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The role of wild carnivore carcasses in the transmission of infectious agents: epidemiological and ecological aspects

El papel de los cadáveres de carnívoros silvestres en la transmisión de agentes infectocontagiosos: aspectos epidemiológicos y ecológicos

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The role of wild carnivore carcasses in the transmission of infectious agents: epidemiological and ecological aspects

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El papel de los cadáveres de carnívoros silvestres en la transmisión de agentes infectocontagiosos: aspectos epidemiológicos y ecológicos

Memoria presentada por el Licenciado en Veterinaria

Moisés Gonzálvez Juan

para optar al grado de Doctor en Ciencias Veterinarias con Mención Internacional

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AUTORIZAN:

La presentación de la Tesis Doctoral titulada “The role of wild carnivore carcasses in the transmission of infectious agents: epidemiological and ecological aspects” (El papel de los cadáveres de carnívoros silvestres en la transmisión de agentes infectocontagiosos: aspectos epidemiológicos y ecológicos), realizada por Moisés Gonzálvez Juan, bajo nuestra supervisión y dirección, para la obtención del grado de Doctor por la Universidad de Murcia.

En Murcia, a uno de septiembre de dos mil veinte.

CARLOS MARTÍNEZ-CARRASCO PLEITE

MARCOS MOLEÓN PAIZ

A mi abuela Dolores y a mi abuelo Antonio,
quienes siempre estuvieron y siempre estarán.

“Cada vez que perdemos una especie rompemos
una cadena de la vida que ha evolucionado
durante 3.500 millones de años.”
Jeffrey McNeely

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Tras terminar la Licenciatura de Veterinaria en el año 2014, me matriculé en el Máster en Gestión de Fauna Silvestre de la Universidad de Murcia. Al finalizar el curso en 2015, y tras quedar cautivado por la fauna, y especialmente por todo lo que envolvía al Parque Natural de Cazorla, decidí adentrarme de lleno en la tesis que ahora estoy culminando. En este punto, siempre tendré mucho que agradecer a mi director y amigo Carlos Martínez-Carrasco Pleite, quien además de darme la oportunidad de trabajar en lo que más me apasiona, ha sido un apoyo importantísimo durante estos años, así como un motor de generar conocimiento, motivación y pasión por la fauna. Podría enumerar decenas de anécdotas de todas las salidas al campo que hemos tenido la suerte de realizar, pero prefiero todavía más que las sigamos viviendo y recordando. ¡Muchas gracias por todo! Por otro lado, debo destacar como otro pilar fundamental de mi tesis a mi director Marcos Moleón Paiz. Gracias por darme la oportunidad de investigar en un campo tan interesante, así como por mostrarme el fascinante entramado ecológico que hay detrás de los parásitos. Te agradezco también la ayuda, dedicación y orientación que me has dado siempre que ha sido necesario. Espero poder seguir aprendiendo de vosotros durante mucho más tiempo.

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SUMMARY

In this PhD dissertation, we have delved into the epidemiological consequences emerged from the interactions between wildlife and carnivorous mammal carcasses in three areas of southeastern Spain. Moreover, we have assessed whether ecological terms and concepts are adequately and accurately used in epidemiological studies about the trophic transmission of pathogens at the wildlife-livestock-human interface. We have also performed a systematic review to analyze the main aspects of these epidemiological studies, as well as to describe the degree of interdisciplinary collaboration and the type of evidence on which their epidemiological inferences and conclusions are based.

Ecological interactions have been traditionally studied considering only the most striking components of the ecosystem, with little attention being paid to smaller and less conspicuous elements, such as parasites. Notwithstanding, these organisms are currently seen as important components of ecosystems that need to be carefully evaluated to get a more realistically understanding of not only the composition but also the functioning of ecological networks. The epidemiology of parasites, which can include trophic and non-trophic transmission routes in their life cycles, is largely influenced by host behavior. The latter is often a result of an evolutionary response to decrease the infection risk. Therefore, due to the high complexity of factors involved in the epidemiology of parasites, an interdisciplinary approach is required for its study. This holistic vision would enable specific terms and concepts associated with each discipline to be known and appropriately used by researchers. Moreover, it would allow a closer collaboration between specialists from the field of Biology and Veterinary, being the basis of new horizons of knowledge in epidemiological research.

In **Chapter 1** we addressed the current state of knowledge about parasite transmission through meat consumption at the wildlife-livestock-human interface. In this systematic review, we analyzed the main characteristics that define the epidemiological studies conducted in this field. Among other aspects, we assessed the degree of interdisciplinarity of the research teams, the accuracy in the use of ecological terms related to meat consumption in the wild, and the scientific reliability of arguments used to support the epidemiological conclusions reached by these studies.

For this purpose, we conducted a systematic review of scientific articles and bibliographic reviews published on or before December 2015, including in the title or in the abstract any of the following combinations of terms: “Carrion” AND “Pathogen” OR

"*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; "Meat" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; "Scaveng*" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; and "Predat*" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*". We used the Web of Science database to perform the bibliographic search. *Trichinella* spp., *Toxoplasma gondii* and *Neospora caninum* were selected for the study because they are meat-borne parasites with a wide range of hosts in their life cycles and indeed they have a relevant impact on animal and public health (this last in the case of *Trichinella* spp. and *T. gondii*). While most of the research studying the trophic behavior of wild mammals has been carried out by biologists, epidemiological studies of meat-borne pathogens have been mainly conducted by veterinarians, showing a remarkable lack of interdisciplinary collaboration among them. In this systematic review, we found that most of the articles analyzed justified the trophic transmission of parasites using exclusively arguments obtained from bibliographic references (51.7%) or using non-science-based assertions (46.1%). The remaining articles based the transmission on indirect evidence (2.2%; e.g., inferring the type of host´s diet from the analysis of its feces composition). On the other hand, ecological terms in many scientific articles and literature reviews were absent and, when mentioned, were inaccurate or even misused. Only one article and one review used the ecological terms correctly and accurately. This lack of precision and rigor may be due because scientific publications are mostly carried out by unidisciplinary research teams, both in the case of scientific articles and bibliographic reviews (74.2% and 80.6%, respectively). Furthermore, these unidisciplinary teams were mostly composed by veterinarians in articles (95.5%) and reviews (76%). These results highlight the need to establish interdisciplinary collaborations between researchers trained in Ecology and Epidemiology to improve the study of trophic transmission of parasites at the wildlife-livestock-human interface. In this sense, this integrated and enriched perspective would enhance the approach, design, interpretation and assessment of scientific studies concerning disease ecology. Moreover, it would promote the use of precise ecological terminology which is essential for describing the trophic behavior of carnivore wild species, and thus avoiding inaccuracies or errors that could cause future non-scientific and incorrect epidemiological interpretations. Therefore, our proposal is that studies on wildlife diseases should be carried out from a holistic perspective within a One Health approach. For this, ecological aspects involved in the maintenance and dispersion of pathogens and, generally, in the epidemiology of diseases of domestic animals, wildlife and humans in the wild should be effectively integrated.

In **Chapter 2** we thoroughly examined the behavior of scavenging vertebrates at carnivore carcasses, with special focus on interaction between red fox (*Vulpes vulpes*) and conspecific carrion. Thereafter, we tried to infer the possible epidemiological consequences that this behavior could have for the transmission of meat-borne parasites through carrion consumption.

Understanding about the ecological factors that influence the epidemiology of wildlife diseases is increasing. Within this context, it is particularly important to understand host avoidance behaviors to reduce the risk of infection by parasites. However, there is very little information about the ecological role of carnivore carcasses and the epidemiological implications that scavenging behaviors may have on parasite transmission through carnivore carrion consumption. The scarcity of detailed studies has led to the widespread assumption that intraspecific carrion consumption is an important route of meat-borne parasite transmission, among which *Trichinella* spp., *T. gondii* and *N. caninum* stand out. The red fox, a ubiquitous facultative scavenger, is particularly relevant in the transmission of parasites. The fox is distributed in numerous ecosystems and is considered one of the most important wild reservoirs of pathogens with zoonotic and veterinary implications. Between November 2016 and March 2018, a fieldwork study was carried out to analyze by camera trapping the trophic behavior patterns established between wild carnivores and mammalian carnivore carcasses. Fifty-six fox carcasses and ten carcasses of other mesocarnivore species were monitored in three areas: Sierras de Cazorla, Segura y Las Villas Natural Park (n=27 foxes), periurban areas of Murcia city (n=19 foxes) and Sierra Espuña Regional Park (n=10 foxes and 10 mesocarnivores other than the fox: four stone martens -*Martes foina*-, three badgers -*Meles meles*-, two genets -*Genetta genetta*- and a wild cat -*Felis silvestris silvestris*-). These areas were selected for having different scavenger communities and degrees of anthropization. An automatic camera was placed in front of each carcass to capture 15-second videos at one-minute intervals, provided that movement was detected. Monitoring extended until carcasses were completely consumed (no remains or only skin) or up to a maximum of 10 weeks if consumption was not complete (bone and skin remains). We found that carrion consumption depended on the type of carcass (conspecific vs. heterospecific for the consumer) and the time elapsed since the carrion was available. Foxes were very efficient in detecting mesocarnivore carrion, but the widespread behavior consisted of avoiding consumption, especially of conspecific carcasses. Only 16.9% of fox events recorded in conspecific carrion corresponded to intraspecific consumption. Cannibalism was recorded in 63% of the carcasses in Cazorla, 32% in Murcia, and 40% at fox carrion sites in Espuña. No intraspecific consumption events were recorded in carrion of other mesocarnivores in Espuña. In addition, consumption events, when recorded, were delayed several days (carrion other than foxes) or weeks (carrion of foxes) from the time of detection. These results suggest that the decision to consume carrion from phylogenetically close species is probably conditioned by two contrasting forces: the use of phylogenetically similar species, which is a resource that has a high nutritional value, as opposed to the risk of acquiring meat-borne parasites shared with these host species. Both conditioning factors, which decrease over time, would be key factors in the delayed consumption of carnivore carcasses. In general, our study demonstrates that carnivore carrion is a fundamental component in the "landscape of disgust" of carnivores.

In **Chapter 3** we investigated the vertebrate behavior (contact, marking by feces and urine, rubbing against or near carrion), especially of the red fox, at carnivore carcass sites, interpreting such non-trophic behavior from the perspective of possible epidemiological consequences related to non-trophic transmitted pathogens.

In general, the heterogeneous spatial and temporal distribution of pathogen transmission risk is characterized by the existence of points with a greater infection risk than others. Trophic resources favoring animal concentration contribute to increase considerably the risk of infection, and therefore may be good examples of local places with high epidemiological relevance or hotspots. When these resources are infected, animals need to assess both the risks and benefits they assume when interacting with them. In this sense, carrion is a paradigmatic example of a resource that may be associated with pathogen transmission through trophic and non-trophic ways. Despite being a brief temporary resource, carnivore carcasses have longer persistence in the ecosystem than the herbivore ones, since they tend to be avoided by other carnivore consumers. Thus, they can become an interesting model to analyze the interactions between wildlife and carrion, as well as the transmission risk of pathogens by non-trophic routes. To this effect, a field study by camera trapping was carried out between November 2016 and March 2018 to assess the behavior of wildlife (scavengers and non-scavengers) at mesocarnivore carcass sites. The same general sampling methodology of Chapter 2 was followed, including the same 66 carcasses and three study areas. Carcass sites were visited by a high variety of vertebrates, whose behavior depended on the visiting species, the study area and the type of carrion. Scavenger species contacted more frequently with carrion, probably as a result of their scavenging habits. Contact events represented 40.6% of total events recorded. Specifically, of total contact events, 64.4% were in Cazorla, 16.6% in Murcia, and 7.6% and 11.5% in Espuña (fox carcasses and carcasses other than fox, respectively). Considering only events of visiting foxes, 43.4% of them were associated with intraspecific contact. Contact events by foxes occurred more frequently and earlier at heterospecific carcasses than at conspecifics ones, being delayed by several weeks especially in the latter. Regarding rubbing events by foxes, a similar pattern was observed at heterospecific and conspecific carrion, although the frequency of rubbing was greater in carcasses other than fox. This result supports the hypothesis that carnivores try to avoid contact with conspecific carrion in order to reduce the risk of acquiring non-trophically transmitted pathogens. In addition, rubbing contact with carrion was more frequent than contact resulting from marking with urine or feces. Thus, close contact caused by rubbing of visitor species with carrion could play an important role in the transmission of ectoparasites, most notably *Sarcoptes scabiei*. Related to marking by foxes, it was most frequently recorded at fox carcass sites, probably because they are used as inter- and intraspecific information points of longer persistence than other carcasses. Marking events (urine and feces) in fox carcasses could pose an epidemiological risk, since there are places where some viruses excreted by these routes are probably more present, such as canine parvovirus and distemper virus, or parasites, such as protozoa and helminths with direct life cycle. Our results also indicate that the propensity to assume risks of pathogen transmission would be higher in more competitive environments (i.e. where obligate scavengers are present, such as griffon vultures -*Gyps fulvus*-), since the availability of food resources for facultative scavengers could be limited. According to our general hypothesis, foxes avoided contact with carrion during the first weeks, probably to reduce the risk of infection by non-trophically transmitted parasites, especially in conspecific carcasses. However, other pathogens that are more persistent in the environment, such as some viruses, bacterial spores, and eggs of certain helminth species, may remain infective in the ecosystem for months or years, so this strategy seems ineffective for some parasites transmitted by non-trophic routes.

In general, this thesis provides a detailed knowledge about ecological interactions between carrion of carnivorous mammals and vertebrate wildlife. This information is a fundamental basis for inferring the epidemiological consequences that could be derived from these relationships, both for trophically and non-trophically transmitted parasites. In

addition, this thesis encourages the need to increase interdisciplinary collaboration to address these studies from a One Health perspective, highlighting the importance of using correct ecological terminology and, above all, epidemiological interpretations based on accurate data.

RESUMEN

En esta tesis doctoral hemos profundizado en el estudio de las consecuencias epidemiológicas que pueden conllevar las interacciones entre la fauna silvestre y los cadáveres de mamíferos carnívoros en tres zonas del sureste de España. Además, hemos evaluado si los términos y conceptos ecológicos se emplean adecuadamente y con precisión en los estudios epidemiológicos sobre la transmisión trófica de patógenos en la interfaz silvestre-doméstico-humano. Asimismo, hemos analizado, mediante una revisión sistemática de la literatura científica publicada, las principales características de este tipo de estudios epidemiológicos, describiendo el grado de colaboración interdisciplinar que los define y el tipo de evidencias sobre las que sustentan las inferencias epidemiológicas y conclusiones a las que llegan.

Tradicionalmente, las interacciones ecológicas han sido estudiadas atendiendo a los componentes más llamativos del ecosistema, prestando poca atención a otros elementos más pequeños y menos evidentes, como los parásitos. No obstante, en la actualidad, los parásitos se consideran componentes fundamentales de los ecosistemas que deben ser evaluados con detenimiento y que ayudan a entender de forma más realista no solo la composición, sino también el funcionamiento de las redes ecológicas. La epidemiología de los parásitos, que pueden utilizar vías de transmisión trófica y no trófica en sus respectivos ciclos biológicos, está muy influenciada por el comportamiento de los hospedadores, que en muchas ocasiones es una respuesta comportamental adquirida evolutivamente para disminuir el riesgo de infección. Por tanto, la complejidad de los factores que intervienen en la epidemiología de los parásitos hace necesario abordar su estudio desde una perspectiva interdisciplinar. Esta visión holística permitiría que los términos y conceptos asociados a cada disciplina fuesen conocidos y usados correctamente por parte de investigadores de otras disciplinas. Además, favorecería una colaboración estrecha entre especialistas del campo de la Biología y la Veterinaria, siendo la base de nuevos horizontes de conocimiento en la investigación epidemiológica.

En el **Capítulo 1** se abordó el estado actual del conocimiento sobre la transmisión de parásitos por consumo de carne en la interfaz silvestre-doméstico-humano. En este trabajo de revisión sistemática analizamos las características principales que definen los estudios epidemiológicos realizados en este campo. Entre otros aspectos, se ha valorado el grado de interdisciplinaridad de los equipos de investigación, la precisión en el uso de los términos ecológicos relacionados con el consumo de carne en la naturaleza, así como la solvencia científica de los argumentos empleados para sostener las conclusiones epidemiológicas a las que llegan dichos estudios.

A tal fin, se realizó una revisión sistemática de artículos científicos y revisiones bibliográficas publicadas con fecha igual o anterior a diciembre de 2015 que incluyeran en el título o en el resumen alguna de las siguientes combinaciones de términos: "Carrion" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; "Meat" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; "Scaveng*" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; and "Predat*" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*". Para la búsqueda se usó la base de datos Web of Science. Se seleccionaron *Trichinella* spp, *Toxoplasma gondii* y *Neospora caninum* para el estudio por ser parásitos transmitidos por consumo de carne, con un amplio rango de hospedadores en su ciclo biológico y con un impacto importante sobre la sanidad animal y la salud pública (en el caso de *Trichinella* spp. y *T. gondii*). Mientras que la mayoría de los trabajos que estudian los comportamientos tróficos de los mamíferos silvestres han sido llevados a cabo por biólogos, los estudios epidemiológicos de patógenos transmitidos por consumo de carne han sido realizados principalmente por veterinarios, evidenciándose una notable falta de colaboración interdisciplinar. En esta revisión sistemática hemos comprobado que la mayoría de los artículos analizados justificaron la transmisión trófica de los parásitos utilizando exclusivamente argumentos obtenidos a partir de referencias bibliográficas (51.7%) o afirmaciones infundadas (46.1%), mientras que el resto de los artículos basaron la transmisión en evidencias indirectas (2.2%; por ejemplo, infiriendo el tipo de dieta del hospedador estudiado a partir del análisis de la composición de sus heces). Por otro lado, en muchos de los artículos científicos y revisiones bibliográficas no se emplearon los términos ecológicos asociados al consumo de carne y, cuando se usaron, se hizo de una forma imprecisa o incluso errónea. Solamente un artículo y una revisión utilizaron los términos ecológicos de forma correcta y precisa. Esta falta de precisión y rigurosidad puede estar motivada por el hecho de que las publicaciones científicas son realizadas mayoritariamente por equipos de investigación unidisciplinares, tanto en el caso de los artículos científicos como en las revisiones bibliográficas (74.2% y 80.6%, respectivamente). Además, estos equipos unidisciplinares están compuestos en su mayoría por veterinarios, tanto en artículos (95.5%) como en revisiones (76%). Estos resultados destacan la necesidad de establecer colaboraciones interdisciplinares entre científicos formados en el campo de la Ecología y de la Epidemiología para profundizar en el estudio de la transmisión trófica de los parásitos en la interfaz silvestre-doméstico-humano. En este sentido, y desde una visión integradora más enriquecedora, se podría mejorar el planteamiento, diseño, interpretación y valoración de los trabajos científicos referentes a la ecología de las enfermedades. Además, podría promover el empleo preciso de la terminología ecológica, que es esencial para describir el comportamiento trófico de los carnívoros silvestres y, de esta manera, evitar imprecisiones o errores que pudieran ser origen de futuras interpretaciones epidemiológicas sin base científica e incorrectas. Por tanto, nuestra propuesta es que los estudios sobre las enfermedades infectocontagiosas en la fauna silvestre sean realizados desde una perspectiva holística y con un enfoque *One Health*. Para ello, deben integrarse de forma efectiva los aspectos ecológicos que intervienen en el mantenimiento y dispersión de los agentes infecciosos en la naturaleza y, en general, en la epidemiología de las enfermedades de los animales domésticos, de la fauna silvestre y del hombre en el medio natural.

En el **Capítulo 2** se estudió en detalle el comportamiento de los vertebrados carroñeros, con especial énfasis en el zorro rojo (*Vulpes vulpes*), ante cadáveres de mesocarnívoros (incluidos cadáveres de zorro). A partir de esta información, tratamos de inferir las posibles consecuencias epidemiológicas que puede conllevar este comportamiento en referencia a los parásitos transmitidos por consumo de carroña.

En general, el conocimiento de los factores ecológicos involucrados en la epidemiología de las enfermedades en la fauna silvestre se ha incrementado durante los últimos años. En este contexto, es particularmente importante comprender los comportamientos de evasión de los hospedadores para disminuir el riesgo de infección por parásitos. Sin embargo, hay muy poca información sobre el papel ecológico de los cadáveres de carnívoros, así como de las implicaciones epidemiológicas que el consumo de carroña puede tener sobre la transmisión de parásitos a través de su consumo. Esta escasez de estudios ha propiciado la suposición generalizada de que el consumo de carroña intraespecífico es una importante vía de transmisión de parásitos, entre los que destacan *Trichinella* spp., *T. gondii* y *N. caninum*. En la transmisión de estos parásitos adquiere una especial relevancia el zorro rojo, un carroñero facultativo presente en una amplia diversidad de ecosistemas y que está considerado como uno de los reservorios silvestres más importantes de patógenos con potencial zoonósico y relevancia veterinaria. Entre noviembre de 2016 y marzo de 2018 se realizó un estudio de campo para conocer en profundidad el patrón de comportamiento trófico entre los carnívoros silvestres y los

cadáveres de mamíferos carnívoros. Se monitorizaron mediante cámaras trampa 56 cadáveres de zorro y 10 de otras especies de mesocarnívoro en tres áreas: el Parque Natural de las Sierras de Cazorla, Segura y Las Villas (n=27 zorros), áreas periurbanas de Murcia (n=19 zorros) y el Parque Regional de Sierra Espuña (n=10 zorros y 10 mesocarnívoros distintos al zorro: cuatro garduñas -*Martes foina*-, tres tejones -*Meles meles*-, dos ginetas -*Genetta genetta*- y un gato montés -*Felis silvestris silvestris*-). Estas áreas fueron seleccionadas por tener diferentes comunidades de carroñeros y grados de antropización. En cada punto de estudio se colocó una cámara de activación automática programada para registrar vídeos de 15 segundos, a intervalos de un minuto, cuando detectase movimiento. El seguimiento duró hasta que los cadáveres fueron completamente consumidos (no quedaron restos o solo piel) o hasta un máximo de 10 semanas si el consumo no fue completo (restos de huesos y piel). Se comprobó que el consumo de carroña dependía tanto del tipo de cadáver (congénere *vs* heteroespecífico respecto al consumidor) como del tiempo transcurrido desde que la carroña estuvo disponible. Los zorros fueron muy eficientes en la detección de la carroña de mesocarnívoros, pero el comportamiento generalizado consistió en rechazar el consumo, especialmente de los cadáveres de congéneres. Únicamente el 16.9% de los eventos registrados de zorro en cadáveres de congéneres correspondieron a consumo intraespecífico. Se registró canibalismo en el 63% de los cadáveres de Cazorla, en el 32% de Murcia y en el 40% de los cadáveres de zorro en Espuña. No se registró ningún evento de consumo intraespecífico en la carroña de otros mesocarnívoros. Además, los eventos de consumo, cuando ocurrieron, se retrasaron varios días (carroña de mesocarnívoros distintos al zorro) o semanas (carroña de zorros) desde el momento de la detección. Estos resultados apoyan la hipótesis de que evitar el consumo de carroña de especies filogenéticamente cercanas es un comportamiento generalizado en los carnívoros que les permite reducir el riesgo de infección por parásitos transmitidos por consumo de carne. Además, nuestro estudio sugiere que la decisión de consumir carroña de especies filogenéticamente cercanas probablemente esté condicionada por dos fuerzas contrarias: el aprovechamiento de la carroña, que es un recurso que tiene un alto valor nutricional, frente al riesgo de adquirir parásitos compartidos. Ambos condicionantes, que disminuyen con el tiempo, serían factores fundamentales involucrados en el consumo tardío de los cadáveres de carnívoros. En general, nuestro estudio demuestra que la carroña de carnívoro es un componente fundamental en el denominado como “paisaje de la aversión” (*landscape of disgust*) de los carnívoros.

En el **Capítulo 3** se estudió el comportamiento (contacto, marcaje mediante heces y orina, frotamiento contra la carroña o cerca de ella) de los vertebrados (especialmente el zorro rojo) ante cadáveres de carnívoros, interpretando dicho comportamiento no trófico desde la perspectiva de las posibles consecuencias epidemiológicas relacionadas con la transmisión no trófica de patógenos.

En general, la heterogénea distribución temporal y espacial del riesgo de transmisión de patógenos se caracteriza por la existencia de puntos que suponen un mayor riesgo de infección que otros. Los recursos tróficos que favorecen la concentración de animales, incrementando así considerablemente el riesgo de infección, pueden ser buenos ejemplos de estos puntos con elevada importancia epidemiológica o *hotspots*. Cuando estos recursos están infectados, los animales deben valorar los riesgos y beneficios que asumen al interactuar con ellos. En este sentido, la carroña es un ejemplo paradigmático de recurso que puede estar relacionado con la transmisión de patógenos a través de rutas tróficas y no tróficas. A pesar de que los cadáveres son un recurso temporal breve, los de carnívoros tienen una persistencia en el ecosistema superior a los de herbívoros, dado que tienden a ser evitados por otros carnívoros, por lo que son un modelo interesante para estudiar las interacciones entre la fauna silvestre y la carroña, así como el riesgo de transmisión de patógenos por vía no trófica. Con tal fin, entre noviembre de 2016 y marzo de 2018 se realizó un estudio de campo para evaluar mediante fototrampeo el comportamiento de la fauna silvestre (especies carroñeras y no carroñeras) en puntos con presencia de cadáveres de mesocarnívoros. Se siguió la misma metodología general de muestreo que en el Capítulo 2, incluyendo los mismos 66 cadáveres y las mismas tres áreas de estudio. Los enclaves de los cadáveres fueron visitados por una elevada variedad de vertebrados, cuyo comportamiento con la carroña dependió de la especie visitante, de la zona de estudio y del tipo de carroña. Las especies carroñeras, probablemente por sus hábitos tróficos, contactaron con más frecuencia con los cadáveres. Los eventos totales de contacto supusieron el 40.6% de todos los eventos registrados. En concreto, de los eventos totales de contacto, el 64.4% se registraron en Cazorla, el 16.6% en Murcia y el 7.6% y 11.5% en Espuña (cadáveres de zorro y cadáveres de otros mesocarnívoros, respectivamente). Considerando exclusivamente los eventos de zorro, el 43.4% de ellos se asoció a contacto intraespecífico. Los contactos fueron más frecuentes y tempranos en los cadáveres heteroespecíficos que en los de congéneres, retrasándose varias semanas especialmente en estos últimos. Con respecto a los eventos de frotamiento de los zorros visitantes, se observó un patrón similar entre los cadáveres heteroespecíficos y los de congéneres, aunque la frecuencia fue mayor en los cadáveres de otras especies. Este resultado apoya la hipótesis de que los carnívoros intentan evitar el contacto con la carroña de congéneres para disminuir el riesgo de adquirir patógenos transmitidos por vía no trófica. Además, los contactos ocasionados por el frotamiento de los visitantes con la carroña fueron más frecuentes que los debidos al marcaje con orina o heces. En este sentido, el contacto mediante frotamiento de la especie visitante con la carroña podría ser un factor clave en la transmisión de ectoparásitos, entre los que destaca *Sarcoptes scabiei*. Respecto al marcaje por parte de los zorros, se registró con mayor frecuencia en cadáveres de zorro, seguramente debido a que son usados como puntos de información inter- e intraespecífico de larga persistencia, en comparación con otro tipo de cadáveres. Este marcaje mediante orina y heces podría suponer un riesgo epidemiológico, creándose puntos con mayor probabilidad de presencia de algunos agentes víricos excretados por estas vías, como es el caso del parvovirus canino y el moquillo, o parásitos, como protozoos y helmintos de ciclo biológico directo. Nuestros resultados también indican que la propensión a asumir riesgos de transmisión de patógenos sería mayor en ambientes más competitivos (es decir, donde hay carroñeros obligados, como los buitres leonados -*Gyps fulvus*-), ya que la disponibilidad de recursos tróficos para los carroñeros facultativos sería menor. Acorde a nuestra hipótesis general, los zorros evitan contactar con la carroña durante las primeras semanas, probablemente para disminuir el riesgo de infección por parásitos transmitidos por vía no trófica, especialmente si se trata de cadáveres de congéneres. No obstante, otros patógenos más resistentes a las condiciones ambientales, como algunos virus, esporas de bacterias y huevos de ciertas especies de helmintos, podrían permanecer viables en el ecosistema durante meses o años, por lo que esta estrategia parece ineficaz para algunos patógenos transmitidos por vía no trófica.

En general, esta tesis aporta un conocimiento detallado de las interacciones ecológicas entre la carroña de mamíferos carnívoros y la fauna silvestre vertebrada. Esta información es una base fundamental para inferir las posibles consecuencias epidemiológicas que pueden derivarse de estas relaciones, tanto para parásitos transmitidos por consumo de carne como para aquellos que emplean rutas no tróficas. Además, esta tesis destaca la necesidad de incrementar la colaboración interdisciplinar para abordar estos estudios desde una perspectiva *One Health*, remarcando la importancia de emplear una correcta terminología ecológica y, ante todo, interpretaciones epidemiológicas que estén fundamentadas en datos precisos.

GENERAL INTRODUCTION

GENERAL BACKGROUND

This investigation focused on the behavioral patterns of wildlife at carcasses of mammalian mesocarnivores, with particular emphasis on the interactions between species that are phylogenetically related. Specifically, this study aimed to describe trophic and non-trophic interactions that take place among wild carnivore species and, based on these observations, draw the epidemiological implications for pathogens transmitted via meat consumption or direct contact, such as *Trichinella* spp. and *Sarcoptes scabiei*, the etiological agents of trichinellosis and sarcoptic mange, respectively.

This introduction touch (1) the importance of understanding in detail the functioning of ecosystems, recognizing them as a complex network of interactions in which all their multiple elements are interconnected and in which viral, bacterial and parasitic agents are a fundamental part that must be studied. In this context, (2) special attention must be paid to a very large number of host species that have an important ecological role in ecosystems, namely vertebrate carnivores. Regarding these species, (3) it is important to further examine their interactions with carrion, one of their most important trophic resources; in the case of mammalian carnivore carcasses, very little is known. Thanks to these studies, the epidemiological consequences that ecological interactions may have on trophic and non-trophic transmission of parasites could be evaluated. Moreover, (4) these epidemiological implications could be especially important in the case of the red fox (*Vulpes vulpes*), since it is the most abundant and ubiquitous carnivore on the Iberian Peninsula. Accordingly, the red fox may be a key element in the maintenance and dispersion of a wide variety of parasites, in both relatively undisturbed natural settings as well as areas subject to different degrees of anthropogenic pressure. Finally, in this introduction (5) we advocate the need to approach the study of wildlife diseases from a broad, holistic perspective, including interdisciplinary research teams comprised of specialists such as epidemiologists and ecologists. Cooperation of these researchers is key to ensuring studies in the field of disease ecology achieve sound and coherent conclusions from a One Health perspective.

THE ECOSYSTEM: A COMPLEX NETWORK OF INTERCONNECTED ELEMENTS

Ecosystems are composed of communities of living organisms that interact with each other and with abiotic factors in their environment. Until relatively recently, these networks of interconnected elements were represented using simple models that did not accurately reflected reality (Brose *et al*., 2005; Anand *et al*., 2010). However, in recent years, as understanding of the elements that make up ecosystems improved, the growing trend has been to study living organisms from a broader perspective that attempts to encompass, as far as possible, the majority of the elements and interactions that occur in these complex networks (Parrott, 2010) (Figure 1).

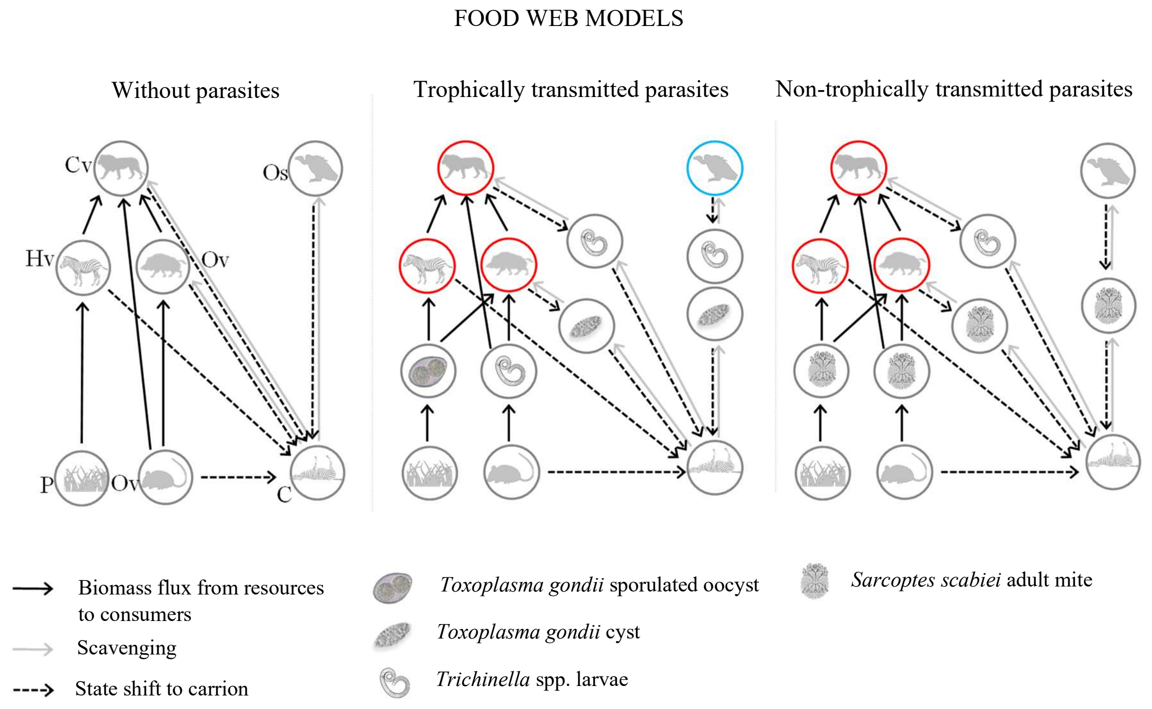

Figure 1. Graphic representation of food webs without parasites, with trophically and non-trophically transmitted parasites. The figure includes primary producers (P), carnivores (Cv), herbivores (Hv), omnivores (Ov), obligate scavengers (Os) and carrion (C). Red circles represent interactions that facilitate the maintenance and dispersion of parasites in the environment, while the blue one promotes their elimination from the ecosystem. Modified from Moleón and Sánchez-Zapata (2015).

In fact, studying the interactions that occur among the components of these ecological networks is key to understanding how an ecosystem works and, accordingly, implementing measures aimed at preserving biodiversity (Landi *et al*., 2018). Furthermore, this more complete and realistic perspective enables us to not only define and assess the effects that a certain change may have on an element of the ecosystem, but also predict the consequences that it will have on other organisms that partake in these ecological interactions (Brose *et al*., 2005). Amid this diversity of organisms, vertebrate animals, among others, have attracted considerable interest from scientists. Nevertheless, other types of organisms have gone unnoticed, and, only in recent years, have they started receiving more attention. Among them are parasites that, possibly due to their small size, their cryptic nature, and the difficulty of evaluating their effects on free-living hosts, have received little attention in ecological studies (Ostfeld *et al*., 2008; Hatcher *et al*., 2012; Sukhdeo, 2012). This lack of scientific studies focusing on the ecology of parasites contrasts with the fact that recent studies have shown the importance of these organisms to the structure of ecological interactions, e.g. influencing the structure of trophic networks and the flow of energy and nutrients (Lafferty *et al*., 2008; Lefèvre *et al*., 2009).

Evidence that parasites are fully integrated into ecosystems is that parasite species richness is a bioindicator of habitat quality (Hudson *et al*., 2006). In fact, in undisturbed natural settings it is more likely to find animals that host more than one parasite species than those that are monoparasitic (Pedersen and Fenton, 2007), which indicates parasites' adaptation to and active participation in ecological interactions. Moreover, parasites are typically so adapted to their hosts that, frequently, they achieve relationships of long-term equilibrium in which both host and parasite survive (Phillips, 2002).

It is crucial to understand the routes of transmission and the life cycles of parasites to describe their ecological and epidemiological characteristics. Parasites that do not involve intermediary hosts have a direct life cycle, which may be completed entirely with the participation of two hosts that act as definitive hosts (Antonovics *et al*., 2017). Parasites with indirect life cycle are, in general, more complex since they require the participation of intermediate hosts, and their transmission involves various host species (Choisy *et al*., 2003; Antonovics *et al*., 2017). Predator-prey relationships are frequently associated with the transmission of a wide range of parasite species, especially those with an indirect life cycle (Parker *et al*., 2015).

The multitude of interactions between parasites and their hosts results in evolutionary changes in hosts and parasites that, on many occasions, are driven by the heterogeneity of other elements that make up the ecosystem (Penczykowski *et al*., 2016). In terms of the host, this evolutionary dynamic leads to a series of changes, some of which are behavioral, aimed at reducing the risk of parasite transmission (Hart, 2011; Poirotte *et al*., 2017). On the other hand, parasites evolve by adopting strategies that allow them to survive in the host, such as immune response evasion (Zambrano-Villa *et al*., 2002) or searching for alternative hosts (Parker *et al*., 2015).

In view of the foregoing, understanding the epidemiological consequences of interspecific interactions between these pathogens and other components of the ecosystem is fundamental to the study of parasites (Marcogliese and Cone, 1997). In this sense, scientists face the challenge of studying complex ecological networks that may respond unpredictably to natural or anthropic disequilibrium (MacDougall *et al*., 2013; Parker *et al*., 2015). To this end, objective and accurate data on the trophic and non-trophic interactions that occur between different components of the ecosystem are needed. In this regard, especially interesting are the behavioral patterns of wildlife species that could be key to understanding and explaining epidemiological aspects directly related to the maintenance and dispersion of parasites in an ecosystem. The use of camera traps has shown to be a very efficient methodology that provides highly useful information without interfering with the animals' behavior (Caravaggi *et al*., 2017). This tool has traditionally been used in the field of Ecology, although it is being used increasingly in scientific studies with an epidemiological focus, especially in relation to nocturnal and evasive fauna, such as mammalian carnivores (Kelly *et al*., 2008; Trolliet *et al*., 2014; Pyšková *et al*., 2018). An example of this is the use of this technology to study parasites with important epidemiological implications for wild carnivores on the Iberian Peninsula, as is the case of sarcoptic mange in wolves (*Canis lupus*) and foxes (Oleaga *et al*., 2011; Carricondo-Sánchez *et al*., 2017).

VERTEBRATE CARNIVORES AND CARRION ECOLOGY

The term carnivore refers to a group of heterotrophic organisms present in all ecosystems that are characterized by a diet based on the consumption of animal tissues. This diet may consist of consuming animals that were either dead or alive before the interaction between the carnivore and the prey, referred to as scavenging or predation (Getz, 2011), respectively. Likewise, this consumption may take place between individuals of different species (interspecific consumption) or the same species (intraspecific consumption, or cannibalism) (Abrams, 1987; Polis, 1991). It is worth mentioning the high nutritional value of meat, especially of prey that are phylogenetically similar to the consumer, which explains the nutritional importance of trophic behavior based on intraspecific consumption (Meffe and Crump, 1987; Mayntz and Toft, 2006).

Within carnivorous vertebrates, there is a gradient between species that depend almost entirely on meat, such as Felidae, and those that also exploit plant-based trophic resources.

Foxes are a paradigmatic example of those that feed on a wide variety of plant and animal sources (Díaz-Ruiz *et al.*, 2013). In general, strict carnivores are more vulnerable to environmental changes than more generalist species.

Another important subdivision in carnivores, based specifically on the consumption of carrion, is whether these species scavenge exclusively or as a complement to other food sources. In the first group are obligate scavengers, such as the griffon vulture *Gyps fulvus* (Buechley and Şekercioğlu, 2016); the second group is composed of facultative scavengers, such as the red fox (Díaz-Ruiz *et al.*, 2013). Competition between and among groups of scavengers is high (Moleón *et al.*, 2014), although consumption is well structured (Selva and Fortuna, 2007), which allows for the maximum coexistence of different scavenger species (Sebastián-González *et al.*, 2016). The presence of specialized scavengers like vultures can reduce the amount of carrion available for opportunistic scavengers like red foxes, which may limit their abundance (Morales-Reyes *et al.*, 2017).

In trophic networks, the energy flow per link associated with scavenging is greater than for predation, which demonstrates its importance in the functioning of ecosystems (Wilson and Wolkovich, 2011). Despite this evidence, the consumption of carrion has traditionally been largely unexplored (Moleón and Sánchez-Zapata, 2015). The presence of carcasses in nature is fundamental for the survival of numerous species (DeVault *et al.*, 2003; Sebastián-González *et al.*, 2019). Apart from the obvious ecological role as a source of nutrients, carcass sites are characterized by the accumulation of a large variety of organic material (carrion remains, invertebrates, urine and feces from visiting species, feathers, etc.). Thus, carcass sites can be regarded as hotspots of biodiversity (Barton *et al.*, 2013).

CARRION: ECOLOGICAL INTERACTIONS AND EPIDEMIOLOGICAL CONSEQUENCES

The role of carrion as a trophic resource has been extensively described in the case of herbivores (DeVault *et al.*, 2003; Sebastián-González *et al.*, 2019). Only recently has carrion from carnivore species begun to be studied in detail (Olson *et al.*, 2016; Moleón *et al.*, 2017). These studies have shown that the pattern of consumption for different types of carrion differs considerably. Specifically, carrion from mammalian carnivores persists longer in the natural environment because scavengers, especially mesocarnivores, tend to avoid it (Moleón *et al.*, 2017). It has been suggested that this behavior is probably the result of an evolutionary adaptation of the host, whose objective is to reduce the risk of transmission of pathogens, given that phylogenetic similarities between two species of carnivores means there is a greater number of shared infectious agents (Huang *et al.*, 2014; Moleón *et al.*, 2017). In this regard, it has been established that some carnivorous species can detect the presence of volatile organic compounds associated with certain pathogens using their olfactory sense (Pradel *et al.*, 2007; Ferrero *et al.*, 2011; Cernosek *et al.*, 2020), which allows them to differentiate carcasses that do not pose a health risk from those that should be avoided. This coincides with recent observations that mammalian carnivores exposed to pieces of meat from herbivores and carnivores of similar external appearances avoid the latter, i.e., those that are of higher parasite risk (Moleón *et al.*, 2017).

The finding that carrion from mammalian carnivores is rejected by phylogenetically similar consumers (mesocarnivores) has also been verified in the case of red fox by other authors that analyzed its diet from scats; they indicated that cannibalism is a highly unusual behavior in this canid species (Cagnacci *et al.*, 2003; Remonti *et al.*, 2005). However, despite this evidence, it is widely believed in part of the scientific community that intraspecific consumption (cannibalism) is a typical behavior among carnivores that favors the transmission of some parasites, especially in relation to the sylvatic life cycle of *Trichinella* spp. (Campbell, 1988; Pozio, 2000; Pozio and Murrell, 2006; Badagliacca *et al.*, 2016). This assumption, which largely lacks empirical support, is most likely due to the authors' incorrect interpretation of data. For example, finding hairs of a given species, such as fox, in its feces has frequently been interpreted as an indicator of cannibalism, without considering that the existence of these hairs could be due to the animal's grooming behavior (Remonti *et al.*, 2005). This connection made by the scientific community between cannibalism and the mode of transmission of parasites among mammalian carnivores becomes apparent when analyzing the most repeated words in scientific articles by performing a search of the literature on this topic. Specifically, the bibliometric map generated using VOSviewer software (Van Eck *et al.*, 2010), based on articles that examined the transmission of *Trichinella* spp. in wildlife species, shows a clear association between the key words 'transmission' and 'cannibalism' in these studies (Figure 2).

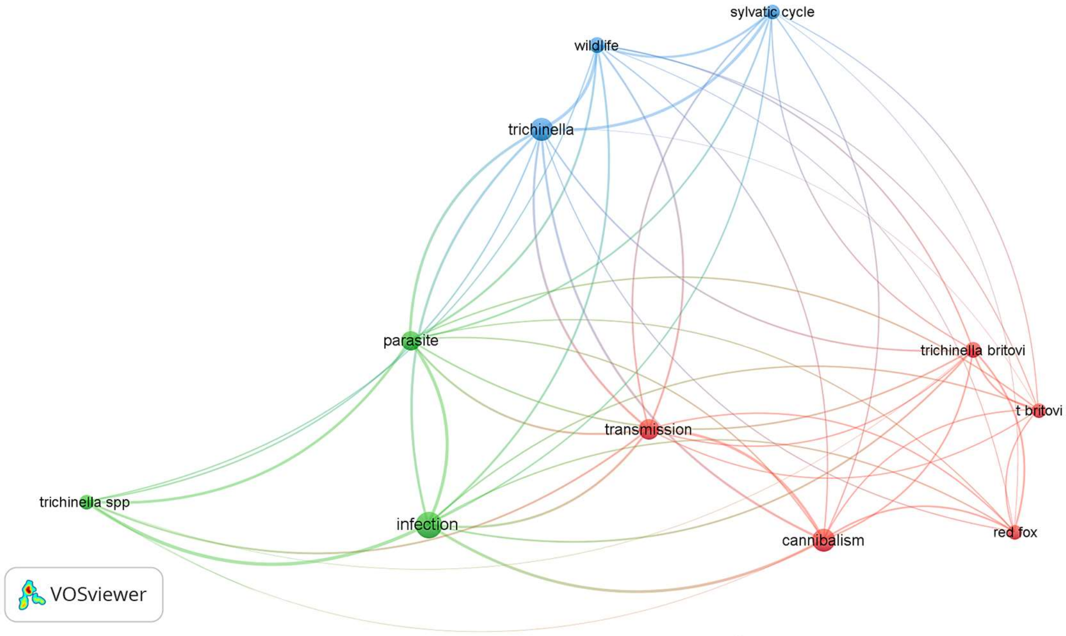

Figure 2. Bibliometric map generated from 23 scientific articles identified using the search term [“*Trichinella*” AND “cannibal*” AND “wild”] on the Web of Science (1900–June 2020). Green cluster: conceptual references to *Trichinella* spp.; red cluster: terms related to the transmission of the parasite; blue cluster: terms related to the existence of the parasite’s sylvatic cycle**.**

Given that the persistence of carrion in the environment largely depends on the community of scavengers present there, it is noteworthy that in areas with few or no vultures, the scavenging rate decreases (Ogada *et al*., 2012; Morales-Reyes *et al*., 2017). Vultures provide important ecosystem services worldwide by eliminating microorganisms present in carcasses that could have repercussions for the health of other wildlife species (Zepeda Mendoza *et al*., 2018). In this respect, carrion may host a wide variety of pathogens (Cantlay *et al*., 2017; Stella *et al*., 2018). For this reason, studies should be performed to determine what role carrion plays in the transmission of viral, bacterial and parasitic agents in ecosystems. This type of studies is of greater necessity in areas where obligate scavengers are not present, as well as in the case of carnivore vertebrate carrion since the risk of transmission to other carnivores is higher.

Regarding the persistence of pathogens in carnivore carrion, some infective stages remain viable from few days to several weeks, depending on the characteristics of each pathogen and environmental factors, in particular temperature. For example, the rabies virus can remain viable for three days at 35ºC, but this figure increases to 18 days at 4ºC (McElhinney *et al*., 2014). Another example is *Trichinella* spp. cyst larvae in muscles, which can be infectious for 2-3 weeks at 23ºC (Oivanen *et al.*, 2002), but are capable of surviving 2-3 months at low temperatures, as was demonstrated in fox carcasses covered by snow (Rossi *et al.*, 2019). The characteristic anaerobic conditions of carcasses are very well tolerated by *Trichinella* spp. due to its adaptation to anaerobic metabolism (Pozio, 2016; Rossi *et al.*, 2019).

Among the most prominent parasites capable of trophic transmission in the wild are the nematode *Trichinella* spp. and the protozoa *Toxoplasma gondii* and *Neospora caninum*. The present eco-epidemiological study focuses on these pathogens because they are some of the most widespread parasites around the world, have a broad range of carnivore hosts, depend entirely (*Trichinella* spp.) or partially (*T. gondii* and *N. caninum*) on trophic transmission to complete their biological life cycle (Dubey, 1991; Gondim, 2006; Pozio and Murrell, 2006) and, in the case of *Trichinella* spp. and *T. gondii*, they are zoonotic agents. Prolonged environmental persistence of mammalian carnivore carcasses could have important epidemiological effects on all susceptible host species present at the wildlife-domestic-human interface (Figure 3).

It is important to consider that carrion can also be an indirect food source for scavengers and predators that feed on necrophagous arthropods (Moreno-Opo and Margalida, 2013). This could have important epidemiological implications given that these invertebrates could act as paratenic hosts (Riva *et al.*, 2015). In this sense, mammalian carnivore carrion, due to its prolonged persistence in the environment compared to herbivore carrion, hosts a well-structured community of necrophagous arthropods (Muñoz-Lozano *et al.*, 2019).

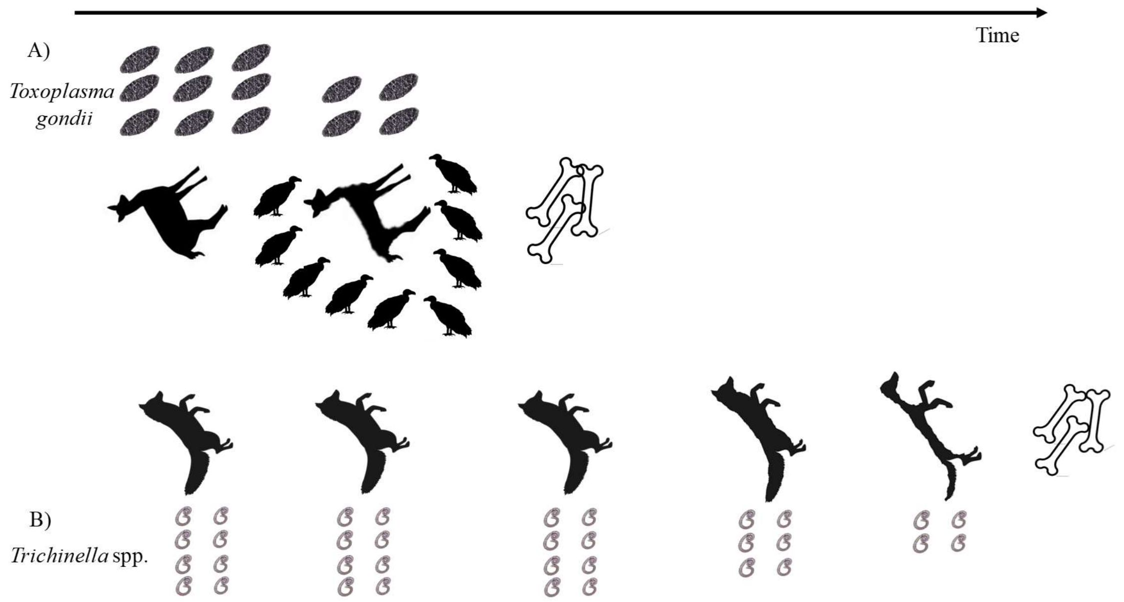

Figure 3. Graphic representation of the persistence of herbivore carrion infected with *T. gondii* (A) and carnivore carrion infected with *Trichinella* spp. (B). The longer carrion persists without being consumed, the more protracted the presence of parasites in the environment. Based on Moleón *et al*. (2017).

Finally, carrion also serves various important non-trophic functions in ecosystems, from being a source of materials for the construction of birds' nests to constituting a key element in the epidemiology of pathogens transmitted by direct contact or through the air (Turner *et al*., 2014; Moleón and Sánchez-Zapata, 2016). As for non-trophic transmission of pathogens, this study focuses on *S. scabiei*, the mite that causes sarcoptic mange, which is mainly transmitted by direct contact. As with the previously mentioned parasites, *S. scabiei* has a wide range of host species that includes mammalian carnivores present on the Iberian Peninsula, can survive for several weeks in the environment, and has a major impact on wild carnivore populations (Arlian *et al*., 1984; Oleaga *et al*., 2011; Arlian and Morgan, 2017).

BIOLOGY AND THE EPIDEMIOLOGICAL ROLE OF RED FOX AND OTHER MESOCARNIVORES

The red fox is one of the most widespread mammals in the world, inhabiting regions of Eurasia, North Africa, North America and Australia. Its ecological plasticity allows it to occupy many geographical regions with different climatic conditions, from the Sahara desert to the Boreal region (Hoffmann and Sillero-Zubiri, 2016).

It is the most widely distributed and abundant carnivore mammal on the Iberian Peninsula, where exhibits a wide trophic spectrum (Díaz-Ruiz *et al.*, 2013). In general, its diet is based on rabbits (*Oryctolagus cuniculus*), small mammals, carrion and fruits (Díaz-Ruiz *et al.*, 2013). Consumption of carrion by foxes depends on many factors. For example, in winter they typically increase carcass consumption due to a lack of alternative resources (Rossi *et al.*, 1992; Selva *et al.*, 2005; Genovart *et al.*, 2010).

The red fox's eclecticism enables it to dwell in urban and periurban areas where it finds abundant human waste, pet food, and even domestic animals (Contesse *et al.*, 2004; Mackenstedt *et al.*, 2015). This has afforded it special attention, not only as a pathogen reservoir with health implications for wildlife species, but also for domestic animals and human beings (Mackenstedt *et al.*, 2015; Karamon *et al.*, 2018). In this sense, the fox's role in the sylvatic life cycle of various zoonotic parasites has been amply documented, with *Trichinella* spp. and *T. gondii* being among the most studied ones (Pozio and Murrell, 2006; Sobrino *et al.*, 2007; Mackenstedt *et al.*, 2015). The fox merits special attention as a reservoir of *Echinococcus multilocularis* (Duscher *et al.*, 2015), a cestode with serious health and economic consequences for humans globally (Budke *et al.*, 2006). The complex life cycle of many parasites makes it difficult to know all the possible interactions between wildlife, domestic animals and humans that could pose a risk of transmission of any of these parasites. For this reason, it is important to carefully assess the presence of wildlife species such as the red fox in anthropized environments, considering the lack of knowledge about many aspects of the life cycles and epidemiological features of these parasites (Mackenstedt *et al.*, 2015).

In addition to foxes, other widespread mesocarnivore scavengers on the Iberian Peninsula, like stone martens (*Martes foina*), genets (*Genetta genetta*) and badgers (*Meles meles*), should be considered when studying ecological and epidemiological aspects of carrion because they all share habitat and resources (Gaubert *et al.*, 2015; Abramov *et al.*, 2016; Hoffmann and Sillero-Zubiri, 2016; Kranz *et al.*, 2016; Amaya-Castaño and Palomares, 2018). Moreover, all of these species are hosts of the previously described parasites affecting foxes (mainly *Trichinella* spp. and *T. gondii*), so they may also play an epidemiological role in the maintenance and dispersion of their sylvatic life cycle (Pozio and Murrell, 2006; Sobrino *et al.*, 2007, 2008). For this reason, disease surveillance should be used to track these pathogens in all the wildlife species that are potential reservoirs of these zoonoses, especially if they inhabit urban or periurban areas (Lempp *et al.*, 2017).

Moreover, the previously mentioned mesocarnivores are hosts of some viruses that may pose a risk to the conservation of threatened Iberian wildlife species, such as the Iberian lynx (*Lynx pardinus*) and the European wildcat (*Felis silvestris silvestris*) (Duarte *et al*., 2013).

ECOLOGY AND EPIDEMIOLOGY: A HOLISTIC VISION

One of the main foundations for driving genuine scientific progress, which also has a practical application, is the promotion of evidence-based science (Jensen and Gerber, 2020). This concept refers to the use and presentation of rigorously interpreted and discussed scientific data obtained by combining researchers' experience and personal skills with the evidence provided by systematic studies (Jensen and Gerber, 2020). Traditionally, one of the main errors scientists have made when studying the epidemiology of pathogens in wildlife, as well as in the wildlife-domestic-human interface, is the lack of general knowledge integration from different expertise disciplines. A good indication of this is that, despite advances in human medicine using antimicrobials, the appearance of zoonotic diseases in wildlife species that affect humans is increasingly prevalent (Mackenzie *et al*., 2013). This demonstrates the pressing need to approach the study of zoonotic diseases from a holistic perspective whereby the conservation of habitats and biodiversity and human health are closely related (Cunningham *et al*., 2017). To this effect, an interdisciplinary approach with the joint participation of specialists with expertise in animal and human diseases is necessary, as suggested by the World Health Organization and the European Union (Busani *et al.*, 2006), with the goal of performing epidemiological studies within the One Health framework (Mackenzie *et al*., 2013; Gyles, 2016; Cunningham *et al*., 2017) (Figure 4).

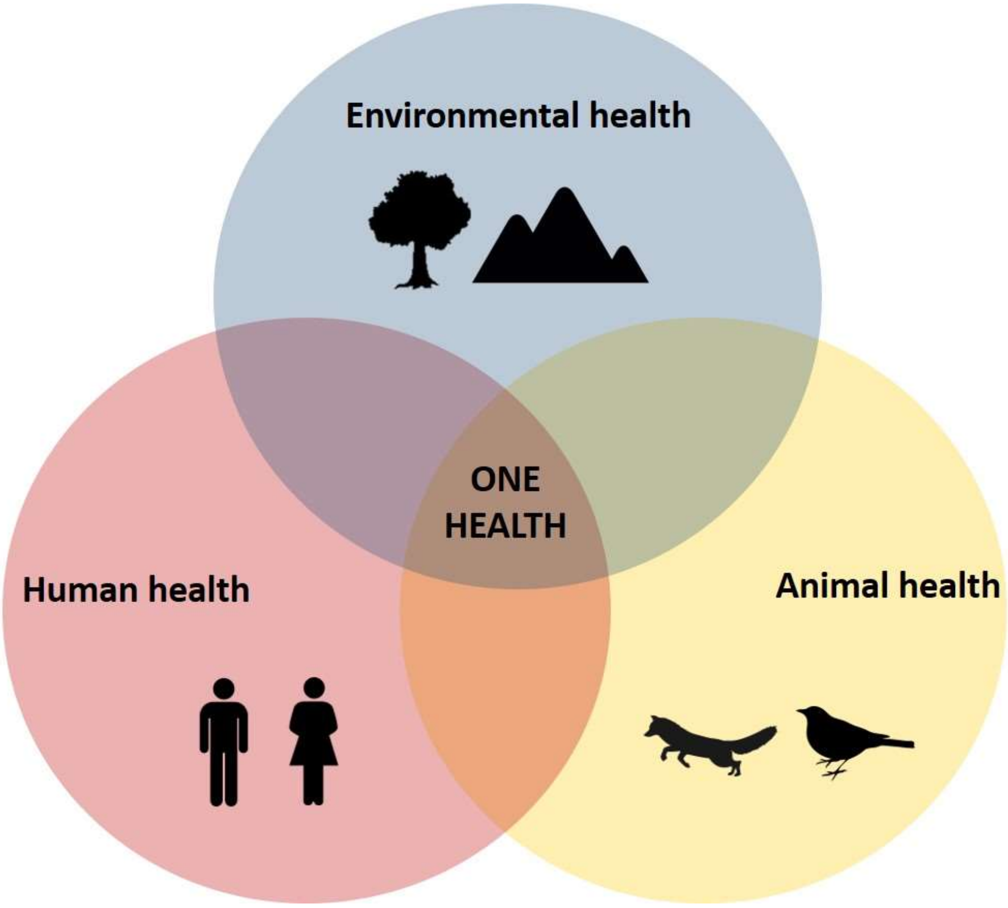

Figure 4. Graphic representation of the One Health concept. Based on Gyles (2016).

Although the first article that mentioned the need to establish collaborations between disciplines with practical applications dates from 1944 (Brozek and Keys, 1944), only in the last decades has this proposal seen renewed support. This coincides with the confirmation that parasites need to be included and considered as fundamental part of ecosystems, while encouraging researchers to approach the study of wildlife diseases from an ecological perspective (Marcogliese and Cone, 1997; Marcogliese, 2003; Sukhdeo, 2012). With this new vision, the contribution of research teams specialized in disciplines such as Epidemiology and Ecology is needed to propose, design, interpret, and assess scientific information concerning ecology and wildlife diseases (Lafferty *et al*., 2008). Moreover, considering future studies will address increasingly complex ecological networks, the need for the participation of researchers with different profiles, such as those with backgrounds in bioinformatics, is anticipated (Michalska-Smith and Allesina, 2019).

When research projects are approached from an interdisciplinary perspective, a key element is the correct and precise use of scientific terminology from each specific field of knowledge. This avoids errors and misunderstandings while promoting an accurate exchange of information and ideas among disciplines (Wells and Richmond, 1995; Hodges, 2008). In this sense, it is desirable to raise interdisciplinary collaboration on scientific studies with the goal of increasing the diversity of approaches to help interpret and discuss the results (Disis and Slattery, 2010). Some unidisciplinary studies may incur in erroneous or imprecise use of scientific terms and concepts, especially if the research is carried out in a field of study different from the researchers' discipline of expertise (Jax *et al*., 1992; Hodges, 2008). In this sense, a lack of rigor and accuracy in the use of terminology and concepts may be the source of the chain of errors that may be repeated in subsequent publications. In the specific case of studying wildlife diseases, these inherited and repeated errors could also have negative health consequences on wildlife and domestic species when they are applied to disease management (Margalida and Colomer, 2012; Gortázar *et al*., 2015).

With the goal of increasing the scientific rigor of research, and, thus, obtaining robust findings that can be used in the management of wildlife species and the conservation of biodiversity in general, detailed fieldwork studies are also recommended (Ríos-Saldaña *et al*., 2018). One possible explanation for the decreasing frequency of studies whose conclusions are based on fieldwork is that they are undervalued from the perspective of publications in comparison to other type of studies (Fitzsimmons and Skevington, 2010). The lesser importance given to fieldwork-based articles, which impedes researchers' professional and career growth (Reich, 2013), may encourage undertaking studies with a less solid empirical basis. Nonetheless, scientific studies with an ecological and epidemiological approach should include rigorous fieldwork, for which a non-invasive methodology may be necessary to provide objective and accurate information; as such, camera trapping may prove very useful in disease ecology studies.

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OBJECTIVES

The overall objective of this doctoral thesis is the study of the behavior of wild species in relation to carnivore carcasses in areas with different degrees of anthropization and biodiversity, underscoring the epidemiological consequences that may be deduced from these interactions.

The recognition of parasites as an integral part of ecosystems has led to an increase in complexity of the epidemiological studies of wildlife diseases. In this sense, the importance of establishing interdisciplinary scientific collaboration that enables improving the assessment and discussion of results brings us to the first objective of this doctoral thesis:

1. **To describe and evaluate the scientific knowledge of the meat-borne parasite transmission to carnivores at the wildlife-domestic-human interface**. This study focuses on parasites transmitted through the consumption of meat that are worldwide distributed (*Trichinella* spp., *Toxoplasma gondii* and *Neospora caninum*). The specific objectives are (a) to explore whether claims that parasites are transmitted through meat consumption in the wildlife are scientifically founded, (b) to determine whether specific ecological concepts and terms are used correctly and accurately in epidemiological studies that address meat-borne parasite transmission in wild species, and (c) to evaluate whether the appropriate use of these concepts and terms is related to the degree of interdisciplinarity of the research teams who participate in this type of studies. This objective will be addressed in **Chapter 1**.

Concerning the trophic transmission of parasites, and in accordance with recently published studies, the apprehension of mammalian carnivores to get infected may condition the consumption of carnivore carrion by this type of scavengers. This avoidance behavior seems especially strong when the carrion belongs to species which are phylogenetically close to the consumer. For this reason, the second objective of this doctoral thesis is:

2. **To evaluate the trophic behavior of vertebrate scavengers regarding the consumption of carnivore carcasses over time in areas with different communities of scavengers and degrees of anthropization**. In this section, special attention will be paid to the scavenging behavior of the red fox (*Vulpes vulpes*), considering from an epidemiological perspective the consequences that such behavior can have on the transmission of meat-borne parasites in the wild. This objective will be addressed in **Chapter 2**.

This avoidance behavior of species visiting carnivore carcasses may include approach and contact patterns of interest for the epidemiological study of non-trophically transmitted pathogens. For this reason, the third objective of this doctoral thesis is:

3. **To describe the pattern of non-trophic interactions among vertebrates, both carnivores and herbivores, and carnivore carcasses in areas with different degrees of anthropization and biodiversity**. Particular focus will be placed on non-trophic interactions between carcasses and red fox, interpreting from an epidemiological approach the possible consequences of such behaviors on the propagation on non-trophically transmitted pathogens. This objective will be addressed in **Chapter 3**.

CHAPTER 1

RESEARCH ON MEAT-BORNE PARASITES IN WILDLIFE: THE CHALLENGE OF BUILDING A SCIENCE-BASED EPIDEMIOLOGY

ABSTRACT

In recent years, the study of parasites has gained notoriety in Ecology, especially from a phylogenetic-evolutionary perspective and in relation to food webs. Thus, a holistic vision that integrates both the epidemiological and ecological perspectives is critical to address the study of infectious diseases in wildlife. Here, we conducted a systematic review of studies on parasite transmission by meat consumption, by either predation or scavenging, at the wildlife-livestock-human interface, with the aim of determine if a) assumptions about the transmission of meat-borne parasites in wildlife are based on accurate evidences, b) the key ecological terms on meat consumption are used correctly and accurately, and c) the precise use of this terminology relates to the degree of interdisciplinarity of the research team. Most of the articles analyzed were carried out by unidisciplinary teams (74.2%), mostly composed of veterinarians, and only a minority (25.8%) were interdisciplinary teams comprising mainly veterinarians, biologists or physicians. To support the epidemiological interpretation of meat-borne parasite transmission, 46.1% of the publications made non-science-based assertions, 51.7% relied exclusively on statements drawn from bibliographical references, and none of the studies based their conclusions on accurate field data. One of the consequences of the lack of interdisciplinary collaboration in the study of meat-borne parasite transmission in wildlife was that ecological terms related to the trophic behavior of carnivores were often not used and, when mentioned, were used inaccurately or even erroneously. We suggest that interdisciplinary collaboration may favor the correct and accurate use of scientific language in research on disease ecology, which could facilitate effective communication among disciplines and thus consolidate future interdisciplinary collaborations.

INTRODUCTION

Parasites are fundamental components of all ecosystems and therefore are involved in the structure and functioning of natural communities (Dobson and Hudson, 1986; Price *et al.*, 1986; Gómez and Nichols, 2013; Seabloom *et al.*, 2015). The diversity of parasites is huge and includes an immense array of taxonomic groups and life-history traits (Poulin, 2007; Fountain-Jones *et al.*, 2018; Llopis-Belenguer *et al.*, 2019). An evidence that parasites are fully integrated into ecosystems is that many of them have life cycles involving different definitive, intermediate, accidental and paratenic host species, as a result of co-evolutionary processes (Price *et al.*, 1986; Brunner and Eizaguirre, 2016;

Sarabian *et al*., 2018). This implies a great number of ecological interactions and strategies for the maintenance and transmission dynamics of parasites (Parker *et al*., 2003). Consequently, the study of the epidemiology of parasites and, in particular, the way they are transmitted in the environment remains one of the major challenges in epidemiological, ecological and evolutionary research (Ezenwa *et al*., 2006; Sukhdeo, 2012).

Currently, it is recommended that the study of infectious diseases be undertaken from a One Health approach (Jenkins *et al*., 2015; Sleeman *et al*., 2019). The implementation of this holistic perspective, although difficult to carry out in wildlife, is necessary to understand the epidemiological role played by wild species. Since any modification of ecological interactions could result in a change in the epidemiology of pathogens (Altizer *et al*., 2013), ecological aspects must be taken into account when studying parasites in wildlife, especially nowadays due to the global environmental change that our planet is undergoing (Parmesan, 2006).

The trophic route is one of the most frequent ways of parasite transmission in the wild (Lafferty and Kuris, 2002). Most studies on the trophic behavior of wild carnivorous mammals have been carried out by biologists, while the epidemiological study of meat-borne pathogens in nature has been undertaken by veterinarians. Epidemiological interpretation of how the sylvatic cycle of parasites is maintained must be supported by scientific evidence of the ecological interactions involved in such a transmission route (Fountain-Jones *et al*., 2018). In this regard, it is particularly widespread in a veterinary epidemiology context that the transmission of meat-borne parasites in wild carnivores (e.g., *Trichinella* spp., *Toxoplasma gondii* and *Neospora caninum*) occurs in part by scavenging behaviors, including intraspecific consumption (i.e., cannibalism) (Campbell, 1988; Pozio, 1998; Pozio, 2000; Gondim, 2006; Pozio and Murrell, 2006; Dubey and Jones, 2008; Almería, 2013; Lopes *et al*., 2015; Badagliacca *et al*., 2016). However, this last statement is in contradiction with recent findings showing that carnivorous mammals generally have a low cannibalistic tendency (Selva *et al*., 2005; Moleón *et al*., 2017). This indicates that the scientific evidence supporting this epidemiological interpretation is often weak (Von Elm and Egger, 2004; Zaccai, 2004) and insufficiently based on accurate fieldwork data (Ríos-Saldaña *et al*., 2018). In addition, it suggests that the interdisciplinary collaboration in epidemiological research is limited (Disis and Slattery, 2010; Blanco, 2014). At this point, we must highlight that wrong scientific statements and unfounded assertions may have important negative consequences on the management of domestic and wild animals' health (Margalida and Colomer, 2012; Gortázar *et al*., 2015).

The existence of many factors that may influence the transmission of parasites in the wild encourages the collaboration between biologists and veterinarians when undertaking epidemiological studies. This interdisciplinary approach requires the use of concepts and terms with specific meaning to each of these scientific disciplines. When researching from an interdisciplinary approach, the precise and correct use of scientific language is essential to avoid errors and misinterpretations (Wells and Richmond, 1995; Pushkin, 1996; Hodges, 2008; Bridle *et al*., 2013; Fischer *et al*., 2015). Only in this way can effective communication and the sharing and integration of accurate ideas between disciplines be successfully achieved (Ripple *et al*., 2016).

The general goal of this study is to systematically review the current status of knowledge about parasite transmission through trophic behavior in terrestrial vertebrate carnivores at the wildlife-livestock-human interface. The systematic review focuses on meat-borne pathogens, in particular three parasites widely distributed around the world (*Trichinella* spp., *T. gondii* and *N. caninum*), with the aim of providing answers to the following questions: a) are statements about the transmission of meat-borne parasites in wildlife based on accurate evidences?; b) are the key ecological concepts and terms on meat consumption used correctly and accurately in epidemiological studies on trophic transmission of parasites in wildlife?; and, c) does the precise use of this terminology relate to the degree of interdisciplinarity of the research team involved in the epidemiological study? We hypothesize that epidemiological studies in wildlife conducted by veterinarians generally assume that certain trophic behaviors, such as cannibalism, are common among wild carnivorous mammals and, therefore, reach epidemiological conclusions that are not science-based. Our prediction is that interdisciplinary studies between ecologists and veterinarians employ the terms and concepts related to trophic behavior with more accuracy. Our study provides information to be taken into account in the design of future epidemiological researches on wildlife, especially those related to the transmission of meat-borne parasites.

MATERIAL AND METHODS

Defining key ecological terms

This systematic review is based on parasites transmitted by meat consumption at the wildlife-livestock-human interface. For this reason, it requires the definition of key ecological terms frequently employed in ecology and other biology disciplines when referring to vertebrate carnivores (Figure 1). First, "carnivore" is any animal that eats meat and other animal tissues, irrespective of its taxonomic identity. Second, the term "predation" refers to the consumption of a prey that has been killed by the consumer, while "scavenging" refers to the consumption of "carrion", i.e., tissues from animals that have died from causes other than predation by the consumer (Getz, 2011; Olea *et al.*, 2019). Third, a distinction can be made depending on the species to which the consumer and the prey belong. When the prey, either predated or scavenged, and the consumer belong to different species, we refer to "interspecific predation/scavenging", and when they belong to the same species, we refer to "intraspecific predation/scavenging" or, generally, "cannibalism" (Polis, 1981; Abrams, 1987). Thus, it should be noted that the concept of cannibalism includes the consumption of both predated and scavenged animals.

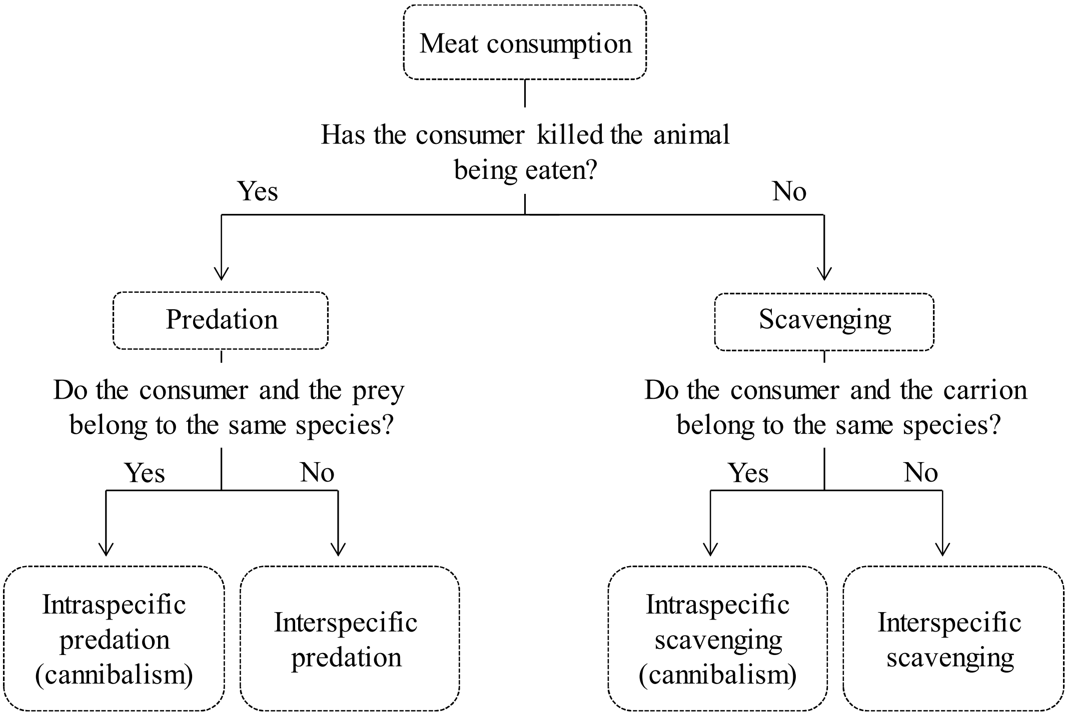

Figure 1. Key ecological terms commonly used to describe meat consumption in carnivore animals.

Search protocol and selection criteria

We conducted a systematic review of scientific publications on pathogens transmitted by meat consumption, with special attention to three parasites (*Trichinella* spp., *T. gondii* and *N. caninum*). The election of these paradigmatic meat-borne parasites is justified by the wide range of wild host species, as well as because they are zoonotic agents (*T. gondii* and *Trichinella* spp.) or have an impact on livestock health (*T. gondii* and *N. caninum*) (Hill and Dubey, 2002; Pozio and Murrell, 2006; Dubey *et al*., 2007). Following guidelines provided by Haddaway *et al*. (2015), and according to the protocol outlined by PRISMA (Moher *et al*., 2009), we used the Web of Science database to search for "articles" and "reviews" published on or before December 2015 that included the following terms in the title or abstract: "Carrion" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; "Meat" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; "Scaveng*" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*"; and "Predat*" AND "Pathogen" OR "*Trichinella*" OR "*Toxoplasma*" OR "*Neospora*". Since the scope of this study was restricted to epidemiological studies at the wildlife-livestock-human interface, including vertebrate hosts, the research was limited to published studies in three scientific categories: "Veterinary Science", "Pathology", and "Parasitology". The search was completed with additional articles found by Google Scholar and PubMed, as well as with references obtained by reading the bibliography sections of the articles found in the consulted bibliographic databases. Data extraction, selection and analysis were conducted by the first author of this study, with co-authors cross-checking data when necessary.

In the first phase duplicated publications were excluded and 12,945 records were obtained. After restricting the search to the scope of the three scientific categories mentioned above, the records were reduced to 2,603. The selection of the final set of publications was performed on the basis of a two-step process following the recommendations of Dressel *et al*. (2015). The first step was to check the title and abstract of each publication in order to assess the relevance of the subject and eligibility and to separate "research articles" from "reviews", excluding other kind of publications different from the previous ones (e.g., letters, book chapters and congress proceedings). The second step was to read the full content of the papers to identify those studies within the scope of this systematic review. At this point, epidemiological studies involving only domestic animals (without referring wildlife trophic interaction), laboratory and experimental studies, articles dealing exclusively with human medicine, food science studies and articles on invertebrate hosts were excluded. This resulted in 89 research articles and 31 reviews for in-depth review (Figure S1 and Appendix S1).

Data extraction and analysis

Each selected publication was carefully read to extract the following general information: “year” of publication; country in which the research was carried out (i.e., the study area; only for articles, following the criterion of assigning the country according to the area where the study was carried out); and “biome” of the study area (from Olson *et al.*, 2001). In addition, the following eco-epidemiological information was extracted from each of the selected articles: wild and domestic “host species” (i.e., those vertebrate species listed in the publication that are susceptible to the pathogen investigated); “class” to which the host species belongs (Amphibia, Reptilia, Aves, Mammalia); “feeding behavior” of the host species (carnivore, herbivore, omnivore); type of “pathogen” studied (helminths, protozoa, bacteria, viruses, prions); the “process” of obtaining the consumed meat, as argued/indicated/suggested by authors (predation, scavenging, cannibalism, meat-borne pathogen transmission in humans, any combination of the above, and not mentioned); and the “type of evidence” on which the parasite transmission route, if any, was inferred (direct evidence, such as direct observation or video recording of animals consuming prey; scientific bibliography; indirect evidence, such as diet studies from feces; and non-science-based assertions). Moreover, we checked whether the ecological terms related to meat consumption by carnivores (Figure 1) were correctly used in the reviewed publications (articles and reviews). The “use of terms” was classified as: not used (when the term was not mentioned in the article), misused (when the term was incorrectly used, i.e., it was used to describe a different process), inaccurately used (for example, when the term cannibalism was used without specifying whether it refers to cannibalistic predation or cannibalistic scavenging), and correctly used (when the context in which the term is applied leaves no doubt as to the precision of its use). Finally, the research “profile” of the co-authors of articles and reviews (veterinarian, biologist, physician, another research profile) was recorded, as inferred from each author´s affiliation. Based on this, “research teams” were classified as unidisciplinary (when all the co-authors belonged to the same discipline) or interdisciplinary teams (when there were co-authors of at least two different disciplines).

From the selected publications, it was evaluated whether a) the type of evidence on which the study based its conclusions about the meat-borne parasite transmission was science-based and b) the correct and precise use of the ecological terms and concepts were related to the unidisciplinary or interdisciplinary character of the research team.

With the aim of revealing relationships between epidemiological and ecological terms used in articles about pathogen transmission through meat consumption at the wildlife-livestock-human interface, we identified clusters of terms extracted from the content of the selected publications. For this purpose, we used VOSviewer (http://www.vosviewer.com/), a free software for creating and visualizing semantic networks or term maps from scientific literature (Van Eck and Waltman, 2010; Perianes-Rodriguez *et al*., 2016). The software applies text mining and clustering functions to analyze co-occurrence of terms (Van Eck and Waltman, 2010). We focused on the terms (n=388 terms; we did not consider general words such as articles, prepositions and pronouns) that co-occurred in the title or abstract of at least two articles. We then examined the terms initially selected by the software and removed those that were not considered key terms directly related to the core of the study and that are usually mentioned, such as “analysis”, “antibody”, “antigen”, “data”, “human infection”, “laboratory”, “patient”, “PCR”, “result”, “sample”, “sex”, “study” or survey”. Thus, we obtained a final subset of 25 terms of epidemiological and ecological relevance (Figure S2) to construct the semantic network.

RESULTS

Type of meat-borne pathogens in wildlife subject to study

In relation to the meat-borne pathogens studied at the wildlife-livestock-human interface, most of the tested articles involved helminths (61.8%; 55/89), being in all cases publications focusing on *Trichinella* spp. Protozoa was the second most studied group of meat-borne parasites (30.3%; 27/89), with most articles targeting *T. gondii* (88.9%). Bacteria, viruses and prions compounded the minority group (14.6%; 13/89) with predominance of articles focused on bacteria of the genera *Salmonella, Leptospira* and *Mycobacterium*. The rest of pathogens (viruses and prions) had a marginal appearance in our search. On the other hand, one article addressed the study of all the groups of pathogens mentioned (helminths, protozoa and others), two papers jointly analyzed protozoa and helminths, and other two studies dealt with protozoan parasites and other pathogens belonging to the minority group (Figure S3, Table S1).

Temporal and geographical distribution of included studies

The majority of articles and reviews have been published since 2000 (Figure S4). Most articles on the transmission of pathogens through meat consumption in wildlife were published in Europe and North America, mainly United States, Italy and Spain (Figure 2). Europe concentrated 63.6% (35/55) and 41.7% (10/24) of articles on *Trichinella* spp. and *T. gondii*, respectively, while 21.8% (12/55) and 16.7% (4/24) of articles on these pathogens, respectively, came from North America. Most of articles were focused on two biomes (Figure S5): temperate broadleaf and mixed forests (34.4%; 44/128 total biomes mentioned in the 89 articles) and Mediterranean forests, woodlands, and scrub (22.1%; 27/128).

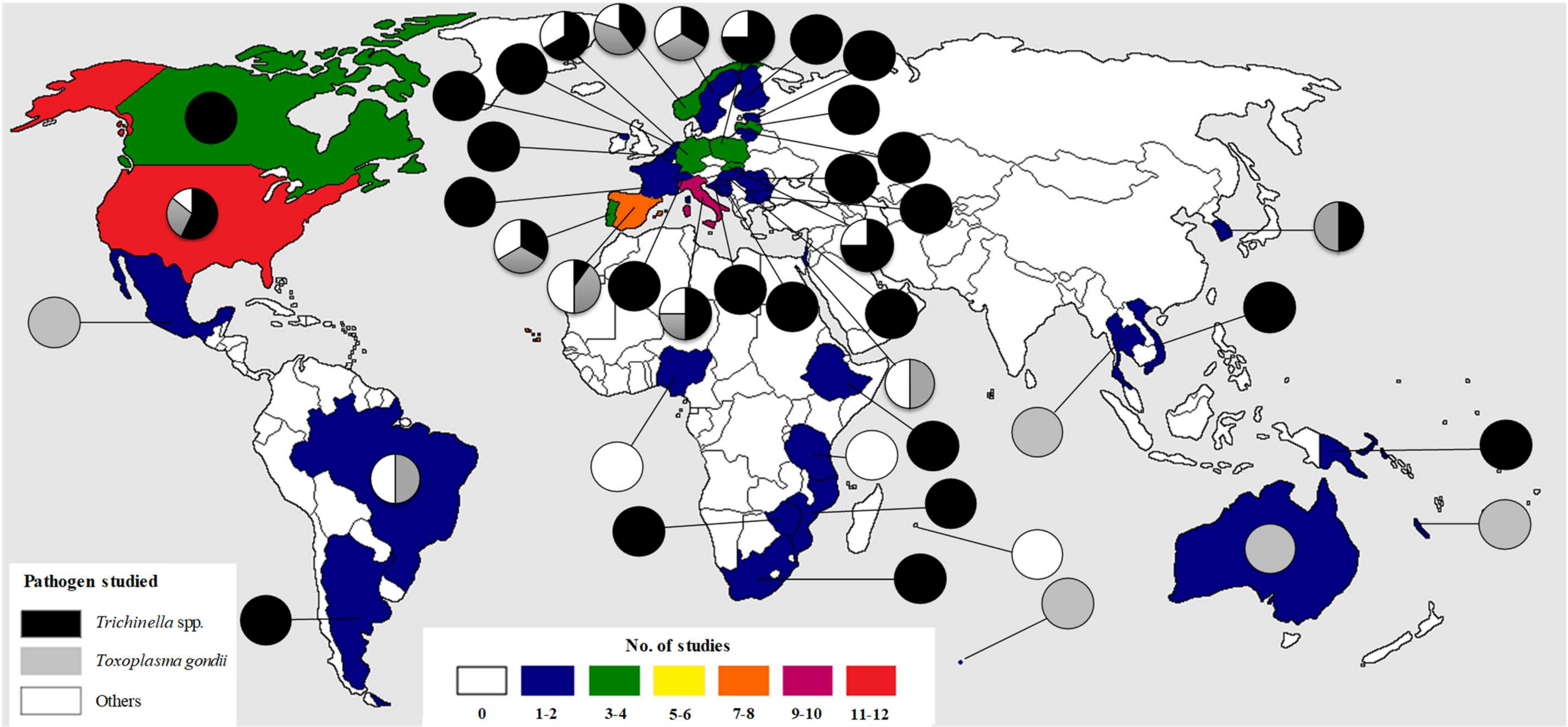

Figure 2. Worldwide geographical distribution of published articles on meat-borne pathogens (*Trichinella* spp., *T. gondii* and other pathogens) at the wildlife-livestock-human interface.

Parasites and host species assessed

In the articles evaluated (n=89), a total of 148 vertebrate species belonging to 104 genera were identified as hosts involved in the transmission of meat-borne parasites. Suidae family constituted the largest group of studied hosts (40.4%; 36/89, including 26 publications on wild boar, two on domestic pig and eight on both), followed by the genera *Vulpes* (32.6%; 29/89), *Canis* (19.1%; 17/89), *Ursus* (15.7%; 14/89), *Rattus* (13.5%; 12/89) and *Felis* (11.2%; 10/89). All articles checked focused on at least one wild species (median: 2; range: 1-33), and 15 publications (16.9%) also addressed at least one domestic species (median: 1; range: 1-4), mainly livestock.

With regard to articles focusing on the study of *Trichinella* spp., 88.1% dealt with mammals, 8.5% with birds and 3.4% with reptiles. Overall, 57.1% of articles addressed omnivorous mammal species, 26% carnivorous mammals and 7.8% herbivorous mammals; the remaining 6.5% and 2.6% corresponded to publications about *Trichinella* spp. affecting carnivorous birds and carnivorous reptiles, respectively.

The articles involving *T. gondii* were mainly conducted on mammals (85.7%), followed by birds (14.3%). Among the former, 32.4%, 32.4% and 24.3% focused on carnivorous, omnivorous and herbivorous species, respectively. The remaining publications (10.8%) dealt with carnivorous bird species. Regarding articles investigating other meat-borne pathogens, 88.9% dealt with mammals (48% omnivores, 32% carnivores and 20% herbivores) and 11.1% with carnivorous birds (Figure 3).

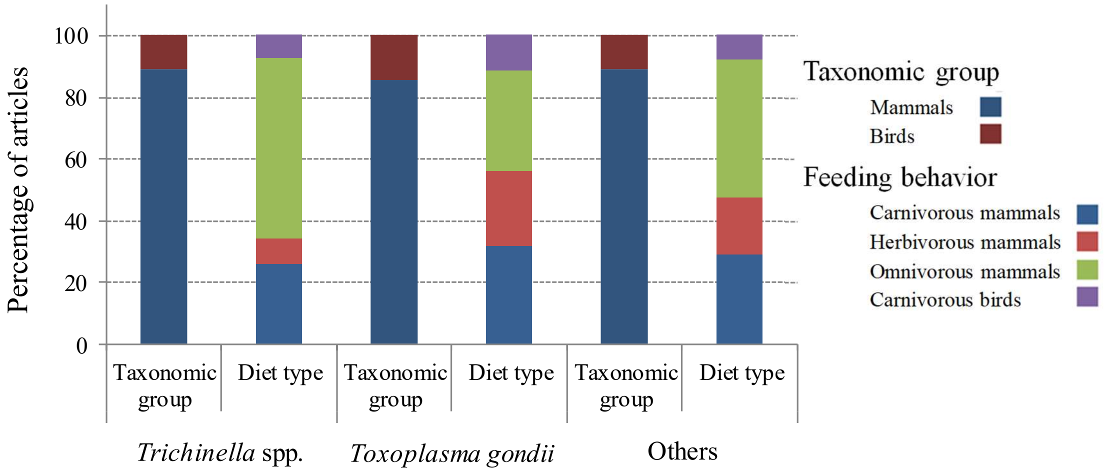

Figure 3. Taxonomic group and feeding behavior of host species of *Trichinella* spp., *T. gondii* and other pathogens, according to the reviewed publications. Reptiles are not shown because their appearance in the reviewed publications was anecdotal.

Evidences supporting epidemiological interpretation on meat-borne parasite transmission

All checked articles indicated some form of transmission; specifically, 52.8% (47/89) of the studies mentioned two or more possible routes of acquiring parasites transmitted by meat consumption, while 47.2% (42/89) mentioned only one way of transmission. Scavenging was the most frequently referred transmission route (62.9%; 56/89), followed by animal meat consumption in humans (41.6%; 37/89), cannibalism (25.8%; 23/89) and predation (24.7%; 22/89).

With regard to the evidences or premises on which the authors supported the mentioned transmission routes (Figure 4), most of the articles used exclusively statements taken from scientific bibliography (51.7%; 46/89), followed by studies with non-science-based assertions about the transmission route (46.1%; 41/89). Only two articles (2.2%; 2/89) used indirect evidences, such as the analysis of host's feces, as a basis for supporting their epidemiological conclusions about the transmission route. None of the 89 articles reviewed supplied direct scientific evidence to support their epidemiological conclusions.

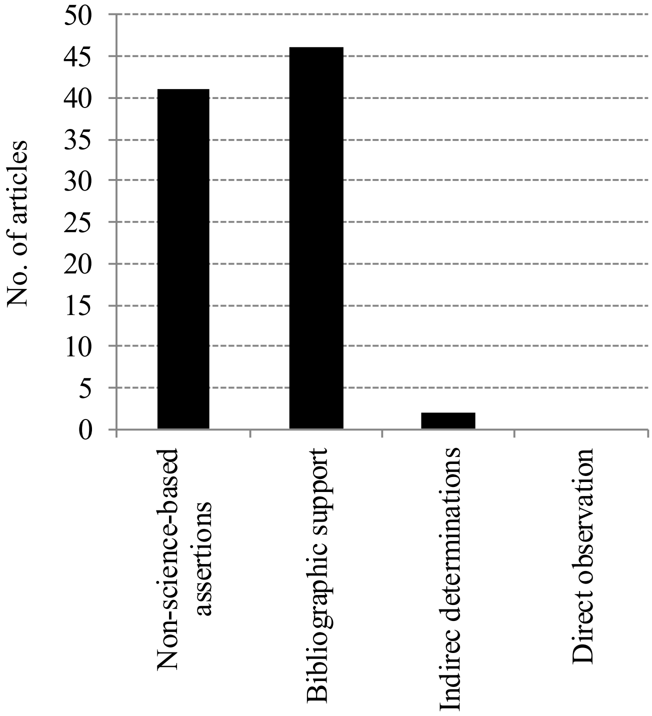

Figure 4. Evidences or assumptions on which the authors supported their conclusions on the transmission routes of the parasites mentioned in their studies.

Degree of team interdisciplinarity and use of key ecological terms related to meat consumption

Articles conducted by unidisciplinary teams represented a higher proportion (74.2%; 66/89) than those done by interdisciplinary teams (25.8%; 23/89) (Table 1). Most epidemiological studies on meat-borne parasites at the wildlife-livestock-human interface have been conducted by unidisciplinary teams of veterinarians (95.5%; 63/66), followed by research teams composed exclusively of physicians (3%; 2/66) and biologists (1.5%; 1/66). Moreover, the studies conducted by interdisciplinary teams were composed mainly of veterinarians and biologists (65.2%; 15/23), followed by veterinarians and physicians (17.4%; 4/23). Only two articles were made by teams integrating veterinarians, biologists and physicians (8.7%; 2/23). Authorship in interdisciplinary collaboration belonged mainly to veterinarians (95.7%; 22/23), followed by biologists (78.3%; 18/23) and physicians (30.4%; 7/23).

Table 1. Distribution of articles (A) and reviews (R) on transmission of meat-borne parasites at the wildlife-livestock-human interface, according to the unidisciplinary or interdisciplinary character of the research team, which may be composed of veterinarians, biologists, physicians and other research profiles, as well as any combination of them.

	Veterinarian		**Biologist**		**Physician**		**Other**	
	A	R	A	R	A	R	A	R
	← 2 articles →						-	-
Veterinarian	63	19	-	-	-	-	-	-
Biologist	15	1	1	-	-	-	-	-
Physician	4	5	1	-	2	6	-	-
Other	1	0	-	-	-	-	-	-

Regarding the scientific reviews checked in our study, most of them were also performed by unidisciplinary teams (80.6%; 25/31) formed by veterinarians (76%; 19/25) and physicians (24%; 6/25). The reviews conducted by interdisciplinary groups (19.4%; 6/31) involved veterinarians and physicians (83.3%; 5/6) and veterinarians and biologists (16.7%; 1/6).

In relation to the unidisciplinary articles analyzed, 30.3% (20/66) did not use key ecological terms, 31.8% (21/66) misused them and 36.4% (24/66) utilized them inaccurately. Only one unidisciplinary article used the ecological terminology correctly (1.5%; 1/66). Regarding articles conducted by interdisciplinary teams, key ecological terms were not used, misused and inaccurately used in 43.5% (10/23), 8.7% (2/23) and 47.8% (11/23) of articles, respectively. None of the articles carried out by interdisciplinary research teams properly used these key ecological terms applied to the trophic transmission of meat-borne parasites. In relation to unidisciplinary reviews, in 32% (8/25) of them the use of key ecological terms was not detected, 32% (8/25) misused them, 32% (8/25) used the terms inaccurately, and only one review (4%; 1/25) used them properly. In the reviews carried out by interdisciplinary teams, these percentages were 16.7% (1/6), 0% (0/6) and 83.3% (5/6), respectively, with no review correctly using these key ecological terms.

Semantic network of epidemiological and ecological terms

In the semantic map constructed with the epidemiological and ecological terms most frequently used in the articles examined, three thematic clusters emerged (Figure 5). One of them was related to key terms commonly mentioned in ecological studies on trophic behavior of wild animals (e.g., “carcass”, “carrion”, “scavenger”, “prey”, “scavenging”). In contrast, the other two clusters included concepts frequently used in epidemiological studies on wildlife diseases, zoonoses and diseases shared with domestic animals (e.g., “pig”, “sylvatic cycle”, “human”, “cannibalism”, “trichinellosis”). In particular, one cluster was related to “*Trichinella* spp.” and Suidae species (“wild boar” and “pig”), while the other cluster was related to “*T. gondii*”, “fox”, “wolf” and, to a lesser extent, “*N. caninum*”.

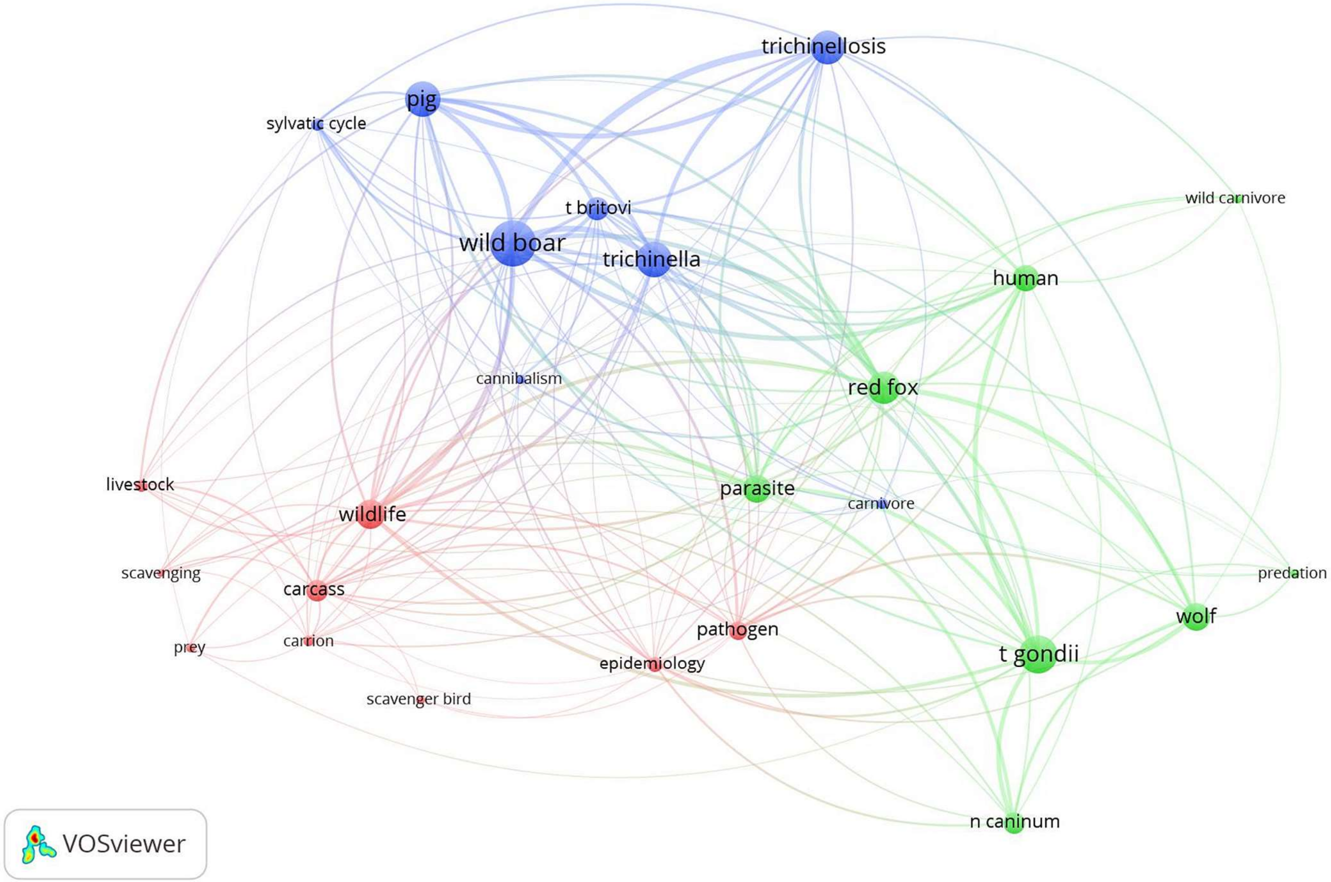

Figure 5. Semantic network to identify relationships between ecological and epidemiological terms in articles on transmission of meat-borne parasites at the wildlife-livestock-human interface. Each color shows a thematic cluster, and the diameter of the colored circles is proportional to the number of times a certain term is cited in the reviewed publications.

DISCUSSION

General patterns in the literature on meat-borne parasite transmission

The growing concern for the study of infectious agents from a One Health perspective has led to a significant increase in the number of scientific publications addressing the study of pathogens at the wildlife-livestock-human epidemiological interface over the past two decades (Wiethoelter *et al*., 2015), as shown in this review for articles and reviews focused on the transmission of parasites by meat consumption. Wildlife constitutes an important reservoir for the maintenance and transmission of a large number of zoonotic pathogens shared with domestic animals, among which *Trichinella* spp., *T. gondii* and *N. caninum* are particularly noteworthy (Bidaisee and Macpherson, 2014; Bird and Mazet, 2018). Since the beginning of the 21st century there has been an increase in the number of articles and scientific reviews focusing on the study of the transmission of parasites by meat consumption in wild species, mainly *Trichinella* spp. and *T. gondii*. It is striking that there was a reduction in the number of publications in 2012, possibly as a result of the impact of the economic crisis on science, as investment in research normally decreases in recession times (Hopwood, 2009; Izsak and Radošević, 2016).

Most of the scientific articles published on topics related to the transmission of meat-borne pathogens at the wildlife-livestock-human interface have been carried out in economically developed areas of the world, mainly Europe and North America, where the investment in science is highest (Tollefson, 2018). These results are consistent with the fact that most publications are from a high-ranking country based on the human development index, a metric correlated with gross domestic product (Livingston *et al*., 2016). In fact, there is a positive relationship between a country's gross domestic product and its research and development spending (Meo *et al*., 2013). These results highlight the need to increase research efforts on carnivorism in areas of the world that are rich in biodiversity, including carnivorous vertebrate species and complex predator-prey and host-parasite relationships (Van der Giessen *et al*., 2001; Ripple *et al*., 2014; Ratnayeke *et al*., 2018). In fact, the majority of the studies published have focused their research on two biomes: temperate broadleaf and mixed forests, and Mediterranean forests, woodlands, and scrub. This geographic bias has been previously described in the ecological literature (Pereira *et al*., 2010). That is, the biomes that have received the greatest attention from the scientific community are those located in the countries that most invest in science. This situation means that other biomes of undoubted scientific interest are neglected (Murphy and Romanuk, 2016), especially in Tropical and Subtropical areas that have a rich community of vertebrate carnivores, and where the epidemiological dynamics of meat-borne pathogens are likely to be different, due to their own ecological particularities.

In relation to the meat-borne pathogens studied, *Trichinella* spp. received by far the highest attention from researchers. This is probably because it is a genus that comprises several nematode species widely distributed, with a large variety of warm-blooded vertebrate hosts distributed in a wide range of biomes (Pozio and Murrell, 2006). In addition, it is one of the meat-borne parasites of greatest concern to public health authorities as a zoonosis (Gottstein *et al*., 2009; Turiac *et al*., 2017), and the most studied meat-borne pathogen at the wildlife-livestock-human epidemiological interface. This is probably due to the fact that *Trichinella* spp. is transmitted to humans through the ingestion of game meat, highlighting the epidemiological role of wild boar, rodents and wild canids in maintaining the sylvatic cycle of *Trichinella* spp. (Pozio, 2000). The second most frequently studied parasite was *T. gondii*. It is a zoonotic protozoa that affects a wide range of domestic and wild hosts, both birds and mammals. Although *T. gondii* has other routes of transmission, for carnivores and omnivores, including humans, infection predominantly occurs by meat consumption (Dubey, 2010). Despite this, our systematic review shows that *T. gondii* has raised less interest in the study of the epidemiology of meat-borne parasites in the wild (Hill and Dubey, 2002; Belluco *et al*., 2016).

The small number of articles dealing with *N. caninum* at the wildlife-livestock-human interface may be explained because researchers seem to focus more exclusively on livestock species, particularly cattle, where this parasite causes significant economic losses (Dubey and Lindsay, 1996; Dubey *et al*., 2007). However, it has been shown that, in addition to dogs (*Canis familiaris*), other wild canids such as coyotes (*C. latrans*), wolves (*C. lupus*) and dingoes (*C. lupus dingo*) are definitive hosts that can be infected by consumption of meat from ungulate intermediate hosts (Donahoe *et al*., 2015). Another reason possibly explaining the reduced number of articles is that *N. caninum* is not a zoonotic agent.

Regarding the host species assessed, most studies focus on the Suidae family (wild boar and domestic pig) and carnivores of the genera *Vulpes*, *Canis*, *Ursus* and *Felis*. This is consistent with the fact that these hosts participate in the sylvatic and peri-domestic life cycle of *Trichinella* spp. (Korhonen *et al*., 2016), which was the most frequently studied meat-borne parasite according to our review. On the other hand, in the case of felids, they are definitive hosts of *T. gondii* and, therefore, a key host in the development of the life cycle of this protozoan (Dubey, 2010).

It should be noted that a total of 148 vertebrate species have been identified in this systematic review. About 90% of them were mammals, the rest being carnivorous birds (hosts of *Trichinella pseudospiralis* and *T. gondii*) and, to a lesser extent, reptiles (hosts of *Trichinella papuae* and *Trichinella zimbabwensis*) (Korhonen *et al*., 2016; Pozio, 2016). In the case of studies of *Trichinella* spp., omnivorous species were analyzed more frequently, possibly due to the key role played by the wild boar in the life cycle of this meat-borne parasite (Pozio *et al*., 2009); the second most studied group was that of carnivorous mammals. These results were expected, taking into account that the selection of publications of the present study was made based on parasites transmitted by meat consumption. In the case of *T. gondii* and other meat-borne pathogens, the results were similar, as was also to be expected for the same reason.

The need of accurate evidences and interdisciplinarity in epidemiological research of meat-borne parasites

Our systematic review shows that the study of the transmission of meat-borne parasites at the wildlife-livestock-human epidemiological interface is weakly supported by accurate evidences. In the case of meat-borne parasites in the wild, most studies indicated that transmission occurs through carrion consumption, and to a lesser extent through cannibalism and predation. However, more than half of articles based these statements exclusively on the scientific literature already published. Moreover, about 46% used in the discussion of their results arguments that have not been scientifically proven, i.e., they mention trophic behaviors of the studied host species that have not been confirmed by scientific investigations. Some studies (2.2%) used indirect methods to demonstrate a certain trophic behavior (e.g., inferring transmission routes from the analysis of the host's feces). This has two main problems: it is very difficult from feces analysis to distinguish between predation and scavenging (Sánchez-Zapata *et al*., 2010), and the presence of a given material in the feces does not necessarily prove prey consumption (e.g., the presence of red fox hairs in red fox feces seems to correspond mainly to the coat-cleaning behavior of foxes rather than to cannibalism; Remonti *et al*., 2005). None of the evaluated studies used direct methods for obtaining accurate field data to demonstrate the mentioned trophic behavior of a host species. Camera trapping could help to gather high-quality information on meat consumption (e.g., Moleón *et al.*, 2017) and reach robust epidemiological conclusions about the transmission of meat-borne pathogens in the wild (Hanna, 2004; Colombo *et al.*, 2017).

Research on the transmission routes of meat-borne parasites was mainly carried out by unidisciplinary teams. The scarce participation of teams formed exclusively by biologists or physicians indicated that the study of wildlife diseases is mainly undertaken by veterinarians. Our semantic map evidenced the scarce collaboration between disciplines in the study of the trophic transmission of parasites by meat consumption at the wildlife-livestock-human interface. Three term clusters were appreciated, one of which was formed by terms commonly used in ecology and was clearly separated from the other two, which included terms usually cited in epidemiological studies conducted by veterinarians. Undoubtedly, epidemiological research on wild animals requires the participation of veterinarians but, if we want to approach it from a One Health perspective (Gyles, 2016; Sleeman *et al.*, 2019), an integrated view of the epidemiological and ecological aspects is required. For this reason, interdisciplinary collaboration between veterinarians, ecologists and physicians needs to be increased in epidemiological studies (Bridle *et al.*, 2013). Although rare, there are examples of research in the field of wildlife diseases undertaken by interdisciplinary teams that have made significant scientific progress (Medlock *et al.*, 2007; Jaenson *et al.*, 2018). Unfortunately, one obstacle to be overcome is the lack of scientific funding, which is often directed towards unidisciplinary teams despite the fact that, in general terms, scientific results obtained by interdisciplinary teams often have a greater impact on the scientific community and, moreover, maintain this interest for more years (Bromham *et al.*, 2016; Kwon *et al.*, 2017).

The lack of interdisciplinary collaboration led to a more deficient use of the key ecological terms and concepts related to the trophic behavior of carnivores. This calls for closer interdisciplinary collaboration between veterinarians, ecologists, physicians and other researchers. Research approached from a holistic perspective implies the creation of new research horizons. However, in order to avoid errors and misinterpretations, the precise and correct use of the scientific language of each of the disciplines involved in the research should be prioritary (Pushkin, 1996; Hodges, 2008; Herrando-Pérez *et al.*, 2014), which facilitates effective communication between disciplines and, consequently, the consolidation of future interdisciplinary collaborations (Perez, 2015; Ripple *et al*., 2016).

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SUPPLEMENTARY FILES

Table S1. Number of scientific articles focusing on the study of the most relevant meat-borne pathogens.

Type of pathogen	Genus or species	Number of articles
Protozoa	*Toxoplasma gondii*	24
	Neospora caninum	7
	Sarcocystis spp.	2
Helminths	*Trichinella* spp.	55
	Echinococcus spp.	1
Others (bacteria, viruses, prions)	*Salmonella* spp.	4
	Leptospira spp.	4
	Mycobacterium spp.	3

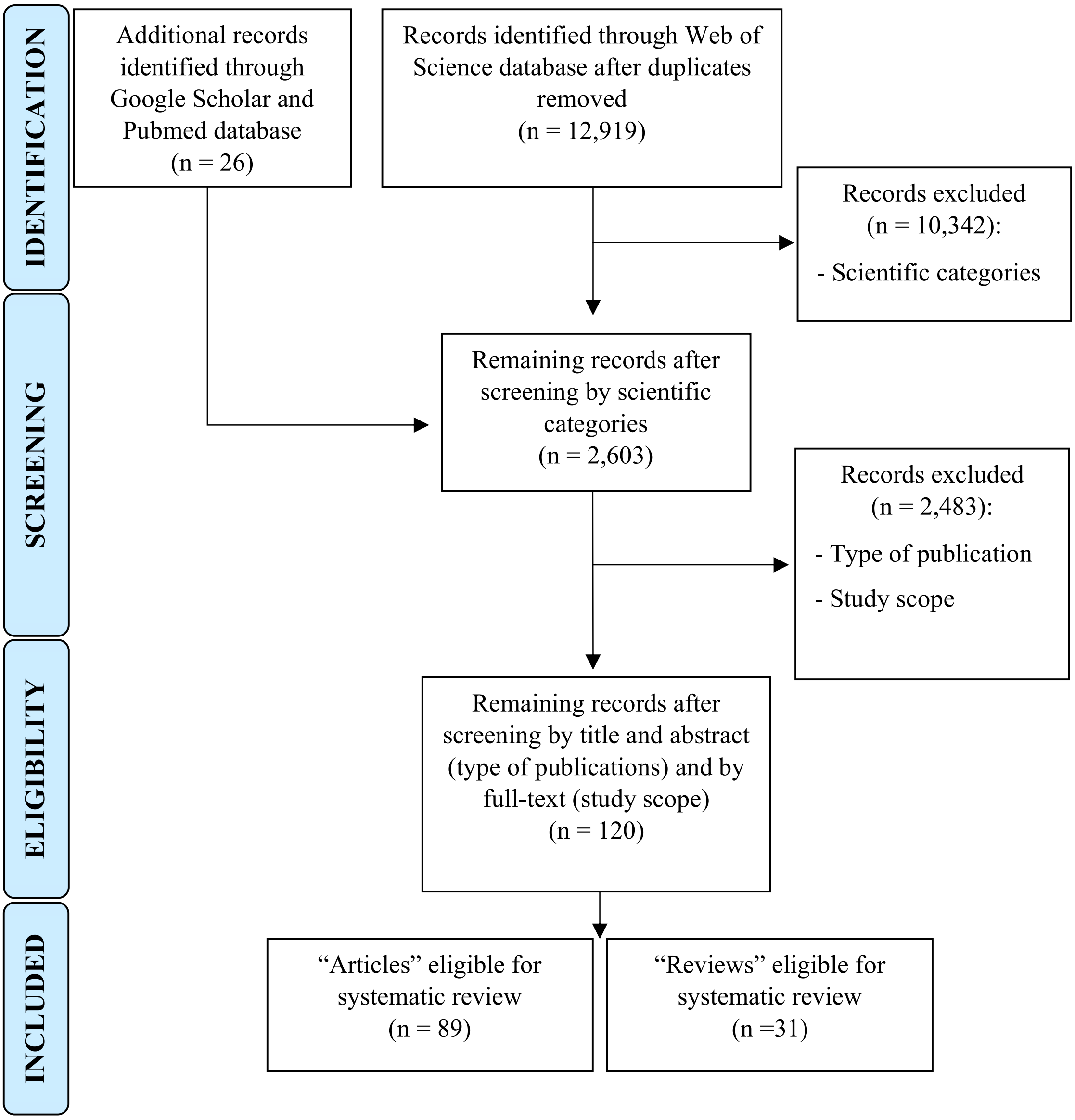


Figure S1. Flow diagram of the results of the identification, screening, eligibility, assessment and inclusion of the reviewed articles and reviews.

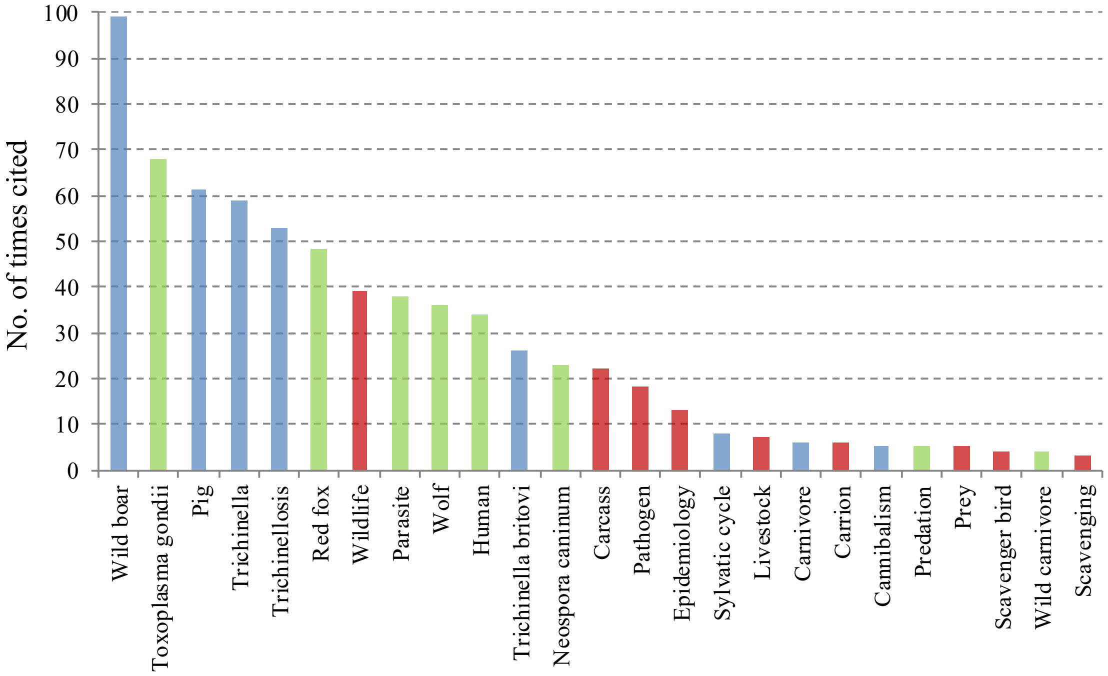


Figure S2. Occurrence of ecological and epidemiological terms selected through VOSviewer, categorized into three clusters (see term interactions in Figure 5).

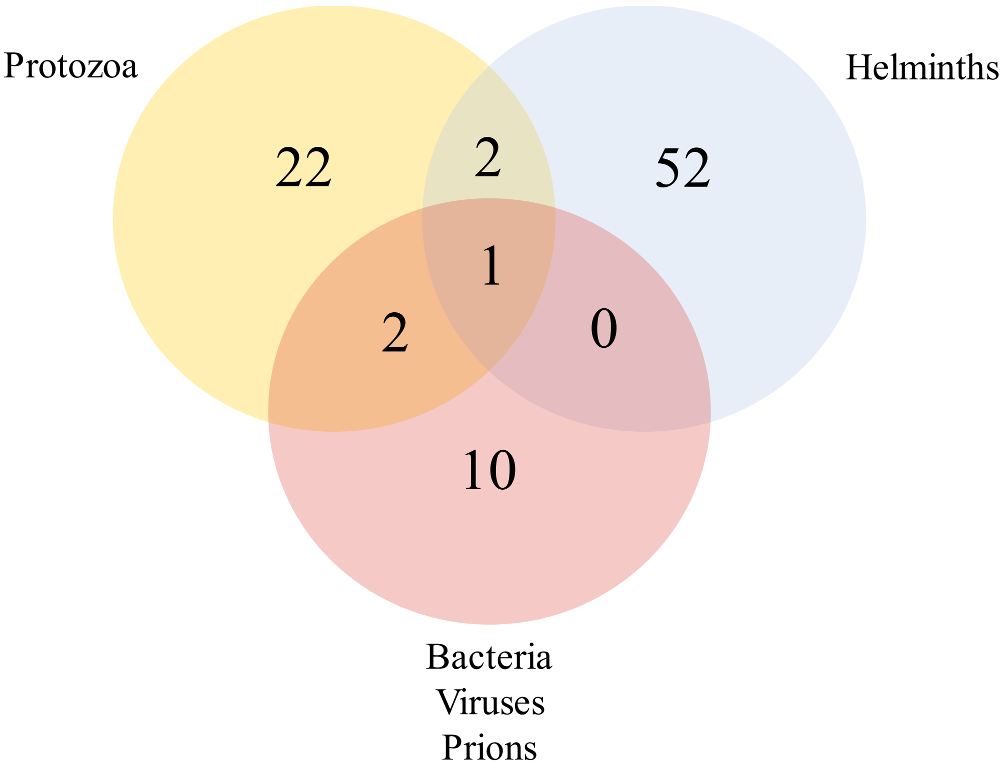
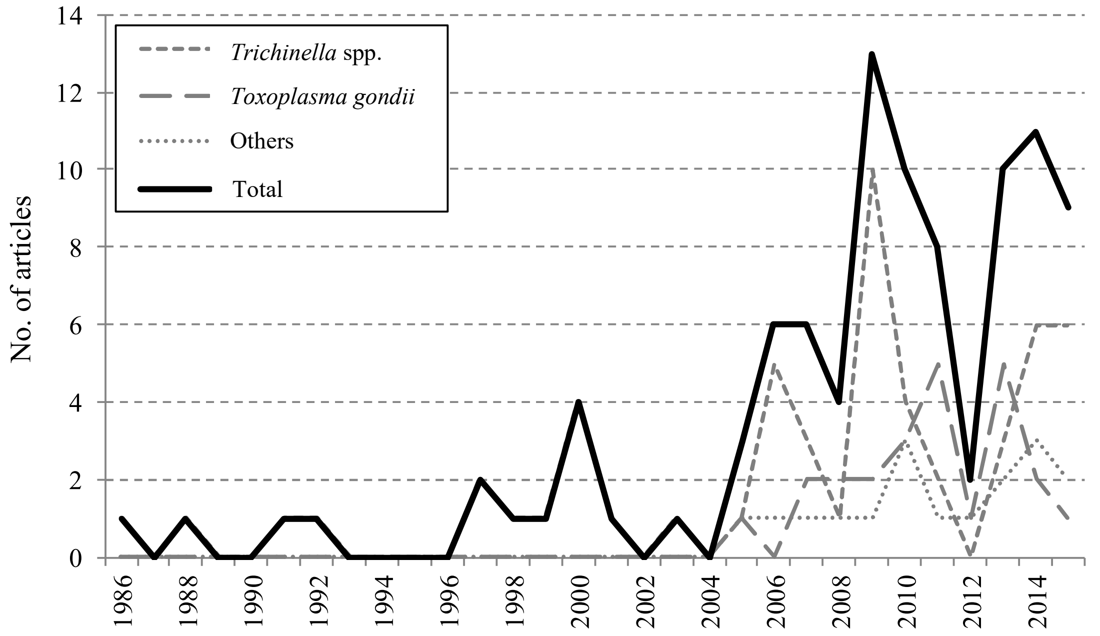


Figure S3. Distribution of the number of articles checked according to the group of meat-borne pathogens at the wildlife-livestock-human interface.



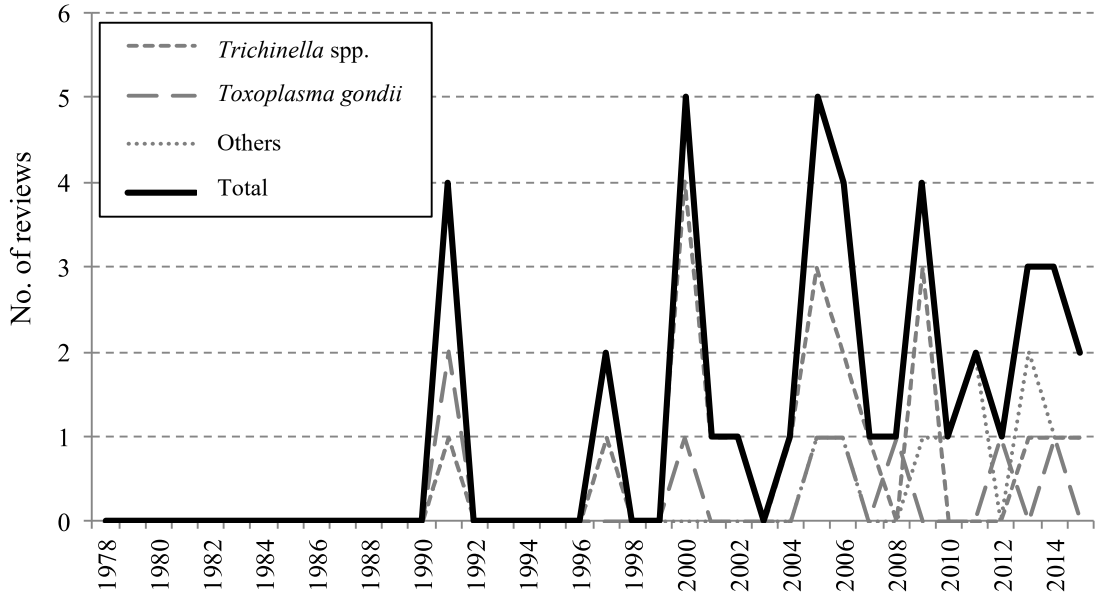


Figure S4. Temporal distribution of articles (upper graph) and reviews (lower graph) published per year addressing the study of meat-borne parasites at the wildlife-domestic-human interface. Publications focusing on *Trichinella* spp., *T. gondii* and other pathogens are shown, as well as the temporal distribution of the sum of all publications.

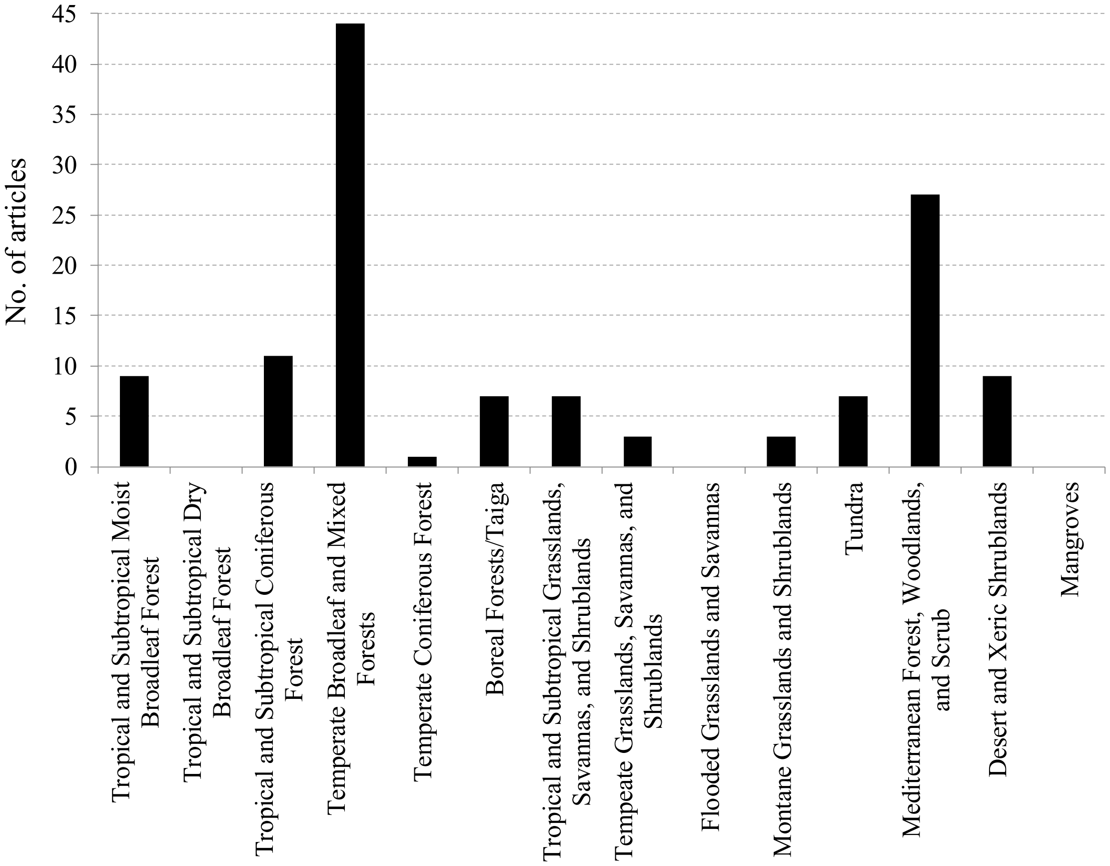


Figure S5. Distribution of evaluated articles according to the fourteen biogeographic biomes described by Olson *et al*. (2001).

Appendix S1. List of articles and reviews selected for this systematic review.

Articles

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CHAPTER 2

SMART CARNIVORES THINK TWICE: SCAVENGING BEHAVIOR OF RED FOX AT CARNIVORE CARCASSES IN RELATION TO THE TRANSMISSION RISK OF MEAT-BORNE PARASITES

ABSTRACT

Parasite avoidance behaviors are essential to understand host-parasite coevolution, as well as wildlife epidemiology and energy flow through food webs. However, the strategies, mechanisms and consequences of avoiding trophically transmitted parasites in mammalian carnivores have received little scientific attention. The absence of detailed behavioral studies has led to the widespread assumption that cannibalistic or intraspecific scavenging is a major transmission route for *Trichinella* spp. and other meat-borne parasites, especially for the red fox (*Vulpes vulpes*). Here, we used videos recorded by camera traps to explore the behavior of red foxes and other mammalian carnivores at 56 intra- and 10 interspecific carnivore carcasses in three areas of southeastern Spain. We found that carrion consumption was dependent on both carcass type (conspecific *vs*. heterospecific to the consumer) and time since the carcass became available. Red foxes were very efficient in detecting mesocarnivore carrion, but they were generally reluctant to consume them, especially conspecific carcasses. In addition, consumption by foxes, when recorded, was delayed several days (carcasses other than fox) or weeks (fox carcasses) after carcass detection. Other mammalian scavengers showed a similar pattern. These findings support the hypothesis that avoidance of carrion from phylogenetically related prey is a widespread behavior in carnivores to reduce the transmission risk of meat-borne parasites. They also suggest that the foraging decisions of scavengers are probably shaped by two 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. Overall, we show that carnivore carcasses are fundamental components in the landscape of disgust for carnivores.

INTRODUCTION

Host-parasite interactions are pervasive in ecosystems and may strongly influence food web structure and function (Lafferty *et al.*, 2006, 2008; Byers, 2009; 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 (Petney and Andrews, 1998; Craft *et al.*, 2008; Morand, 2015). Through an astonishing diversity of direct and indirect pathways, parasites may alter consumer-resource dynamics (Hudson *et al.*, 2006; Hatcher *et al.*, 2012). 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 (hereafter, referred as protozoan and metazoan parasites), including immunological and behavioral responses. Among them, behavior may be regarded as the animals' first line of defence against infection (Hart, 1990, 2011). Given that detecting parasites is challenging, usually due to their small size, animals have "learned", probably at an evolutionary scale, to identify indirect signs of parasitism risk 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 (Curtis, 2014; Buck *et al*., 2018; Hart and Hart, 2018; Weinstein *et al*., 2018). For instance, herbivores usually avoid grazing close to feces (Ezenwa, 2004). At a landscape scale, hosts are thus forced to change their use of space and time to reduce exposure to parasites (Weinstein *et al*., 2018). Hosts may perceive parasite infection risk on a three-dimensional "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 behaviors may alter energy flow through food webs (Wood and Johnson, 2015).

Despite the important ecological, evolutionary and epidemiological implications of host behavior (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 (Fox, 1975; Palomares and Caro, 1999; Caro and Stoner, 2003), 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). Given that phylogenetically related carnivores harbor 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 highest for conspecific flesh (Meffe and Crump, 1987; Mayntz and Toft, 2006), and its associated parasite risk (Pfennig *et al*., 1998; Pfennig, 2000; Rudolf and Antonovics, 2007; Moleón *et al*., 2017). Both the nutritive value and the parasite risk decrease with time (Parmenter and MacMahon, 2009; Rossi *et al*., 2019). Whether and when a scavenger decides to feed on a risky conspecific carcass while obtaining sufficient nutritional revenue are largely unresolved questions in scavenging and disease ecology.

Trichinella spp. (phylum Nematoda) and *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 Eurasian mammalian carnivores, including the red fox (*Vulpes vulpes*) and several mustelids (Pérez-Martín *et al*., 2000; Oivanen *et al*., 2002a; Sobrino *et al*., 2007; Kirjušina *et al*., 2016; Lukášová *et al*., 2018). 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 behavior in relation to the risk of parasite transmission (Vercammen *et al*., 2002; Díaz-Ruiz *et al*., 2013).

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. (Campbell, 1988; Pozio, 2000; Pozio and Murrell, 2006; Badagliacca *et al*., 2016). However, recent empirical and modeling 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 (Moleón *et al*., 2017). Thus, further research on carnivore scavenging behavior in relation to carcass identity is needed.

The main objective of this study is to assess the consumptive patterns of mammalian carnivore carcasses over time, including the final stages of carcass consumption by scavengers, and in several areas that differ in their scavenging communities and degree of anthropization. We pay particular attention to red fox scavenging behavior in relation to meat-borne parasite risk. Our general hypothesis is that the risk of acquiring parasites through scavenging is dependent on both carcass identity (conspecific *vs*. heterospecific to the consumer) and time since the carcass became available. We predict that carcasses of heterospecifics will be more readily consumed than those of conspecifics, and that carnivores will engage in cannibalism later when facing conspecific carrion compared to heterospecific carrion. This study may provide a basis for a more accurate interpretation of the epidemiological aspects that characterize the transmission of parasites in the wild (Polley and Thompson, 2015), which is especially relevant in a global context of zoonotic diseases (Evans *et al.*, 2020).

MATERIAL AND METHODS

Study areas

Fieldwork was conducted in three areas of southeastern Spain: Sierras de Cazorla, Segura y Las Villas Natural Park (hereafter Cazorla; 2,099 km^2, 38º09'N 2º44'W), Sierra Espuña Regional Park (hereafter Espuña; 178 km^2, 37º51'N 1º32'W) and periurban areas of Murcia city (hereafter Murcia; 415 km^2, 37º57'N 1º02'W). All areas, especially Cazorla and Espuña, have a mountainous orography. Natural vegetation is dominated by pine forests (mostly *Pinus halepensis* at low altitudes and *P. nigra* and *P. pinaster* at higher altitudes), aromatic shrubs and patches of oak forests (*Quercus ilex* and *Q. faginea*; Rivas-Martínez *et al.*, 1987). There is an altitudinal and meteorological gradient from Cazorla (500-2,107 m a.s.l.; mean annual temperature: 12-16ºC; mean annual precipitation: 300-950 mm) to Espuña (200-1,583 m a.s.l.; mean annual temperature: 13-18ºC; mean annual precipitation: 300-500 mm) and Murcia (190-490 m a.s.l.; mean annual temperature: 17-23ºC; mean annual precipitation: 200-450 mm; www.juntadeandalucia.es; siam.imida.es). Meso-, Supra- and Oro-Mediterranean stages are represented in Cazorla, Thermo-, Meso- and Supra-Mediterranean stages in Espuña, and Thermo- and Meso-Mediterranean stages in Murcia. While Cazorla and Espuña are protected areas, Murcia supports moderate to high levels of anthropization, including scattered residential areas and herbaceous and fruit tree cultivations (mainly citrus trees).

In Cazorla, there is a rich representation of both obligate (i.e., vultures) and facultative scavengers. The scavenging community is similar in Espuña, though vultures are less abundant. In Murcia, vultures are mostly absent, and the presence of domestic carnivores (dogs *Canis lupus familiaris* and cats *Felis silvestris catus*) is more frequent. The red fox is the commonest wild mammalian carnivore in all areas, though it is more abundant in Espuña than in Cazorla (there are no detailed data for Murcia; see Moleón *et al.* (2017), Morales-Reyes *et al.* (2017) for more details on the study areas of Cazorla and Espuña).

Data collection

From November 2016 to March 2018, a total of 66 mesocarnivore carcasses were monitored in Cazorla (n=27 red foxes), Murcia (n=19 red foxes) and Espuña (n=20 carcasses, including ten red foxes, four martens *Martes foina*, three badgers *Meles meles*, two genets *Genetta genetta* and one wild cat *Felis silvestris silvestris*). Hereafter, carcasses of carnivores other than foxes are designated as “other carcasses”. Carcasses came from authorized hunting and recent road kills. Immediately after collection, carcasses were eviscerated, and a serum sample was taken from each animal to perform enzyme-linked immunosorbent assays for antibody detection (ELISA kits, Ingenasa®, Madrid, Spain) against some infectious diseases (canine distemper virus CDV, feline coronavirus FCoV, canine and feline parvovirus CPV/FPV, feline leukemia virus FeLV and feline immunodeficiency virus FIV). In addition, muscle samples from the base of the tongue, the forearms and diaphragm were processed by artificial digestion to detect the presence of *Trichinella* spp. larvae (Kapel *et al*., 1994; Gamble *et al*., 2000). Carcasses used in the study were free from these pathogens. In the case of hunted animals, the tissues adjacent to the shot were removed to eliminate any trace of lead. After necropsy, carcasses were frozen at -20ºC in individual plastic bags, with the time elapsed between carnivore death and freezing being less than 18 h (Moleón *et al*., 2017).

Carcasses were defrosted before their placement in the field for 12-24 h at room temperature. Carcasses were randomly distributed throughout the study areas (minimum distance between neighboring cameras: c. 1 km; Moleón *et al*., 2017). Each carcass was fixed to a rock or a tree trunk by wires to avoid movement of the carcasses by scavengers away from the recording field of the camera. The wires were camouflaged with plant material and soil (Moleón *et al*., 2015). Altitudinal range for carcass sites was 772-1676 in Cazorla, 433-1432 in Espuña and 125-448 in Murcia. On the micro-habitat scale (i.e., radius of 10 m around carcasses), sampling places were categorized as “close areas”, when the vertical projection of trees and shrubs exceeded 50%, and “open areas” otherwise.

Carcasses were monitored using automatic cameras (Bushnell Trophy Cam and Bushnell Agressor) until complete consumption (i.e., no remains, or only fur left) or for a maximum of 10 weeks if carcasses were not completely consumed (i.e., bones and skin remained). Cameras were placed in discreet locations close to the carcasses (3-4 m) and were programmed to record a 15-second video every minute when detecting movement.

Each carcass site was visited weekly to check batteries and memory cards. Cameras provided information on scavenger species presence and behavior. Recorded scavenging species, with scavenging species defined as any carrion-feeding vertebrate that had previously been recorded feeding at carcasses in our study areas (Sebastián-González *et al*., 2019), were grouped into three groups: red fox, other mammals and birds. According to O'Brien *et al*. (2003) and Ridout and Linkie (2009), we defined independent events for each carcass as: a) consecutive videos of unequivocally different individuals of the same species or individuals of different species; b) when individual identification was not possible, consecutive videos of individuals of the same species taken more than 30 min apart; and c) non-consecutive videos of individuals of the same species. We then made a distinction between "consumption events", when we observed unequivocal carrion biting and feeding behavior, and "non-consumption events" otherwise.

Data analyses: weekly scavenging patterns

First, we explored the general spatiotemporal patterns of mesocarnivore carcass use by the studied scavenging communities. For each study area and carcass type (foxes and others), we calculated, 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 group. We did the same for the number of consumption and non-consumption events.

We then explored the changing propensity of red foxes to scavenge mesocarnivore carcasses by calculating these ratios per week: a) consumed:non-consumed carcasses and b) consumption:non-consumption events. In addition, we calculated 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. We used Kruskal-Wallis and Mann-Whitney tests to compare detection time by red foxes between fox carcasses in Cazorla, Espuña and Murcia and between other carcasses and fox carcasses in Espuña, respectively.

Data analyses: determinants of carrion consumption by fox

We used generalized linear models (GLMs) to analyze 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). Time of first consumption was calculated as the time elapsed since carcass detection by foxes until the first consumption event by foxes. The sample unit for these analyses was the carcass. The explanatory variables were study “area” (Cazorla, Espuña, Murcia), “habitat” (close, open), “year”, “season” (winter –November-February, spring –April and May), “hour” of carcass placement (morning –from dawn to 12:00h, afternoon –from 12:00h to dusk), “carcass type” (fox, other), and carcass “detection time” by foxes (in days). For the ratio consumption:non-consumption events, we also used “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. Model selection was based on Akaike’s Information Criterion, which allows the identification of the most parsimonious model (lowest AIC) and ranks the remaining models. For each model, the AIC value was corrected for small sample sizes (AICc). Model selection was done in four steps. First, we constructed univariate models with all the explanatory variables. Second, we constructed bivariate models using all combinations that included the variable retained in the univariate model with lowest AICc. Third, we constructed models with three and four variables (guaranteeing at least c. 10 observations per parameter) with the combinations of variables that provided the lowest AICc values. Fourth, delta AICc (ΔAICc) was calculated as the difference in AICc between each model and the best model in the evaluated set, and models with ΔAICc<2 were considered to have similar support (Burnham and Anderson, 2002). 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). We used R studio software v1.0.143 (R Core Team, 2018).

RESULTS

The scavenging community

A total of 1,617 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 species in the three study areas (59.4% of total events). Consumption events represented 15.7% of the total events recorded (Cazorla: 75.9% of total consumption events; Murcia: 5.1%; Espuña, fox carcasses: 2.7%; Espuña, other carcasses: 16.3%). Considering all study areas together, the red fox was responsible for most consumption events (53.4% of total consumption 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). Intraspecific consumption (i.e., cannibalism) was recorded at 63% of carcasses in Cazorla, 32% in Murcia, and 40% (fox carcasses) and 0% (other carcasses) in Espuña. Cannibalism represented 16.9% of the total events recorded for the red fox at fox carcasses. Considering avian scavengers that scavenge more frequently, consumption events were more frequent than non-consumption events, while the opposite was true for all mammalian scavengers (Table S1).

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. Carcasses visited and consumed were highest in Cazorla, and lowest in Murcia (Figures 1a and S1; Table 1). In relation to events, we observed a similar general pattern, with far more non-consumption events than consumption events, and the highest number of events being recorded in Cazorla. When focusing on Espuña, the main difference was that foxes clearly had more consumption events for other carcasses than for fox carcasses (Figures 1b and S2).

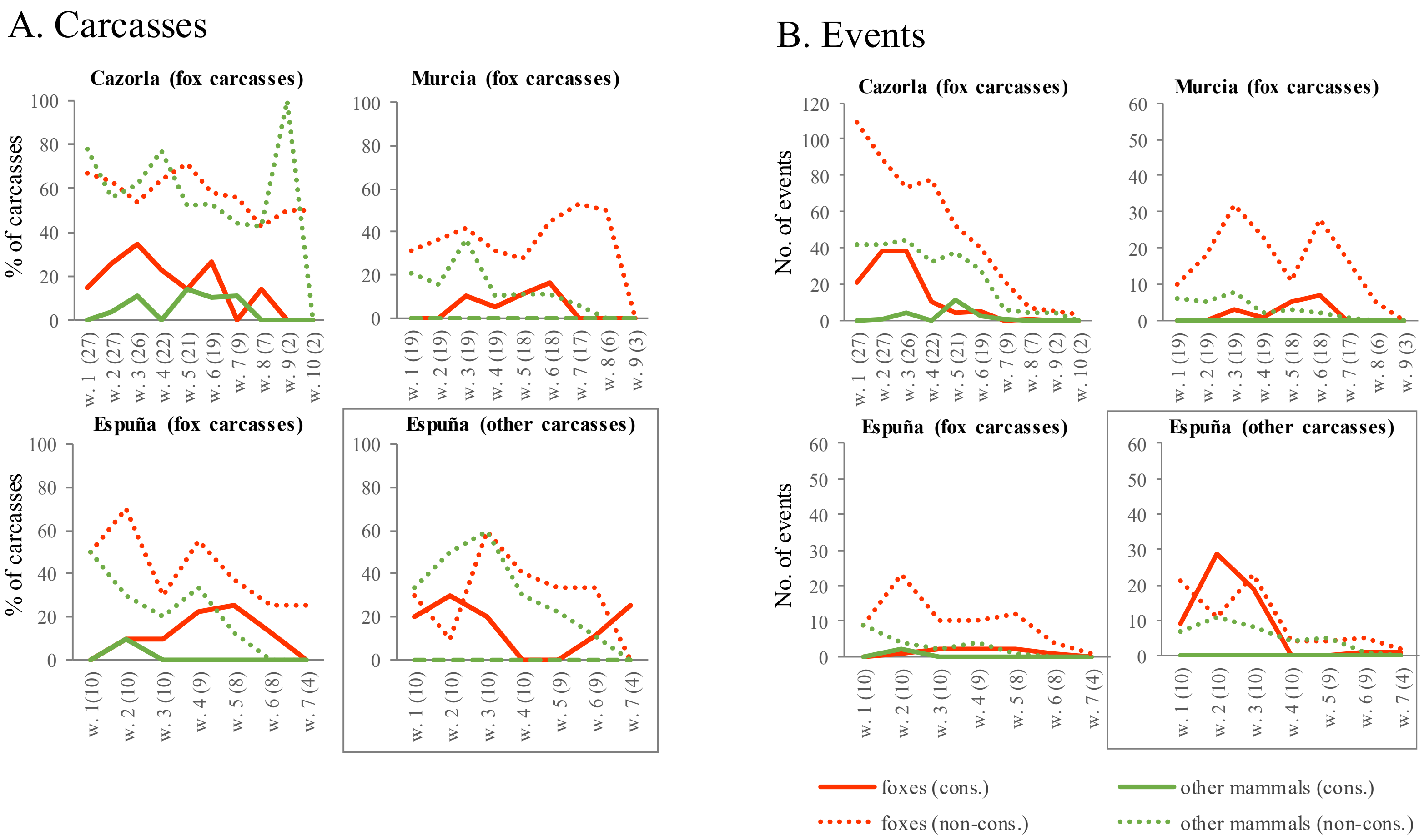

Figure 1. Weekly variation in consumption patterns of mesocarnivore carcasses by red fox and other mammalian scavengers in three areas of southeastern Spain. A) Weekly percentage of consumed (“cons.”; i.e., with at least one consumption event) and non-consumed (“non-cons.”; i.e., visited, but no consumption 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 carcasses available to scavengers is given in parentheses. Panels for carcasses of carnivores other than foxes are in boxes.

Table 1. Scavenging patterns of red fox carcasses and carcasses of other mesocarnivores in the three study areas of southeastern Spain, according to different scavenger groups. 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. 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	77.5±104.5 (4-395)	465.1±371.0 (4-1,191)	27 (100%)	17 (63.0%)	22.0±13.8 (5-53)	4.3±7.0 (0-27)
			Other mammals	132.2±127.5 (2-530)	622.7±212.9 (324-880)	26 (96.3%)	7 (25.9%)	9.6±7.0 (0-24)	0.7±2.0 (0-10)
			Birds	292.5±292.6 (1-890)	231.2±246.8 (20-791)	18 (66.7%)	10 (37.0%)	9.2±11.9 (0-45)	5.5±10.3 (0-37)
			Total	43.7±57.5 (1-195)	371.8±380.7 (4-1,191)	27 (100%)	21 (77.8%)	40.7±21.2 (15-85)	10.5±12.6 (0-40)
Murcia	Foxes	19	Red fox	301.3±244.5 (17-901)	631.8±216.6 (359-932)	16 (84.2%)	6 (31.6%)	8.4±8.8 (0-31)	0.8±1.9 (0-7)
			Other mammals	395.4±342.8 (1-981)	-	12 (63.2%)	0 (0%)	1.4±1.8 (0-7)	0
			Birds	212.8±131.8 (34-350)	386	3 (15.8%)	1 (5.3%)	1.2±3.2 (0-13)	0.2±0.7 (0-3)
			Total	270.5±298.5 (1-974)	626.7±222.8 (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	133.8±103.8 (9-290)	601.0±235.2 (267-795)	9 (90.0%)	4 (40.0%)	7.7±6.2 (0-21)	0.8±1.3 (0-4)
			Other mammals	234.4±194.1 (33-583)	199	10 (100%)	0 (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	102.7±73.4 (9-200)	520.6±271.7 (199-795)	10 (100%)	5 (50.0%)	13.7±13.5 (1-48)	1.0±1.3 (0-4)
	Other	10	Red fox	222.0±184.8 (4-462)	365.4±342.6 (88-927)	10 (100%)	5 (50.0%)	12.9±24.1 (2-81)	5.9±15.6 (0-50)
			Other mammals	292.5±267.0 (34-972)	-	10 (100%)	0 (0%)	3.6±3.1 (1-10)	0
			Birds	502.0±418.3 (257-985)	745	3 (30.0%)	1 (10.0%)	0.6±1.1 (0-3)	0.2±0.6 (0-2)
			Total	150.5±152.9 (4-427)	428.7±343.4 (88-927)	10 (100%)	6 (60.0%)	17.1±23.6 (3-83)	6.1±15.5 (0-50)

The ratio between consumed and non-consumed carcasses by foxes showed a nearly Gaussian 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 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 were there more consumed than non-consumed carcasses. 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 in 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 number of consumption events in relation to non-consumption events at fox carcasses was found in Espuña, were consumption events of other carcasses exceeded non-consumption events during the peak (Figure 2).

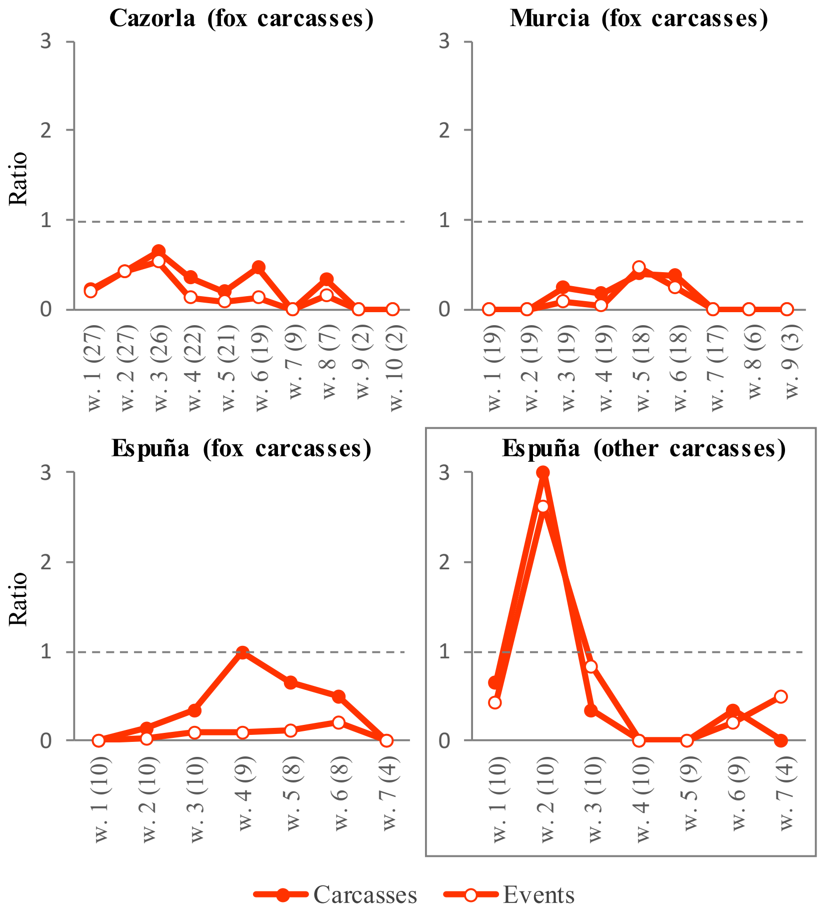

Figure 2. Weekly variation in the ratios consumed:non-consumed carcasses and consumption:non-consumption events by the red fox per study area and carcass type. Values above and below the dashed horizontal gray line indicate, respectively, ratios biased towards consumption and non-consumption. For a given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

Red foxes detected 94% of studied carcasses, but we recorded consumption events only in one-third to two-thirds of them (Cazorla: 63%; Murcia: 38%; Espuña, fox carcasses: 44%; Espuña, other carcasses: 50%). 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 carcasses of other scavengers (Figure 3).

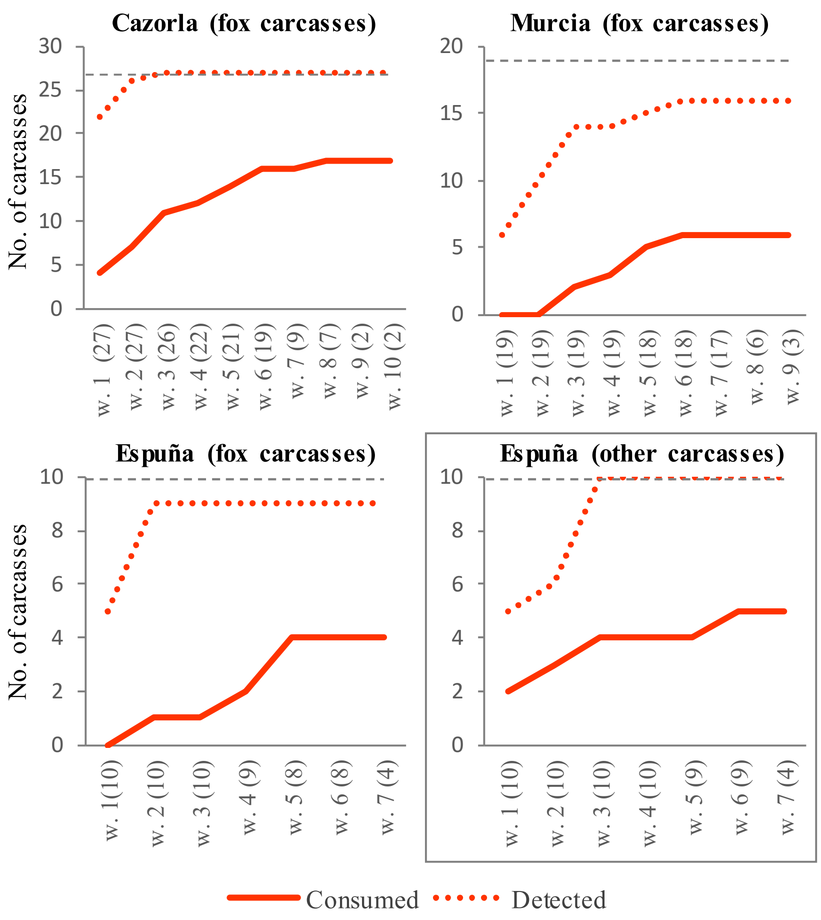

Figure 3. Accumulated weekly number of detected (i.e., with at least one event recorded; dashed line) and consumed (i.e., with at least one consumption event; continuous line) carcasses by the red fox per study area and carcass type. Dotted horizontal gray lines represent the accumulated number of available carcasses. 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.

Determinants of carrion consumption by fox

As revealed by the GLM analyses, time of first consumption by foxes since the carcass was detected by foxes was mostly related to detection time by foxes and carcass type, according to the model with the highest D^2 (Table S2). In particular, foxes started to consume earlier carcasses that were detected earlier, as well as carcasses of mesocarnivores other than fox (Table 2, Figure 1). The ratio consumption:non-consumption events of foxes was related to season, detection time by foxes, carcass type, consumption by other scavengers and study area (Table S2), with a ratio more biased towards consumption events in spring than in winter, as well as at carcasses of other mesocarnivores, carcasses detected earlier, and carcasses also consumed by other scavengers and in Murcia, Cazorla and Espuña, in that order (Table 2, Figure 2).

Table 2. 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; "carcass" type: fox, other; "season": winter, spring; "scav. cons.": consumption by scavengers other than fox; "area": Cazorla, Espuña, Murcia). Only the models with highest D^2 are shown for simplicity. 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	Model	Parameter	Estimate	SE	df
Time to first consumption	detection time + carcass	Intercept	18.598	3.165	31
		detection time	-0.475	0.311	
		carcass (other)	-6.778	6.456	
Ratio consumption:non-consumption events	season + detection time + carcass + scav. cons. + area	Intercept	-0.269	0.270	61
		season (winter)	-1.814	0.270	
		detection time	-0.059	0.023	
		carcass (other)	1.889	0.416	
		scav_cons (yes)	0.784	0.209	
		area (Espuña)	-1.646	0.462	
		area (Murcia)	0.170	0.327	

DISCUSSION

Parasite avoidance behaviors in carnivore species have received little scientific attention, despite being a key defensive barrier against trophically transmitted parasites such as *Trichinella* spp. (Hart, 1990, 2011; Ezenwa *et al.*, 2016; Sarabian *et al.*, 2018; Weinstein *et al.*, 2018). Here, we found that red foxes were very efficient in detecting mesocarnivore carrion, as they visited nearly all monitored carcasses. However, as expected, they were generally reluctant to consume them, especially conspecific carcasses. In addition, consumption by foxes, when recorded, was delayed several days (carcasses other than fox) or weeks (fox carcasses) after carcass detection. Other mammalian scavengers showed a similar pattern: 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, mainly by vultures, foxes, wild boars and dogs (Mateo-Tomás *et al.*, 2017; Moleón *et al.*, 2017; Arrondo *et al.*, 2019). Overall, our results are in agreement with diet studies on red fox (Fairley, 1970; Remonti *et al*., 2005) and other mammalian carnivores (Fox, 1975; Palomares and Caro, 1999; Caro and Stoner, 2003) 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 behavior in carnivores to prevent meat-borne parasite risk (Moleón *et al*., 2017).

Why do foxes and other carnivores not feed on carcasses, especially conspecific carrion, upon detection? Our results suggest that the foraging decisions of scavengers are probably shaped by two contrasting forces (Figure 4), namely the nutritional reward provided by carrion of phylogenetically similar species (Meffe and Crump, 1987; Mayntz and Toft, 2006) and the risk of acquiring meat-borne parasites shared with these species (Pfennig *et al*., 1998; Pfennig, 2000; Rudolf and Antonovics, 2007; Huang *et al*., 2014; Moleón *et al*., 2017). 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 (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 (Figure 4).

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, *Trichinella* spp. does 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. Finally, as can be deduced from Figure 4, the risk of acquiring infective meat-borne parasites is probably much more determinant than the nutritive value of the carcass when guiding foraging decisions. Within a carnivore-animal flesh context, all prey can be considered of relatively high-quality (Swift *et al*., 1979).

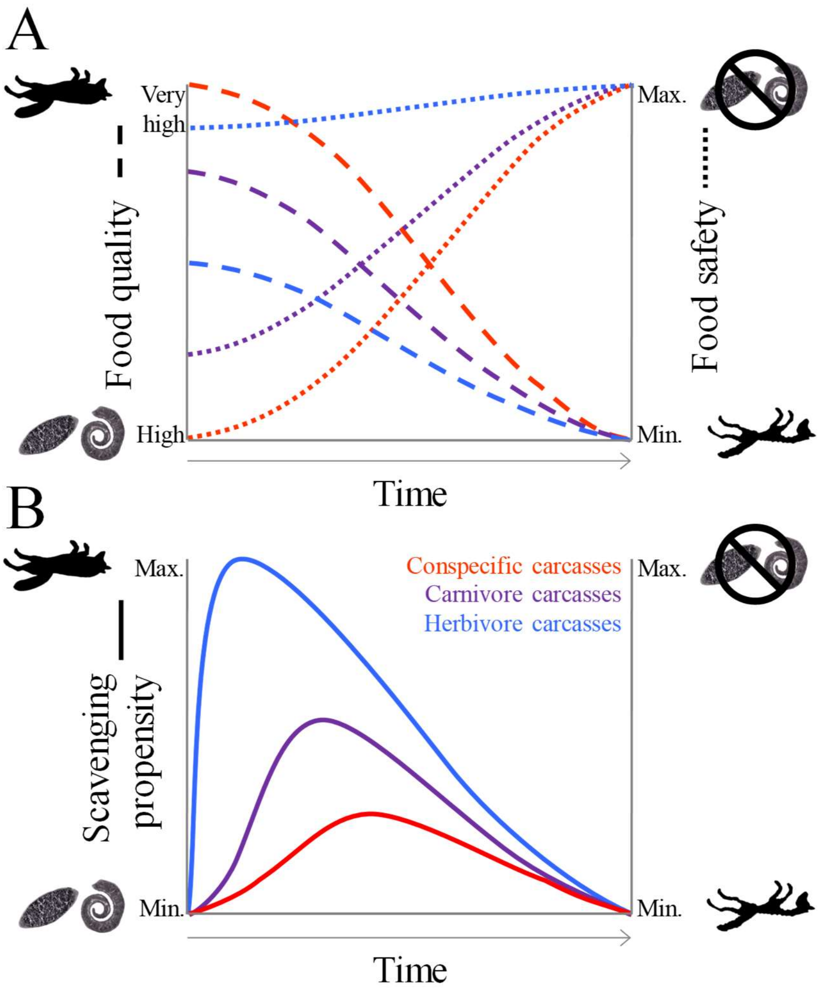

Figure 4. Conceptual model showing how food quality and safety shape the propensity of mammalian carnivores to scavenge on carcasses of species differing in their phylogenetic distance to the consumer. A) On one hand, the nutritive value, which is maximum for conspecific carcasses, decreases with time. Note that all meat can be regarded as high- to very high-quality food for a carnivore (Swift *et al*., 1979). On the other hand, the probability that a carcass is free of infective stages of meat-borne parasites increases with time. In fresh carcasses, the risk of acquiring infective meat-borne parasites for a consumer is maximum for conspecific carcasses, and minimum for carcasses belonging to weakly related species. Non-linearity is probably a fundamental property of all of these functions. B) These contrasting forces probably shape the observed patterns of carcass consumption (e.g., this study, Moleón *et al*., 2017, Morales-Reyes *et al*., 2017, Arrondo *et al*., 2019).

When this nutritional value-parasite risk trade-off favors feeding on conspecific and phylogenetically related carcasses may depend on several extrinsic and intrinsic factors. First, the infectivity of *Trichinella* spp. and other meat-borne parasites is highly dependent on environmental conditions (Pozio, 2000). In particular, high humidity and low temperature favors the survival and transmission of these parasites (Oivanen *et al*., 2002b; Riva *et al*., 2012; Pozio, 2016; Fariña *et al*., 2017; Rossi *et al*., 2019). At constant low temperatures, such as those reached beneath the snow, the infective capacity of *Trichinella* *britovi* larvae in red fox carcasses does not show important reductions during the first four months. However, above the snow, with more oscillating temperatures, the 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 *Trichinella 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 Mediterranean 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, carrion decomposes faster than in colder latitudes (Selva *et al*., 2005), with most non-scavenged flesh disappearing within the first two months due to necrophagous invertebrates, decomposers and dehydration (Muñoz-Lozano *et al*., 2019). All of this is consistent with our findings. In addition, we found that consumption events were more frequent in relation to non-consumption events in spring than in winter. At first sight, this result could seem counterintuitive because scavenging by facultative scavengers in general (Sebastián-González *et al*., 2019), and red fox in particular (Padial *et al*., 2002; Cagnacci *et al*., 2003), is more frequent during winter in temperate ecosystems. However, our findings make sense when considering that survival of parasites in decaying meat is temperature-dependent (Riva *et al*., 2012). Thus, the survival time of these parasites and subsequent risk of parasite transmission associated with carnivore carcasses would be lower in spring compared to winter, especially in mild springs such as those occurring in our study areas.

Overall, foxes fed more and earlier when carcasses were detected earlier, probably because the resource was known for a longer period and/or by more individuals. 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 interspecific facilitative process, as is typical in scavenging assemblages (Moleón *et al*., 2014). Carrion consumption by other scavenger species could be a signal that the carcass is safe, so foxes may have partly relied on these indirect cues to guide their foraging decisions. Differences in the ratio between consumption and non-consumption events among areas suggest that different populations are subject to different environmental constraints besides climate, including different trajectories of anthropization, contrasting local parasite communities and different competition levels. For instance, in Cazorla, foxes are deprived of a large portion of carrion resources due to abundant vultures (Morales-Reyes *et al*., 2017), and thus they could be more prone to assuming the risk of consuming carnivore carcasses in this location.

Finally, the fact that some foxes practiced cannibalism while most rejected conspecific carcasses indicates 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 (Mukherjee and Heithaus, 2013).

Epidemiological and ecological consequences

The results of this and previous studies (Moleón *et al*., 2017) show that cannibalistic scavenging is a rare feeding strategy in mammalian mesocarnivores. In the case of red fox, all mesocarnivore carcasses are risky carcasses, but the risk associated with fox carcasses is highest. 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 other wild carnivores. This challenges the widespread assumption that multi-host parasites such as *Trichinella* spp. are closely linked to intraspecific consumption, including both predation and scavenging (Campbell, 1988; Pozio, 2000; Badagliacca *et al*., 2016). This assumption may be partially rooted in the frequent presence of fox hairs in fox feces, which has traditionally interpreted as evidence of cannibalism. However, Remonti *et al*. (2005) argued that undigested fox hairs found in feces 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 flesh. Secondary 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 favorable environmental conditions is five days (Maroli and Pozio, 2000).

Carnivore carcass avoidance by carnivores results in slower nutrient cycling compared to other types of carrion (Moleón *et al.*, 2017). In turn, the longer persistence of carnivore carrion in the environment means an important trophic opportunity for invertebrates and decomposers, especially during the first stages of carcass decomposition. In our study areas, we found a highly structured community of necrophagous and necrophilous insects that exploit mammalian carnivore carcasses (Muñoz-Lozano *et al.*, 2019). While herbivore carcasses are mainly exploited by vertebrates (DeVault *et al.*, 2003; Mateo-Tomás *et al.*, 2015), carnivore carcasses are mostly consumed by smaller organisms (especially in the absence of large avian scavengers), which distribute nutrients at shorter distances. Thus, ecological effects of carnivore carrion are expected to be pervasive mainly at a micro-habitat scale.

Future directions and conclusions

Carnivore carcasses offer many ecological, evolutionary and epidemiological research opportunities (Moleón *et al.*, 2017). At the population level, exploring patterns of carnivore carrion use and scavenger behavior at carcasses in different systems with contrasting environmental conditions and scavenger and parasite communities could be the first step to disentangle the role of carnivore carcasses in disease transmission. In addition, detailed knowledge about the diversity of potential hosts of multi-host parasites is crucial to fully understand the dynamics of parasitic diseases (Gandon, 2004). Exploring the role of necrophagous insects as vectors and paratenic hosts of meat-borne parasites (Riva *et al.*, 2015) could widen the knowledge on the epidemiological implications of carnivore carrion to different trophic levels through indirect interactions. Individual-level studies on patterns of individual variation in parasite avoidance behavior and their causes and evolutionary and epidemiological consequences are virtually nonexistent. These studies may benefit from the combination of different individual monitoring techniques, such as radiotracking and camera trapping. Recent research has highlighted that, even for species with few distinctive individual features such as red foxes, individual identification may be successfully achieved from camera trapping data (Dorning and Harris, 2019). In general, videos may offer high-quality behavioral information and show details (e.g., confirm consumption events) that can be overlooked by using photographs only.

Overall, we have shown the advantages of detailed behavioral studies that combine different metrics to test –and challenge– widely accepted assumptions on meat-borne parasite transmission. Carnivore carcasses are fundamental components in the landscape of disgust for carnivores (Buck *et al.*, 2018; Weinstein *et al.*, 2018). Our findings support the view that the indirect, nonconsumptive effects of parasites may strongly impact host behavior, with potential effects that propagate through food webs (Buck *et al.*, 2018; Sarabian *et al.*, 2018). 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.

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SUPPLEMENTARY FILES

Table S1. Non-consumption (“Non-cons. events”) and consumption events (“Cons. events”) by scavengers recorded per study area and carcass type.

			Cazorla (foxes)		**Murcia (foxes)**		**Espuña (foxes)**		**Espuña (others)**	
Class	**Common name**	**Scientific name**	**Non-cons. events**	**Cons. events**	**Non-cons. events**	**Cons. events**	**Non-cons. events**	**Cons. events**	**Non-cons. events**	**Cons. events**
Birds	Griffon vulture	*Gyps fulvus*	0	1	0	0	0	0	0	0
	Golden eagle	*Aquila chrysaetos*	0	8	0	0	0	0	0	0
	Little owl	*Athene noctua*	1	0	19	3	0	0	0	0
	Common raven	*Corvus corax*	4	16	0	0	0	0	0	0
	Carrion crow	*Corvus corone*	34	69	0	0	0	0	0	0
	Eurasian jay	*Garrulus glandarius*	60	54	0	0	38	0	4	2
Mammals	Red fox	*Vulpes vulpes*	478	117	144	16	69	8	70	59
	Domestic dog	*Canis lupus familiaris*	13	0	8	0	0	0	2	0
	Wild cat	*Felis silvestris silvestris*	7	0	2	0	0	0	0	0
	Domestic cat	*Felis silvestris catus*	0	0	1	0	0	0	0	0
	Stone marten	*Martes foina*	62	11	1	0	8	0	18	0
	Eurasian badger	*Meles meles*	2	0	0	0	0	0	0	0
	Common genet	*Genetta genetta*	27	3	5	0	4	0	2	0
	Wild boar	*Sus scrofa*	128	5	10	0	8	2	14	0
Total			**816**	**284**	**190**	**19**	**127**	**10**	**110**	**61**

Table S2. AICc-based model selection to assess the effect of study “area”, “habitat”, “year”, “season”, “hour”, “carcass type”, other “scavenger” presence, consumption by other scavenger (“scav. cons.”), and carcass “detection time” on “time of first consumption” by foxes and the “ratio consumption:non-consumption events” by foxes on mesocarnivore carcasses in southeastern Spain (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 models explained by the predictors (deviance, D^2) are shown. Selected models are in bold.

Response variable	**Model**	**k**	**AICc**	**ΔAICc**	**D^2**
Time to first consumption	**detection time**	**1**	**261.12**	**0**	**3.62**
	carcass	**1**	**262.41**	**1.29**	**7.42**
	detection time + carcass	**2**	**262.55**	**1.43**	**10.81**
	detection time + habitat	2	263.26	2.14	
	hour	1	263.28	2.16	
	habitat	1	263.54	2.42	
	season	1	263.56	2.44	
	detection time + season	2	263.60	2.48	
	detection time + hour	2	263.67	2.55	
	year	2	263.85	2.73	
	detection time + carcass + habitat	3	264.10	2.98	
	detection time + year	3	265.09	3.97	
	detection time + carcass + hour	3	265.15	4.03	
	detection time + carcass + season	3	265.37	4.25	
	area	2	265.94	4.82	
	detection time + area	3	266.39	5.27	
Ratio consumption:non-consumption events	**season + detection time + carcass + scav. cons. + area**	**6**	**337.66**	**0**	**34.44**
	season + detection time + carcass + scav. cons.	4	348.20	10.54	
	season + detection time + carcass + scav. cons. + year	6	349.00	11.34	
	season + detection time + carcass + area	5	349.71	12.05	
	season + detection time + carcass + scav. cons. + hour	5	349.94	12.28	
	season + detection time + carcass + scav. cons. + scavenger	5	350.48	12.82	

Table S2 (continued). AICc-based model selection to assess the effect of study “area”, “habitat”, “year”, “season”, “hour”, “carcass type”, other “scavenger” presence, consumption by other scavenger (“scav. cons.”), and carcass “detection time” on “time of first consumption” by foxes and the “ratio consumption:non-consumption events” by foxes on mesocarnivore carcasses in southeastern Spain (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 models explained by the predictors (deviance, D^2) are shown. Selected models are in bold.

Response variable	**Model**	**k**	**AICc**	**ΔAICc**	**D^2**
Ratio consumption:non-consumption events	season + detection time + carcass + scav. cons. + habitat	5	350.66	13.00	
	season + detection time + scav. cons.	3	358.47	20.81	
	season + detection time + carcass + habitat	4	362.70	25.04	
	season + scav. cons.	2	366.91	29.25	
	season + detection time + carcass	3	372.54	34.88	
	season + detection time + habitat	3	373.76	36.10	
	season + detection time + carcass + scavenger	4	374.81	37.15	
	season + detection time + carcass + hour	4	374.90	37.24	
	season + detection time + area	4	374.99	37.33	
	season + detection time + carcass + year	5	375.99	38.33	
	season + detection time	2	376.66	39.00	
	season + detection time + scavenger	3	378.86	41.20	
	season + detection time + hour	3	378.93	41.27	
	season + detection time + year	4	379.94	42.28	
	season + habitat	2	381.51	43.85	
	season + area	3	381.76	44.10	
	season + carcass	2	383.48	45.82	
	season	1	388.20	50.54	
	season + scavenger	2	388.93	51.27	
	season + year	3	389.68	52.02	
	season + hour	2	390.36	52.70	
	carcass	1	402.57	64.91	

Table S2 (continued). AICc-based model selection to assess the effect of study “area”, “habitat”, “year”, “season”, “hour”, “carcass type”, other “scavenger” presence, consumption by other scavenger (“scav. cons.”), and carcass “detection time” on “time of first consumption” by foxes and the “ratio consumption:non-consumption events” by foxes on mesocarnivore carcasses in southeastern Spain (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 models explained by the predictors (deviance, D^2) are shown. Selected models are in bold.

Response variable	**Model**	**k**	**AICc**	**ΔAICc**	**D2**
Ratio consumption:non-consumption events	area	2	423.54	85.88	
	detection time	1	434.04	96.38	
	year	2	444.69	107.03	
	scavenger	1	446.16	108.50	
	scav. cons.	1	446.78	109.12	
	habitat	1	448.95	111.29	
	hour	1	450.14	112.48	

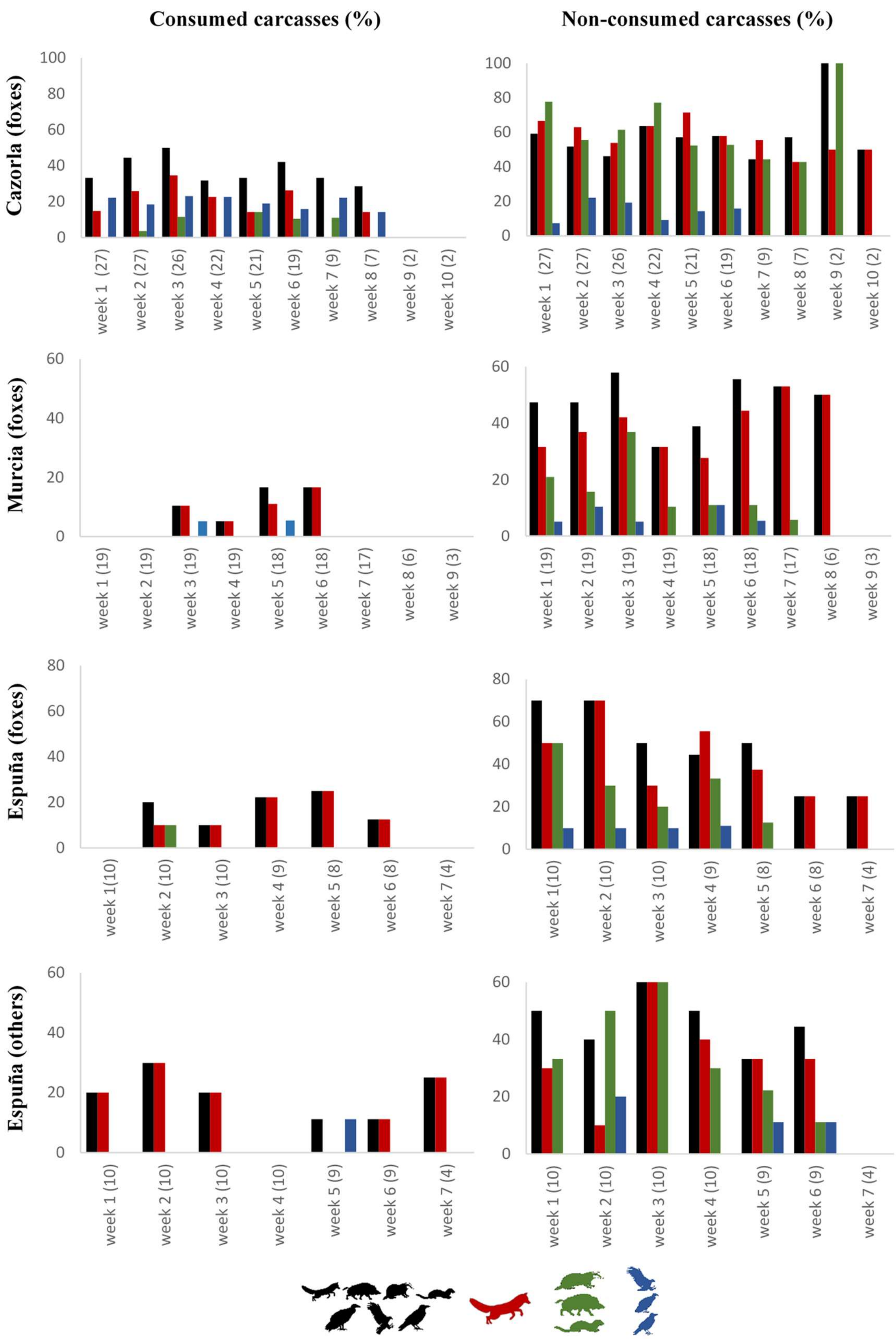

Figure S1. Weekly percentage of consumed (i.e., with at least one consumption event) and non-consumed (i.e., visited, but no consumption events recorded) carcasses by each scavenger group per study area and carcass type. For a given week, the number of carcasses available to scavengers is given in parentheses. To facilitate comparisons, Y-axis's scale is equal for each study area.

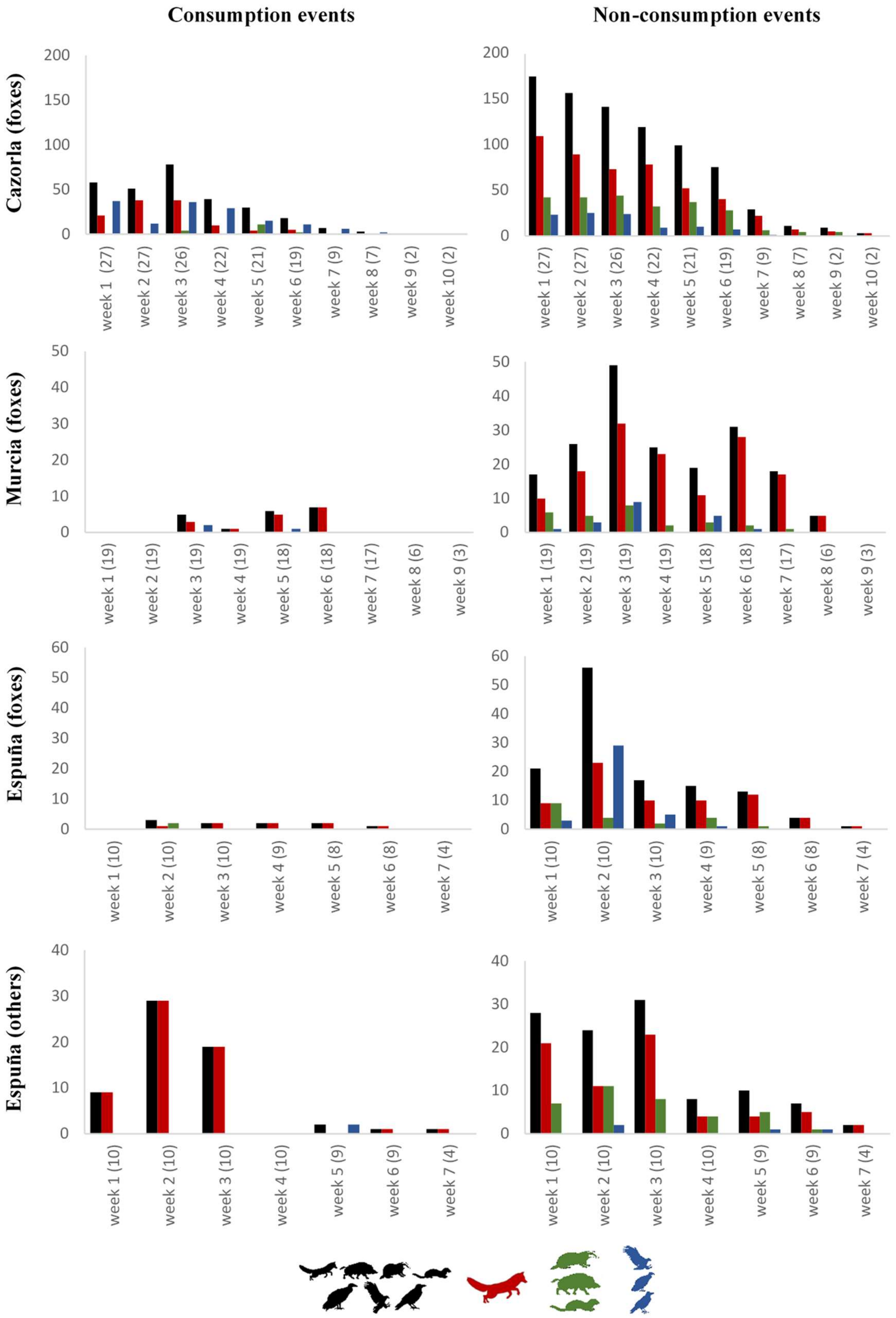

Figure S2. Weekly percentage of consumption and non-consumption events by each scavenger group per study area and carcass type. For a given week, the number of carcasses available to scavengers is given in parentheses. To facilitate comparisons, Y-axis's scale is equal for each study area.

CHAPTER 3

DESCRIBING THE RISK OF NON-TROPHICALLY TRANSMITTED PARASITES BASED ON RED FOX BEHAVIOR VIS-À-VIS CARNIVORE CARCASSES

ABSTRACT

The spatial and temporal distribution of pathogens in wildlife is heterogeneous, with specific areas and periods of greatest transmission risk. Trophic resources usually favor the concentration of animals, so the risk of infection associated with these is often greater. In this sense, carrion is an ephemeral trophic resource that can act as a hotspot for meat-borne pathogens, but also for other non-trophically transmitted ones. Carnivore carrion has a greater persistence in the environment than herbivore carrion, which makes it, a priori, an attractive site for different animal species, with a greater number of ecological interactions and, possibly, with epidemiological consequences regarding non-trophic transmission of parasites. In order to investigate this last issue, we used videos recorded by camera traps to evaluate the behavior of wildlife species in three areas of the Iberian Peninsula where a total of 56 fox carcasses and 10 carcasses other than fox were placed. Concerning foxes, contact events were more frequent and earlier at heterospecific carrion than at conspecific ones. These contacts used to be delayed several weeks, especially in conspecific carcasses. In relation to rubbing events, a similar pattern between heterospecific and conspecific carrion was detected, although the frequency was higher in mesocarnivore sites other than fox. Moreover, rubbing contact events by foxes were more frequently detected than contacts resulting from marking. This behavior pattern could be interpreted, from an epidemiological point of view, as an infection risk of pathogens transmitted by direct contact, most notably *Sarcoptes scabiei*. Marking events were more frequently recorded at fox carcasses, suggesting that they are used as inter- and intraspecific information points of longer persistence. This finding is evidence of the risk posed by carrion sites in the transmission of infective stages eliminated by feces or urine, such as certain viruses and helminth eggs. Overall, foxes were reluctant to contact carrion during the first weeks, especially in conspecific carcasses, probably to reduce the risk of infection by non-trophically transmitted parasites. However, this strategy seems ineffective for the most persistent pathogens in the environment. Our research highlights the importance of the ecological study of wildlife diseases, relating ecological interactions with possible modes of transmission of emerging and re-emerging pathogens.

INTRODUCTION

Pathogen distribution is spatially and temporally heterogeneous, so epidemiological landscapes frequently consist of hotspots for transmission risk within a matrix of reduced or even no exposure to parasites (Bousema *et al.*, 2012; Buck *et al.*, 2018; Weinstein *et al.*, 2018a). Infection risk hotspots may be driven by either resources that favor aggregation of animals, such as water ponds, food-rich patches or by pathogen-contaminated resources, such as latrines (Buck *et al.*, 2018; Weinstein *et al.*, 2018a, 2018b). The epidemiological risk may also be increased by species-specific behaviors, such as social interaction between individuals of gregarious species or family groups, or during certain times of the year, such as during mating (Altizer *et al.*, 2003; Patterson and Ruckstuhl, 2013; Ezenwa *et al.*, 2016). The infection risk also depends on the diversity of susceptible and alternative hosts in the environment (Johnson and Thieltges, 2010). When food resources and other points of attraction are apparently infected, hosts must weigh perceived infection risk against foraging gains and other benefits (Weinstein *et al.*, 2018b). Understanding host behavioral responses to potential risk of infection associated with food resources is relevant from an ecological and evolutionary perspective, but also provides a solid basis for better interpretation of epidemiological risk factors (Hart, 1990; Kuris, 2003; Penczykowski *et al.*, 2015).

Carcasses are a paradigmatic example of food resource that may be regarded as hotspots for both trophically and non-trophically transmitted pathogens (Turner *et al.*, 2014; Dmitric *et al.*, 2017). This nutrient-rich resource attracts many scavengers in all ecosystems (DeVault *et al.*, 2003; Beasley *et al.*, 2012; Mateo-Tomás *et al.*, 2015; Sebastián-González *et al.*, 2019), leading to concentrations within few meters of up to hundreds of different individuals in the case of vultures (Donázar, 1993). In the absence of vultures, which are very efficient carrion consumers, many opportunistic or facultative scavengers such as mammalian mesocarnivores may readily access carrion (Morales-Reyes *et al.*, 2017). In these conditions, parasite transmission may occur not only from the carcass to the scavenger, but also among different scavengers that co-occur at carcass sites (Ogada *et al.*, 2012). Moreover, the dead animal can be a source of pathogens for non-scavenging species that approach the carcass without the intention of eating it, for other species that contact the carcass with the aim of ingesting the necrophagous invertebrates found on it, as well as for animal species that use the carcass for non-trophic purposes, such as marking behavior and taking material for nest construction (Moleón and Sánchez-Zapata, 2016).

Carcasses are normally an ephemeral resource (DeVault *et al.*, 2003; Barton *et al.*, 2013). However, not all of them have the same duration in the environment. Carcasses of carnivore species generally persist longer than those of herbivore species (Selva *et al.*, 2005; Olson *et al.*, 2016; Moleón *et al.*, 2017, 2020). This is because not all carnivorous species that may feed on herbivore carcasses feel safe to feed on carcasses of phylogenetically related species, especially on conspecific carcasses, given increased risk of acquiring species-specific meat-borne parasites (Hart, 2011; Moleón *et al.*, 2017). Therefore, the opportunities for contact between carcasses and the visiting host species, as well as between the latter, are more numerous in the case of carnivore carcasses. Consequently, the possibility of the host becoming infected through this type of carcasses, especially by non-trophically transmitted pathogens, may also increase. Thus, carnivore carcasses are an excellent model to study host behavior around carcasses in relation to the risk of acquiring non-trophically transmitted parasites, and how this behavior changes with time. However, fine-grained behavioral studies about the risk associated with carcass sites are largely lacking, particularly for carnivore carrion.

In the case of mammalian carnivores, non-trophically transmitted pathogens include a wide range of parasites, fungus, bacteria and virus. These pathogens have characteristics that largely condition their transmission, such as survival time in the environment of the infective stages, the route of infection they have, the number of host species that are susceptible, as well as the life cycle they present (Poulin, 2007). In general, the infection risk of these pathogens through carcasses decreases over time, conditioned by survival in the environment of the infective stages. In addition, this risk increases as the distance between the susceptible host and the carcass decreases. Among the pathogens that cause most impact on wildlife is *Sarcoptes scabiei*, which produces sarcoptic mange (Niedringhaus *et al.*, 2019). This multi-host ectoparasite is widely distributed and affects an ample range of mammals, including ungulates and carnivores (Pisano *et al.*, 2019; Turchetto *et al.*, 2020). Sarcoptic mange mites are located on the epidermis of the animal, and can be transmitted through direct contact between individuals or indirectly when a susceptible host acquires free mites that have shed the skin of an infected animal, especially in dens and other sheltered sites where *S. scabiei* may survive for several days (Pence and Ueckermann, 2002). Another infectious agent of major concern for its health impact on wildlife populations is the bacterium *Bacillus anthracis*, which cause anthrax in ungulates and, to a lesser extent, in carnivores. After the death of the infected animal, this virulent pathogen produces spores around the carcass that can persist in the environment for years, infecting new hosts via ingestion or inhalation (Bellan *et al.*, 2013; Turner *et al.*, 2014). Other widely distributed, non-trophically transmitted infectious agents that can seriously affect wild carnivore populations are rabies, distemper virus and canine parvovirus, which can be acquired through the saliva, respiratory secretions and feces of infected animals, respectively (Truyen *et al*., 1998; Gottstein *et al*., 2009; Nouvellet *et al*., 2013; McElhinney *et al*., 2014; Carricondo-Sánchez *et al*., 2017).

The most ubiquitous mammalian carnivore worldwide is the red fox (*Vulpes vulpes*), a typical generalist species that feeds upon a wide array of animal, plant and fungal foods, including carrion (Wilson and Mittermeier, 2009; Mateo-Tomás *et al*., 2015). Foxes inhabit a wide range of habitats, including urban and peri-urban areas (Wilson and Mittermeier, 2009). Thus, much has been discussed about the epidemiological role of foxes as reservoirs of pathogens with potential zoonotic and veterinary significance (Di Cerbo *et al*., 2008; Karamon *et al*., 2018).

Our main goal is to explore the behavior of potential hosts of non-trophically transmitted pathogens at carnivore carcass sites, with an especial emphasis on the red fox. For this purpose, we monitored the decomposition process of fox and other mesocarnivore carcasses in several areas that differ in their communities of vertebrate carnivores and in a gradient of anthropization. Analyzed behaviors include contact, marking and rubbing, on either the carcass or its vicinities. Our main hypothesis is that the risk of acquiring pathogens through direct contact is dependent on both carcass types (conspecific *vs*. heterospecific regarding the consumer) and time since the carcass became available, and that hosts rely on these indirect cues to shape their behavior. Overall, we predict that risky behaviors will be more frequent in heterospecific carcasses than in conspecific ones. This study may provide important insights to further understand the landscape of disgust associated with carrion, as well as the possible epidemiological consequences of this host behavior (Buck *et al*., 2018; Weinstein *et al*., 2018a). This kind of studies may be especially welcome in the current SARS-CoV-2 pandemic context, which has highlighted the need to investigate the form of transmission of this emerging pathogen in wild species, especially in mesocarnivores (Leroy *et al*., 2020; Tiwari *et al*., 2020).

MATERIAL AND METHODS

Study areas

Fieldwork was done in three mountainous areas of southeastern Spain: Sierras de Cazorla, Segura y Las Villas Natural Park (hereafter Cazorla; 2,099 km^2, 38º09'N 2º44'W), Sierra Espuña Regional Park (hereafter Espuña; 178 km^2, 37º51'N 1º32'W) and periurban areas of Murcia city (hereafter Murcia; 415 km^2, 37º57'N 1º02'W). Natural vegetation in the three areas is dominated by pine forests (mostly *Pinus halepensis* at low altitudes and *P. nigra* and *P. pinaster* at higher altitudes), aromatic shrubs and patches of oak forests (*Quercus ilex* and *Q. faginea*) (Rivas-Martínez *et al*., 1987). There is an altitudinal and meteorological gradient from Cazorla (500-2,107 m.a.s.l.; mean annual temperature: 12-16ºC; mean annual precipitation: 300-950 mm) to Espuña (200-1,583 m.a.s.l.; 13-18ºC; 300-500 mm) and Murcia (190-490 m.a.s.l.; 17-23ºC; 200-450 mm) (www.juntadeandalucia.es; siam.imida.es). Meso-, Supra- and Oro-Mediterranean stages are represented in Cazorla, Thermo-, Meso- and Supra-Mediterranean stages in Espuña, and Thermo- and Meso-Mediterranean stages in Murcia. Cazorla and Espuña are protected areas, while Murcia supports moderate to high levels of anthropization, including scattered residential areas and herbaceous and fruit tree cultivations (mainly citrus trees).

In general, vertebrate communities are much richer in Cazorla, which holds a large and permanent population of obligate scavengers (i.e., vultures) and a wide variety of facultative scavengers. The scavenging community is similar in Espuña, though vultures are less abundant. In Murcia, vultures are mostly absent, and the presence of domestic carnivores, such as the dog (*Canis lupus familiaris*) and the cat (*Felis silvestris catus*), is more frequent. The fox is the commonest wild mammalian carnivore in the three study areas, though it is more abundant in Espuña than in Cazorla; there are no detailed data for Murcia. For more information on Cazorla and Espuña, see Moleón *et al*. (2017) and Morales-Reyes *et al*. (2017), respectively.

Data collection

A total of 66 mesocarnivore carcasses were monitored in Cazorla (n=27 foxes), Murcia (n=19 foxes) and Espuña (n=20 carcasses, including ten foxes, four martens (*Martes foina*), three badgers (*Meles meles*), two genets (*Genetta genetta*) and one wild cat (*Felis silvestris silvestris*) from November 2016 to March 2018. The main research model was the fox because it is the most abundant carnivore in the studied areas. Hereafter, carcasses of carnivores other than foxes are designated as “other carcasses”. Carcasses came from authorized hunting (only in the case of foxes) and recent road kills (foxes and other carnivores). Immediately after collection, carcasses were eviscerated, and a serum sample was taken from each animal to perform enzyme-linked immunosorbent assays for antibody detection (ELISA kits, Ingenasa®, Madrid, Spain) against some infectious diseases (canine distemper virus CDV, feline coronavirus FCoV, canine and feline parvovirus CPV/FPV, feline leukemia virus FeLV and feline immunodeficiency virus FIV). Also, muscle samples from the base of the tongue, the forearms and diaphragm were processed by artificial digestion to detect the presence of *Trichinella* spp. larvae (Kapel *et al*., 1994; Gamble *et al*., 2000). Carcasses used in the study were free from these pathogens, and no lesions compatible with sarcoptic mange, mycosis or other pathologies were detected. In the case of hunted foxes, the tissues adjacent to the shot were removed to eliminate any trace of lead. After necropsy, carcasses were frozen at -20ºC in individual plastic bags, with the time elapsed between carnivore death and freezing being less than 18 h (Moleón *et al*., 2017).

Carcasses were defrosted before their placement in the field for 12-24 h at room temperature. Carcasses were randomly distributed throughout the study areas, with a minimum distance between neighboring cameras of at least 1 km (Moleón *et al*., 2017). Each carcass was fixed to a rock or a tree trunk by 1.5 mm diameter steel wires to avoid movement of the carcasses by scavengers away from the recording field of the camera. The wires were camouflaged with plant material and soil (Moleón *et al*., 2015). Altitudinal range for carcass sites was 772-1676 m a.s.l. in Cazorla, 433-1432 m a.s.l. in Espuña and 125-448 m a.s.l. in Murcia. On the micro-habitat scale (i.e., radius of 10 m around carcass), sampling places were categorized as “close areas”, when the vertical projection of trees and shrubs exceeded 50%, and “open areas” otherwise.

Carcasses were monitored using automatic cameras (Bushnell Trophy Cam and Bushnell Agressor) until complete consumption (i.e., no remains, or only fur left) or for a maximum of 10 weeks if carcass was not completely consumed (i.e., bones and skin remained). Cameras were placed in discreet locations close to the carcasses (3-4 m) and were programmed to record a 15-second video every minute when detecting movement. Each carcass site was visited weekly to check batteries and memory cards. Cameras provided information on the presence of vertebrate species and their behavior at carcass sites. Recorded vertebrate species were classified into three groups: “red fox”, “other mammals” and “birds” (including in this last group one reptile: *Timon lepida*). According to O’Brien *et al.* (2003) and Ridout and Linkie (2009), we defined independent events for each carcass as: a) consecutive videos of unequivocally different individuals of the same species or individuals of different species; b) when individual identification was not possible, consecutive videos of individuals of the same species taken more than 30 minutes apart; and c) non-consecutive videos of individuals of the same species. For each event, we recorded a) the species group, b) the number of different individuals, c) the existence of contact between the visitor and the carcass, d) the existence of marking behavior (urine and feces deposition), e) the existence of rubbing behavior, and, f) when visitors contacted the carcass, the part of it that was contacted (“anterior”: head, neck and forelimbs; “middle”: trunk; “posterior”: tail, perianal region and hindquarters). All events were categorized according to the minimum distance between the visitor and the carcass as “contact” (distance: 0 cm), “close” (distance: >0-50 cm), “moderate” (distance: >50-200 cm) and “far” (distance: >200 cm). These distance intervals were also used to classify marking and rubbing sites.

Data analyses: weekly behavioral patterns

First, we explored the general spatiotemporal patterns of mesocarnivore carcass use by the studied vertebrate communities. For each study area and carcass type (foxes and others), we calculated, on a weekly basis, the proportion of carcasses that were contacted (i.e., with at least one contact event), marked (i.e., with at least one event showing marking behavior), rubbed (i.e., with at least one event showing rubbing behavior on the carcass or on the ground next to it), and visited but not contacted (i.e., no contact events recorded), for all vertebrates together and separately for each vertebrate group. We did the same for the number of contact, marking, rubbing and no contact events.

We then explored the changing propensity of foxes to contact mesocarnivore carcasses by calculating these ratios per week: a) contacted:non-contacted carcasses, b) marked:non-marked carcasses, c) rubbed:non-rubbed carcasses, d) contact:non-contact events, e) marking:non-marking events, and f) rubbing:non-rubbing events. In addition, we calculated the accumulated number of carcasses that were a) detected, b) contacted (i.e., at least one contact event), c) marked (i.e., at least one marking event), and d) rubbed (i.e., at least one rubbing event) each week by foxes.

Data analyses: determinants of fox behavior

We used generalized linear models (GLMs) to analyze the factors influencing “time of first contact” (only carcasses with at least one contact event by foxes were used; n=54). Time of first contact was calculated as the time elapsed since carcass detection by foxes until the first contact event by foxes. The sample unit for these analyses was the carcass. The explanatory variables were study “area” (Cazorla, Espuña, Murcia), “habitat” (close, open), “year”, “season” (winter –November-February, spring –April and May), “hour” of carcass placement (morning –from dawn to 12:00h, afternoon –from 12:00h to dusk), “carcass type” (fox, other), and carcass “detection time” by foxes (i.e., time elapsed since carcass placement and its detection by fox, expressed in days).

We then proceeded with model construction, using Gaussian error distributions and identity functions. Model selection was based on Akaike’s Information Criterion, which allows the identification of the most parsimonious model (lowest AIC) and ranks the remaining models. For each model, the AIC value was corrected for small sample sizes (AICc). Model selection was done in four steps. First, we constructed univariate models with all the explanatory variables. Second, we constructed bivariate models using all combinations that included the variable retained in the univariate model with lowest AICc. Third, we constructed models with three and four variables (guaranteeing at least c. 10 observations per parameter) with the combinations of variables that provided the lowest AICc values. Fourth, delta AICc (ΔAICc) was calculated as the difference in AICc between each model and the best model in the evaluated set, and models with $\Delta AICc<2$ were considered to have similar support (Burnham and Anderson, 2002). 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).

Finally, we used Chi-square analyses to compare the parts of the carcass that were contacted by foxes a) among study areas (only fox carcasses) and b) carcass types (only in Espuña). We also used Chi-square analyses to compare the minimum distance between visiting foxes and the carcass a) among study areas (only fox carcasses) and b) carcass types (only in Espuña). All analyses were done with R studio software v1.0.143 (R Core Team, 2018).

RESULTS

Visiting species and their general behavior

We recorded a total of 2,383 events of vertebrate species visiting the carcasses (58.9% in Cazorla, 23.9% in Murcia, 7.9% in Espuña at fox carcasses, 9.3% in Espuña at other carcasses). We detected 41 species (19 birds, 21 mammals and one reptile). The average richness of visiting species per carcass was approximately double in Cazorla than in Murcia and Espuña (Tables S1 and S2). Domestic species (mainly dogs, but also cats, goats and sheep) were rarely recorded (1.4% of total events; Table S2). The fox was the most frequently recorded species in the three study areas (40.3% of total events). Mean number of different individuals per event was 1.1±0.9 (range: 1-29), and groups of visitors (i.e., more than one individual) were recorded at 8.0% of total events. Groups were more frequently recorded for carrion crow (*Corvus corone*), wild boar (*Sus scrofa*), mouflon (*Ovis aries musimon*) and eurasian jay (*Garrulus glandarius*) in Cazorla. The fox was very rarely observed in groups (Table S2).

Contact events represented 40.6% of the total recorded events. Specifically, contact events in Cazorla were 64.4% of total contact events; in Murcia 16.6%; and in Espuña were 7.6% and 11.5% at fox carcasses and at other carcasses, respectively (Figure 1, Table 1). Considering all study areas together, the fox was the species that most frequently contacted with carcasses (45.0% of total contact events; Figure 1, Table 1). Carcasses were contacted by 21 vertebrate species (nine birds and 12 mammals) in Cazorla, 15 species in Murcia (five birds and 10 mammals), seven species in Espuña at fox carcasses (three birds and four mammals), and 10 species in Espuña at other carcasses (three birds and seven mammals; Table S2). Intraspecific contact was recorded at 100% of carcasses in Cazorla, 63.2% in Murcia, and 60.0% (fox carcasses) and 30.0% (other carcasses) in Espuña. In foxes, intraspecific contact was detected in 43.4% of the total events recorded. In Espuña, events (especially contact events) of foxes and other mammals, but not of birds, were more frequently recorded at carcasses of other mesocarnivores (Figure 1). Contact of both domestic and wild species with the same carcass took place at six carcasses in Cazorla (22.2% of total carcasses in this area), three in Murcia (15.8%) and two carcasses of other mesocarnivores in Espuña (20% of total non-fox carcasses). Contact between individuals of different visiting species at carcass sites was recorded only once, between a golden eagle and a griffon vulture in Cazorla.

Marking and rubbing behaviors were recorded in 5.7% and 2.4% of total events, respectively. In detail, the results obtained in Cazorla were 64.7% and 59.7% of total marking and rubbing events, respectively; in Murcia were 16.2% and 19.3%; at fox carcasses from Espuña were 8.1% and 8.7%, and 11.0% and 12.3% at other carcasses (Figure 1, Table 1). The fox was the most frequently recorded species marking (83.1% of total marking events) and rubbing on the carcass or on the ground (70.1% of total rubbing events), and no marking and rubbing behaviors were observed for birds (Figure 1, Table 1). Regarding total marking events, urination was the most frequently recorded behavior in foxes (85.2% of total marking events) and other mammals (73.9%), while defecation only represented 14.8% and 26.1% of marking events, respectively.

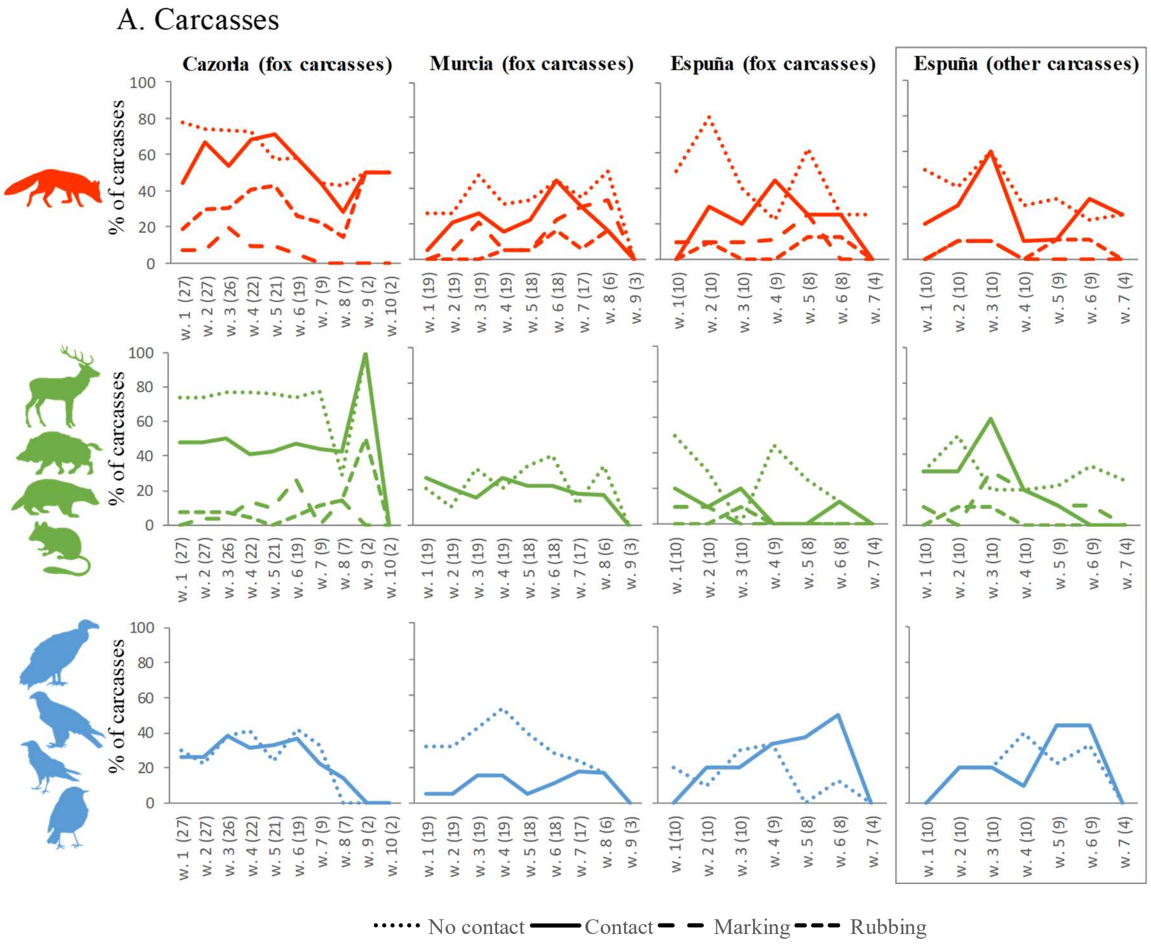
A. Carcasses

Figure 1. Weekly variation in patterns of use of mesocarnivore carcasses by red fox, other mammals and birds in three areas of southeastern Spain. A) Weekly percentage of contacted (i.e., with at least one contact event), non-contacted (i.e., visited, but no contact events recorded), marked (i.e., with at least one marking event), and rubbed (i.e., with at least one rubbing event) carcasses by red fox, other mammals and birds per study area and carcass type. B) Weekly number of contact, non-contact, marking, and rubbing events by red fox, other mammals and birds per study area and carcass type. For a given week, the number of carcasses available is given in parentheses. Panels for carcasses of carnivores other than foxes are in boxes.

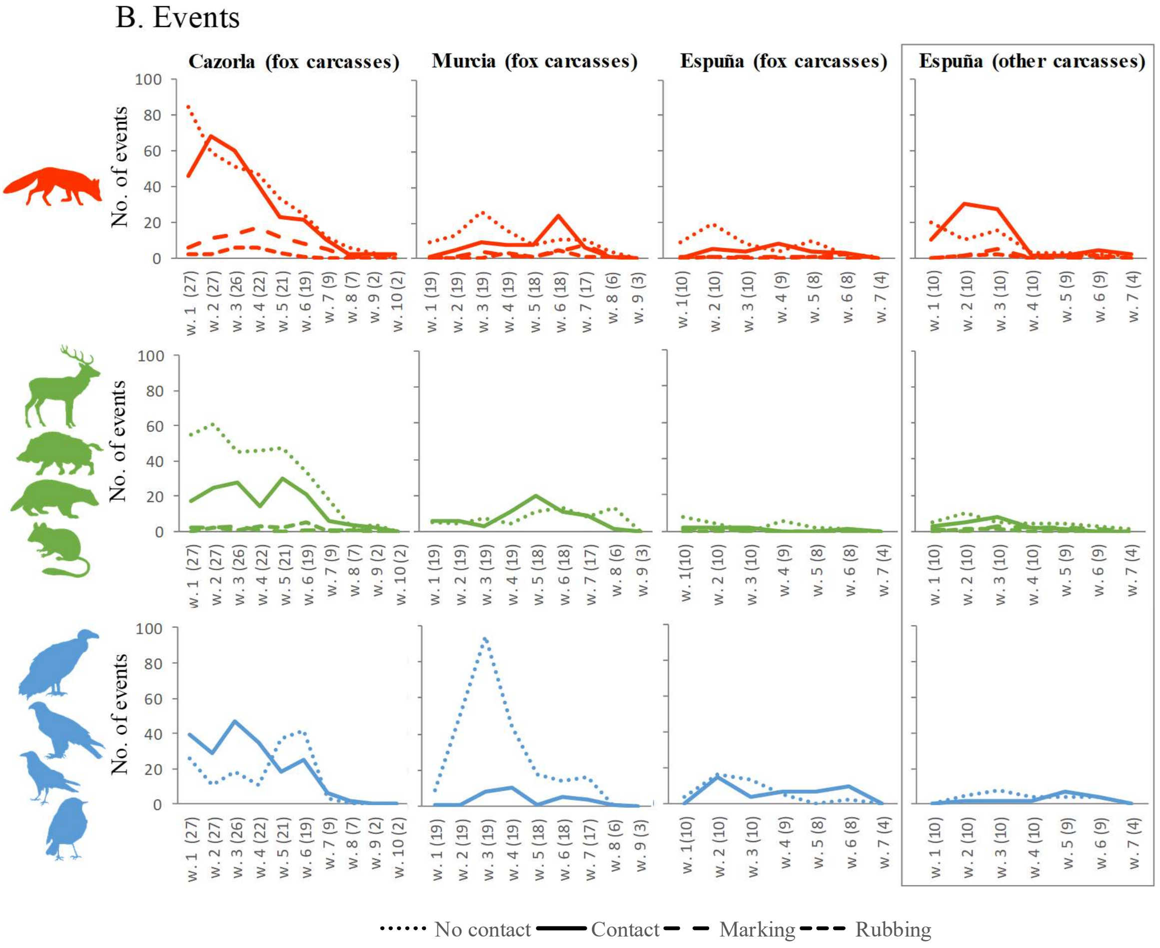

Figure 1 (continued). Weekly variation in patterns of use of mesocarnivore carcasses by red fox, other mammals and birds in three areas of southeastern Spain. A) Weekly percentage of contacted (i.e., with at least one contact event), non-contacted (i.e., visited, but no contact events recorded), marked (i.e., with at least one marking event), and rubbed (i.e., with at least one rubbing event) carcasses by red fox, other mammals and birds per study area and carcass type. B) Weekly number of contact, non-contact, marking, and rubbing events by red fox, other mammals and birds per study area and carcass type. For a given week, the number of carcasses available is given in parentheses. Panels for carcasses of carnivores other than foxes are in boxes.

Table 1. Carcass use patterns per study area and carcass type, according to different vertebrate species groups. Number of monitored carcasses is indicated for each study area and carcass type. The number of carcasses visited, contacted, marked and rubbed by each vertebrate group is shown together with the percentage relative to the total carcasses monitored per area and carcass type (in parentheses). Mean number of events per carcass±SD is shown for total, contact, marking and rubbing events. We considered carcasses contacted, marked and rubbed as those carcasses with at least one event with contact, marking or rubbing by a given vertebrate group. Similarly, we considered contact, marking and rubbing events as those events with at least one contact, marking or rubbing behavior recorded.

Area	Carcass type	N	Group	Carcasses visited	Carcasses contacted	Carcasses marked	Carcasses rubbed	Total events	Contact events	Marking events	Rubbing events
Cazorla	Foxes	27	Red fox	27 (100%)	27 (100%)	20 (74.1%)	9 (33.3%)	22.0±13.8	10.2±9.0	2.8±4.1	0.7±1.6
			Other mammals	27 (100%)	23 (85.2%)	9 (33.3%)	8 (29.7%)	17.0±9.6	1±5.0	0.4±0.8	0.5±0.9
			Birds	21 (77.8%)	18 (66.7%)	0 (0%)	0 (0%)	12.9±15.6	7.4±10.3	0	0
			Total	27 (100%)	27 (100%)	22 (81.5%)	14 (51.2%)	51.9±25.6	23.1±16.7	3.3±4.6	1.2±1.9
Murcia	Foxes	19	Red fox	16 (84.2%)	12 (63.2%)	9 (47.4%)	4 (14.8%)	8.4±8.8	3.3±3.9	1.2±1.6	0.6±1.3
			Other mammals	16 (84.2%)	9 (47.4%)	0 (0%)	0 (0%)	6.9±10.6	3.5±8.1	0	0
			Birds	15 (78.9%)	9 (47.4%)	0 (0%)	0 (0%)	14.6±17.3	1.6±2.6	0	0
			Total	19 (100%)	16 (84.2%)	9 (47.4%)	4 (14.8%)	30.0±25.2	8.4±9.0	1.2±1.6	0.6±1.3
Espuña	Foxes	10	Red fox	9 (90.0%)	6 (60.0%)	4 (40.0%)	1 (10.0%)	7.7±6.2	2.4±3.5	0.9±1.5	0.4±1.3
			Other mammals	10 (100%)	6 (60.0%)	2 (20.0%)	1 (10.0%)	2.8±2.4	0.7±0.7	0.2±0.4	0.1±0.3
			Birds	8 (80.0%)	6 (60.0%)	0 (0%)	0 (0%)	8.3±15.2	4.3±6.7	0	0
			Total	10 (100%)	10 (100%)	5 (50.0%)	2 (20.0%)	18.8±18.4	7.4±8.7	1.1±1.6	0.5±1.3
	Other	10	Red fox	10 (100%)	9 (90.0%)	1 (10.0%)	2 (20.0%)	12.9±24.1	7.5±16.8	0.6±1.9	0.5±1.1
			Other mammals	10 (10.0%)	8 (80.0%)	5 (50.0%)	2 (20.0%)	5.1±4.3	1.9±1.6	0.9±1.3	0.2±0.4
			Birds	7 (70.0%)	5 (50.0%)	0 (0%)	0 (0%)	4.2±4.9	1.7±2.2	0	0
			Total	10 (100%)	10 (100%)	6 (60.0%)	3 (30.0%)	22.2±22.4	11.1±16.1	1.5±2.0	0.7±1.3

Weekly patterns in fox behavior

Maximum values in the ratio between contacted and non-contacted carcasses by fox took place from the fourth (in Espuña) to the seventh (in Cazorla) week in the case of fox carcasses (Figure 2). In the carcasses of other species, the maximum took place from the second week, i.e., two weeks earlier than the maximum for fox carcasses in the same study area (Espuña). We observed a similar general pattern for events, with peaks occurring from the fourth week on in the case of fox carcasses and in the second week in the case of other carcasses, i.e., two weeks earlier than the peak for fox carcasses in the same study area. While fox carcasses in Cazorla and Murcia, and other carcasses in Espuña, began to be contacted in the first week after their deployment, the first events of contact of fox carcasses in Espuña began to be recorded from the second week. In Espuña, the ratio contact:non-contact events was generally higher at other carnivore carcasses than at fox carcasses (Figure 2).

Carcasses in all the study areas were detected by foxes during the first week. The number of contacted carcasses by fox stabilized by the fourth to seventh week in fox carcasses, and by the fourth week in other carcasses (Figure 3). In Espuña, by the fourth week (i.e., when the maximum number of contacted carcasses was reached for both types of carcasses), less fox carcasses were contacted (60% of total fox carcasses) than carcasses of other carnivores (90% of total other carcasses). While marking by fox was anecdotal for other carcasses (10%), foxes marked 40-74% of fox carcasses, with a direct relationship between marked and contacted carcasses in this case (Figure 3). In contrast, rubbing on the carcass or on the ground next to it by fox was more frequent at other carcasses, especially in late weeks (Figure 3).

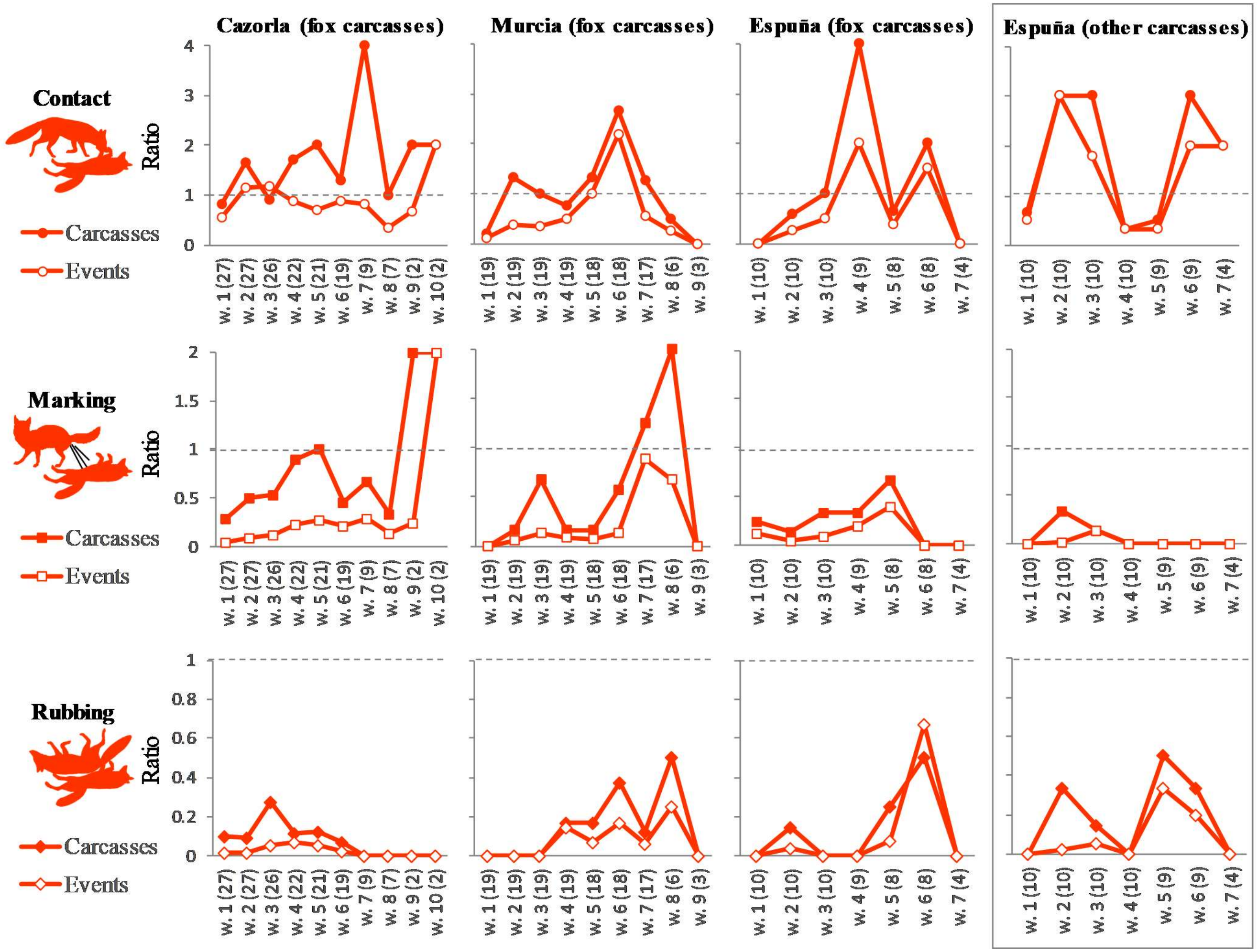

Figure 2. Weekly variation in the ratios contacted:non-contacted carcasses, contact:non-contact events, marked:non-marked carcasses, marking:non-marking events, rubbed:non-rubbed carcasses, and rubbing:non-rubbing events by the red fox per study area and carcass type. Values above and below the dashed horizontal gray line indicate, respectively, ratios biased towards contact/marking/rubbing and non-contact/non-marking/non-rubbing. For a given week, the number of carcasses available is given in parentheses. Panel for carcasses of carnivores other than foxes is in the box.

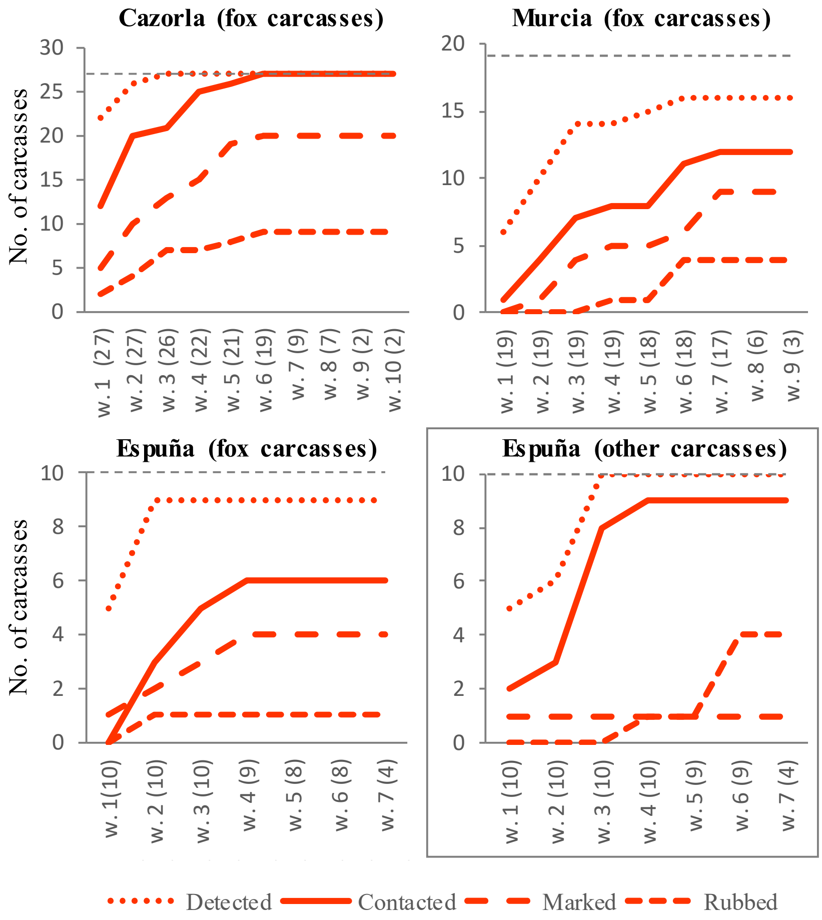

Figure 3. Accumulated weekly number of detected (i.e., with at least one event recorded), contacted (i.e., with at least one contact event), marked (i.e., with at least one marking event), and rubbed (i.e., with at least one rubbing event) carcasses by the red fox per study area and carcass type. Dotted horizontal gray lines represent the accumulated number of available carcasses. For a given week, the number of carcasses available is given in parentheses. Panel for carcasses of carnivores other than foxes is in the box.

According to the GLMs, the time elapsed since carcass detection by foxes until they contacted it was related to the type of carcass, season, hour of carcass placement and, mostly, by habitat (Table 2). In particular, foxes started to contact earlier carcasses in open habitats, carcasses of mesocarnivores other than fox (Figure 1), in spring and carcasses that were placed during the morning (Table 3). However, selected models explained little of the variability in the response variable, as revealed by their low D^2 values (<10%; Table 2).

Table 2. AICc-based model selection to assess the effect of study “area”, “habitat”, “year”, “season”, “hour”, and “carcass type” on “time of first contact” by foxes on mesocarnivore carcasses in southeastern Spain (see main 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 models explained by the predictors (deviance, D^2) are shown. Selected models are in bold.

Model	k	AICc	ΔAICc	D^2
habitat	**1**	**406.78**	**0**	**6.02**
habitat + carcass	**2**	**407.48**	**0.70**	**8.83**
habitat + season	**2**	**408.08**	**1.30**	**7.81**
habitat + hour	**2**	**408.66**	**1.88**	**6.82**
habitat + carcass + hour	3	409.27	2.49	
season	1	409.53	2.75	
carcass	1	409.67	2.89	
habitat + carcass + season	3	409.81	3.03	
hour	1	409.83	3.05	
year	2	410.88	4.10	
habitat + area	3	410.98	4.20	
habitat + year	3	411.40	4.62	
habitat + carcass + hour + season	4	411.65	4.87	
area	2	411.89	5.11	
habitat + carcass + year	4	411.94	5.16	
habitat + carcass + area	4	412.27	5.49	
habitat + carcass + hour + year	5	413.63	6.85	
habitat + carcass + hour + area	5	414.25	7.47	

Table 3. Generalized linear models (GLMs) showing the relationship between “time of first contact” by foxes with the explanatory variables included in the selected models (“habitat”: open, close; “carcass” type: fox, other; “season”: winter, spring; “hour”: morning, afternoon). Only selected models are shown, ordered from highest to lowest D^2. 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.

Model	Parameter	Estimate	SE	df
habitat + carcass	Intercept	11.402	1.823	53
	habitat (open)	-6.665	3.157	
	carcass (other)	-4.749	3.794	
habitat + season	Intercept	8.545	2.392	53
	habitat (open)	-5.907	3.069	
	season (winter)	2.863	2.878	
habitat + hour	Intercept	10.743	1.747	53
	habitat (open)	-5.681	3.071	
	hour (morning)	-2.430	3.691	
habitat	Intercept	10.306	1.607	53
	habitat (open)	-5.569	3.050	

Spatial patterns of fox behavior

The direct contact of foxes with the different anatomical regions of the carcass followed a heterogeneous pattern (Figure 4). In general, the part of fox carcasses that was less frequently contacted by foxes was the anterior region. Patterns of direct contact with fox carcasses were similar in Cazorla and Murcia (χ^2=2.240, d.f.=2, p=0.3) and Cazorla and Espuña (χ^2=4.728, d.f.=2, p=0.09). However, foxes contacted most frequently the posterior region of fox carcasses in Espuña and the central part in Murcia (χ^2=7.528, d.f.=2, p=0.02). In Espuña, foxes showed different behaviors vis-à-vis fox carcasses than those of other carnivores (χ^2=25.002, d.f.=2, p<0.00001). In particular, foxes contacted mostly the central region of other carnivore carcasses, while the posterior part was the less frequently contacted part (Figure 4).

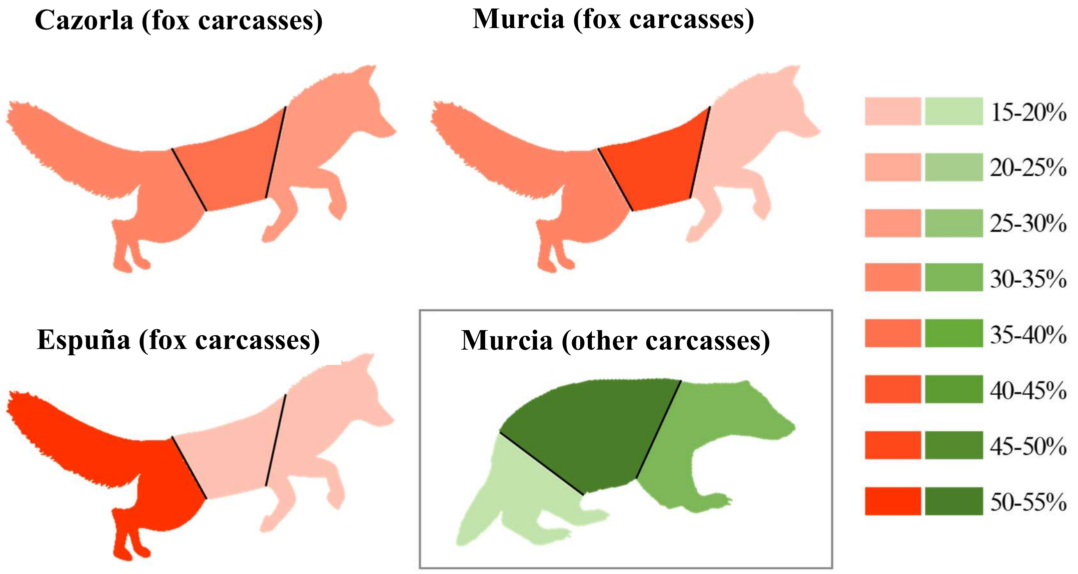

Figure 4. Carcass parts contacted by foxes per study area and carcass type. Percentages are based on total contact events recorded per carcass type and study area.

While most events by foxes were recorded close to the carcasses, we observed some differences among areas and carcass types (Figure 5). In particular, the pattern of distance maintained between the fox and the conspecific carcass was similar in Cazorla and Murcia (χ^2=1.603, d.f.=3, p=0.7), and Murcia and Espuña (χ^2=5.883, d.f.=3, p=0.1). However, while the frequency of fox occurrence follows a gradient that decreases with distance from the carcass in Cazorla, the most frequent minimum distance between visiting foxes and conspecific carcasses in Espuña was within the >0-50 cm interval (χ^2=8.036, d.f.=3, p=0.04). At carcass sites of other carnivore carcasses in Espuña, events were strongly concentrated within a distance of 50 cm from the carcass, with most events touching the carcass (χ^2=16.430, d.f.=3, p<0.001; Figure 5). Most marking (62.8%) and rubbing (82.5%) events were made with direct contact with the carcass.

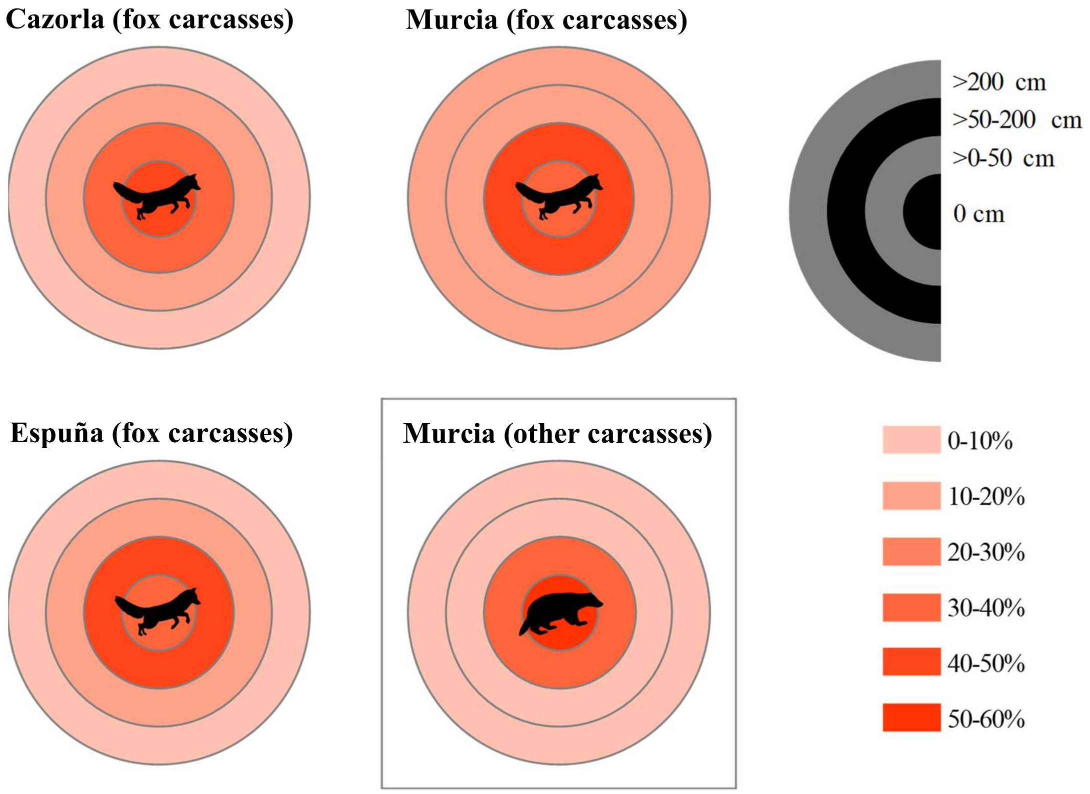

Figure 5. Minimum distance between visiting foxes and carcasses per study area and carcass type. Percentages are based on total events recorded per carcass type and study area.

DISCUSSION

Here we conducted a detailed behavioral study of carnivore hosts, including scavenging and non-scavenging species, vis-à-vis mammalian carnivore carcasses, which represent potential hotspots for non-trophically transmitted pathogens. Few studies have addressed to date how perceived risk of acquiring non-trophically transmitted pathogens may shape the landscape of disgust of hosts (Buck *et al.*, 2018; Weinstein *et al.*, 2018a), and none has focused on carnivore carcasses. Thus, patterns arisen from our study may provide a basis for a more accurate interpretation of the ecological aspects that characterize the transmission of pathogens in the wild (Polley and Thompson, 2015), which is especially relevant in a global context of zoonotic diseases (Evans *et al.*, 2020; Leroy *et al.*, 2020; Tiwari *et al.*, 2020).

Visitor behavior at carnivore carcass sites

Carnivore carcass sites were visited by a rich community of vertebrates, though their behavior differed widely among species groups, study areas and carcass types. The long persistence of mesocarnivore carcasses in the environment due to their relatively low consumption rate (Moleón *et al*., 2017; Muñoz-Lozano *et al*., 2019) probably favored the visiting of numerous species during the long decomposition period, which lasted up to ten weeks. Contact between the visitor and the carcass was frequently recorded. However, direct contact between two different visitor species was hardly ever recorded, and it was never observed between mammals. This contrasts with herbivore carcasses, in which mammalian scavengers may have more opportunities to contact, especially in the absence of competition with vultures (Ogada *et al*., 2012). In carnivore carcasses, visits of mammals are more spaced than in herbivore carcasses, where many scavengers may gather in the short interval during which meat is available. Thus, at carnivore carcass sites, infection risk may take place mainly for visitor-carcass contact rather than direct contact between visitors.

Visitor behavior at carcass sites is probably highly dependent on the scavenging habits of the species. In our study, scavenging species were responsible for most contact events (53.1-96.5%, depending on the study area; see Table S2). Contacts by non-scavengers were mainly done by small passerine birds and garden dormice that were observed taking hair from carcasses for nest construction (Moleón and Sánchez-Zapata, 2016; Moleón *et al*., 2017; authors' pers. observ.; note that these species can also scavenge occasionally and prey on necrophagous insects; Moreno-Opo and Margalida, 2013). Herbivores may avoid carcasses because they pose a risk of predation by scavenging predators (Cortés-Avizanda *et al*., 2009), so carnivore carcasses should represent a low infection risk for these species in the short-term. In the mid- and long-term, however, the vegetation that vigorously grows around carcass sites (Barton *et al*., 2013) may attract herbivores and, consequently, it may increase the risk of infection by certain pathogens with persistent infective stages in the environment (Johnson and Thieltges, 2010), such as eggs of *Taenia* spp., a cestode genus that includes several species of parasites whose intermediate hosts are ungulates and definitive hosts are carnivores (Lesniak *et al*., 2017).

Marking and rubbing behaviors were only observed for mammals. Scent-marking is very frequent in carnivores and many other mammals for interspecific and, mostly, intraspecific communication (e.g., territory delimitation and defense; Ralls, 1971; Johnson, 1973; Sillero-Zubiri and Macdonald, 1998). Rubbing, or scent-rubbing, is also very frequent in mammals such as carnivores, though the eco-evolutionary significance of this behavior is far from being clear (Rieger, 1979; Gosling and McKay, 1990). Direct contact with the carcass was much more frequent for rubbing than marking, which indicates that the risk of acquiring shared pathogens such as *S. scabiei* is higher for wild canids, mustelids and viverrids undergoing rubbing behavior (Arlian, 1989; Kołodziej-Sobocińska *et al.*, 2014). In addition to ectoparasites, there may be other endoparasite infective stages in the hair of the carcass, such as *Toxocara canis* eggs (Roddie *et al.*, 2008). Thus, touching, rubbing against or sniffing the carcass can also be a way of infection for this type of nematode specific to wild canids. The frequent marking behavior observed also suggests that carcass sites may concentrate more persisting infective stages excreted by saliva, urine or feces from the host than in the surrounding landscape. This is the case, for example, of canine parvovirus (Miranda *et al.*, 2017), canine distemper virus (Beineke *et al.*, 2015), *Leptospira* spp. (Millán *et al.*, 2019), *Brucella* spp. (Kosoy and Goodrich, 2019) and ascarids (Okulewicz *et al.*, 2012).

As expected, the richer community of visiting species and the highest number of total contacts, marking and rubbing events were observed in Cazorla, which is the most biodiverse area. In Cazorla, which has important vulture populations, facultative scavengers found less scavenging opportunities (Morales-Reyes *et al.*, 2017), so they may be forced to assume higher risk and scavenge on the few carrion resources that are available (Chapter 2). This suggests that carnivore carcasses that remain unconsumed by vultures may pose a highest infection risk for scavenging mammals in areas with high competition for carrion. The time elapsed in detecting carcasses was usually less than a week. From an epidemiological point of view, this indicates that, even if there is no direct contact with the carcass, there is still a risk of acquiring ectoparasites, especially in the case of those with greater mobility and capacity to leave the carcass, such as fleas, *Otodectes cynotis* and ticks (Domínguez, 2004; Perruci *et al.*, 2016). These ectoparasites are detached from the body within a few hours after host death (Nelder and Reeves, 2005), remaining around the carcass while waiting for a new host. Therefore, mesocarnivore carcass sites could be considered as an epidemiological factor influencing the transmission of vector-borne pathogens (Millán *et al.*, 2016; Hofmeester *et al.*, 2018). However, it should be noted that, in our study, we used carcasses that were frozen (i.e., free from ectoparasites) before their placement in the field.

Domestic species, represented by livestock (goats and sheep) and pets (dogs and cats), were recorded in a very low proportion of total and contact events even for the most anthropized area (Murcia). This suggests that carnivore carcasses are not important hotspots of pathogen transmission for these species, at least in our study areas, where presence of domestic species was generally low. There is concern for rabies circulation among dogs, other domestic animals, wildlife and humans in several parts of the world (Hughes and Macdonald, 2013), though there are no recent cases of rabies in our study area (http://www.who-rabies-bulletin.org/; King *et al.*, 2004). Further studies are recommended in regions where potential contact between wildlife and domestic animals is higher.

Fox behavior in relation to carcass type

We found important behavioral differences of red foxes against fox carcasses and carcasses of other mesocarnivores in Espuña. Foxes contacted more heterospecific carcasses than conspecific ones, and the propensity to contact, measured as the ratio contact:non-contact events, was higher for heterospecific carcasses. Moreover, foxes contacted heterospecific carcasses earlier than conspecific ones, as confirmed by the GLMs, and they were more frequently observed at <50 cm from heterospecific carcasses than from fox carcasses. While propensity to rubbing, most of which took place directly against the carcass, was similar between conspecific and heterospecific carcasses, rubbing by fox was more frequent for the later. All of this is in accordance with the hypotheses that, in general, infection risk is higher for phylogenetically related species (Huang *et al.*, 2014), and that carnivores avoid feeding upon conspecific carcasses because the risk of acquiring species-specific meat-borne pathogens is maximum (Hart, 2011; Moleón *et al.*, 2017). In the case of sarcoptic mange, the fox's greater fear of contact conspecific carrion is consistent with the fact that canids have a higher susceptibility to sarcoptic mange than other mesocarnivore species (Astorga *et al.*, 2018; Niedringhaus *et al.*, 2019). Again, we must emphasize here that carcasses used in our study belonged to healthy animals that presented a good body condition and no skin lesions compatible with sarcoptic mange. However, in the initial stages of the disease, mangy animals do not present evident lesions, which suggests that even carrion that does not have sarcoptic lesions may be infectious to the host that contacts it.

Maximum propensity to contact carcasses took place several weeks after carcass deployment, especially for conspecific carcasses. Off-host survival of ectoparasites such as mites and lice decrease with time after host dead, with survival being affected by environmental temperature and humidity (Arlian *et al.,* 1984, 1989; Pérez-Jiménez *et al*., 1990). In our Mediterranean study areas, characterized by mild and dry environmental conditions, off-host survival of ectoparasites and other pathogens is probably lower than in colder and more humid environments. Foxes visiting carcasses seemed to avoid the period of maximum risk of acquiring ectoparasites, i.e., the first weeks after the carcass was available. However, other infective stages of ascarid eggs, viruses and spore-forming bacteria may survive for longer periods in the carcass vicinities (Turner *et al*., 2014; Beineke *et al*., 2015; Holland, 2017; Miranda *et al*., 2017). In this case, the strategy of foxes of delaying the propensity to contact carcasses would be ineffective to avoid infection risk.

Fox marking behavior was also conditioned by carcass type, as urination and defecation were more frequent for conspecific carcasses. This behavior does not entail, *a priori*, a direct contact with the carcass, so the risk of acquiring some pathogens that are usually transmitted by direct contact and have reduced mobility outside the host, such as lice and, especially, *S. scabiei*, is greatly reduced (Millán *et al*., 2016). This also suggests that marking behavior of the red fox is weakly inhibited by the infection risk associated with the presence of carcasses. In mammalian carnivores, marking is mainly associated with intraspecific communication (e.g. Sillero-Zubiri and Macdonald, 1998). However, why foxes marked more conspecific than heterospecific carcasses is unclear. A possible explanation could be that fox carcasses could be more valuable in terms of persistent information points. This is because the persistence of fox carcasses in the environment is higher than the persistence of carcasses of other mesocarnivores, given that foxes are more prone to feed upon the later (Moleón *et al*., 2017; Muñoz-Lozano *et al*., 2019), and foxes are one of the most abundant scavengers in our study areas (Morales-Reyes *et al*., 2017).

Finally, we found differences regarding the anatomical regions of the conspecific and heterospecific carcasses that were touched by fox. This behavior may reveal that there are certain pathogens whose infective stages are distributed unequally on the body surface. For example, ascarid eggs are located in the skin of the perianal area; the mite *O. cynotis* and *Malassezia* yeast are preferably in the ear canal (Perrucci *et al*., 2016); or *Linguatula serrata*, a pentastomid with adult stages located in nasal cavities (Riley, 1986). Our results suggest that scavenger behavior tends to focus primarily on specific anatomical parts of the carcass. This could have epidemiological consequences that should be investigated.

Conclusions

Here we disentangled the behavior of animals visiting mesocarnivore carcass sites, which may have important implications not only to understand the epidemiology of non-trophically transmitted parasites, but also several eco-evolutionary questions. Contact events between scavengers and carcasses were far more frequent than consumption events (Moleón *et al.*, 2017; Muñoz-Lozano *et al.*, 2019; Chapter 2), which suggests that scavenger behavior is more constrained by the transmission risk of meat-borne parasites than the risk of acquiring non-trophically transmitted parasites. Observed fox behavior may be effective against species-specific ectoparasites with short off-host survival as lice and *S. scabiei*, but not for other pathogen such as ascarids, viruses and spore-forming bacteria that may have persistent infective stages around carcass sites. Overall, this study shows the promising and varied research opportunities of studying animal behavior associated with carrion resources. The impact that emerging and re-emerging diseases associated with wildlife are having on modern societies makes it necessary to address these types of studies, providing scientific evidence that is key to advancing our understanding of the epidemiological factors that occur in the wild.

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SUPPLEMENTARY FILES

Table S1. Vertebrate species richness recorded at carcasses, per study area and carcass type, according to different vertebrate species groups and behavior. Number of monitored carcasses is indicated for each study area and carcass type. Mean number of species±SD is shown. We considered carcasses contacted, marked and rubbed as those carcasses with at least one event with contact, marking or rubbing by a given scavenger group.

Area	Carcass type	N	Group	Visit	Contact	Marking	Rubbing
Cazorla	Foxes	27	Red fox	1.0±0	1.0±0	0.7±0.5	0.3±0.5
			Other mammals	4.9±1.7	1.9±1.4	0.3±0.5	0.3±0.6
			Birds	1.9±1.9	1.1±1.1	0	0
			Total	7.8±2.7	4.0±1.9	1.1±0.7	0.7±0.7
Murcia	Foxes	19	Red fox	0.9±0.4	0.6±0.5	0.5±0.5	0.2±0.4
			Other mammals	1.8±1.3	0.9±1.1	0	0
			Birds	1.6±1.3	0.7±0.9	0	0
			Total	4.2±2.3	2.2±1.7	0.5±0.5	0.2±0.4
Espuña	Foxes	10	Red fox	0.9±0.3	0.6±0.5	0.4±0.5	0.1±0.3
			Other mammals	1.7±1.1	0.6±0.5	0.2±0.4	0.1±0.3
			Birds	1.2±0.9	0.8±0.9	0	0
			Total	3.8±1.9	2.0±1.2	0.6±0.7	0.2±0.4
	Other	10	Red fox	1.0±0	0.9±0.3	0.1±0.3	0.2±0.4
			Other mammals	2.2±1.1	1.4±0.9	0.5±0.5	0.2±0.4
			Birds	1.5±1.2	0.7±0.8	0	0
			Total	4.7±1.8	3.0±1.2	0.6±0.5	0.4±0.7

Table S2a. Carcass use patterns by vertebrate species in Cazorla (fox carcasses). Mean number of individuals±SD per carcass is shown, together with the total number of events with contact, marking and rubbing behavior for each species recorded. Species that scavenge frequently in our study areas are indicated by an asterisk.

Class	Common name	Scientific name	Individuals	Contact	Marking	Rubbing
Birds	Golden eagle*	*Aquila chrysaetos*	1.0±0	8	0	0
	Griffon vulture*	*Gyps fulvus*	20.0±0	1	0	0
	Common raven*	*Corvus corax*	1.6±0.6	16	0	0
	Carrion crow*	*Corvus corone*	1.6±0.8	96	0	0
	Eurasian jay*	*Garrulus glandarius*	1.1±0.2	64	0	0
	Little owl*	*Athene noctua*	1.0±0	0	0	0
	Red-legged partridge	*Alectoris rufa*	-	-	-	-
	European greenfinch	*Chloris chloris*	-	-	-	-
	Common chaffinch	*Fringilla coelebs*	2.0±0	0	0	0
	Blue tit	*Cyanistes caeruleus*	1.0±0	0	0	0
	Great tit	*Parus major*	1.7±1.9	4	0	0
	Black redstart	*Phoenicurus ochruros*	1.0±0	1	0	0
	European robin	*Erithacus rubecula*	1.0±0	10	0	0
	Rock dove	*Columba palumbus*	1.0±0	0	0	0
	Woodchat shrike	*Lanius senator*	-	-	-	-
	Wood lark	*Lullula arborea*	1.0±0.2	1	0	0
	Blackcap	*Sylvia atricapilla*	-	-	-	-
	Common blackbird	*Turdus merula*	1.0±0	0	0	0
	Hoopoe	*Upupa epops*	-	-	-	-

Table S2a (continued). Carcass use patterns by vertebrate species in Cazorla (fox carcasses). Mean number of individuals±SD per carcass is shown, together with the total number of events with contact, marking and rubbing behavior for each species recorded. Species that scavenge frequently in our study areas are indicated by an asterisk.

Class	Common name	Scientific name	Individuals	Contact	Marking	Rubbing
Mammals	Barbary sheep	*Ammotragus lervia*	-	-	-	-
	Goat	*Capra aegagrus hircus*	-	-	-	-
	Spanish ibex	*Capra pyrenaica*	1.4±0.8	1	0	0
	Sheep	*Ovis aries*	9.1±10.2	1	0	0
	Mouflon	*Ovis aries musimon*	1.6±0.8	1	0	0
	Red deer	*Cervus elaphus*	1.2±0.4	0	0	0
	Fallow deer	*Dama dama*	1.4±0.7	1	0	0
	Wild boar*	*Sus scrofa*	1.3±0.9	79	0	12
	Domestic dog*	*Canis lupus familiaris*	1.3±0.5	9	0	2
	Red fox*	*Vulpes vulpes*	1.0±0.1	275	76	20
	Domestic cat*	*Felis silvestris catus*	-	-	-	-
	Wild cat*	*Felis silvestris silvestris*	1.0±0	1	0	0
	Common genet*	*Genetta genetta*	1.0±0	16	1	0
	Stone marten*	*Martes foina*	1.0±0	36	11	0
	Eurasian badger*	*Meles meles*	1.0±0	0	0	0
	Long-tailed field mouse	*Apodemus sylvaticus*	-	-	-	-
	Rat	*Rattus* spp.	1.0±0	1	0	0
	Garden dormouse	*Eliomys quercinus*	1.0±0	0	0	0
	Red squirrel	*Sciurus vulgaris*	1.1±0.3	1	0	0
	European rabbit	*Oryctolagus cuniculus*	-	-	-	-
	White-toothed shrew	*Crocidura russula*	-	-	-	-
Reptiles	Ocellated lizard	*Timon lepidus*	-	-	-	-
Total				**623**	**88**	**34**

Table S2b. Carcass use patterns by vertebrate species in Murcia (fox carcasses). Mean number of individuals±SD per carcass is shown, together with the total number of events with contact, marking and rubbing behavior for each species recorded. Species that scavenge frequently in our study areas are indicated by an asterisk.

Class	**Common name**	**Scientific name**	**Individuals**	**Contact**	**Marking**	**Rubbing**
Birds	Golden eagle*	*Aquila chrysaetos*	-	-	-	-
	Griffon vulture*	*Gyps fulvus*	-	-	-	-
	Common raven*	*Corvus corax*	-	-	-	-
	Carrion crow*	*Corvus corone*	-	-	-	-
	Eurasian jay*	*Garrulus glandarius*	-	-	-	-
	Little owl*	*Athene noctua*	1.0±0	6	0	0
	Red-legged partridge	*Alectoris rufa*	1.5±1.2	0	0	0
	European greenfinch	*Chloris chloris*	1.0±0	0	0	0
	Common chaffinch	*Fringilla coelebs*	-	-	-	-
	Blue tit	*Cyanistes caeruleus*	-	-	-	-
	Great tit	*Parus major*	-	-	-	-
	Black redstart	*Phoenicurus ochruros*	1.1±0.3	4	0	0
	European robin	*Erithacus rubecula*	1.0±0.1	19	0	0
	Rock dove	*Columba palumbus*	-	-	-	-
	Woodchat shrike	*Lanius senator*	1.0±0	1	0	0
	Wood lark	*Lullula arborea*	1.0±0.2	0	0	0
	Blackcap	*Sylvia atricapilla*	1.0±0	1	0	0
	Common blackbird	*Turdus merula*	1.0±0	0	0	0
	Hoopoe	*Upupa epops*	1.0±0	0	0	0

Table S2b (continued). Carcass use patterns by vertebrate species in Murcia (fox carcasses). Mean number of individuals±SD per carcass is shown, together with the total number of events with contact, marking and rubbing behaviour for each species recorded. Species that scavenge frequently in our study areas are indicated by an asterisk.

Class	**Common name**	**Scientific name**	**Individuals**	**Contact**	**Marking**	**Rubbing**
Mammals	Barbary sheep	*Ammotragus lervia*	-	-	-	-
	Goat	*Capra aegagrus hircus*	2.0±0	0	0	0
	Spanish ibex	*Capra pyrenaica*	-	-	-	-
	Sheep	*Ovis aries*	-	-	-	-
	Mouflon	*Ovis aries musimon*	-	-	-	-
	Red deer	*Cervus elaphus*	-	-	-	-
	Fallow deer	*Dama dama*	-	-	-	-
	Wild boar*	*Sus scrofa*	1.7±1.9	7	0	0
	Domestic dog*	*Canis lupus familiaris*	1.1±0.4	7	0	0
	Red fox*	*Vulpes vulpes*	1.0±0.7	62	22	11
	Domestic cat*	*Felis silvestris catus*	1.0±0	0	0	0
	Wild cat*	*Felis silvestris silvestris*	1.0±0	1	0	0
	Common genet*	*Genetta genetta*	1.0±0	2	0	0
	Stone marten*	*Martes foina*	1.0±0	0	0	0
	Eurasian badger*	*Meles meles*	-	-	-	-
	Long-tailed field mouse	*Apodemus sylvaticus*	1.0±0	5	0	0
	Rat	*Rattus* spp.	-	-	-	-
	Garden dormouse	*Eliomys quercinus*	1.0±0	39	0	0
	Red squirrel	*Sciurus vulgaris*	1.0±0	1	0	0
	European rabbit	*Oryctolagus cuniculus*	1.0±0	1	0	0
	White-toothed shrew	*Crocidura russula*	1.0±0	4	0	0
Reptiles	Ocellated lizard	*Timon lepidus*	-	-	-	-
Total				**160**	**22**	**11**

Table S2c. Carcass use patterns by vertebrate species in Espuña (fox carcasses). Mean number of individuals±SD per carcass is shown, together with the total number of events with contact, marking and rubbing behavior for each species recorded. Species that scavenge frequently in our study areas are indicated by an asterisk.

Class	**Common name**	**Scientific name**	**Individuals**	**Contact**	**Marking**	**Rubbing**
Birds	Golden eagle*	*Aquila chrysaetos*	-	-	-	-
	Griffon vulture*	*Gyps fulvus*	-	-	-	-
	Common raven*	*Corvus corax*	-	-	-	-
	Carrion crow*	*Corvus corone*	-	-	-	-
	Eurasian jay*	*Garrulus glandarius*	1.2±0.4	13	0	0
	Little owl*	*Athene noctua*	-	-	-	-
	Red-legged partridge	*Alectoris rufa*	-	-	-	-
	European greenfinch	*Chloris chloris*	-	-	-	-
	Common chaffinch	*Fringilla coelebs*	-	-	-	-
	Blue tit	*Cyanistes caeruleus*	-	-	-	-
	Great tit	*Parus major*	1.1±0.3	26	0	0
	Black redstart	*Phoenicurus ochruros*	-	-	-	-
	European robin	*Erithacus rubecula*	1.0±0	0	0	0
	Rock dove	*Columba palumbus*	-	-	-	-
	Woodchat shrike	*Lanius senator*	-	-	-	-
	Wood lark	*Lullula arborea*	-	-	-	-
	Blackcap	*Sylvia atricapilla*	-	-	-	-
	Common blackbird	*Turdus merula*	1.5±1.0	0	0	0
	Hoopoe	*Upupa epops*	-	-	-	-

Table S2c (continued). Carcass use patterns by vertebrate species in Espuña (fox carcasses). Mean number of individuals±SD per carcass is shown, together with the total number of events with contact, marking and rubbing behavior for each species recorded. Species that scavenge frequently in our study areas are indicated by an asterisk.

Class	**Common name**	**Scientific name**	**Individuals**	**Contact**	**Marking**	**Rubbing**
Mammals	Barbary sheep	*Ammotragus lervia*	1.7±1.2	1	0	0
	Goat	*Capra aegagrus hircus*	-	-	-	-
	Spanish ibex	*Capra pyrenaica*	-	-	-	-
	Sheep	*Ovis aries*	-	-	-	-
	Mouflon	*Ovis aries musimon*	-	-	-	-
	Red deer	*Cervus elaphus*	-	-	-	-
	Fallow deer	*Dama dama*	-	-	-	-
	Wild boar*	*Sus scrofa*	2.3±3.5	5	1	1
	Domestic dog*	*Canis lupus familiaris*	-	-	-	-
	Red fox*	*Vulpes vulpes*	1.0±0	24	9	4
	Domestic cat*	*Felis silvestris catus*	-	-	-	-
	Wild cat*	*Felis silvestris silvestris*	-	-	-	-
	Common genet*	*Genetta genetta*	1.0±0	0	1	0
	Stone marten*	*Martes foina*	1.0±0	1	0	0
	Eurasian badger*	*Meles meles*	-	-	-	-
	Long-tailed field mouse	*Apodemus sylvaticus*	-	-	-	-
	Rat	*Rattus* spp.	-	-	-	-
	Garden dormouse	*Eliomys quercinus*	-	-	-	-
	Red squirrel	*Sciurus vulgaris*	2.0±1.7	0	0	0
	European rabbit	*Oryctolagus cuniculus*	-	-	-	-
	White-toothed shrew	*Crocidura russula*	-	-	-	-
Reptiles	Ocellated lizard	*Timon lepidus*	1.0±0	4	0	0
Total				**74**	**11**	**5**

Table S2d. Carcass use patterns by vertebrate species in Espuña (other carcasses). Mean number of individuals±SD per carcass is shown, together with the total number of events with contact, marking and rubbing behavior for each species recorded. Species that scavenge frequently in our study areas are indicated by an asterisk.

Class	Common name	Scientific name	Individuals	Contact	Marking	Rubbing
Birds	Golden eagle*	*Aquila chrysaetos*	-	-	-	-
	Griffon vulture*	*Gyps fulvus*	-	-	-	-
	Common raven*	*Corvus corax*	-	-	-	-
	Carrion crow*	*Corvus corone*	-	-	-	-
	Eurasian jay*	*Garrulus glandarius*	1.0±0	3	0	0
	Little owl*	*Athene noctua*	-	-	-	-
	Red-legged partridge	*Alectoris rufa*	1.5±0.7	0	0	0
	European greenfinch	*Chloris chloris*	-	-	-	-
	Common chaffinch	*Fringilla coelebs*	-	-	-	-
	Blue tit	*Cyanistes caeruleus*	-	-	-	-
	Great tit	*Parus major*	1.1±0.3	13	0	0
	Black redstart	*Phoenicurus ochruros*	-	-	-	-
	European robin	*Erithacus rubecula*	-	-	-	-
	Rock dove	*Columba palumbus*	-	-	-	-
	Woodchat shrike	*Lanius senator*	-	-	-	-
	Wood lark	*Lullula arborea*	1.0±0	0	0	0
	Blackcap	*Sylvia atricapilla*	-	-	-	-
	Common blackbird	*Turdus merula*	1.0±0	0	0	0
	Hoopoe	*Upupa epops*	-	-	-	-

Table S2d (continued). Carcass use patterns by vertebrate species in Espuña (other carcasses). Mean number of individuals±SD per carcass is shown, together with the total number of events with contact, marking and rubbing behavior for each species recorded. Species that scavenge frequently in our study areas are indicated by an asterisk.

Class	Common name	Scientific name	Individuals	Contact	Marking	Rubbing
Mammals	Barbary sheep	*Ammotragus lervia*	1.3±0.5	0	0	0
	Goat	*Capra aegagrus hircus*	-	-	-	-
	Spanish ibex	*Capra pyrenaica*	-	-	-	-
	Sheep	*Ovis aries*	-	-	-	-
	Mouflon	*Ovis aries musimon*	-	-	-	-
	Red deer	*Cervus elaphus*	-	-	-	-
	Fallow deer	*Dama dama*	-	-	-	-
	Wild boar*	*Sus scrofa*	1.5±1.1	7	0	0
	Domestic dog*	*Canis lupus familiaris*	1.5±0.7	2	0	2
	Red fox*	*Vulpes vulpes*	1.0±0.1	75	6	5
	Domestic cat*	*Felis silvestris catus*	-	-	-	-
	Wild cat*	*Felis silvestris silvestris*	-	-	-	-
	Common genet*	*Genetta genetta*	1.0±0	1	1	0
	Stone marten*	*Martes foina*	1.0±0	5	8	0
	Eurasian badger*	*Meles meles*	-	-	-	-
	Long-tailed field mouse	*Apodemus sylvaticus*	-	-	-	-
	Rat	*Rattus* spp.	1.0±0	1	0	0
	Garden dormouse	*Eliomys quercinus*	1.0±0	3	0	0
	Red squirrel	*Sciurus vulgaris*	1.0±0	0	0	0
	European rabbit	*Oryctolagus cuniculus*	1.0±0	0	0	0
	White-toothed shrew	*Crocidura russula*	-	-	-	-
Reptiles	Ocellated lizard	*Timon lepidus*	1.0±0	1	0	0
Total				**111**	**15**	**7**

GENERAL DISCUSSION

Host-parasite interactions are considered fundamental elements of ecosystems (Lafferty *et al.*, 2006, 2008; Byers, 2009; Sukhdeo, 2012; Gómez and Nichols, 2013). Carrion ecology should be taken into account in epidemiological studies on wildlife diseases, as it is a nutrient-rich food resource that attract many carnivores (DeVault *et al.*, 2003, Wilson and Wolkovich, 2011; Moleón *et al.*, 2014; Sebastián-González *et al.*, 2019) and a potential source of infection (Turner *et al.*, 2014; Rossi *et al.*, 2019). In this doctoral thesis, we have shown that scavenger behavior is shaped by two contrasting forces: the nutritive value of carrion and the risk of acquiring pathogens, both of which are higher for phylogenetically related species (Huang *et al.*, 2014; Moleón *et al.*, 2017). The described behavior may have a great impact on the epidemiology of worldwide distributed parasites that depend on trophic interactions (e.g., *Trichinella* spp.; Pozio and Murrell, 2006) or close contacts (e.g., *Sarcoptes scabiei*; Arlian and Morgan, 2017) for their transmission. The detailed study of wildlife diseases requires a deep knowledge of multiple factors related to the ecology and epidemiology of infectious agents. For this purpose, establishing interdisciplinary teams can allow to get a holistic vision based on the One Health approach (Mackenzie *et al.*, 2013; Gyles, 2016; Cunningham *et al.*, 2017).

Results gathered in this doctoral thesis highlight the lack of interdisciplinary collaborations in topics related to trophically transmitted parasites (Chapter 1), which is associated with the use in the scientific literature of widely accepted assumptions but that lack a solid scientific basis. Chapters 2 and 3 exemplify the approach to the study of disease ecology from an interdisciplinary perspective, which has been useful to get objective and relevant information about the possible consequences of carnivore ecology in the epidemiology of wildlife diseases. In addition to generating information about some of the most paradigmatic meat-borne parasites of carnivores in the wild (Chapter 2), we have also deepened into the study of non-trophically transmitted pathogens (Chapter 3).

Throughout Chapter 1 of this doctoral thesis, the composition of work teams studying the trophic transmission of parasites were evaluated. We encourage both ecologists with specific knowledge on trophic interactions and epidemiologists to be involved in studies related to the transmission of pathogens by meat consumption. This point may be important to promote the correct use of ecological terminology in epidemiological contexts, among other benefits (Herrando-Pérez *et al.*, 2014), avoiding misconceptions in future wildlife research and management programs. Contrary to our expectations, most studies about meat-borne parasites were carried out by unidisciplinary veterinary teams, who are not usually experts in Ecology. For this reason, it was common to find imprecise and erroneous ecological terms in the articles and reviews analyzed. Moreover, in Chapter 1, we also observed that the vast majority of articles based their conclusions on unfounded information or previous, also frequently unfounded, scientific literature. The scarcity of articles that used accurate methodologies makes it difficult to obtain correct and precise data, preventing the reach of "science-based science" standards (Hanna, 2004; Colombo *et al.*, 2017). The lack of rigor in the use of terminology, and the use of poorly science-based hypotheses associated to unidisciplinary articles, indicate the need to increase interdisciplinary collaborations between experts in biological and veterinary sciences.

Probably due to the scarce interdisciplinary collaboration observed in the scientific literature related to the trophic transmission of parasites, several dogmatic and non-realistic assumptions have traditionally pervaded the literature. One of the most remarkable examples is related to intraspecific or cannibalistic consumptions, which have been strongly associated to the transmission of some worldwide distributed and zoonotic parasites, such as *Trichinella* spp. (Campbell, 1988; Pozio & Murrell, 2006; Badagliacca *et al.*, 2016). These results have been refuted by researchers based on diet studies (Fairley, 1970; Remonti *et al.*, 2005), which indicate that cannibalism is a very uncommon behavior in foxes. This hypothesis is supported by Moleón *et al.*, (2017), who have shown that the consumption of conspecifics is rejected by carnivores as a strategy to reduce the risk of parasite infection. This carnivore behavior has received little attention in the scientific literature, despite being a major defensive barrier to avoid trophically transmitted parasite (Hart, 1990; Hart, 2011; Ezenwa *et al.*, 2016; Sarabian *et al.*, 2018; Weinstein *et al.*, 2018).

Contrary to the assumption about the major role of cannibalism in trophic transmission of parasites, Chapter 2 remarks that transmission and maintenance of these parasites in the wild should depend mostly on routes other than intraspecific consumption. Moreover, we provide detailed information about non-trophic interactions between scavenging and non-scavenging species with carnivore carcasses, which can also be hotspots for non-trophically transmitted pathogens (Chapter 3). This last point has received scarce attention in the scientific literature.

The long persistence of mammalian carnivore carrion in the environment, due to their low consumption rate in comparison to herbivore carcasses (Moleón *et al.*, 2017; Muñoz-Lozano *et al.*, 2019), favors the visit of several species that can interact with the carrion

(Chapters 2 and 3). Among these species, our study mainly focused on interactions between foxes and conspecific (foxes) or heterospecific carcasses (other than foxes), though our findings may be probably applied to many other carnivore species. We showed a high efficiency of foxes in detecting mesocarnivore carcasses (Chapters 2 and 3), but consumption events were uncommon (Chapter 2). The main novelty of our work in relation to previous studies is that consumption events were delayed from few days (heterospecific carcasses) to several weeks (conspecific carcasses). The time elapsed between carcass detection and consumption can be explained by the action of two contrasting forces: the nutritional value of phylogenetically close carrion (Meffe and Crump, 1987; Mayntz and Toft, 2006) and the risk of parasite infection (e.g., *Trichinella* spp.) by the consumption of this type of carcasses (Pfennig *et al.*, 1998; Pfennig, 2000; Rudolf and Antonovics, 2007; Huang *et al.*, 2014; Moleón *et al.*, 2017). Based on our findings, carrion consumption is carried out when the carcass is considered “safe” by the scavenger. This point is reached when the transmission risk of viable parasites by trophic route decreases, despite the loss of nutritional quality of carcass over time (Parmenter and MacMahon, 2009; Pozio, 2016). Thus, scavengers of mammalian carnivore carcasses must face a trade-off between the nutritional gains and the risk of acquiring meat-borne parasites. These scavenger decisions may be shaped by additional factors, such as seasonality in alternative food resources and individual variation in body condition (Mukherjee and Heithaus, 2013).

As described for carcass consumption, the higher proportion of contact events with carnivore carcasses (Chapter 3) took place by scavenging species after several weeks from carcass placement, especially in conspecific carrion, being contact events less frequent and later than in heterospecific ones. These results suggest that carnivores avoid the contact with carnivore carrion to reduce the risk of acquiring non-tropically transmitted pathogens. Concerning rubbing events, although a similar propensity in heterospecific and conspecific carrion was described, this behavior was more frequent in heterospecific carcasses, which supports the hypothesis that the risk of infection is greater in phylogenetically close species (Huang *et al.*, 2014). Moreover, contact rubbing events were more frequent than contact marking events, which indicate the key role of rubbing in the risk of acquiring ectoparasites, such as *S. scabiei*. Other endoparasite infective stages, such as *Toxocara canis* eggs (Roddie *et al.*, 2008), could be in the hair of the carcass and infect new hosts trough contact, rubbing or sniffing. In contrast, marking events were more common in fox carrion, probably because they are used as intra- and interspecific information points due to their long persistence in the environment. The marking events observed suggest that urine and feces on carcasses can be a reservoir of some pathogens, such as canine parvovirus (Miranda *et al.*, 2017), *Leptospira* spp. (Millán *et al.*, 2019) or ascarids (Okulewicz *et al.*, 2012). The part of carcass where visiting foxes contacted was different according to the carrion type, (i.e., conspecific or heterospecific), which could have some influence on the transmission risk of certain pathogens. However, further studies are needed to determine species-specific differences in the risk of infection.

Our findings (Chapter 2 and 3) are consistent with the fact that the survival of trophically and non-trophically transmitted parasites (e.g., *Trichinella* spp. and *S. scabiei*) in decaying carcasses is mainly temperature-dependent (Smith *et al.*, 1999; Chen and Mullens, 2008; Riva *et al.*, 2012). In this sense, the persistence of meat-borne and non-trophically transmitted parasites in carrion should be lower in spring and, therefore, also the risk of parasites transmission associated with their consumption or contact. In addition, individual factors (hungry, young, senescent and sick animals) can predispose animals to eat poor quality food and to assume the risk of consuming or contacting unsafe carrion (Mukherjee and Heithaus, 2013) (Chapter 2 and 3). Although foxes seem to avoid the period of greatest risk of acquiring ectoparasites (i.e., first weeks) (Chapter 3), other pathogens such as some viruses and helminth infective forms can survive for a long time in the vicinity of carrion (Shen and Gorham, 1980; Gordon and Angrick, 1986). In this case, the fox's strategy of delaying contact with the carcass would not be effective. Regarding herbivores, they usually avoid carrion because it poses a risk of predation, so pathogens that are at carcass sites represent a low risk of infection for them in the short-term. However, in the medium- and long-term, the risk increases when vegetation grows around the carcass and herbivores feed on it, since it can be a transmission route for pathogens that survive for months or years in the environment (e.g., *Bacillus anthracis* spores) (Turner *et al.*, 2014).

Differences in the ratio of consumption:non-consumption and contact:non-contact events (Chapters 2 and 3) between areas suggest that differences in populations, environmental conditions, levels of anthropization, local parasite communities and interspecific competition could be operating. The richer community of visiting species, as well as the highest number of total, consumption, contact, marking and rubbing events were observed in the area with the highest biodiversity (Cazorla). In this area, due to the presence of vultures, scavengers could be forced to assume a higher risk of infection, since the availability of carrion is lower than in vulture-lacking areas (Morales-Reyes *et al.*, 2017).

Overall, the results reported in this doctoral thesis represent a significant advancement in the knowledge of wildlife diseases. Our interdisciplinary research provides an essential ecological basis for studying the epidemiology of meat-borne and non-trophically transmitted parasites through interactions with mammalian carnivore carcasses, which are important nutritional resources in the ecosystems.

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CONCLUSIONS

FIRST: Scientific articles addressing meat-borne parasites at the wildlife-domestic-human interface mostly support their statements using previous bibliographic references or non-science-based assertions. Therefore, it is necessary to promote the design of studies based on methods that enable science-based results to be obtained and, consequently, plausible epidemiological conclusions and interpretations to be reached.

SECOND: Most articles and reviews on meat-borne pathogens at the wildlife-domestic-human interface are conducted by veterinarians. This unidisciplinary character of the research teams leads to the imprecise or incorrect use of scientific terms and concepts concerning trophic interactions of carnivore species. Therefore, it would be advisable to approach this type of studies from an interdisciplinary perspective, which would favor the appropriate use of the specialized scientific language, a solid interpretation of the ecological and epidemiological results and, consequently, an unequivocal communication between disciplines.

THIRD: Intraguild and especially intraspecific carrion consumption is an uncommon behavior in foxes and other mesocarnivores. Moreover, when it occurs, consumption is mainly delayed several weeks from the carrion placement. This trophic behavior of mesocarnivore scavengers is possibly a consequence of balancing the decision to feed on carrion with high nutritional value against assuming the lowest possible risk of acquiring an infection by meat-borne pathogens.

FOURTH: The low number of cannibalism events in mesocarnivores contrasts with the widespread statement in the scientific community that intraspecific consumption is an important way for parasite transmission in the wild, notably in epidemiological studies conducted on *Trichinella* spp. This highlights the need to undertake empirical fieldwork in order to understand the ecological trophic interactions that occur between wild hosts and, consequently, that favor the maintenance and transmission of pathogens through carrion consumption.

FIFTH: Behavioral pattern of visiting species on mesocarnivore carcasses may also be conditioned by, among other factors, the risk of acquiring non-trophically transmitted pathogens. This elusive behavior during the first weeks after the detection of the carrion is consistent with an attitude intended to reduce the risk of acquiring parasites with low survival outside a live host (e.g., lice and *Sarcoptes scabiei*). However, it does not seem to be an efficient strategy to avoid the transmission of pathogens whose infective stages can remain viable for a long time on the carcass or its vicinities.

SIXTH: The frequent marking behavior of visiting foxes on carnivore carrion, especially when they are of conspecifics, suggests that these carcass sites could concentrate infective stages of several viruses, bacteria and endoparasites excreted mainly by urine and feces. Thus, these places could become hotspots with a higher epidemiological risk of pathogen transmission among foxes.

CONCLUSIONES

PRIMERA: Los artículos científicos que abordan la transmisión de parásitos por consumo de carne en la interfaz silvestre-doméstico-humano sostienen de forma mayoritaria sus afirmaciones con citas bibliográficas previas o con asunciones no corroboradas científicamente. Por ello, es necesario promover el diseño de estudios basados en métodos que permitan obtener resultados con rigor científico y, en consecuencia, poder llegar a conclusiones e interpretaciones epidemiológicas plausibles.

SEGUNDA: La mayoría de los artículos y revisiones sobre la transmisión trófica de patógenos en la interfaz silvestre-doméstico-humano están realizados por veterinarios. Este carácter unidisciplinar de los equipos de investigación propicia el uso impreciso o incorrecto de los términos y conceptos científicos referentes a interacciones tróficas de especies carnívoras. Por ello, sería recomendable que el abordaje de este tipo de estudios se realizase desde una perspectiva interdisciplinar, lo que favorecería el uso apropiado del lenguaje científico especializado, una sólida interpretación de los resultados ecológicos y epidemiológicos y, en consecuencia, una comunicación inequívoca entre disciplinas.

TERCERA: El consumo intragremial y, particularmente, intraespecífico de carroña es un comportamiento infrecuente en zorros y otros mesocarnívoros. Además, cuando se produce, el consumo ocurre principalmente después del trascurso de varias semanas desde que la carroña está disponible. Este comportamiento trófico de los mesocarnívoros carroñeros es posiblemente consecuencia de sopesar entre la decisión de ingerir carroña con un alto valor nutritivo y la de asumir el menor riesgo posible de adquirir una infección por patógenos transmitidos por la carne.

CUARTA: El reducido número de eventos de canibalismo detectado en mesocarnívoros contrasta con la afirmación ampliamente difundida en la comunidad científica de que es una importante forma de transmisión de parásitos en la naturaleza, sobre todo en los estudios epidemiológicos realizados sobre *Trichinella* spp. Este hecho pone de manifiesto la necesidad de realizar estudios empíricos de campo que permitan conocer las interacciones ecológicas tróficas que ocurren entre hospedadores silvestres y, por consiguiente, que favorecen el mantenimiento y transmisión de patógenos por consumo de carne.

QUINTA: El patrón de comportamiento de las especies visitantes de cadáveres de mesocarnívoros también parece estar condicionado, entre otros factores, por el riesgo de adquirir patógenos transmitidos por vía no trófica. Este comportamiento elusivo durante las primeras semanas desde la detección de la carroña concuerda con una actitud tendente a reducir el riesgo de adquirir parásitos con escasa supervivencia fuera de un hospedador vivo (por ejemplo, piojos y *Sarcoptes scabiei*). No obstante, no parece ser una estrategia eficiente para evitar la transmisión de patógenos cuyas formas infectivas pueden permanecer viables durante mucho tiempo en la carroña o en sus inmediaciones.

SEXTA: El comportamiento frecuente de marcaje de los zorros visitantes en las carroñas de carnívoros, especialmente cuando son de congéneres, sugiere que estos lugares podrían concentrar formas infectivas de diversos virus, bacterias y endoparásitos excretados principalmente por orina y heces. Por lo tanto, estas zonas podrían convertirse en puntos calientes con un mayor riesgo epidemiológico de transmisión de patógenos entre zorros.

APPENDICES

Appendix 1: Laboratory and fieldwork

Figure 1. Red fox (left) and stone marten (right) before necropsy.

Figure 2. Camera trap placement in front of a fox carcass.

Figure 3. Detail of a camera trap placed in a study point (left) and during the setup process (right).

Appendix 2: Fox interaction with conspecific carrion

Figure 1. Fox detecting a conspecific carcass.

Figure 2. Intraspecific consumption of fox carcass.

Figure 3. Intraspecific contact at fox carcass site.

Figure 4. Intraspecific rubbing at fox carcass site.

Figure 5. Intraspecific marking at fox carcass site.

Appendix 3: Relevant visitors other than foxes at carcass site

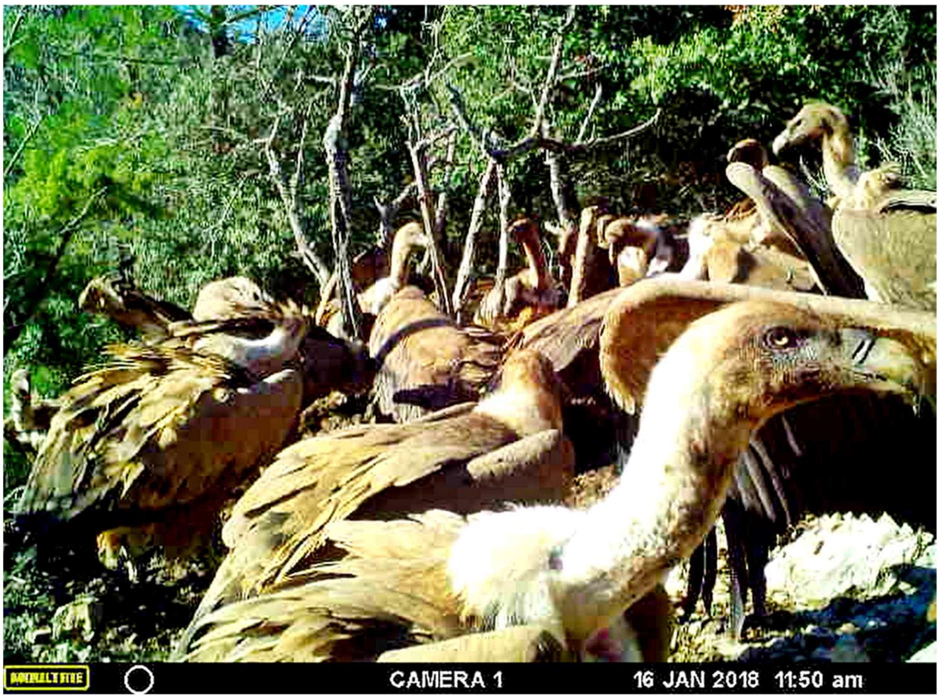

Figure 1. Griffon vultures scavenging a fox carcass.

Figure 2. Golden eagle scavenging a fox carcass.

Figure 3. Carrion crows at fox carcass site.

Figure 4. Eurasian jay at fox carcass site.

Figure 5. Wild boars contact with a fox carcass.

Figure 6. Stone marten at fox carcass site.

Figure 7. Common genet at fox carcass site.