Basic and Applied Ecology 83 (2025) 12–22

Contents lists available at ScienceDirect

Basic and Applied Ecology

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

RESEARCH PAPER

The extended role of carrion: Insect consumption and hair taking at fox carcasses

Daniel Redondo-Gómez [a,*], José M. Gil-Sánchez [a], Moisés Gonzálvez [b,c], Carlos Martínez-Carrasco [b], Esther Sebastián-González [d], Lidia Rosell [b], Pablo Jiménez-Nájar [b], José A. Sánchez-Zapata [e], Daniel Martín-Vega [f], Marcos Moleón [a]

[a] *Department of Zoology, University of Granada, Spain*
[b] *Department of Animal Health, University of Murcia, Spain*
[c] *Department of Animal Health, Animal Health and Zoonoses Research Group (GISAZ), University of Cordoba, Cordoba, Spain*
[d] *Department of Ecology, University of Alicante, Spain*
[e] *Department of Applied Biology, University Miguel Hernández, Spain*
[f] *Department of Life Sciences, University of Alcalá, Spain*

ARTICLE INFO

Keywords:
Carnivore carcasses
Larvae
Necrokleptotrichy
Nest building
Non-scavenging functions
Non-trophic functions

ABSTRACT

Scavenging has been profusely studied in the last decades. However, carrion is more than a direct source of food for scavengers and decomposers, as it may provide many non-scavenging ecological functions. These include the provision of carrion insects to insectivores and hair to nest-building species. However, the patterns of use of these resources are greatly unknown. In this context, carnivore carcasses may represent an outstanding study model because they usually persist in the environment for longer than herbivore carcasses. Here, we used video-trapping to explore the consumption of carrion insects and hair taking at 99 red fox (*Vulpes vulpes*) carcasses in three areas of southeastern Spain. Carcasses were frequently used for consuming insects and taking hair (7.3 events in total on average per carcass). These non-scavenging behaviors were observed over eight weeks for most carcasses, peaking around the fifth week. Birds were the main users of carcasses, distantly followed by mammals; reptiles were only recorded feeding occasionally on carrion insects. These behaviors were more frequent during spring, when the demand for insects for offspring feeding and hair for nest building is maximized by many vertebrates. Moreover, the community of species exhibiting each of these behaviors was highly organized, as evidenced from their nested structure. We observed co-occurrence of insect consumption and hair taking in a quarter of carcasses, with co-occurrence being mostly due to chance and certain individuals and groups that used some carcasses for both purposes. Overall, non-scavenging uses of fox carcasses by vertebrates in our study area is more frequent than scavenging, which highlights the broad ecological relevance of carnivore carcasses and opens exciting future research avenues.

Introduction

Carrion, i.e., dead animal tissue, is a nutrient-rich, ephemeral, and relatively unpredictable trophic resource that is readily exploited by a myriad of decomposers and invertebrate and vertebrate scavengers (DeVault et al., 2003; Wilson & Wolkovich, 2011; Barton et al., 2013). However, carrion is much more than a direct source of food for decomposers and scavengers. For instance, humans have obtained bones, skin, and other raw materials from carcasses since our origins to make tools and ornaments (Quaggiotto et al., 2022). Also, carrion is considered a key element in disease dynamics, as it may carry pathogens (Markandya et al., 2008; Turner et al., 2014) and favor their transmission among the animals gathering around carcasses (Ogada et al., 2012). Other less known ecological functions of carcasses include their role as fecal marking nuclei for mammalian carnivores (Barja & List, 2014; Gonzálvez et al., 2021a) and in shaping the landscape of fear for scavenging and non-scavenging animals (Moleón & Sánchez-Zapata, 2021; Redondo Gómez et al., 2023). All these non-scavenging functions – and others that may remain undiscovered – may be of great importance for the maintenance of biodiversity and represent a promising research

---

* Corresponding author.
E-mail address: drg@ugr.es (D. Redondo-Gómez).

https://doi.org/10.1016/j.baae.2024.12.008
Received 23 March 2024; Accepted 25 December 2024

avenue with wide ecological, evolutionary, behavioral, epidemiological, and anthropological implications.

In this study, we focus on two non-scavenging functions of carrion that have been largely overlooked in the scientific literature. First, carcasses may hold an abundant community of necrophagous and necrophilous insects (Barton et al., 2013), which represent a rich and highly nutritive food that may be exploited by insectivorous animals during the carcass decomposition process (Mason et al., 2023; Melville et al., 2023; Hashizume et al., 2024),). Many studies have investigated the succession of the carrion insect assemblage in carcasses of domestic animals for forensic purposes (Wang et al., 2008; Voss et al., 2011; Martín-Vega et al., 2019; Matuszewski et al., 2020; Matuszewski & Mądra-Bielewicz, 2024). However, further entomological studies on carcasses of wild species in natural conditions are needed (Braack, 1987; Watson & Carlton, 2005; Anderson, 2019; Von Hoermann et al., 2021; Hashizume et al., 2024), and very little is known about the role of carrion insects as a food resource (Moreno-Opo & Margalida, 2013; Mason et al., 2023; Schwegmann et al., 2023).

Second, in addition to direct and indirect (or secondary) trophic resources, carcasses provide non-trophic resources, such as hair and feathers. These materials are widely used for nest building by birds (Tóth, 2008; Ondrušová & Adamík, 2013) and mammals (Gil-Delgado et al., 2010). Adding hair and feathers to the nests can influence bird reproductive success through mechanisms that range from nest insulation (Perez et al., 2020) to the prevention of nestlings' diseases (Aubretch et al., 2013) and sexual selection processes (García-López de Hierro et al., 2013). Hair and feathers may come from live animals (the so-called *kleptotrichy* and *kleptoptily*, respectively, from Greek "klepto-"=to steal and "trich-"=hair or "ptero-"=feather; Whitney, 2007; Pollock et al., 2021) or from their carcasses (a phenomenon that could be termed *necrokleptotrichy* and *necrokleptoptily*, from Greek "necro-"=death). Necrokleptotrichy and necrokleptotily have already been observed in nature (Tóth, 2008; Moreno-Opo & Margalida, 2013; Moleón & Sánchez-Zapata, 2016; Harničárová & Adamík, 2016; Sarlin & Morris, 2022), but these behaviors are still poorly understood.

These non-scavenging roles of carrion require that the carcass persists over a sufficient period in the environment, to allow its detection by species potentially using it as well as the development of the carrion insect community (Muñoz-Lozano et al., 2019; Hashizume et al., 2023). Carcasses of herbivore vertebrates such as lagomorphs and ungulates may be completely eaten within hours, especially in the presence of highly efficient scavengers such as vultures and large carnivores (Sebastián-González et al., 2013; Mateo-Tomás et al., 2017). This largely prevents the establishment of abundant communities of carrion insects and could reduce the availability of fur and its detectability. In contrast, carcasses of carnivorous mammals are usually avoided by other scavenging mammals, which generally leads to a longer persistence of these carcasses in the environment than herbivore carcasses (Moleón et al., 2017; Gonzálvez et al., 2021a; Peers et al., 2021; Butler-Valverde et al., 2022; Hashizume et al., 2023). This could allow many species to use carnivore carcasses for non-scavenging purposes such as insect consumption and/or hair taking (Moleón et al., 2017). In southeastern Spain, the abundance of insects at carnivore carcasses in mid-winter to early spring sharply increases from the second week after carcass placement, and decreases mainly after 1–2 months, with fly larvae dominating the first stages of carcass decomposition and then being progressively replaced by beetles. After that, carcass remains, including fur, are still observable in and around the carcass site (Muñoz-Lozano et al., 2019). Thus, carnivore carrion is a particularly promising study model to explore non-scavenging functions of carcasses in ecosystems, as well as potential associations between different non-scavenging functions. These associations may appear when the same individual uses the carcass for different purposes, or simply by chance. Also, co-occurrence of different behaviors in a given carcass may be favored by facilitative processes among carcass users, as observed in scavenging assemblages (Moleón et al., 2014).

Here, we study two non-scavenging behaviors at red fox (V*ulpes vulpes*) carcasses: 1) consumption of carrion insects, which represents a non-scavenging or indirect trophic function, and 2) hair taking or necrokleptotrichy, as an example of a non-trophic function. After describing the patterns of insect consumption and hair taking and analyzing the factors influencing them, we explore the potential association between these two behaviors. We predict that (1) insect-consumption behavior will be more frequent during the peak phase of carrion insect larvae biomass availability; (2) hair-taking behavior will extend beyond the depletion of the insect resource; and (3) both behaviors will (a) be connected by insectivorous species that construct nests and by species that may signal carcass location to other species, and (b) be more frequent during the breeding season, i.e., when the demand for insects and hair is maximized by carrion-visiting species. Fully acknowledging these non-scavenging behaviors could notably extend our understanding of the ecological role of carrion.

Materials and methods

Study areas

The study was conducted in three areas of southeastern Mediterranean Spain: Sierras de Cazorla, Segura y Las Villas Natural Park (hereafter, Cazorla), Sierra Espuña Regional Park (hereafter, Espuña), and the surroundings of Murcia city (hereafter, Murcia). These areas represent three different scenarios according to orography, anthropization, weather conditions, and vertebrate communities. Cazorla (500–2107 m a.s.l.) is a vast protected mountain range with a relatively low degree of anthropization. The mean annual temperature is 12–16 °C and the mean annual precipitation is 300–950 mm. Espuña (200–1583 m a.s.l.) is a protected mountainous area with a medium level of anthropization. This area is slightly warmer (13–18 °C), and drier (300–500 mm) than Cazorla. The third area (100–315 m a.s.l.) is ca. 10 km from the city of Murcia, so the level of anthropization is high. The climate is the warmest and driest of the three study areas (17–23 °C, 200–450 mm). Wild vertebrate richness is highest in Cazorla, and the red fox is the most abundant wild mammalian carnivore in the three study areas (Gonzálvez et al., 2021a; b).

Monitoring of carcasses

Between 2017 and 2022, we monitored 99 red fox carcasses during winter and spring (November-April) through camera trapping in the three study areas (see Table 1). The carcasses, coming from recent roadkills or approved hunting, were necropsied and eviscerated for veterinary examination and immediately stored at −20 °C inside plastic bags. We analyzed the carcasses in the laboratory to exclude the presence of *Trichinella* spp., *Sarcoptes scabiei*, and the most common viral diseases affecting carnivores (canine distemper virus and canine parvovirus). Then, carcasses were defrosted for 12–24 h at laboratory temperature and placed in areas of natural vegetation (primarily oaks *Quercus ilex* and pines *Pinus nigra*) in both open and closed habitats (<50 % and >50 % tree cover within a radius of 10 m, respectively), with a minimum distance of 1.5 km between neighboring simultaneous carcasses. Some of the placement sites were reused in subsequent years.

Table 1
Number of red fox carcasses monitored per study area, habitat, and season (according to carcass deployment date).

	Season		Habitat		
Area	Non-breeding	Breeding	Open	Closed	Total
Cazorla	24	13	17	20	37
Espuña	22	10	11	21	32
Murcia	20	10	1	29	30
Total	**66**	**33**	**28**	**71**	**99**

Carcasses were attached to a rock or a tree trunk to avoid displacement from the camera focus. Cameras (Bushnell Trophy Cam and Bushnell Aggressor) were placed 3–4 m from the carcass and they were programmed to record one picture and one 15 s video every minute while detecting movement (Gonzálvez et al., 2021a; b). Carcass monitoring lasted until the carcasses were completely consumed/decomposed (i.e., only skin, bones, and other hard tissues remained), which was generally observed approximately after 50 days.

Definition of insect-consumption and hair-taking behaviors

We identified insect-consumption and hair-taking behaviors from the videos recorded by the cameras. First, we considered consumption of insects when the recorded images showed: 1) an animal unequivocally consuming an insect (at any life stage) directly from the carcass or within a 1.5-m radius around it, 2) an animal carrying insects in its beak, or 3) an animal taking something directly from the carcass or within a 1.5-m radius around it followed by swallowing (for birds) or chewing (for mammals), as long as the carcass itself was not consumed (Fig. 1). Meat consumption was identified because it usually implies a vigorous action that often includes jerks, as opposed to the more delicate capture of insects. Although this approach can wrongly include some consumption of food other than insects, the insectivorous habits of most consuming species and the presence of many insects around the monitored carcasses minimized this potential bias. Moreover, we did not assign insect-consumption behavior unless we had clear evidence. Second, we considered that the hair-taking behavior occurred when the recorded images showed: 1) an animal taking hair directly from the carcass or within a 1.5-m radius around it, or 2) an animal holding hair (compatible with the carcass) in its beak/mouth within a radius of 1.5 m around the carcass (Fig. 1).

General treatment of data

First, we grouped the recorded files into independent events, namely groups of videos or photos separated by <30 min that show the same individual or group performing a certain behavior (O'Brien et al., 2003; Ridout & Linkie, 2009; Gonzálvez et al., 2021a; b). Individuals of the same species appearing in videos separated <30 min were considered as the same individual to avoid overestimation of events unless individual identification was possible. To ensure independence between events, monospecific groups of individuals consuming insects or taking hair were considered as a single event.

Second, we defined our response variables. For each carcass and behavior (insect consumption and hair taking), we calculated the *number of events* (sum of all recorded events), *species richness* (number of different species observed displaying the behavior), and *time of first use* (days elapsed between carcass deployment and the first recorded behavior). We also calculated the *weekly number of events*, i.e., the number of events per week, and the *weekly co-occurrence* of behaviors, as a binomial variable indicating whether the two behaviors occurred in the same carcass within a given week. In addition, we explored co-occurrence of insect consumption and hair taking at a shorter temporal scale. In particular, for each carcass with co-occurrence of these two behaviors, we determined the number of times that a hair-taking event was immediately preceded by an insect-consumption event (and vice versa), as well as the time ($\leq$1 h vs. >1h) elapsed between these consecutive events of different behaviors.

Third, using the carcass as sample unit ($n = 99$), we fitted Generalized Linear Models (GLMs) to explain the changes in the *number of*

Fig. 1. Frames of videos showing insect-consumption and hair-taking (i.e., *necrokleptotrichy*) behaviors performed by several species (**a**: wild boar *Sus scrofa*; **b**: European robin *Erithacus rubecula*; **c**: ocellated lizard *Timon lepidus*; **d**: garden dormouse *Eliomys quercinus*; **e**: red-billed chough *Pyrrhocorax pyrrhocorax*; **f**: great tit *Parus major*; **g**: red-billed chough) in fox carcasses, detected through camera trapping. Mammals, birds, and reptiles are represented by orange, blue, and green, respectively.

events, species richness, and *time of first use* of each behavior (response variables) according to these explanatory variables: *area* (Cazorla, Espuña, or Murcia), *season* (according to the carcass deployment date: November-February or March-April; non-breeding and breeding season, respectively, for most local birds and micromammals; Moreno, 1988; Catalan & Haeger, 1996; Roldán et al., 2013), and *habitat* (open or closed). *Number of events* and *species richness* were modeled using Poisson error distribution and log link function, while we used Gaussian error distribution and identity link function for *time of first use*. For each response variable, we fitted the complete set of uni- and multi-variate models with $\geq$10 observations per parameter (Hardy & Bryman, 2004), including a null model without explanatory variables. We selected the most parsimonious model based on Akaike's Information Criterion for small sample sizes (AICc; using the function *AICc* of the package AICcmodavg; Mazerolle, 2019). The model with the lowest AICc and all other models within delta-AICc<2 were considered equally supported (Burnham & Anderson, 2002). For these selected models, we calculated the proportion of explained deviance according to this formula: D^2 = (null deviance-residual deviance)/null deviance*100 (Burnham & Anderson, 2002).

Fourth, to study temporal trends in insect-consumption and hair-taking behaviors, we fitted Generalized Linear Mixed Models (GLMMs) with carcass as random factor. We assessed the effect of *area, season, habitat*, and *week* (number of week since carcass deployment; both normal and quadratic functions) in the *weekly number of events*, separately for insect consumption and hair taking, and the *weekly co-occurrence* (response variables). For model construction and selection, we used a multi-model inference approach like the one described above for GLMs. Models were built using the optimal random structure, previously determined by comparing the model with all fixed terms and different combinations of the random structure (i.e., with and without the random term; Martin-Díaz et al., 2018). We used Poisson error distribution and log link function for *weekly number of events*, and binomial error distribution and logit link function for *weekly co-occurrence*. To calculate the variance explained by fixed factors, we computed the marginal coefficient of determination for generalized mixed-effect models (R^2; Nakagawa & Schielzeth, 2013; Johnson, 2014; using the function *r.squaredGLMM* from the package MuMIn in R; Barton, 2023).

Network analyses

To further investigate the potential association between insect-consumption and hair-taking behaviors, we ran network analyses. For this purpose, we created an interaction network where each row *i* represented a carcass and each column *j* was a species. Each matrix cell *aij* was filled with the number of times that each species was detected in each carcass. We created one matrix for insect consumption and another for hair taking. Then, we used these two matrices to build a tripartite network that shows the interactions among carcasses, species that used them, and types of behavior, using the *plotweb2* function from the *bipartite* package in R (Dormann et al., 2009).

In addition, we created another matrix including both insect-consumption and hair-taking behaviors. Thus, species performing both behaviors appeared twice in the dataset. Then, we evaluated how different species and behaviors co-occurred in the same carcasses by using cluster analysis. We calculated the clustering coefficient in R with the *igraph* package (Dormann, 2011). To identify if the clustering coefficient was larger than expected by random, we created 100 random matrices where the proportion of interactions per column and row was kept constant. Finally, we estimated whether the observed clustering coefficient fell within 95 % of the clustering values found for the random matrices.

Finally, we analyzed the nestedness of the community, separately for each behavior, using the *nested* function from the bipartite package in R (Dormann et al., 2009). In our case, the community would be nested if the species consuming insects (or taking hair) at carcasses visited by few insect-consuming (or hair-taking) species are subsets of those species consuming insects or (taking hair) at carcasses visited by more insect-consuming (or hair-taking) species. We measured the nestedness of the network by using the NODF metric (nestedness metric based on overlap and decreasing fill; Almeida-Neto et al., 2008). Perfectly nested matrices show an NODF value of 100, but random matrices show intermediate NODF values. Thus, to identify if the matrix was more nested than expected by random, we compared the NODF metric with that obtained by randomizing the value using a null model that controlled for the effects of species richness and sample size and maintains the heterogeneity in the number of interactions across species and carcasses (Sebastián-González et al., 2015). To identify the most important species in maintaining the network structure, we calculated the contribution to nestedness (N) of each species (Saavedra et al., 2011; Silva et al., 2023) using the *nestedncontribution* function from the bipartite package in R (Dormann et al., 2009). The N metric aims to assess how each individual species affects the community nestedness compared to a random species. To do so, the *nestedcontribution* function randomizes the interactions of the focal species, recalculates nestedness and then compares the observed and randomized values. Species enhancing overall nestedness will have positive values, while those with a negative contribution will have negative values. All analyses were conducted in R 4.0.5 (R Core Team, 2020).

Results

Insect consumption

In total, we recorded 355 insect-consumption events, performed by 19 different species (16 birds, two mammals, and one reptile species; see Appendix A: Table 1) at 51 different carcasses (51.5 % of the 99 monitored red fox carcasses; 45.9–59.4 % of total carcasses per area; Table 2). Corvids (carrion crow *Corvus corone*, red-billed chough *Pyrrhocorax pyrrhocorax*, Eurasian jay *Garrulus glandarius,* and Eurasian magpie *Pica pica*) performed 26.8 % of the recorded insect-consumption events. The European robin (*Erithacus rubecula*) and Eurasian stone-curlew (*Burhinus oedicnemus*) were also frequently recorded consuming insects (19.2 % and 14.6 % of events, respectively). Two mammals (wild boar *Sus scrofa* and garden dormouse *Eliomys quercinus*) and one reptile species (ocellated lizard *Timon lepidus*) were also detected consuming insects at carcass sites.

The number of events was explained by area, habitat and season (Tables 3, see Appendix A: Tables 2 and 5), being higher in Murcia, in open habitats, and during the breeding season (Table 2, see Appendix A: Table 5). However, the selected model showed a very low explanatory capacity (D^2<7 %; Table 3, see Appendix A: Table 5). There were no better models than the null model to explain changes in species richness and the time of first use (Table 3). In relation to the temporal trends, the weekly number of events was particularly dependent on the time after carcass deployment, as revealed by the GLMs (though the explained deviance was low; Table 3, see Appendix A: Table 5), increasing progressively until the sixth week and sharply decreasing afterwards (Fig. 2). The richness of the species consuming insects and the percentage of carcasses in which this behavior was observed followed a similar pattern, though less skewed (Fig. 2).

The community performing insect-consumption behavior showed a nested structure (Z=6.65; p<0.001). The species with higher contribution to nestedness were the black redstart (*Phoenicurus ochruros*), the Eurasian stone-curlew, and the ocellated lizard (N=1, N=0.99, and N=0.98, respectively)

Hair taking

In total, we recorded 358 hair-taking events, performed by 12 different species (11 birds and one mammal) at 42 different carcasses (42.4 % of the 99 carcasses monitored; 37.5–48.6 % of total carcasses

Table 2

Mean ± standard deviation (n: number of carcasses used to calculate the variable) of 1) the "number of events" per carcass, 2) the number of different species performing the behavior per carcass ("species richness"), and 3) the time of the first recorded event per carcass ("time of first use", in hours). Data are shown separately by behavior (insect consumption or hair taking), season, and area.

			Season		
Behavior	Variable	Area	Non-breeding	Breeding	**Total**
Insect consumption	Number of events	Cazorla	0.88 ± 2.09 (24)	12.46 ± 25.37 (13)	4.95 ± 15.77 (37)
		Espuña	1.14 ± 2.03 (22)	2.60 ± 4.27 (10)	1.59 ± 2.93 (32)
		Murcia	1.40 ± 5.58 (20)	9.90 ± 9.10 (10)	4.23 ± 7.92 (30)
		Total	**1.12 ± 3.47 (66)**	**8.70 ± 16.96 (33)**	**3.65 ± 10.71 (99)**
	Species richness	Cazorla	0.38 ± 0.58 (24)	1.08 ± 1.04 (13)	0.62 ± 0.83 (37)
		Espuña	0.45 ± 0.74 (22)	0.80 ± 1.03 (10)	0.56 ± 0.84 (32)
		Murcia	0.15 ± 0.37 (20)	1.70 ± 1.16 (10)	0.67 ± 1.03 (30)
		Total	**0.33 ± 0.59 (66)**	**1.18 ± 1.10 (33)**	**0.62 ± 0.89 (99)**
	Time of first use	Cazorla	31.67 ± 15.68 (8)	16.20 ± 13.91 (10)	22.00 ± 16.06 (18)
		Espuña	36.43 ± 22.15 (7)	22.75 ± 16.7 (5)	31.45 ± 20.63 (12)
		Murcia	37.00 ± 10.00 (3)	20.78 ± 10.44 (9)	24.83 ± 12.30 (12)
		Total	**34.75 ± 17.25 (18)**	**19.13 ± 12.81 (24)**	**25.54 ± 16.53 (42)**
Hair taking	Number of events	Cazorla	2.46 ± 4.33 (24)	3.46 ± 6.63 (13)	2.81 ± 5.18 (37)
		Espuña	4.68 ± 7.92 (22)	1.10 ± 1.73 (10)	3.56 ± 6.80 (32)
		Murcia	1.35 ± 2.94 (20)	11.60 ± 15.18 (10)	4.77 ± 10.07 (30)
		Total	**2.86 ± 5.6 (66)**	**5.21 ± 10.07 (33)**	**3.65 ± 7.42 (99)**
	Species richness	Cazorla	0.71 ± 0.91 (24)	0.62 ± 0.77 (13)	0.68 ± 0.85 (37)
		Espuña	0.95 ± 0.90 (22)	0.40 ± 0.52 (10)	0.78 ± 0.83 (32)
		Murcia	0.40 ± 0.68 (20)	1.70 ± 0.48 (10)	0.83 ± 0.87 (30)
		Total	**0.70 ± 0.86 (66)**	**0.88 ± 0.82 (33)**	**0.76 ± 0.85 (99)**
	Time of first use	Cazorla	15.75 ± 14.05 (11)	12.33 ± 7.06 (6)	14.29 ± 11.34 (17)
		Espuña	15.60 ± 11.08 (15)	14.67 ± 5.77 (4)	15.44 ± 10.26 (19)
		Murcia	15.80 ± 2.17 (6)	18.56 ± 12.81 (9)	17.57 ± 10.21 (15)
		Total	**15.68 ± 10.75 (32)**	**15.83 ± 10.21 (19)**	**15.74 ± 10.43 (51)**

Table 3

AICc-based selected models for insect-consumption and hair-taking behaviors to assess the effect of area (Cazorla, Espuña, and Murcia), season (breeding and non-breeding), and habitat (open, closed) on the number of events per carcass, the number of different species performing the behavior per carcass (species richness) and the time of first recorded behavior per carcass (in hours); and the effect of area (Cazorla, Espuña, and Murcia), season (breeding and non-breeding), habitat (open, closed), and time (weeks) on the number of weekly events, and the co-occurrence of hair-taking and insect consumption behaviors. The number of estimated parameters (k), AICc values, AICc differences (ΔAICc) with the highest-ranked model (i.e. the one with the lowest AICc), and the variability of the models explained by the predictors (deviance D^2 for GLMs and marginal R^2 for GLMMs) are shown. Only selected models are shown (see Appendix A: Tables 2, 3 and 4 for all models). N = 99 carcasses in all models.

Behavior	Response variable	Model	k	AICc	ΔAICc	D^2/R^2
Insect consumption	Number of events	area + season + habitat	4	1001.30	0	6.9
	Richness	1 (null model)	1	228.00	0	0.0
		season	1	229.15	1.15	0.9
		habitat	1	229.83	1.82	0.2
	Time of first use	1 (null model)	1	349.50	0	0.0
	Weekly number of events	week + week^2 + (1|carcass)	2	526.52	0	<0.4
		week + (1|carcass)	1	527.01	0.49	<0.1
		week + week^2 + habitat + (1|carcass)	3	528.18	1.66	<0.5
Hair taking	Number of events	area + season + habitat	4	902.45	0	35.3
	Richness	season	1	193.79	0	19.9
		season + habitat	2	195.74	1.95	20.1
	Time of first use	season	1	325.36	0	22.2
		season + habitat	2	325.54	0.18	26.7
	Weekly number of events	week + week^2 + (1|carcass)	2	519.84	0	0.2
		week + week^2 + season + (1|carcass)	3	521.38	1.54	0.2
Both	Weekly co-occurrence	week + week^2 + season + (1|carcass)	3	231.12	0	0.13
		week + week^2 + area + season + (1|carcass)	5	233.03	1.91	0.14
		week + week^2 + season + habitat + (1|carcass)	4	233.04	1.91	0.13

per area; Table 2). Tits (great tit *Parus major*, European crested tit *Lophophanes cristatus,* and coal tit *Periparus ater*) performed 57.5 % of the total recorded hair-taking events. The garden dormouse (*Eliomys quercinus*) and carrion crow (*Corvus corone*) were also frequently recorded taking hair (19.6 % and 9.8 % of events, respectively).

As revealed by the selected GLMs, which showed a moderate explanatory capacity (D^2 = *c.* 20–35 %), the number of events, the species richness, and the time of first use were mostly dependent on season (Table 3, see Appendix A: Tables 3 and 5). Importantly, differences due to season were always higher than differences among areas and habitat types (Table 2). The number of events and species richness were higher in the breeding season; accordingly, the time of first use was lower in the breeding season (Table 3, see Appendix A: Tables 3 and 5). In relation to the temporal trends, the weekly number of events was highly dependent on the time after carcass deployment, as revealed by the GLMs (Table 3, see Appendix A: Tables 3 and 5), substantially increasing from the second week and decreasing after the sixth week (Fig. 2). The richness of the species taking hair and the percentage of carcasses in which this behavior was observed followed a similar pattern, though less pronounced for richness. Interestingly, when correcting for the number of available carcasses, the percentage of carcasses used as a source of hair and, especially, the number of species performing this behavior, showed an increasing trend, with maximum values toward the final stages of carcass decomposition. Similarly, the

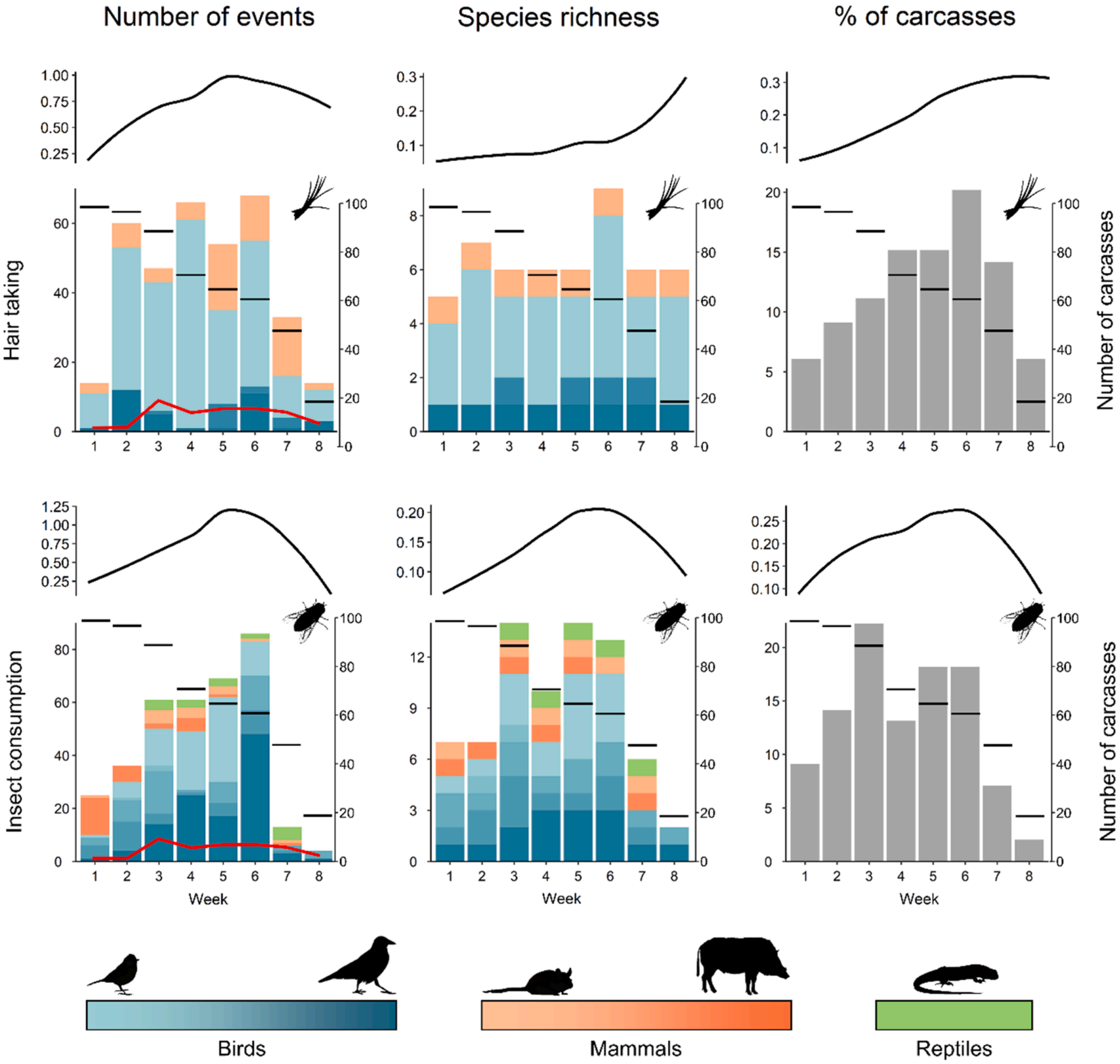

Fig. 2. Weekly development since carcass deployment of the number of events, the number of different species performing the behavior, and the percentage of carcasses showing insect-consumption (upper row) and hair-taking (lower row) behaviors. The right axis and the black horizontal lines represent the weekly development of the number of monitored carcasses. The curves above the graphs show the trend line of the ratio between the variables (number of events, species richness, or percentage of carcasses) and the number of monitored carcasses in that week. The red line inside the graphs for the number of events represents co-occurrence, i.e., the number of carcasses showing both insect-consumption and hair-taking behaviors each week. Mammals, birds, and reptiles are represented by orange, blue, and green, respectively, and the darkness of the color is proportional to the average weight of the species (darker color: higher weight). Note that temporal changes in the studied variables are not exclusively due to changes in the number of monitored carcasses. There was one hair-taking event in week 12 that is not represented in the graphs for better visualization.

number of hair-taking events at this final stage decreased less sharply than insect-consumption events (Fig. 2).

As for insect consumption, the community of species taking hair from carcasses also showed a nested structure ($Z = 2.07$; $p = 0.02$). The two species of corvids detected taking hair, the red-billed chough and the carrion crow, contributed the most to the nested structure of the network (N = 1, and N = 0.98, respectively).

Co-occurrence and interaction between behaviors

Overall, we detected both insect consumption and hair taking in 26.2 % of carcasses, and co-occurrence within a given week was recorded at 19.2 % of carcasses. As found for each behavior separately, the weekly co-occurrence of both behaviors followed a bell-shaped distribution, with a maximum 3–6 weeks after carcass deployment (Fig. 2), as shown by the GLMMs; moreover, co-occurrence was higher during the breeding season, in open habitats, and in Cazorla (R^2=0.13–0.14; Tables 3, see Appendix A: Tables 4 and 5). We detected only eight hair-taking events within 1 h after the last insect-consumption event (total number of consecutive events of different behaviors: 54), and six insect-consumption events within 1 h after the last hair-taking event (total number of consecutive events of different behaviors: 52). Nine (five insect-consumption events preceded by hair-taking events and four hair-taking events preceded by insect-consumption events) of these 14 co-occurrences of different behaviors within a 1h-interval corresponded to the same individual (one co-occurrence by garden dormouse) or group (eight co-occurrences by corvids) that performed the two behaviors in the same carcass. The other five co-occurrences within a 1h-interval (one insect-consumption event preceded by hair-taking event and four hair-taking events preceded by insect-consumption events) occurred between different species of birds.

The tripartite network (Fig. 3) revealed differences in the number of events of each behavior recorded in every carcass: some carcasses were used very intensely as a source of hair but not as an insect supply, and vice versa. In addition, the tripartite representation suggests different strategies adopted by the species exploiting the monitored carcasses. In particular, while some species concentrated most of their events on a few carcasses and used intensively these carcasses upon detection (this was the case of the insect consumption by the Eurasian stone-curlew), other species distributed their events across a greater number of carcasses and used them less frequently (this was the case of insect consumption by thrushes *Turdus* sp.; Fig. 3). Besides, other species, such as the great tit, appeared to use both strategies (Fig. 3).

The observed clustering coefficient (0.292) was significantly larger than the clustering coefficients calculated for the null matrices (mean coefficient of the null matrices = 0.052, SD = 0.056, p = 0.01). The clustering analysis identified six different modules, three of them being mono-specific and the other three including 5–13 species (Fig. 4). Within the multi-species groups, one of them only included species consuming insects, while the other two included the two behaviors.

Discussion

Around two decades after the scientific community started to recognize that the scavenging community is not randomly assembled (e.g. Selva & Fortuna, 2007), our findings strongly indicate that non-scavenging uses of carnivore carcasses may also be common and structured (i.e., nested) behaviors, rather than occasional and random. In our study, an important proportion of the monitored carcasses were used as a source of insects (52 %), hair (42 %), and both resources simultaneously (26 %), and we recorded an average of 7.3 non-scavenging carrion use events per carcass throughout the c. 50 days in which their decomposition process was monitored (Table 2; note that this does not include other non-scavenging uses of carrion, such as marking). These results indicate that the non-scavenging use by vertebrate species of red fox carcasses in our study area is more frequent than the consumption of meat (2.6 scavenging events per carcass on average for carcasses monitored in 2016–2018, $n = 56$; Gonzálvez et al., 2021a). Moreover, most of the species exhibiting these non-scavenger behaviors were non-scavengers, suggesting that carrion may serve important ecological functions for a broader range of species beyond the scavenger guild.

Insect consumption

The number of insect-consumption events and the richness of species performing this behavior roughly followed the pattern of temporal variation in insect abundance in fox carcasses previously described in southeastern Spain (Muñoz-Lozano et al., 2019). These authors observed a decrease in the number of blow fly larvae after the first month, whereas the number of Coleoptera larvae (mainly from the family Dermestidae) gradually increased (Muñoz-Lozano et al., 2019), as the later are specialized in the consumption of dry tissues that are commonly associated with carcasses in advanced stages of decomposition (Matuszewski et al., 2008; Magni et al., 2019). After the sixth week, we detected a sharp decrease in the number of insect-consumption events

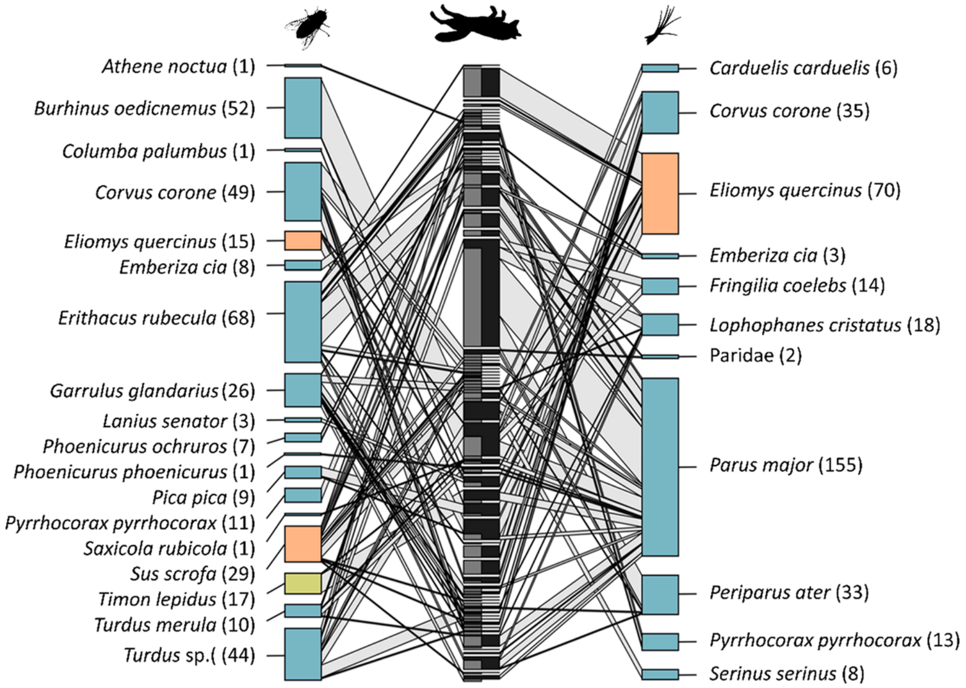

Fig. 3. Graphical representation of a tripartite network showing species performing insect-consumption (left column), hair-taking (right column) behavior and carcasses in which these behaviors have been performed (center column). Lines connect each species with the specific carcass where they were detected consuming invertebrates or taking hair. The number of events of each species for each behavior is indicated in brackets and the width of the boxes (only the black section in the central column) and lines is proportional to the number of interactions. Reptiles, mammals, and birds are represented by green, orange, and blue respectively.

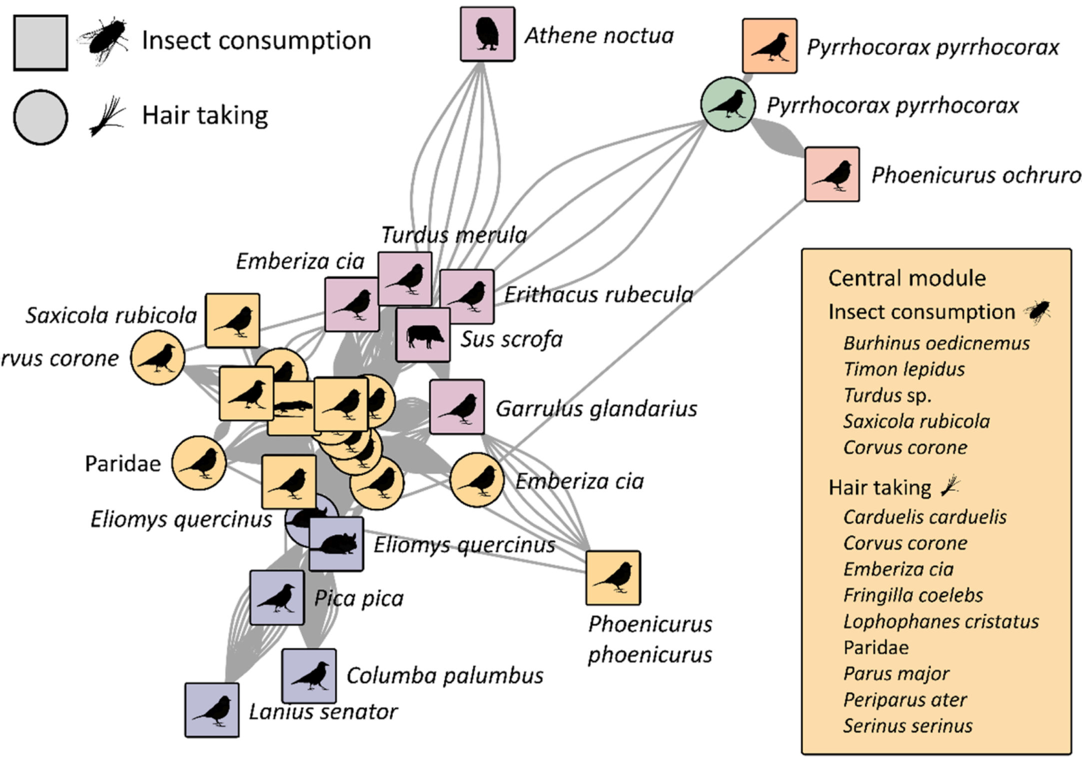

Fig. 4. Clustering structure of the co-occurrence patterns of species performing insect-consumption (represented by circles) and hair-taking behavior (represented by squares). Species co-occurring in the same carcass are connected by a line. Species are colored according to the cluster to which they belong.

and the richness of species performing this behavior (see Fig. 2). This pattern cannot be entirely explained by the decrease in available insect larvae, which are still abundant during these stages (especially beetle larvae; Muñoz-Lozano et al., 2019). The preference of birds for Diptera larvae against the heavily fuzzy and strongly sclerotized carrion beetle larvae could explain this decline, though this possibility needs to be tested.

These insect pulses might play an essential role in the trophic ecology of many species (Hashizume et al. 2024), similar to locust outbreaks (Goriup & Schulz, 1991; Sánchez-Zapata et al., 2007) or the bark beetle infestation spots (Przepióra et al., 2020), but at a more local spatial scale, i.e., within the home range of a few insectivorous animals. In our case, several recorded videos showed birds from the same species (e.g., *Turdus* spp.) repeatedly visiting carcasses in April and collecting and accumulating larvae in the beak, which could be indicative of the use of carcasses as an insect source to feed nestlings during the breeding season. The number of insect-consumption events does not seem to be greatly affected by the degree of human impact, as it was higher in the most anthropized area (Murcia), especially in open habitats.

Hair taking

The weekly evolution of the number of hair-taking or *necrokleptotrichy* events was similar to that described above for the insect-consumption behavior, although hair was exploited more than insects in the last stages of carcass decomposition, due to the longer persistence of hair compared to insects. Indeed, a longer monitoring time could have detected new species exploiting this resource (Fig. 2). The low number of events during the first week may be due to a) the progressive detection of the carcass by the animals in the area (Gonzálvez et al., 2021a) and/or b) the reluctance to approach a fresh carnivore carcass due to uncertainty about its death (Redondo-Gómez et al., 2023). In addition, visitors could find greater facility to pull out the hair a few days after the death of the animal (due to the autolytic process occurring in the dermis). However, our observations indicate that even small birds are able to take hair from fresh carcasses. Finally, *necrokleptotrichy* started earlier in carcasses in open habitats, probably because they were more easily located than carcasses in more vegetated habitats.

There was a large proportion of recorded hair-collection events by species that frequently incorporate hair into their nests, especially Paridae species (Ondrušová & Adamík, 2013; Harničárová & Adamík, 2016; Pollock et al., 2021), Corvidae (the carrion crow; Bolopo et al., 2015; and the red-billed chough; McKay, 1996), and the garden dormouse (Gil-Delgado et al., 2010; see Fig. 3). Although hair and other animal-derived materials seem to be rare in mammal nests (Deeming, 2023), such a behavior is mostly found in small species (i.e., <1 kg), which agrees with our dormouse findings, as well as the occasional observation by our team of red squirrels (*Sciurus vulgaris*) taking hair from fox carcasses in our study areas. Most events were observed during the breeding season of these avian and mammalian species (March--April; Moreno, 1988; Catalan & Haeger, 1996; Roldán et al., 2013; see Table 2), suggesting that the hair collected from fox carcasses might have been used for nest construction or decoration. The specific use of mammalian carnivore hair in nests may not be arbitrary, as some studies suggest that predator odors could act as an olfactory deterrent to other predators (Schuetz, 2005; Adamík & Král, 2008; Liu & Liang, 2021). Irrespective of the confirmation of this hypothesis by further research, given the risk of taking hair from live carnivores (Pollock et al., 2021), carrion must be a prominent and long-lasting source of hair.

Co-occurrence and interaction between behaviors

We found co-occurrence of insect consumption and *necrokleptotrichy* in one quarter of the monitored carcasses. As could be expected, both behaviors co-occurred more frequently 3–6 weeks after carcass deployment, during the breeding season, in Murcia, and in open habitats, i.e., when and where the number of events of each behavior was higher (Fig. 2). Weekly co-occurrences could be the result of 1) the same individual or group using the carcass for both insect consumption and hair taking, 2) some facilitation process between visiting species (e.g.

signaling carcass location; see Moleón et al., 2014 for carcass signaling among scavengers), or 3) chance. According to our findings at the shorter temporal scale, co-occurrences are more likely to result mostly by chance, though also from insectivorous species that use hair in their nests, performing both behaviors once they have detected the carcass.

The results of the cluster analysis also suggest that insect-consumption and hair-taking events are somehow related, since they are frequently performed in the same group of carcasses by the same species (core set in Fig. 4). However, the existence of a module exclusively containing insect-consumption events (Fig. 4), as well as the differences found between the number of insect-consumption and hair-taking events in some carcasses (Fig. 3), shows that these behaviors can also occur independently. The grouping of some species consuming insects in the same set of carcasses may reflect large insect concentrations in those carcasses, although this could not be confirmed because it is not always possible to see the insect larvae availability at the carcasses from the camera trap images. Moreover, the clustering of insect-consumption and hair-taking events performed by the same species in different modules (e.g., the black redstart; Fig. 4) suggests that many species that detect carcasses use them exclusively either as a source of hair or to feed on insects.

Conclusion and further directions

Analyzing in more detail the wide variety of unexplored and unknown roles that carrion plays in ecosystems can improve our understanding of ecosystems and lead to great advances in carrion ecology and other related disciplines. Our findings support the importance of carnivore carrion, which has traditionally been neglected in carrion ecology research (Moleón et al., 2017), as a source of both insects and hair, with potential implications for the trophic and reproductive ecology of many vertebrate species. Moreover, these two behaviors seem to be mostly independent of each other. The growing number of papers on non-scavenging uses of wild carcasses highlight the ecological relevance of these unexplored facets of carrion (Tóth, 2008; Moleón & Sánchez-Zapata, 2016; Harničárová & Adamík, 2016; Sarlin & Morris, 2022). Our results provide additional support against regulations prohibiting the leaving of wildlife carcasses in the field (e.g., Margalida & Moleón, 2016), as many species, including endangered ones (e.g., the red-billed chough in our case), could benefit from the supply of resources such as insects and hair. Further research on other carcass species – both carnivorous and herbivorous –, seasons, and systems is needed to understand the ultimate ecological, evolutionary, and practical consequences of these non-scavenging uses of carcasses. More broadly, a more comprehensive view of the multiple non-scavenging functions of carrion would represent a significant step forward in carrion ecology.

CRediT authorship contribution statement

Daniel Redondo-Gómez: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **José M. Gil-Sánchez:** Writing – review & editing, Visualization, Supervision, Investigation, Formal analysis, Data curation, Conceptualization. **Moisés Gonzálvez:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carlos Martínez-Carrasco:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Esther Sebastián-González:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lidia Rosell:** Methodology, Investigation, Conceptualization. **Pablo Jiménez-Nájar:** Methodology, Investigation, Conceptualization. **José A. Sánchez-Zapata:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Daniel Martín-Vega:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Formal analysis. **Marcos Moleón:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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

Acknowledgments

This study was funded by the Spanish Ministry of Economy, Industry and Competitiveness and EU ERDF funds through project CGL2017–89905-R, and by the Spanish Ministry of Science and Innovation and EU ERDF funds through project PID2021–128952NB-I00. DRG was funded by a predoctoral grant from the Junta de Andalucía (PREDOC_00262). ESG and MM received the Ramón y Cajal grants RYC-2019–027216-I & RYC-2015–19231, respectively, funded by MCIN/ AEI/ 10.13039/501100011033 and by ESF Investing in your future. MG was supported by a postdoctoral contract Margarita Salas (University of Murcia) from the Program of Requalification of the Spanish University System (Spanish Ministry of Universities) financed by the European Union-NextGenerationEU.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.12.008.

References

Adamík, P., & Král, M. (2008). Nest losses of cavity nesting birds caused by dormice (Gliridae, Rodentia). *Acta Theriologica, 53*(2), 185–192.

, J.r. Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement *Oikos, 117*, 1227–1239 (Copenhagen, Denmark)

Anderson, G. S. (2019). Factors that influence insect succession on carrion. *Forensic entomology* (pp. 103–139). CRC press.

Aubrecht, G., Huber, W., & Weissenhofer, A. (2013). Coincidence or benefit? The use of Marasmius (horse-hair fungus) filaments in bird nests. *Avian Biology Research, 6*(1), 26–30.

Barja, I., & List, R. (2014). The role of spatial distribution of faeces in coyote scent marking behavior. *Polish Journal of Ecology, 62*(2), 373–384.

Barton, P. S., Cunningham, S. A., Lindenmayer, D. B., & Manning, A. D. (2013). The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia, 171*(4), 761–772.

Barton K. (2023). MuMIn: Multi-model inference_. R package version 1.47.5, <https://CRAN.R-project.org/package=MuMIn>.

Bolopo, D., Canestrari, D., Marcos, J. M., & Baglione, V. (2015). Nest sanitation in cooperatively breeding carrion crows. *The Auk: Ornithological Advances, 132*(3), 604–612.

Braack, L. E. O. (1987). Community dynamics of carrion-attendant arthropods in tropical African woodland. *Oecologia, 72*(3), 402–409.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference. a practical information-theoretic approach.* New York: Springer.

Jr Butler-Valverde, M. J., DeVault, T. L., Rhodes, O. E., & Beasley, J. C (2022). Carcass appearance does not influence scavenger avoidance of carnivore carrion. *Scientific Reports, 12*(1), 18842.

Catalan, R. M., & Haeger, J. F. (1996). Breeding patterns of the great tit (Parus major) in a pine plantation and a holm oak forest in a Mediterranean region (southern Spain). *Revue d'Ecologie, Terre et Vie, 51*(4), 341–357.

Deeming, D. C. (2023). Nest construction in mammals: A review of the patterns of construction and functional roles. *Philosophical Transactions of the Royal Society B, 378*(1884), Article 20220138.

Jr DeVault, T. L., Rhodes, O. E., & Shivik, J. A (2003). Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos, 102*(2), 225–234 (Copenhagen, Denmark).

Dormann, C. F., Frueund, J., Bluethgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal, 2*, 7–24.

Dormann, C. F. (2011). How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology, 1*(1), 1–20.

García-López de Hierro, L., Moleón, M., & Ryan, P. G. (2013). Is carrying feathers a sexually selected trait in house sparrows? *Ethology: formerly Zeitschrift fur Tierpsychologie, 119*(3), 199–211.

Gil-Delgado, J. A., Mira, O., Viñals, A., Gómez, J., Banyuls, N., & Vives-Ferrándiz, C. (2010). Diet of the garden dormouse (*Eliomys quercinus* Linnaeus 1766) in orange groves: Seasonal variation and use of available resources. *Mammalia, 74*(2), 147–151.

Gonzálvez, M., Martínez-Carrasco, C., Sánchez-Zapata, J. A., & Moleón, M. (2021a). Smart carnivores think twice: Red fox delays scavenging on conspecific carcasses to reduce parasite risk. *Applied Animal Behavior Science, 243*, Article 105462.

Gonzálvez, M., Martínez-Carrasco, C., & Moleón, M. (2021b). Understanding potential implications for non-trophic parasite transmission based on vertebrate behavior at mesocarnivore carcass sites. *Veterinary Research Communications, 45*(4), 261–275.

Goriup P.D. & Schulz H. (1991). Conservation Management of the White Stork. in Salathe T. Eds. Conserving migratory birds. Cambridge: P. 112.

Hardy, M., & Bryman, A. (2004). *Handbook of data analysis*. London: SAGE Publications.

Harničárová, K., & Adamík, P. (2016). Mammal hair in nests of four cavity-nesting songbirds: Occurrence, diversity and seasonality. *Bird study : the journal of the British Trust for Ornithology, 63*(2), 181–186.

Hashizume, A., Koda, R., & Nakashima, Y. (2023). Intraguild scavenging on carnivore carcasses is delayed enough to allow successful dispersal of maggots for pupation. *Journal of Zoology, 321*(2), 156–164.

Hashizume, A., Koda, R., & Nakashima, Y. (2024). Infection risk associated with carnivore carcasses may govern trophic interactions between maggots and insectivorous passerine birds. *Biology Letters, 20*(6), Article 20240069.

Johnson, P. C. (2014). Extension of Nakagawa & Schielzeth`s R2GLMM to random slopes models. *Methods in Ecology and Evolution, 5*(9), 944–946.

Liu, J., & Liang, W. (2021). Snake slough in birds' nests acts as a nest predator deterrent. *Ethology Ecology & Evolution, 33*(6), 591–602.

Magni, P., Zwerver, M., & Dadour, I. R. (2019). Insect succession pattern on decomposing pig carcasses in Tasmania: A summer study. *Papers and Proceedings of the Royal Society of Tasmania, 153*, 31–38.

Margalida, A., & Moleón, M. (2016). Toward carrion-free ecosystems? *Frontiers in Ecology and the Environment, 14*, 183–184.

Markandya, A., Taylor, T., Longo, A., Murty, M. N., Murty, S., & Dhavala, K. (2008). Counting the cost of vulture decline—An appraisal of the human health and other benefits of vultures in India. *Ecological Economics, 67*(2), 194–204.

Martin-Díaz, P., Gil-Sánchez, J. M., Ballesteros-Duperón, E., Barea-Azcón, J. M., Virgós, E., Pardavila, X., et al. (2018). Integrating space and time in predator-prey studies: The case of wildcats and rabbits in SE Spain. *Mammalian Biology, 88*, 114–122.

Martín-Vega, D., Baz, A., Cifrián, B., Gómez-Gómez, A., & Díaz-Aranda, L. M. (2019). Long-term insect successional patterns on pig carcasses in central Spain. *International Journal of Legal Medicine, 133*, 1581–1592.

Mason, D. S., Jones, A. K., Barton, B. T., Proctor, M., Webb, S. L., & Lashley, M. A. (2023). *Coyotes Eat Flies at Carrion. Food Webs, 37*, e00309.

Mateo-Tomás, P., Olea, P. P., Moleón, M., Selva, N., & Sánchez-Zapata, J. A. (2017). Both rare and common species support ecosystem services in scavenger communities. *Global Ecology and Biogeography, 26*(12), 1459–1470.

Matuszewski, S., Bajerlein, D., Konwerski, S., & Szpila, K. (2008). An initial study of insect succession and carrion decomposition in various forest habitats of Central Europe. *Forensic Science International, 180*(2–3), 61–69.

Matuszewski, S., Hall, M. J., Moreau, G., Schoenly, K. G., Tarone, A. M., & Villet, M. H. (2020). Pigs vs people: The use of pigs as analogues for humans in forensic entomology and taphonomy research. *International Journal of Legal Medicine, 134*, 793–810.

Matuszewski, S., & Mądra-Bielewicz, A. (2024). Field validation of post-mortem interval estimation based on insect development. Part 1: Accuracy gains from the laboratory rearing of insect evidence. *Forensic Science International, 354*, Article 111902.

Mazerolle, M. J. (2019). *AICcmodavg: Model selection and multi- model inference based on (Q)AIC(c)*. R Package Version 2.2-4.

McKay, C. R. (1996). *Conservation and ecology of the red-billed chough pyrrhocorax pyrrhocorax*. University of Glasgow. Doctoral dissertation.

Melville, H., Gaines, M., Slater, K., & Strauss, W. M. (2023). Ecological gatekeeping: Black-backed jackals are left to crave carrion in absence of large facultative scavengers. *Food Webs, 37*, e00310.

Moleón, M., Sánchez-Zapata, J. A., Selva, N., Donázar, J. A., & Owen-Smith, N. (2014). Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews, 89*(4), 1042–1054.

Moleón, M., & Sánchez-Zapata, J. A. (2016). Non-trophic functions of carcasses: From death to the nest. *Frontiers in Ecology and the Environment, 14*, 340–341.

Moleón, M., Martínez-Carrasco, C., Muellerklein, O. C., Getz, W. M., Muñoz-Lozano, C., & Sánchez-Zapata, J. A. (2017). Carnivore carcasses are avoided by carnivores. *Journal of Animal Ecology, 86*(5), 1179–1191.

Moleón, M., & Sánchez-Zapata, J. A. (2021). The role of carrion in the landscapes of fear and disgust: A review and prospects. *Diversity, 13*(1), 28.

Moreno, S. (1988). Reproduction of garden dormouse *Eliomys quercinus lusitanicus*, in southwest Spain. *Mammalia, 52*(3), 401–408.

Moreno-Opo, R., & Margalida, A. (2013). Carcasses provide resources not exclusively to scavengers: Patterns of carrion exploitation by passerine birds. *Ecosphere, 4*(8), 1–15 (Washington, D.C).

Muñoz-Lozano, C., Martín-Vega, D., Martínez-Carrasco, C., Sánchez-Zapata, J. A., Morales-Reyes, Z., Gonzálvez, M., et al. (2019). Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. *PloS One, 14*(8), Article e0221890.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from Generalized Linear Mixed-effects Models. *Methods in Ecology and Evolution, 4*, 133–142.

O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal conservation forum* (pp. 131–139). Cambridge University Press (Vol. 6, No. 2.

Ogada, D. L., Torchin, M. E., Kinnaird, M. F., & Ezenwa, V. O (2012). Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology, 26*(3), 453–460.

Ondrušová, K., & Adamík, P. (2013). Characterizing the mammalian hair present in great tit (Parus Major) nests. *Bird study : the journal of the British Trust for Ornithology, 60* (3), 428–431.

Peers, M. J., Konkolics, S. M., Majchrzak, Y. N., Menzies, A. K., Studd, E. K., Boonstra, R., et al. (2021). Vertebrate scavenging dynamics differ between carnivore and herbivore carcasses in the northern boreal forest. *Ecosphere, 12*(8), e03691 (Washington, D.C).

Perez, D. M., Gardner, J. L., & Medina, I. (2020). Climate as an evolutionary driver of nest morphology in birds: A review. *Frontiers in Ecology and Evolution, 8*, 424.

Pollock, H. S., MacDonald, S. E., Vizentin-Bugoni, J., Brawn, J. D., Sutton, Z. S., & Hauber, M. E. (2021). What the pluck? The theft of mammal hair by birds is an overlooked but common behavior with fitness implications. *Ecology, 102*(12), e03501.

Przepióra, F., Loch, J., & Ciach, M. (2020). Bark beetle infestation spots as biodiversity hotspots: Canopy gaps resulting from insect outbreaks enhance the species richness, diversity and abundance of birds breeding in coniferous forests. *Forest Ecology and Management, 473*, Article 118280.

Quaggiotto, M. M., Sánchez-Zapata, J. A., Bailey, D. M., Payo-Payo, A., Navarro, J., Brownlow, A., et al. (2022). Past, present and future of the ecosystem services provided by cetacean carcasses. *Ecosystem Services, 54*, Article 101406.

R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Redondo-Gómez, D., Rossi, L., Cardello, M., De Pasquale, S., Martínez-Carrasco, C., Sánchez-Zapata, J. A., et al. (2023). Top-predator carrion is scary: Fight-and-flight responses of wild boars to wolf carcasses. *Ecology and Evolution, 13*(4), e9911.

Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics, 14*, 322–337.

Roldán, M., Gálvez, D. M., Rodríguez, J., & Soler, M. (2013). Breeding biology and fledgling survival in a Carrion Crow *Corvus corone* population of southern Spain: A comparison of group and pair breeder. *Acta Ornithologica, 48*(2), 221–235.

Saavedra, S., Stouffer, D. B., Uzzi, B., & Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature, 478*, 233–235. https://doi.org/10.1038/nature10433

Sánchez-Zapata, J. A., Donázar, J. A., Delgado, A., Forero, M. G., Ceballos, O., & Hiraldo, F. (2007). Desert locust outbreaks in the Sahel: Resource competition, predation and ecological effects of pest control. *Journal of Applied Ecology, 44*(2), 323–329.

Sarlin, P. J., & Morris, S. (2022). First report of kleptotrichy by Large-billed Crows (Corvus macrorhynchos culminatus) from a live mammal. *The Wilson Journal of Ornithology, 134*(4), 717–719.

Schuetz, J. G. (2005). Common waxbills use carnivore scat to reduce the risk of nest predation. *Behavioral Ecology, 16*(1), 133–137.

Schwegmann, S., Storch, I., & Bhardwaj, M. (2023). Use of viscera from hunted roe deer by vertebrate scavengers in summer in central European mountainous mixed forest. *Wildlife Biology, 2023*(5), e01117.

Sebastián-González, E., Sánchez-Zapata, J. A., Donázar, J. A., Selva, N., Cortés-Avizanda, A., Hiraldo, F., et al. (2013). Interactive effects of obligate scavengers and scavenger community richness on lagomorph carcass consumption patterns. *Ibis, 155* (4), 881–885.

Sebastián-González, E., Dalsgaard, B., Sandel, B., & Guimaraes, P. R. (2015). Macroecological trends in nestedness and modularity of seed-dispersal networks: Human impact matters. *Global Ecology and Biogeography, 24*, 293–303.

Selva, N., & Fortuna, M. A. (2007). The nested structure of a scavenger community. *Proceedings of the Royal Society B: Biological Sciences, 274*(1613), 1101–1108.

Silva, G. G., Pizo, M. A., Green, A. J., Sebastián-González, E., Bugoni, L., & Maltchik, L. (2023). A waterfowl seed-dispersal network from the Neotropical region is nested and modular. *Biotropica, 55*(2), 480–488.

Tóth, M. (2008). A new noninvasive method for detecting mammals from birds' nests. *Journal of Wildlife Management, 72*, 1237–1240.

Turner, W. C., Kausrud, K. L., Krishnappa, Y. S., Cromsigt, J. P. G. M., Ganz, H. H., Mapaure, I., et al. (2014). Fatal attraction: Vegetation responses to nutrient inputs attract herbivores to infectious anthrax carcass sites. *Proceedings of the Royal Society B: Biological Sciences, 281*(1795), Article 20141785.

Von Hoermann, C., Lackner, T., Sommer, D., Heurich, M., Benbow, E., & Müller, J. (2021). Carcasses at fixed locations host a higher diversity of necrophilous beetles. *Insects, 12*, 412.

Voss, S. C., Cook, D. F., & Dadour, I. R. (2011). Decomposition and insect succession of clothed and unclothed carcasses in Western Australia. *Forensic Science International, 211*(1–3), 67–75.

Wang, J., Li, Z., Chen, Y., Chen, Q., & Yin, X. (2008). The succession and development of insects on pig carcasses and their significances in estimating PMI in south China. *Forensic Science International, 179*(1), 11–18.

Watson, E. G., & Carlton, C. E. (2005). Insect succession and decomposition of wildlife carcasses during fall and winter in Louisiana. *Journal of Medical Entomology, 42*, 193–203.

Whitney, B. M. (2007). Kleptoptily": How the fork-tailed palm-swift feathers its nest. *The Auk, 124*(2), 712–715.

Wilson, E. E., & Wolkovich, E. M. (2011). Scavenging: How carnivores and carrion structure communities. *Trends in Ecology & Evolution, 26*(3), 129–135.