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Rewilding traditional grazing areas affects scavenger assemblages and carcass consumption patterns

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Abstract

The abandonment of traditional livestock farming systems in Mediterranean countries is triggering a large-scale habitat transformation, which, in general, consists of the replacement of open grazing areas by woodlands through non-managed regeneration. As a consequence, wild ungulates are occupying rapidly the empty niche left by domestic ungulates. Both types of ungulates represent the main trophic resource for large vertebrate scavengers. However, a comparison of how vertebrate scavengers consume ungulate carcasses in different habitats with different ungulate species composition is lacking. This knowledge is essential to forecast the possible consequences of the current farmland abandonment on scavenger species. Here, we compared the scavenging patterns of 24 wild and 24 domestic ungulate carcasses in a mountainous region of southern Spain monitored through camera trapping. Our results show that carcasses of domestic ungulates, which concentrate in large numbers in open pasturelands, were detected and consumed earlier than those of wild ungulate carcasses, which frequently occur in much lower densities at more heterogenous habitats such as shrublands and forest. Richness and abundance of scavengers were also higher at domestic ungulate carcasses in open habitats. Vultures, mainly griffons (*Gyps fulvus*), consumed most of the carcasses, although mammalian facultative scavengers, mainly wild boar (*Sus scrofa*) and red fox (*Vulpes vulpes*), also contributed importantly to the consumption of wild ungulate carcasses in areas with higher vegetation cover. Our findings evidence that the abandonment of traditional grazing may entail consequences for the scavenger community, which should be considered by ecologists and wildlife managers.

Keywords: Facultative scavengers; Farmlands abandonment; Livestock; Rewilding; Vultures; Wild ungulates

Introduction

Since the onset of farming around 12,000 years ago, human activities have modified species distribution and abundance

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as well as the structure and functioning of communities and ecosystems (Barnosky et al. 2012). The anthropic habitat transformation harmed some species (especially large mammals such as ungulates and large carnivores) to benefit livestock (Gaston & Blackburn 1995; Cardillo, Mace, & Jones 2005). In the Mediterranean Basin, traditional livestock shaped pasture landscapes and, along with direct persecution and hunting, has contributed to displace wild ungulates to difficult access areas (San Miguel-Ayanz, García-Calvo, & García-Olalla 2010; Giguet-Covex et al. 2014). However, in the last decades, traditional farming practices are being replaced by modern techniques in many parts of Europe. Understanding the ecological consequences of such a major change is a prominent challenge for wildlife conservation in these areas.

During the mid-20th century, agricultural and livestock communities have experienced severe socioeconomic changes that have led to the transfer of human population from rural to urban areas. Such changes have triggered the abandonment of many farming lands (Sirami, Brotons, Burfield, Fonderflick, & Martin 2008; Bernués, Ruiz, Olaizola, Villalba, & Casasús 2011; Cocca, Sturaro, Gallo, & Ramanzin 2012; Beilin et al. 2014; Plieninger, Hui, Gaertner, & Huntsinger 2014), especially in hardly accessible zones and areas with low-quality pastures (Gellrich & Zimmermann 2007; Plieninger et al. 2014). Simultaneously, in high-productivity areas historical activities have largely been replaced by more productive techniques. For instance, transhumance supposes huge efforts to move herds (mainly sheep) from winter to summer pastures. This practice is being replaced by stabling (Olea & Mateo-Tomás 2009), which means that animals do not move from the vicinity of the farm and have supplementary feeding (Cortés-Avizanda, Donázar, & Pereira 2015). Indeed, Navarro and Pereira (2015) estimated that, between 1990 and 2010, traditional grazing livestock heads in Europe declined by 25%. The drastic reduction of free grazing herds has led to an increment of niche availability for wild ungulates (mainly Cervidae and wild boars *Sus scrofa*) which, along with stricter hunting regulations and active population reinforcements, introductions and reintroductions, has positively contributed to their population increase and expansion in most European countries (Apollonio, Andersen, & Putman 2010; Vingada, Fonseca, Cancela, Ferreira, & Eira 2010; Acevedo et al. 2011). A land-abandonment process entails a passive "rewilding" phenomenon (Soulé & Noss 1998; Navarro & Pereira 2015; Corlett 2016), involving the recovery of ecological succession without human intervention. Understanding the ecological consequences of this complex process has become a great research challenge for ecologists during the last decades (Plieninger et al. 2014; Queiroz, Beilin, Folke, & Lindborg 2014).

There is a growing literature about the impact of the rewilding processes on wild ungulates (Acevedo et al. 2011) and on agro-ecosystem-related species such as song birds and pastureland grasses (see e.g. Hedlund et al. 2003; Regos et al. 2016). Other functional groups such as scavengers, however, have received attention only recently (Mateo-Tomás & Olea 2015; Cortés-Avizanda et al. 2015; García-Barón et al. 2018), despite this group provides important ecological functions and ecosystem services (Moleón et al. 2014; DeVault et al. 2016). Ungulate carcasses are an important food source for many avian and mammalian scavengers (Selva & Fortuna 2007; Kelly, Sparks, DeVault, & Rhodes 2007; Mateo-Tomás et al. 2015). This includes both obligate scavengers (i.e. vultures), which are the most efficient terrestrial vertebrate scavengers (Cortés-Avizanda, Jovani, Carrete, & Donázar 2012; Sebastián-González et al. 2016; Morales-Reyes, Sánchez-Zapata et al. 2017), and facultative scavengers, such as other raptors, corvids, mesocarnivores and top predators (Pereira, Owen-Smith, & Moleón 2014; Mateo-Tomás et al. 2015).

The abandonment of traditional agro-grazing systems and the subsequent rewilding might affect carrion resources by altering the abundance of carcasses, the habitat in which they occur, and the wild and domestic ungulate carcass ratio. First, the expected increase in wild ungulate populations (Acevedo et al. 2011) will probably not be sufficient to supplant in terms of biomass the current domestic ungulate populations (Margalida, Colomer, & Sanuy 2011). Second, each ungulate group dominates different habitats in relation to vegetation cover, with domestic species occurring mostly in open habitats (e.g., pasturelands) and wild ungulates in a wider variety of habitats, using frequently shrubby and woody areas (Apollonio et al. 2010; Acevedo et al. 2011). In turn, these differences in ungulate population density and habitat use may decisively affect the detectability and accessibility of carrion by scavengers (Selva, Jędrzejewska, Jędrzejewski, & Wajrak 2005; Bamford, Monadjem, & Hardy 2009; Ruzicka & Conover 2012; Moleón et al. 2019). Whereas Old-World vultures are highly efficient in detecting carcasses in open areas thanks to an acute eyesight, the ability to perform long-distance movements and the capacity of transferring information on carcass location (Ruxton & Houston 2004; Cortés-Avizanda, Jovani, Carrete, Donázar, & Grimm 2014), terrestrial vertebrates with fine smell sense such as mammalian carnivores will be able to find carcasses even in woody and shrub vegetation patches (Selva et al. 2005; Moleón et al. 2019). Thus, we can hypothesize that because both kind of carcasses appear at different densities and are linked to different habitats, they would be consumed by unequal scavenger assemblages. Identifying possible differences in the use of ungulate carcasses by vertebrate scavengers in relation to hypothetical future scenarios of abandonment is a relevant ecological question with profound conservation implications due to the ongoing change in land use and farming practices, especially for endangered scavengers such as vultures (Ogada, Keesing, & Virani 2012; Ogada, Torchin, Kinnaird, & Eznewa 2012; Cortés-Avizanda et al. 2015; Pfeiffer, Venter, & Downs 2015).

Here, we developed a camera trapping experiment to compare how avian and mammal scavengers exploit ungulate carrion where carcasses are usually available. The Mediterranean mountains of southern Spain are an excellent case study because free grazing livestock (mainly sheep) still coexist with a diverse guild of wild ungulates and scavengers. Our main prediction was that carcasses of domestic ungulates, which concentrate in large numbers in open pasturelands, would be detected and consumed earlier than wild ungulate carcasses, which frequently occur in much lower densities at more heterogenous habitats, such as shrublands and forest. This would result in differences in scavenger guild composition and species consumption rates between domestic and wild ungulate carcasses, with vultures dominating domestic ungulate carcasses and facultative scavengers, especially mammalian carnivores, mostly scavenging at wild ungulate carcasses. These local findings may be easily transferred to other scenarios of change in traditional farming activities.

Material and methods

Study area

The study area comprises the Sierras de Cazorla, Segura y Las Villas Natural Park (Fig. 1), the largest protected area in Spain and the second one in Europe (214,300 ha). The landscape is mountainous, and altitude ranges from 500 to 2107 m above the sea. Climate is Mediterranean, with an annual mean temperature ranging from 12 to 16 °C and mean precipitation ranging from 300 to 1600 mm. The park is mainly covered by woodlands of pines (*Pinus nigra*, *Pinus pinaster*, and *Pinus halepensis*) and oaks (*Quercus ilex* and *Quercus faginea*). Moreover, karstic plains covered mostly by pastures are frequent above 1700 m a.s.l. (Rivas-Martínez 1986).

The park holds breeding populations of three obligate scavenger species: griffon vultures (*Gyps fulvus*; >400 pairs, distributed over the whole park), Egyptian vultures (*Neophron percnopterus*; 4 pairs) and bearded vultures (*Gypaetus barbatus*; 3 pairs; Arenas, Benítez, & Rodríguez-Peinado 2015). Cinereous vultures (*Aegypius monachus*) are also common although they do not breed within the park. Among the avian facultative scavengers, corvids are the most abundant group, with large populations of common ravens (*Corvus corax*), carrion crows (*Corvus corone*), European jays (*Garrulus glandarius*) and common magpies (*Pica pica*). Scavenging raptors other than vultures are mainly represented by golden eagles (*Aquila chrysaetos*) (18 pairs; Bautista et al. 2006), black kites (*Milvus migrans*) and red kites (*Milvus milvus*). Among mammals, red foxes (*Vulpes vulpes*), stone martens (*Martes foina*) and wild boars are the most frequent scavengers (Morales-Reyes, Sánchez-Zapata et al. 2017). Free-ranging shepherd dogs (*Canis lupus familiaris*) are also common (Morales-Reyes, Sánchez-Zapata et al. 2017), although these herding dogs are domestic and fed by farmers. Apparently, the density of the major scavenger species in the study area (e.g. golden eagles and griffon vultures) has not changed greatly during the study period (CMAYOT 2015; pers. observ.).

Within the protected area, grazing is only allowed on the upper plateau in a 22,633 ha grassland area, where around 35,000 sheep graze from the end of May to November. During autumn and winter, in a transhumance movement, the herds of sheep are transferred to warmer pastures (mainly towards the west). Considering an annual mortality rate of 5% (Morales-Reyes, Pérez-García et al. 2017), the potential availability of domestic ungulate carcasses to scavengers would be around 146 sheep/month. Wild ungulates in the park move freely in the whole park but tend to aggregate at areas covered by forests and shrubs and are subject to culling and sport hunting. The last available census of wild ungulates was conducted in 2015 within the Andalusian Game Reserve (65,752 ha; see Fig. 1), where most culling and hunting activities are performed (http://www.juntadeandalucia.es/medioambiente/site/pcp). According to this census, the wild ungulate population inside the Game Reserve includes 740 Spanish ibexes (*Capra pyrenaica*), 1402 red deer (*Cervus elaphus*), 1047 mouflons (*Ovis aries*), and 1247 fallow deer (*Dama dama*). Although no census data are available for the wild boar, this species is abundant throughout the park, probably exceeding in number the populations of all other wild ungulate species together.

Data collection

In July 2015, we monitored 24 domestic ungulate carcasses (23 sheep and one goat) within the pastureland area (Fig. 1; see Appendix A in Supplementary material for details on date and time of carcasses placement). Carcasses were placed randomly (always separated by >1.5 km from each other to maximize the independence of samples; Morales-Reyes, Sánchez-Zapata et al. 2017) and before 12:30 h (see Appendix A: Table 1 in Supplementary material). Cameras (Bushnell NatureView Cam HD Max) were placed in front of the carcasses (5–20 m away), were active between 6:30 h and 21:30 h, and were programmed to take a picture every minute. We programmed cameras to work only during daytime to save batteries, as previous field experience indicated that livestock carcasses were usually depleted before night by large vulture numbers. We searched for feces and tracks to detect the presence of nocturnal scavengers. This limited our capacity to identify different individuals and the contribution to carrion biomass consumption by these species. However, most domestic ungulate carcasses (79.2%) were depleted before the first night, thus reducing this potential bias. In addition, in July and August 2007 (see Table S1 in Supplementary material), we monitored 24 carcasses of wild ungulates, which had been culled by park rangers and subsequently left in the place of death (13 fallow deer, 7 mouflons and 4 red deer) (Fig. 1). Automatic cameras (Bushnell Trail Scout 2.1 MP) were located 5–10 m away from

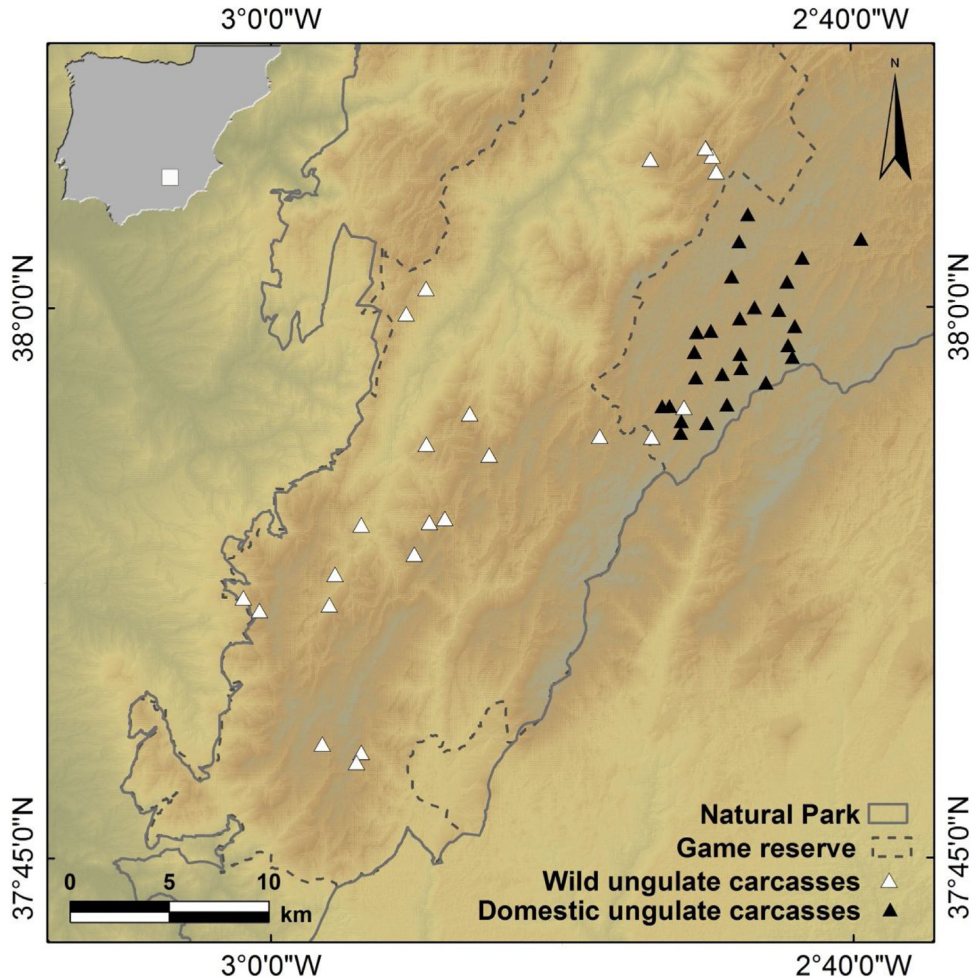

Fig. 1. Study area. We show the spatial distribution of monitored carcasses of wild (white triangles) and domestic (black triangles) ungulates, the limits of Sierras de Cazorla, Segura y Las Villas Natural Park (solid gray line) and the Andalusian Game Reserve (dashed gray line).

the carcasses. In this case, cameras were programmed for 24-h operation, recording two pictures when movement was detected (Morales-Reyes, Sánchez-Zapata et al. 2017). We visited the cameras every two days to check them, replace batteries and download existing pictures, until the carcass was completely consumed. According to Moleón, Sánchez-Zapata, Sebastián-González, and Owen-Smith (2015), both wild and domestic ungulate carcasses studied are equivalent in size (i.e. medium-size carcasses; 10–100 kg), so we do not expect carcass type to substantially affect their scavenging patterns.

We used CORINE Land Cover habitat categories (CEC 2012) to assign vegetation cover to each carcass location at the local scale. We defined it as the predominant category within a 25 m radius around carcasses (Pardo-Barquín, Mateo-Tomás, & Olea 2018).

For each carcass, we used the pictures (and, in the case of domestic ungulate carcasses, scavenger feces and tracks) to estimate: (i) 'detection time' (time elapsed since carcass placement until the arrival of first scavenger); (ii) 'consumption time' (time elapsed between the arrival of the first scavenger and the last picture of a scavenger); (iii) 'richness' (number of scavenger species recorded); (iv) maximum 'abundance' (maximum number of unequivocally different individuals of each scavenger species recorded per day); (v) 'percentage of carrion biomass consumed by obligate scavengers'; (vi) 'percentage of carrion biomass consumed by avian facultative scavengers'; and (vii) 'percentage of carrion biomass consumed by mammalian facultative scavengers'. To estimate these last three variables, we followed the methodology described in Mateo-Tomás, Olea, Moleón, Selva, and Sánchez-Zapata (2017). Some parameters were impossible to estimate for several carcasses due to the lack of information (see Table 1).

Data analyses

We used the non-parametric Mann–Whitney U test to compare the consumption patterns of wild and domestic ungulate carcasses. Also, we tested the relation between carcass consumption time and the maximun number of griffon vultures recorded in a picture (separately for domestic and wild ungulate carcasses) by means of Spearman correlations. We focused this analysis on the griffon vulture

Table 1. Carcass detection and consumption times, richness of species per carcass, maximum abundance of individuals of all species, and percentage of carrion biomass consumed by obligate, avian and mammalian facultative scavengers (values represent mean ± standard deviation, minimum, maximum and sample size) for each carcass type. p-Values and z-values of the differences between domestic and wild ungulate carcasses are shown. Sample size in the case of abundance and the variables related to biomass consumption is <24 because of sampling failure in several carcasses.

	Domestic ungulate carcasses				Wild ungulate carcasses				Comparison	
	Mean ± SD	Min.	Max.	n	Mean ± SD	Min.	Max.	n	p	z
Detection time (h)	8.83 ± 17.48	0.25	79.67	24	18.44 ± 17.49	0.17	54	24	0.005	−2.79
Consumption time (h)	12.56 ± 16.87	0.21	76.87	24	82.27 ± 73.81	3.5	310	24	<0.001	−4.15
Scavenger richness	4.17 ± 1.63	1	7	24	2.67 ± 0.92	1	4	24	0.002	3.06
Scavenger abundance	83.26 ± 25.03	38	142	19	35.93 ± 18.23	5	72	15	<0.001	5.88
Biomass consumed by obligate scavengers (%)	97.92 ± 2.10	91.42	100	19	47.16 ± 46.66	0	100	15	<0.001	4.61
Biomass consumed by avian facultative scavengers (%)	0.80 ± 0.45	0	1.51	19	2.23 ± 2.79	0	8.03	15	0.071	−1.96
Biomass consumed by mammalian facultative scavengers (%)[a]	1.28 ± 1.93	0	7.06	19	50.61 ± 46.66	0	100	15	0.011	2.71

[a] The livestock carrion biomass consumed by mammalian scavengers is a conservative estimation (see Methods and Discussion for details).

because this species consumed most of carrion biomass and is the most efficient scavenger of Mediterranean systems (Cortés-Avizanda et al., 2014; Sebastián-González et al., 2016). Analyses were performed in R 3.2.4 (R Core Team, 2016).

Results

Cameras recorded 4341 and 7388 pictures of vertebrate scavengers at wild and domestic ungulate carcasses, respectively. According to CORINE Land Cover (CEC, 2012), all the domestic ungulate carcasses were assigned to natural grasslands, whereas wild ungulate carcasses sites were more heterogeneous (coniferous forest: n = 17; sclerophyllous vegetation: n = 3; transitional woodland-shrub: n = 3; natural grasslands: n = 1). Consequently, the vegetation cover associated with both kind of carcasses was clearly different ($\chi^2 = 44.16$, df = 3, p-value <0.001). Mean detection time of wild ungulate carcasses was significantly higher than that of domestic ungulate carcasses. Mean consumption time of wild ungulate carcasses was significantly higher (6–7 times) compared to domestic ungulate carcasses (see Table 1 for the results of statistical tests).

Scavenger assemblages and the species-specific pattern of carrion biomass consumed differed greatly between wild and domestic ungulate carcasses (Fig. 2A and B; Appendix A: Table 2 in Supplementary material). Domestic ungulate carcasses were visited in total by fewer scavenger species (n = 9 species) than wild ungulate carcasses (n = 12). However, mean richness of scavenger species per carcass was significantly higher in domestic ungulate carcasses (see Table 1). The average maximum abundance of scavenger individuals was significantly higher at domestic ungulate carcasses (see Table 1 for the results of statistical tests). Vultures visited more frequently, and more vultures gathered, at domestic ungulate carcasses. In contrast, the richness and abundance of facultative scavenger species were higher at wild ungulate carcasses. The griffon vulture was the most abundant scavenger in both types of carcasses, especially in domestic ungulate carcasses. Red fox and wild boar were the scavenger species that visited more wild ungulate carcasses (Fig. 2A; Appendix A: Table 2 in Supplementary material).

Obligate scavengers consumed significantly more domestic ungulate carrion biomass than wild ungulate carrion (mean = 97.92% vs. 47.16%; $t = -4, 76$, $p < 0.001$). In particular, griffon vultures consumed on average 96.98% and 47.05% of the biomass of domestic and wild ungulate carcasses, respectively (see Table S2 in Supplementary material). Avian facultative scavengers consumed very low carrion biomass of both domestic and wild ungulate carcasses (1% vs. 2%; t = 2.20, p-value <0.02). Mammalian facultative scavengers, mainly represented by wild boar, consumed significantly more wild ungulate carrion biomass than domestic ungulate carrion (52% vs. 1%; t = 4.62, $p < 0.001$). The time needed to consume a carcass was significantly and negatively correlated with the maximum number of griffon vultures recorded at carcasses (Z = 2932.2, $p < 0.001$ for domestic ungulate carcasses; Z = 4104.8, $p < 0.001$ for wild ungulate carcasses) (Fig. 2C; Appendix A: Table 2 in Supplementary material).

Discussion

Our results reveal important, differences in the consumption patterns of domestic and wild ungulate carcasses and the composition of their scavenger assemblages. First, carcasses of domestic ungulates, which appeared in open grazing areas, were detected and consumed faster than those of wild ungulates, which were found in more heterogeneous habitats including shrub and woodlands. Second, livestock carcasses were exploited on average by a richer scavenger guild in terms of species and individuals. Third, while vultures depleted almost all the livestock carrion, facultative scavengers consumed an important portion of wild ungulate carrion. Overall, our findings highlight the pivotal role of vultures in relation to carrion consumption efficiency: when large number of vultures were present, carcasses were rapidly depleted, irrespective of carcass type.

There are many abiotic and biotic factors that may modulate the structure and functioning of scavenger communities at the local and regional level (Turner, Abernethy, Conner, Rhodes, & Beasley 2017). For example, carcass size (Moleón et al., 2015), carcass type (Olson, Beasley, & Rhodes 2016; Moleón et al., 2017; Muñoz-Lozano et al., 2019) and season (Selva & Fortuna 2007; Pereira et al. 2014) largely influence scavenging assemblages and consumption patterns. In this study, however, we focused on carcasses of wild and domestic ungulates, which in our case are of similar size, and monitored the carcasses during the same season (i.e. summer). Thus, the differences found should be explained by other factors.

Microhabitat structure may play a relevant role in carcass detection by scavengers (Ruzicka & Conover, 2012; Moleón et al., 2019). For scavengers that rely mostly on visual cues to detect carrion, such as vultures (Ruxton & Houston 2004), carrion encounter rate and speed is highly dependent on vegetation structure (Bamford et al., 2009; Ogada, Keesing et al., 2012; Ogada, Torchin et al., 2012; Smith, Laatsch, & Beasley 2017). In our study system, there was a strong asymmetry regarding the habitats associated to each carcass type: whereas all livestock carcasses were located in open habitats (i.e. pastureland), carcasses of wild ungulates were mostly found in more heterogeneous environments. This might explain why vultures, particularly griffons (i.e. the most abundant vulture species in the study area), exploited domestic ungulate carrion more efficiently than wild ungulate carrion. Griffon vultures arrived quickly and in large numbers to domestic ungulate carcasses, depleting the resource in a short time as indicated by the correlation between the number of vultures recorded at carcasses

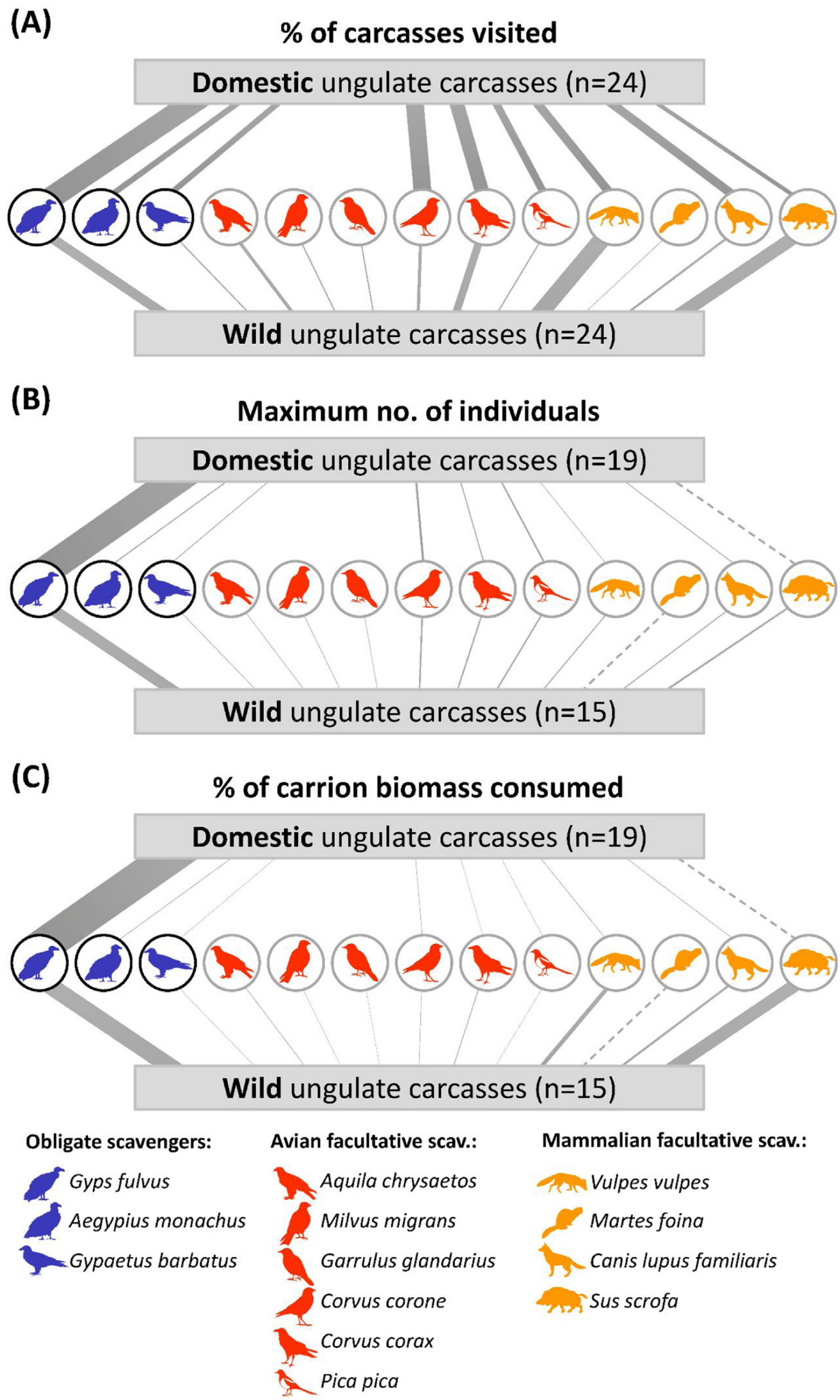

Fig. 2. Differential scavenging patterns of domestic and wild ungulate carcasses. Note that domestic ungulate carcasses usually occur at higher densities and in more open habitats than wild ungulate carcasses. Differences are shown in terms of percentage of carcasses visited by each scavenger species, maximum number of individuals of each scavenger species recorded at carcasses, and percentage of carrion biomass consumed by each scavenger species. Line width is proportional to the percentage of carcasses visited, the maximum number of individuals recorded, and the percentage of carrion biomass consumed, respectively. Dashed lines represent cases with insufficient data to infer quantitative values. Detailed results per scavenger species are provided in Table S2 in Supplementary material.

and carcass consumption time (see Results and Fig. 2B). In turn, griffon vulture scavenging activity could decrease carrion consumption opportunities even for major facultative scavengers of Mediterranean systems such as golden eagles, red foxes and wild boars (Blázquez, Sánchez-Zapata, Botella, Carrete, & Eguía 2009; Sánchez-Zapata, Eguía, Blázquez, Moleón, & Botella 2010; Ballari & Barrios-García 2014; Morales-Reyes, Sánchez-Zapata et al. 2017). Although many scavengers visited livestock carcasses, little carrion was available to them, especially to nocturnal scavengers because most livestock carcasses had been consumed before the first night by vultures, which dominate predictable carrion resources in Mediterranean habitats (Cortés-Avizanda, Carrete, & Donázar 2010, 2012).

In contrast, higher coverage of trees and shrubs might hinder visual detection of wild ungulate carcasses by soaring vultures, thus allowing facultative scavengers, especially mammals with finer sense of smell (Savage 1977), to access this carrion source (DeVault, Brisbin, & Rhodes 2004; Selva et al. 2005; Bamford et al. 2009). Recent research suggests that local processes such as species sorting through habitat heterogeneity would dominate scavenger metacommunity dynamics together with stochastic forces (e.g. carrion unpredictability) in Mediterranean ecosystems (Mateo-Tomás et al. 2017). The longer time required depleting wild ungulate carcasses, partly due to the lower presence of vultures at these carcasses, and the territorial behavior of carnivorous mammals and other raptors might contribute to a more equitable distribution of the biomass consumed among the different consumers.

In addition to the effect of the habitat structure, domestic ungulates have larger population sizes and also a higher spatial concentration within pasturelands (usually around shepherd habitations). The consequence is a remarkable difference in terms of density and spatial and temporal predictability of domestic ungulate carcasses as compared to the wild ungulate carcasses, which gives an advantage to the most competitive species, especially the griffon vulture (Cortés-Avizanda et al. 2012). Unravelling the relative contribution of habitat type and ungulate carcass density on scavenging patterns and scavenger communities deserves further investigation. Other factors linked to sheep farming might have contributed to the observed differences. In grazing areas, it is usually the presence of shepherd dogs which also consumed part of our experimental carcasses. Free-ranging dogs are efficient scavengers (Butler & du Toit 2002) and are able to exclude other less competitive facultative scavengers (e.g. foxes; Vanak & Gompper 2010). Thus, dogs might favor a “landscape of fear” scenario (Weinstein, Buck, & Young 2018) around carcasses, as has been observed in other areas (Butler & du Toit 2002; Schlacher et al. 2015).

Carcasses of wild and domestic ungulates may play an overall distinct role in the food webs of Mediterranean ecosystems. According to current predictions, the abandonment of extensive farmlands in many parts of Europe will increase during the next years (Verburg & Overmars 2009), leading to a decrease in the number of free-ranging herds. Besides, these land-abandonment processes have led to the substitution of part of the current pasture lands by shrublands and forest linked to an increment of wild ungulate populations (e.g. Apollonio et al. 2010). Despite the increasing number of wild ungulates which also could occupy the remaining pasturelands, it is unquestionable that, in general terms, land-abandonment is going to entail a decrease in the density of carrion available and a drastic change in their detectability. Thus, scavenging vertebrates might face a changing scenario in their main trophic resource. Our results indicate that domestic ungulate carcasses, which normally aggregate in open areas, held a higher richness and a larger number of individuals of scavenger species. It is remarkable that bearded and cinereous vultures were mainly detected at domestic ungulate carcasses. Consequently, farmland abandonment and the subsequent reduction in the availability of livestock carcasses could have negative consequences for the conservation of these endangered vultures. A recent study highlights a dual effect of farmland abandonment and the subsequent forest expansion for cinereous vultures, as they depend on forested areas for nesting, while foraging habitats are located in open areas (García-Barón et al. 2018).

The observed differences should also be taken into account to estimate environmental carrying capacity of scavenger populations, especially vultures. Most studies usually assume as a starting point that carcasses of domestic and wild ungulate are ecologically equivalent and that the individuals of scavenger bird species have a similar probability of accessing one or the other resource (Mateo-Tomás & Olea 2010; Margalida et al. 2011). However, our results demonstrate that this assumption would lead to important biases because both types of carcasses appear in different habitats and at different densities that make them differently available for scavengers. In the end, this can lead to misinterpreting the role of wild ungulates in the conservation of scavenger guilds. Thus, we encourage policy makers and wildlife managers to be aware of the wide and complex ecological consequences of the ongoing rewilding process. Overall, our results call attention to the need of fine-tuning estimations on the role that the abandonment of traditional grazing activities and rewilding processes may have in the availability of carrion resources to scavengers, the subsequent structure of trophic networks and, finally, in the long-term maintenance of scavenger populations.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.baae.2019.10.006.

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