

From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting

Patricia Mateo-Tomás¹*, Pedro P. Olea^{1,2}, Marcos Moleón³, Joaquín Vicente¹, Francisco Botella³, Nuria Selva⁴, Javier Viñuela¹ and José Antonio Sánchez-Zapata³

¹Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ronda de Toledo s/n, 13071 Ciudad Real, Spain, ²Departamento de Ecología, Universidad Autónoma de Madrid, 28049 Madrid, Spain, ³Departamento de Biología Aplicada, Universidad Miguel Hernández, Avda. de la Universidad, s/n, 03202 Elche, Alicante, Spain, ⁴Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland

ABSTRACT

Aim Anthropogenic food subsidies are increasingly present in ecosystems, but their impacts remain poorly understood. Big game hunting is a growing activity that annually subsidizes ecosystems with tonnes of carrion world-wide. By feeding on carrion, scavengers support key ecosystem functions and services, becoming key vectors to transfer the impacts of human-mediated food subsidies across ecosystems. We characterize and compare the structure of vertebrate communities feeding on these subsidies, namely big game hunting remains, at a global scale.

Location Global.

Methods We collected data from a countrywide field study in Spain and broadened it up to nine regions in four continents by reviewing scientific literature. We analysed the structure of the scavenger communities considering species composition, richness and scavenging frequency.

Results Seventy-nine vertebrate species, 19% globally threatened, scavenged food subsidies from big game hunting world-wide. Scavenger richness (2.0–11.0% of vertebrates/region) positively correlated with total vertebrate richness. Although scavenger communities at hunting remains varied among regions, we describe a general structural pattern. Birds and mammals dominate consumption, with birds scavenging twice more frequently than mammals – but more mammal species scavenge compared to birds. Generalists dominate scavenging globally, especially where the presence of obligate scavengers (vultures) and apex predators (e.g. wolves, hyenas, eagles) is low.

Main conclusions Anthropogenic food from hunting subsidizes many vertebrate species from different trophic levels and conservation status and thus is expected to affect from populations to ecosystems. Obligate scavengers and apex predators seem to play a key role structuring the scavenger community through top-down mechanisms. The general structure of scavenger communities we describe here provides a benchmark for comparisons of subsidized and non-subsidized communities. More data on the spatio-temporal availability of anthropogenic food subsidies and their consumption by scavengers world-wide are needed to efficiently preserve biodiversity, and the associated ecological functions and services, in increasingly subsidized ecosystems.

Keywords

Anthropogenic food subsidies, apex predators, carrion, food webs, generalists, vultures.

Spain.

A Journal of Conservation Biogeography

E-mail: rktespejos@gmail.com

*Correspondence: Patricia Mateo-Tomás,

Plaza de los Pueblos 9, 24900 Riaño, León,

INTRODUCTION

Food wasted into ecosystems by human activities such as livestock farming, fishing or hunting is rapidly increasing across the planet, but their ecological impacts, although recognized, remain poorly understood (Oro et al., 2013). A large part of these anthropogenic food subsidies are provided as carrion, which is a high-quality resource (i.e. nutrient-rich food without consumers exerting energy to chase it; Wilson & Wolkovich, 2011). Thus, carrion predictable availability in nature is expected to affect different ecological levels from individuals to ecosystems (DeVault et al., 2003; Oro et al., 2013). Vertebrate scavengers, which feed at a variable extent on carrion, are therefore one of the guilds thought to be more strongly affected by the presence of anthropogenic food subsidies in ecosystems (Oro et al., 2013). According to their widespread presence in ecosystems, they become also key vectors for transferring such impacts across ecological levels and food webs (Wilson & Wolkovich, 2011).

Carrion consumption, scavenging, is a widespread strategy with a noticeable contribution to energy transfer. Scavenging supports key ecosystem services (e.g. accelerating nutrient recycling, limiting disease spreading; DeVault et al., 2003; Wenny et al., 2011; Moleón et al., 2014a). However, its role in ecosystems is frequently underestimated (e.g. by 16-fold in food webs; Wilson & Wolkovich, 2011), and thus, detailed knowledge on most ecological processes related to scavenging is lacking. To identify key structural attributes of the scavenger community (e.g. species diversity, scavenging frequency, trophic links) is necessary to advance our understanding of the ecological processes underlying ecosystem functions and services (DeVault et al., 2003; Wilson & Wolkovich, 2011; Moleón et al., 2014b). This knowledge will facilitate management and conservation of ecosystems under global change, especially regarding previous conservation and socioeconomic conflicts arisen from the mismanagement of some anthropogenic food subsidies (e.g. livestock carcasses in Asia and Europe; Tella, 2001; Oaks et al., 2004; Markandya et al., 2008). In this context, it is urgent to understand better the role of severely threatened species such as most obligate scavengers (i.e. vultures; Ogada et al., 2012a) and apex predators (Ripple et al., 2014).

Hunting was the first human activity subsidizing natural ecosystems with food through prey carcasses left by early human hunters (Oro *et al.*, 2013). The appearance of agriculture and domesticated farm animals reduced the relative importance of food subsidies from hunting (Moleón *et al.*, 2014a). Nonetheless, the rapid growth of sport hunting in modern societies and the recovery of wild ungulate populations (Lindsey *et al.*, 2007; Gortázar, 2012; Weinbaum *et al.*, 2013) has increased again the role of hunting as food subsidizer in ecosystems. In this regard, big game trophy hunting (i.e. sport hunting of large animals, mainly wild ungulates and predators; Lindsey *et al.*, 2007) is particularly relevant. This activity captures millions of animals each year (e.g. \sim 14.4·10⁶ wild ungulates in USA in 2008; Fig. 1), involving

millions of people and dollars world-wide (e.g. 11.6.10⁶ hunters and \$16.9.109 in USA; US Fish & Wildlife Service, 2011). Unlike subsistence hunting (i.e. intended for food provisioning), in trophy hunting, a sizeable proportion of the hunted individual is often abandoned in the field (Vicente et al., 2011). Although these trophy hunting remains are additionally exploited by local communities in some regions (e.g. Africa; Baldus et al., 2008), tonnes of carrion yearly subsidize ecosystems world-wide (e.g. ~1.0.10⁸ tonnes per year in Europe, ~6.9·10⁵ tonnes per year in USA; Vicente et al., 2011; Oro et al., 2013). Wildlife cropping can also provide extra food subsidies from selective elimination of certain classes (e.g. females, juveniles) and handicapped animals to regulate ungulate populations (Torres-Porras et al., 2014). Hunting remains are thus likely exerting a noticeable impact on ecosystems (Wilmers et al., 2003; Selva & Fortuna, 2007; Mateo-Tomás & Olea, 2010; Oro et al., 2013).

Here we characterize the vertebrate scavenger communities consuming anthropogenic food subsidies (i.e. big game hunting remains) world-wide. We present results of a large-scale field study covering mainland Spain (i.e. \sim 500.000 km²) and complement it with scientific works (N = 7) from around the world (i.e. \sim 100.000 km²). We examine how the vertebrate scavenger community consuming hunting remains varies across world regions in terms of species composition and scavenging frequency, further assessing changes in its structure and deriving a general structural pattern. We discuss the possible consequences of scavenging on big game remains and provide further insights useful to inform conservation and management and guide future research on the topic.

METHODS

Data recording

We used motion-triggered remote cameras to monitor 361 carcasses consisting of hunting remains of wild ungulate species in temperate and Mediterranean ecosystems in mainland Spain in 2006–2013 (Fig. 1; Table S1 in Supporting Information).

We assessed the existing knowledge on vertebrate consumption of hunting remains world-wide by reviewing 113 research works retrieved through a search in Scopus (i.e. 'scaveng* AND (carcass* OR carrion) AND (hunt* OR harvest* OR cull*)' in 'Title, Abstract and Keywords') up to 30 June 2014. We obtained valid data (i.e. systematic monitoring providing a complete list of scavenging species and quantifying their scavenging frequencies) from six locations world-wide, including Europe (N = 3; Selva, 2004; Killengreen et al., 2012; Wikenros et al., 2013; Fig. 1), North America (N = 2; Magoun, 1976; Wilmers *et al.*, 2003) and Australia (N = 1; Read & Wilson, 2004). We also considered unpublished data from camera trapping of ungulate carcasses in South Africa (M. Moleón, unpublished data; Table S1). All the hunting remains came from big game herbivores (Table S1).



Figure 1 Large ungulates and marsupials hunted world-wide. Hunting bags, that is the number of animals of big game ungulate and marsupial species hunted each year by country (individuals km^{-2}), are shown. Locations of the study areas (i.e. those with detailed data on the scavenging community consuming hunting remains) are shown, including our study areas in Temperate and Mediterranean Spain (i.e. the dotted line in the inset northward and southward, respectively). Photographs show the species accounting for most captures or emblematic species regarding their distribution, conservation status and/or value as trophies for hunters. See Appendix S1 for the complete list of species, data sources and photograph credits.

To provide a complete list of vertebrate species scavenging hunting remains world-wide, we compiled non-systematic data scattered through the remaining works retrieved by our Scopus search (Table S2). These data were excluded from analyses on the structure of the scavenger community.

Data analyses

We calculated scavenger's species diversity (i.e. Shannon diversity hereafter) following (Jost, 2007) framework of 'true' diversities, equivalent to the exponential of Shannon entropy (i.e. e^H , where $H = -\sum_{i=1}^{s} p_i \ln p_i$). S was the number of scavenger species within a site (i.e. species richness), and p_i was the scavenging frequency of the *i*th species in each world region. The scavenging frequency of each vertebrate species was the proportion of carcasses at which that species was recorded scavenging from the total number of carcasses monitored in each region. For works where the sample units were not the monitored carcasses (N = 3), we estimated scavenging frequencies using photographs (Killengreen et al., 2012), 10day periods (i.e. visits; Wikenros et al., 2013) and kilograms of hunting remains (Wilmers et al., 2003) as sample units. We show raw data of scavenger species richness and Shannon diversity in each ecosystem. Because of the different number of sample units among ecosystems, we also compared these

two parameters for an equal sampling level. We standardized all sampling of each ecosystem to an equal completeness (or coverage). We used the incidence-based data to build coverage-based rarefaction and extrapolation curves up to achieve a base coverage level (i.e. a sampled fraction of the total of individuals in the community equal for all the study locations to compare, i.e. 96% for our analysis, Table 1; see Chao *et al.*, 2014). We used this sample standardization only for the six regions using monitored carcasses as sample units (see above).

We used Spearman correlations (i.e. r_s ; significance level: P < 0.05) to explore the existence in the scavenger community of broad-scale spatial patterns often described for biodiversity (Gaston, 2000). We assessed the correlations of scavenger species richness and Shannon diversity with environmental variables (latitude, elevation, precipitation, temperature; Table S3). We also explored the relationships between these environmental variables and the scavenging frequencies of the main scavenging groups (i.e. apex predators, obligate scavengers and generalists; see Table S2 for a detailed description). To infer possible interspecific relationships, we calculated correlations between the scavenging frequencies of these scavenging groups. We also used chi-square tests to compare the scavenger communities regarding the presence of mammals, birds and reptiles (Table 1).

					Norwegian	Greater	Alaskan	South		
	Temperate	Mediterranean	Bialowieza	Scandinavian	Arctic	Yellowstone	Arctic	African		
	Spain	Spain	Primeval	Boreal Forest	Tundra	Ecosystem	Tundra	Savanna	Arid South	World-
	(TSP)	(MSP)	Forest (BPF)	(SBF) ⁸	(NAT)	(GYE) [¶]	(AAT)	(SAS)	Australia (ASA)	wide
Observed richness (Sobs) *	20	29	23	6	11	6	6	16	6	69
Estimated richness [†]	14	20	16	na	na	na	6	21	6	na
[S 0.96 (IC95%)]	(13 - 16)	(18–21)	(15-18)				(7-11)	(14-27)	(5-7)	
Observed Shannon diversity*	10.3	12.5	12.4	4.3	1.4	2.0	6.1	9.9	5.2	24.9
Estimated Shannon diversity [†]	9.6	11.6	11.6	na	na	na	6.7	10.6	5.0	na
[Shannon 0.96 (IC95%)]	(8.2 - 10.5)	(10.8 - 12.4)	(10.9 - 12.4)				(5.2 - 8.2)	(8.7 - 12.4)	(4.3 - 5.7)	
Observed coverage [†]	0.978	0.990	0.988	na	na	na	0.987	0.942	0.999	0.10
% of all vertebrates	8.4	8.3	6.4	2.0	3.3	1.5	10.8	2.3	2.2	5.5**
% of all birds and mammals	10.4	10.8	7.5	2.4	3.7	1.6	11.0	2.6	2.3	5.9**
Number of scavenging birds	11	19	6	6	7	4	5	8	4	36
(percentage of total scavengers	(55.0%)	$(65.5\%)^{\ddagger\dagger}$	$(39.1\%)^{\ddagger\ddagger}$	$(75.0\%)^{\dagger\dagger}$	$(63.6\%)^{\dagger\dagger}$	$(66.7\%)^{\dagger\dagger}$	(55.6%)	(50.0%)	$(66.7\%)^{\dagger\dagger}$	(52.2%)
recorded)										
% of all birds [‡]	9.5	9.2	3.6 ^{§§}	1.8	2.6 ^{\$\$}	1.3	7.8 ^{\$\$}	1.6	2.6	4.4^{**}
Number of scavenging mammals	9	10	13	2	4	2	4	8	1	31
(percentage of total scavengers	(45.0%)	$(34.5\%)^{\dagger\dagger}$	$(56.5\%)^{\ddagger\ddagger}$	$(25.0\%)^{\dagger\dagger}$	$(36.4\%)^{\dagger\dagger}$	$(33.3\%)^{\dagger\dagger}$	(44.4%)	(50.0%)	$(16.7\%)^{\dagger\dagger}$	(44.9%)
recorded)										
% of all mammals [‡]	14.2	19.7	22.4 ^{\$\$}	4.1	12.9 ^{\$\$}	3.0	22.2 ^{\$\$}	5.8	4.5	12.9^{**}
Number of scavenging reptiles	0	0	1	0	0	0	0	0	1	2
(percentage of total scavengers	(0.0%)	(%0.0)	(4.4%)	(0.0%)	(0.0%)	(0.0%)	(0,0,0)	(0.0%)	(16.7%)	(2.9%)
recorded)										
% of all reptiles [‡]	0	0	14.3	0	0	0	0	0	2.5	1.9^{**}
World region	Europe	Europe	Europe	Europe	Europe	North	North	Africa	Australia	World
						America	America			
Data source	This study	This study	Selva, 2004	Wikenros	Killengreen	Wilmers	Magoun,	Moleón,	Read &	
				et al., 2013	et al., 2012	et al., 2003	1976	unpublished	Wilson, 2004	
								data		
	-		-	-	-					

*Scavenger richness and true Shannon diversity based on the data recorded in each region with systematic monitoring. [†]Calculated according to Chao et al. (2014). See main text. na: no data available for calculations.

calculated according to Chao *et al.* (2014). See main text, na. no data avalable for cal *Relative to total bird/mammal/reptile species richness in the area.

retative to total photomaticular species from the area. ⁸Nine species recorded at hunting remains but only eight listed (see Wikenros *et al.*, 2013).

The species recorded at mutual remains out only usin made (see Wilmers et al., 2013). [Methodological constraints limit some calculations for this region (see Wilmers et al., 2003).

**Mean value considering all regions.

⁺⁺Significant (i.e. P < 0.05 in chi-squared test) or ^{‡‡}marginally significant (i.e. P < 0.10) differences among the percentages of scavenging mammals and birds relative to the total number of scavengers recorded in the region.

^{\$\$}Significant (i.e. P < 0.05 in chi-squared test) or [¶] marginally significant (i.e. P < 0.10) differences among the percentages of scavenging mammals and birds relative to the total number of species within each class.

Table 1 Main characteristics of the scavenger communities recorded at hunting remains world-wide (different colours for different continents, dotted/darker for mainland Spain within Europe).

Similar to food web research (Thompson *et al.*, 2012), we analysed the structure of the scavenger community according to three different degrees of aggregation of biological species (hereafter scavenger groups), based on species taxonomy, body mass and main trophic habits (Table S2). We assessed the structural similarity of scavenging communities worldwide using a nonmetric multidimensional scaling (NMDS) computed over a Bray–Curtis distance matrix. To compute the distance matrix, we built a group-by-region data matrix (M_{ij}) with G rows and R columns. G were the different scavenger groups (Table S2) and R each of the nine world regions available (Fig. 1). The value of each element in row i and column j of this matrix (M_{ij}) was the scavenging frequency of each scavenger group in each region. We plotted the best two dimensions (axes) from the NMDS.

We performed all the analyses in the statistical programming language R (R Development Core Team, 2014).

RESULTS

Richness and diversity of the scavenger community

Up to 79 vertebrate species were reported scavenging hunting remains world-wide (Table S2), 69 species at ecosystems with systematic monitoring (Fig. 2). Vertebrate scavenger richness varied among ecosystems (6–29 species; Fig. 2; Table 1), representing 2–11% of the total terrestrial vertebrate species richness in each biome (Table 1). Vertebrate scavenger's

species Shannon diversity widely ranged between regions (i.e. 1.4–12.5; Table 1). When all the ecosystems were posed over an equal sample coverage, estimated species richness and Shannon diversity showed similar trends to those of raw data (Table 1). Extreme biomes (i.e. arid Australia, Alaskan tundra; Fig. 2) exhibited two to three times lower scavenger richness and diversity than other regions, agreeing with general biodiversity patterns (Gaston, 2000). Estimated scavenger richness positively correlated with total vertebrate and bird and mammal species richness ($r_s = 0.89$, P = 0.03 for both). No significant correlations were detected regarding the environmental factors considered.

Fifteen scavenging species (19%) – including eight obligate scavengers and six apex predators – were globally listed as threatened according to The IUCN Red List of Threatened Species (Table S2; IUCN, 2014). From none (in arid Australia) up to 50.0% of the total species recorded in a region were globally threatened (0–56.3% when considering national red lists; Fig. 2, Table S2). Locations with a higher presence of vultures and large felids showed the highest rates of threatened scavengers (i.e. Mediterranean and Tropical regions; Fig. 2).

Structure of the scavenger community

Only birds and mammals were recorded at hunting remains in all regions but arid South Australia and Bialowieza Primeval forest (where reptiles were detected; Fig. 2 and 3a). The



Figure 2 Scavenging frequency of vertebrate species recorded at hunting remains world-wide (a) and at each considered region (b–i). Capital letters after bars indicate the species' conservation status according to national/regional legislation. Least concern species have no letters. Red letters show globally threatened species (Table S2; IUCN 2014). *Martes* spp. includes *M. foina* Erxleben and *M. martes. Stercorarius* spp. includes *S. longicaudus* Vieillot and *S. parasiticus* L. Terrestrial ecoregions are shown. See main text and Appendix S1 for further details.

number of bird species was slightly higher than that of mammals (52.2%, 36 species, vs. 44.9%, 31 species; $\chi^2 = 0.55$, P = 0.46), but this pattern was the opposite in Bialowieza forest (Table 1). When considering species' scavenging frequencies, birds dominated the scavenger community in most regions (Fig. 3a). Nonetheless, the percentage of bird species consuming hunting remains relative to the total bird richness was lower than that of mammals in all regions (Table 1).

Obligate (nine vulture species; 13.0%) and facultative (60 bird, mammal and reptile species; 87.0%) scavengers were recorded consuming hunting remains world-wide (Figs 2 and 3c; Table S2). Facultative scavengers (i.e. mainly generalists and apex predators) dominated consumption everywhere (Fig. 3a). They were the only consumers in most regions because obligate scavengers were only present in Spanish and South African ecosystems (Fig. 3a). Vulture presence in these regions seemed to contribute strongly to the structural similarity of their scavenger communities when compared with other ecosystems (Fig. 3b).

Where present, vultures scavenged hunting remains at notable frequencies (i.e. 16.1–32.0%; Fig. 3a), but with marked differences among species (Fig. 2). Generalist species

(57.2% of the total species recorded; Table S2) dominated scavenging in all regions (i.e. 71.1-98.1%), but Alaskan Arctic tundra and South African savanna (Fig. 3a). Corvids (i.e. Corvus spp.) and mesocarnivores (e.g. red fox Vulpes vulpes L., European pine marten Martes martes L.) were dominant species in all regions but South Africa (Fig. 2). The presence of mesocarnivores seemed to be a common structural feature of European scavenger communities (Fig. 3b). Suids (i.e. wild boar Sus scrofa L. and bushpig Potamochoerus larvatus Cuvier) were also noticeable scavengers (i.e. > 20%; Figs 2 and 3a) where present, contributing to the similarity among South African and European scavenger communities (Fig. 3b). Apex predators (i.e. eight birds and seven mammals; 24.5%) scavenged hunting remains world-wide, showing highly variable frequencies (i.e. 1.9-48.5%; Fig. 3a). Large eagles scavenged at noticeable frequencies elsewhere (Figs 2 and 3). Among mammals, large canids (i.e. wolf Canis lupus L.) were the apex predators more frequently scavenging hunting remains (10.9-80.0%) but in South Africa (Figs 2 and 3). Here, the spotted hyena Crocuta crocuta Erxleben dominated scavenging (i.e. 82.4%; Fig. 3a). Large felids were frequently recorded in South African savanna



Figure 3 Structure and composition of scavenger communities at hunting remains world-wide. (a) Bar plot showing consumption (as percentage relative to the sum of all the consumption frequencies at each study location) by each group represented in the two inner rings of panel 'c' in each study location. In the thicker bars, warm colours show mammals and cold colours birds. (b) NMDS showing the similarity of the scavenger communities considering the groups in the inner ring of panel 'c'. Group names are placed according to their contribution for classifying world regions (i.e. different background colours for different continents). See Appendix S1 for photograph credits. (c) General structure of the scavenger community consuming hunting remains world-wide. Rings show the relative contribution of each considered group according to the mean frequency of consumption of the species included in that group across all the regions analysed. Arcs provide mean \pm standard error (SE, dotted lines) for the groups with the same colour in the two external rings. See Table S2 for further details on the groups.

(> 14.7%; Fig. 2h), sharply contrasting with the scarce presence of felids in other regions (Fig. 3a and b). Other apex predators scavenged hunting remains at low frequencies elsewhere (Fig. 2).

From regional to global scavenger communities: a general pattern

Although some noticeable differences arise regarding the composition and structure of scavenger communities at anthropogenic food subsidies from hunting world-wide (Fig. 3a), some similarities exist, mainly related to their geographic location (Fig. 3b). Furthermore, the scavenger communities at hunting remains world-wide seem to share a general structural pattern (Fig. 3c). This pattern consists almost only of birds and mammals. Birds scavenge more frequently than mammals (i.e. mean \pm SE: 65.8 \pm 7.6% vs. 34.2 \pm 7.6% respectively) – but proportionally, more mammal species scavenge compared to birds. Generalist species (mainly corvids, mesocarnivores and suids) globally dominate scavenging at hunting remains (68.1 \pm 8.3%), with obligate scavengers where present $(7.3 \pm 3.9\%)$. Apex predators often scavenge these remains $(22.1 \pm 5.8\%)$, with eagles and large canids being the main apex species in all regions except Africa. Here, hyenas and large felids dominate the resource (Fig. 3a and b). The scavenging frequency of apex predators negatively correlated with that of generalists ($r_s = -0.82$, P = 0.01).

DISCUSSION

Anthropogenic food from big game hunting annually subsidizes natural ecosystems with tonnes of carrion (Fig. 1), feeding a wide range of terrestrial vertebrate species (up to 79, 19% globally threatened; Fig. 2a; Table S2). These are minimum figures as we have reported a paucity of data on vertebrate consumption of hunting remains. < 6% of the scientific literature reviewed on this topic provided detailed data (i.e. systematic monitoring to identify scavengers and quantify their presence) on the vertebrate community that scavenges hunting remains (see Methods). Moreover, the techniques used to record scavenging (Table S1) could underestimate it (O'Connell et al., 2010). Nonetheless, the high monitoring coverage in most regions (i.e. > 94%; Table 1) indicates that the observed figures are highly representative of the actual scavenger communities. Even using only minimum figures, the vertebrate species subsidized by hunting remains represent a significant proportion of the terrestrial vertebrate species pool (Table 1). Indeed, our results show that the estimated scavenger richness seems to be function of the total vertebrate richness in each region, supporting the notion that scavenging is a widespread foraging strategy among vertebrates (DeVault et al., 2003; Selva, 2004; Wilson & Wolkovich, 2011; Moleón et al., 2014a).

Anthropogenic food subsidies released into ecosystems can exert noticeable impacts at individual and population levels (Oro *et al.*, 2013; Newsome *et al.*, 2015). Hunting remains

are an important food resource for some species with high scavenging frequencies (e.g. fox, corvids, eagles; Fig. 2), especially during the breeding period (Read & Wilson, 2004), or under harsh conditions (e.g. food scarcity, extreme weather; Wilmers et al., 2003; Read & Wilson, 2004; Selva, 2004; Killengreen et al., 2012). Although further evidence is lacking on how hunting subsidies affect species' demographic parameters (but see White, 2006), food availability is expected to improve individual fitness (e.g. breeding performance, survival), potentially affecting population dynamics (Wilmers et al., 2003; Mateo-Tomás & Olea, 2010; Newsome et al., 2015). However, consumption of hunting remains can also limit individual fitness. Lead poisoning through ingestion of game killed with lead ammunition is a significant hazard to wildlife (and even to humans; Pain et al., 2010; Kelly et al., 2011). Our data show that large eagles and vultures, including endangered species, often scavenge hunting remains (Figs 2 and 3), which is a major concern for their conservation (Kelly et al., 2011; Finkelstein et al., 2012).

The higher spatio-temporal predictability of anthropogenic food subsidies compared with naturally generated carrion (e.g. predator kills; Wilmers et al., 2003; Selva, 2004) would promote consumption by species with a higher ability to track pulsed food resources (Oro et al., 2013). Social birds with higher foraging and recruitment abilities (e.g. corvids, vultures) dominate the consumption of hunting remains at global scale and/or where present (Fig. 2). The abundance and distribution of both groups show a strong spatio-temporal adjustment to big game hunting (White, 2006; Mateo-Tomás & Olea, 2010). Abundant generalist species such as the red fox can also effectively track this pulsed resource (Oro et al., 2013), becoming the dominant species at hunting remains (Fig. 2a). Abundant food resources from hunting would thus play a role in the expansion of species frequently scavenging anthropogenic food subsidies (e.g. red fox in Norwegian Arctic tundra; Killengreen et al., 2012). Moreover, frequent scavengers of hunting remains are among the world's worst invasive species (i.e. red fox, wild boar; Lowe et al., 2004). Apex predators such as wolves and hyenas, with noticeable scavenging frequencies at hunting remains (Fig. 2a), could also change their distributions in response to anthropogenic food subsidies (Newsome et al., 2015). Besides numerical and distributional responses, scavengers could respond functionally to hunting remains through dietary shifts (e.g. Andean condors Vultur gryphus L. changed their diet from native fauna to exotic game species; Lambertucci et al., 2009). The implications of consuming this predictable resource on evolutionary processes - as already noticed for other anthropogenic food subsidies (Oro et al., 2013; Newsome et al., 2015) - should be further considered.

Structure of the scavenger community consuming hunting remains

By altering species' abundance and distribution, hunting remains added into ecosystems could also impact

communities, mainly by affecting the interspecific interactions (e.g. competition, predation) structuring them (Moleón et al., 2014a). Interestingly, despite some variations in species' composition and richness among world regions, scavenger communities at hunting remains share a general structure (Fig. 3c). This agrees with highly structured patterns (instead of randomness) found in some scavenger communities (Selva & Fortuna, 2007) and with ecological theory predicting similarity of communities consuming the same resources (Segar et al., 2013). These similarities might respond to some taxa filling the same niches in each community (i.e. phylogenetic niche conservatism) but also to ecological convergence (i.e. different lineage species shifting their trophic niche or with similar pre-adaptations to exploit anthropogenic food subsidies; see above). Nonetheless, dispersal and anthropogenic constraints on some guilds (e.g. vultures, apex predators; Ripple et al., 2014) may explain structural differences in the scavenger communities between regions.

The scavenger community exploiting hunting remains is dominated globally by generalist species, while apex predators and obligate scavengers show lower scavenging frequencies (Fig. 3). Bottom-up forces from hunting remains could trigger a numerical response, especially in species with a higher ability to track this pulsed resource and in cosmopolitan opportunistic species known to benefit from predictable anthropogenic food subsidies (e.g. generalists; see above; Oro *et al.*, 2013; Newsome *et al.*, 2015). This would increase their relative importance in the community and their associated cascading effects. High numbers of generalist scavengers could alter top-down forces, leading to higher levels of predation (i.e. hyperpredation) on alternative prey once carrion is consumed (Wilmers *et al.*, 2003; Killengreen *et al.*, 2012; Moleón *et al.*, 2014a). Human–wildlife conflicts (e.g. illegal poisoning; Mateo-Tomás *et al.*, 2012) could arise with increasing predation pressure on species of human interest (e.g. game, livestock; Read & Wilson, 2004; Newsome *et al.*, 2015).

Obligate scavengers (i.e. vultures) and apex predators can limit the presence of generalists at hunting remains (Moleón *et al.*, 2014a; Ripple *et al.*, 2014), out-competing them for food (Ruxton & Houston, 2004; Cortés-Avizanda *et al.*, 2012; Ogada *et al.*, 2012b). As keystone species, apex predators could also exert top-down control through both lethal

Table 2 Structure of scavenger communities at different carrion types. Percentages show the relative scavenging frequencies of each group (e.g. the proportion of carcasses scavenged by a species based on the total number of carcasses monitored; see main text for further details). Only studies with detailed datasets are included. Class and main scavenger groups defined according to criteria in Table S2. Colours as in Table 1. See Appendix S1 for references.

			Class		Main scaver	nger groups			
Type of carrion	Sample size*	Scavenging species N	Birds	Mammals	Generalists	Obligate scavengers	Apex predators	Study area	Reference
Rodents (Mus, Rattus)	26	11	7.7%	92.3%	100.0%	0	0	US-SC, SE USA	DeVault and Rhodes, 2002
Lagomorphs	14	7	95.9%	4.1%	na	37.4%	na	NW Patagonia	Sebastián-González <i>et al.</i> , 2013
(Lepus, Oryctolagus)	13	4	80.0%	17.0%	na	0	na	SE Australia	
	20	11	86.2%	13.8%	62.1%	37.9%	0	NE Spain	
	27	8	48.0%	59.0%	100.0%	0	0	SW Spain	
Naturally dead ungulates [†]	24	17	30.9%	69.1%	82.2%	0	16.7%	BPF, Poland [§]	Selva, 2004
Predator kills	74¶	19	48.9%	51.1%	88.9%	0	10.0%	BPF, Poland [§]	Selva, 2004
(ungulates [¶] , wild mammals [‡])	11¶	10	58.6%	41.4%	89.2%	0	3.5%	SBF, Sweden [§]	Wikenros <i>et al.</i> , 2013
	202"	12	33.2%	66.8%	92.6%	< 1.0%	7.4%	GYE, USA [§]	Wilmers et al., 2003
	460^{\ddagger}	12	55.6%	44.4%	25.1%	48.9%	26.0%	Tanzania	Hunter <i>et al.</i> , 2007
Domestic and wild ungulates	16	17	59.5%	40.5%	35.7%	42.9%	21.4%	NW Zimbabwe	Butler and Du Toit, 2002
Livestock (cows, goats)	61	22	91.6%	8.3%	19.8%	73.9%	6.3%	Central Kenya	Ogada <i>et al.</i> , 2012b; Ogada unpublished data

na, no data available.

*Number of individual carcasses monitored.

[†]Ungulates dead from other causes than predator kills or hunting (e.g. disease, malnutrition). [§]Study areas already considered in this work, see main text and Figs 1 and 2.

[¶]Ungulates and lagomorphs.

(i.e. predation) and non-lethal (e.g. spatio-temporal exclusion) effects (Ripple et al., 2014). Accordingly, in those areas with both obligate scavengers and apex predators (e.g. South African savanna), the already stated dominance of generalist species at hunting remains is considerably reduced (Fig. 3a and b; see also Table 2). The global dominance of generalist species in the scavenger community shown by our data (Fig. 3c) suggests an alteration of the top-down mechanisms exerted by obligate scavengers and apex predators likely due to their general decline across the planet (Ogada et al., 2012a; Ripple et al., 2014). Although information is lacking on the mechanisms linking structural and functional alterations in scavenger communities, the potential role of some overabundant generalist scavengers (e.g. wild board, feral dog) in spreading or maintaining diseases has been suggested (Pain et al., 2003; Vicente et al., 2011). This could be so especially in highly degraded ecosystems with low scavenger diversity where obligate scavengers that rapidly dispose of carcasses are absent (Markandya et al., 2008; Ogada et al., 2012a,b). Nonetheless, while aggregation and intraspecific contact at carcasses is often reported as a likely source of horizontal disease transmission for several scavengers (e.g. carnivores; Markandya et al., 2008; Ogada et al., 2012b; Newsome et al., 2015), the role of most scavengers in the transmission dynamics of diseases from carcasses remains widely unknown and even misunderstood (Bellan et al., 2013).

The general structure of the scavenger community at hunting remains provides a useful benchmark to which compare scavenger communities at other carrion types, advancing knowledge on the impacts of anthropogenic food subsidies on ecosystems (Oro et al., 2013). Similar to hunting remains, birds and mammals dominate scavenging at other carrion types (e.g. predator kills, naturally dead ungulates, small carcasses, livestock; Table 2). Generalist species and obligate scavengers are often reported consuming anthropogenic food subsidies world-wide (Oro et al., 2013), with large canids being the most prevalent consumers among apex predators (Newsome et al., 2015). As already described for hunting remains, the importance of generalists in the scavenger community decreases considerably when both obligate scavengers and apex predators are present (e.g. African ecosystems; Table 2). Further similarities emerge when comparing scavenging at different types of ungulate carcasses (Table 2). As already recorded at hunting remains, generalists dominate scavenging at predator kills and naturally dead ungulates while apex predators are present at lower frequencies. The scavenger communities at these ungulate carcasses (i.e. hunting remains, predator kills and naturally dead ungulates) share a similar nested structure (Selva & Fortuna, 2007) but opposite to that reported for small-sized carcasses (Sebastián-González et al., 2013). Predator kills are less aggregated in space and time than hunting remains (Wilmers et al., 2003; Selva, 2004; Wikenros et al., 2013) and thus might promote higher species diversity (Wilmers et al., 2003; Cortés-Avizanda et al., 2012). This has been noted in areas where both types of carrion have been monitored (i.e.

Yellowstone and Scandinavian forest, Fig. 2; Wilmers *et al.*, 2003; Wikenros *et al.*, 2013). Nonetheless, the opposite trend has also been reported (i.e. Bialowieza forest, Fig. 2e; Selva, 2004), highlighting the need for more research on the topic to properly deal with other factors that could further explain such differences in species richness (e.g. sample size, carcass characteristics; Wilmers *et al.*, 2003). Further analysis should assess the role of the type of carrion (i.e. entire corpses, guts, mixed remains, see Table S1) in shaping vertebrate scavenger communities. For example, carcass openness might affect species composition and/or richness by excluding/favouring some species according to their feeding preferences (Selva, 2004).

Additional efforts should be undertaken to get detailed data on the scavenger communities consuming different carrion types world-wide, especially in the current context of global change (Wilson & Wolkovich, 2011; Beasley et al., 2012). For example, data on scavenger communities at hunting remains are lacking for most terrestrial biomes (Fig. 2). Data on the availability of anthropogenic food subsidies are also needed for a better assessment of their potential impacts on scavenging and ecosystems (Weinbaum et al., 2013). Special attention should focus on Africa, Asia and South America. These regions harbour several biodiversity hotspots (Myers et al., 2000) and an increasing presence of food-subsidizing activities such as hunting and livestock rearing (Baldus et al., 2008; Lambertucci et al., 2009). Moreover, similar to that already described for livestock (Tella, 2001; Oaks et al., 2004; Donázar et al., 2009; Mateo-Tomás, 2009), most of the negative impacts of anthropogenic food subsidies on ecosystems could increase under intensification (Vicente et al., 2011; Oro et al., 2013). Nonetheless, more information on scavenging is necessary to improve our knowledge on the impacts of human activities on community and ecosystem processes, including nutrient and energy flows and provisioning of key ecosystem services associated with scavenging (e.g. disease control). As a first key step, characterizing scavenging links (as provided here) would allow their inclusion in food webs, further advancing our understanding of the ecological processes linking biodiversity, ecosystem functions and services (Wilson & Wolkovich, 2011; Thompson et al., 2012).

ACKNOWLEDGEMENTS

We thank D.L. Ogada and one anonymous referee for useful comments on the manuscript. We thank people at IREC, J. Sánchez, J.R. Lana, S. Eguía, A. Margalida, J.A. Donázar, G. Molleda, J.A. Ballester, J. Royo and forest rangers in Asturias, S. Espuña and S. Nevada for field assistance. Environmental authorities from Asturias, Andalucía, Conselh de Arán, Murcia and Comunidad Valencia, J.L. Marcos, G. Clinning, D. Druce, D. Kelly and Ezemvelo KZN Wildlife provided support and permissions. E. Osorio, A. Wajrak, A. Martínez, S. Justicia and S. Macaskill provided wildlife photographs. C.H. Flather provided data on hunting, and D.L. Ogada, data on scavenging in Central Kenya. PMT

was supported by a grant from Junta de Comunidades de Castilla-La Mancha and Fondo Social Europeo, MM by the Spanish Ministry of Education (Plan Nacional de I+D+i 2008-2011) and NS by the National Research Centre (project 2013/08/M/NZ9/00469) and by the National Centre for Research and Development in Poland, Norway grants (POL-NOR/198352/85/2013). JASZ, FBR, MM and NS were partially financed through projects RNM-1925 (Junta de Andalucía), CGL2006-10689/BOS, CGL2009-12753-C02-02 and CGL2012-40013-C02-01-02 (Ministerio Economía y Competitividadd, Spain), EU FEDER funds and the Access to Unique Technological and Scientific Infrastructure Programme 'Doñana Scientific Reserve' project 23/2007 ICTS-RBD. In memory of Miguel Blázquez.

REFERENCES

- Baldus, R.D., Damm, G.R. & Wollscheid, K. (2008) *Best Practices in Sustainable Hunting – A Guide to Best Practices from Around the World.* CIC – International Council for Game and Wildlife Conservation and FAO, Rome, Italy.
- Beasley, J.C., Olson, Z.H. & Devault, T.L. (2012) Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. *Oikos*, **121**, 1021–1026.
- Bellan, S.E., Turnbull, P.C.B., Beyer, W. & Getz, W.M. (2013) Effects of experimental exclusion of scavengers from carcasses of anthrax-infected herbivores on *Bacillus anthracis* sporulation, survival, and distribution. *Applied and Environmental Microbiology*, **79**, 3756–3761.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, **84**, 45–67.
- Cortés-Avizanda, A., Jovani, R., Carrete, M. & Donázar, J.A. (2012) Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology*, **93**, 2570–2579.
- DeVault, T.L., Rhodes, O.E. Jr & Shivik, J.A. (2003) Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, **102**, 225–234.
- Donázar, J.A., Margalida, A., Carrete, M. & Sánchez-Zapata, J.A. (2009) Too sanitary for vultures. *Science*, **326**, 664.
- Finkelstein, M.E., Doak, D.F., George, D., Burnett, J., Brandt, J., Church, M., Grantham, J. & Smith, D.R. (2012) Lead poisoning and the deceptive recovery of the critically endangered California condor. *Proceedings of the National Academy of Sciences USA*, **109**, 11449–11454.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gortázar, C. (2012) Wildlife research—science for a changing environment. *European Journal of Wildlife Research*, **58**, 1–4.
- IUCN (2014) The IUCN Red List of Threatened Species. Version 2014.1.

- Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**, 2427–2439.
- Kelly, T.R., Bloom, P.H., Torres, S.G., Hernandez, Y.Z., Poppenga, R.H., Boyce, W.M. & Johnson, C.K. (2011) Impact of the California lead ammunition ban on reducing lead exposure in golden eagles and turkey vultures. *PLoS ONE*, **6**, e17656.
- Killengreen, S.T., Strømseng, E., Yoccoz, N.G. & Ims, R.A. (2012) How ecological neighbourhoods influence the structure of the scavenger guild in low arctic tundra: neighbourhood effects on tundra scavenger guild. *Diversity and Distributions*, **18**, 563–574.
- Lambertucci, S.A., Trejo, A., Di Martino, S., Sánchez-Zapata, J.A., Donázar, J.A. & Hiraldo, F. (2009) Spatial and temporal patterns in the diet of the Andean condor: ecological replacement of native fauna by exotic species. *Animal Conservation*, **12**, 338–345.
- Lindsey, P., Roulet, P. & Romanach, S. (2007) Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation*, **134**, 455–469.
- Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2004) 100 of the World's Worst Invasive Alien Species. A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN).
- Magoun, A.J. (1976) Summer Scavenger Activity in Northeastern Alaska. University of Alaska, USA, M.Sc.
- 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**, 194–204.
- Mateo-Tomás, P. (2009) Management and conservation of vultures in the Cantabrian Mountains, NW Spain. PhD thesis. Universidad de León, Spain.
- Mateo-Tomás, P. & Olea, P.P. (2010) When hunting benefits raptors: a case study of game species and vultures. *European Journal of Wildlife Research*, **56**, 519–528.
- Mateo-Tomás, P., Olea, P.P., Sánchez-Barbudo, I.S. & Mateo, R. (2012) Alleviating human-wildlife conflicts: identifying the causes and mapping the risk of illegal poisoning of wild fauna: mapping illegal poisoning of wildlife. *Journal of Applied Ecology*, **49**, 376–385.
- Moleón, M., Sánchez-Zapata, J.A., Margalida, A., Carrete, M., Owen-Smith, N. & Donázar, J.A. (2014a) Humans and scavengers: the evolution of interactions and ecosystem services. *BioScience*, **64**, 394–403.
- Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donázar, J.A. & Owen-Smith, N. (2014b) Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews*, **89**, 1042–1054.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

- Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. & Dickman, C.R. (2015) The ecological effects of providing resource subsidies to predators: resource subsidies and predators. *Global Ecology and Biogeography*, 24, 1–11.
- Oaks, J.L., Gilbert, M., Virani, M.Z., Watson, R.T., Meteyer, C.U., Rideout, B.A., Shivaprasad, H.L., Ahmed, S., Chaudhry, M.J.I., Arshad, M., Mahmood, S., Ali, A. & Khan, A.A. (2004) Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature*, **427**, 630– 633.
- O'Connell, A.F., Nichols, J.D. & Karanth, K.U. (2010) *Camera Traps in Animal Ecology: Methods and Analyses.* Springer Science & Business Media, Japan.
- Ogada, D.L., Keesing, F. & Virani, M.Z. (2012a) Dropping dead: causes and consequences of vulture population declines worldwide: Worldwide decline of vultures. *Annals of the New York Academy of Sciences*, **1249**, 57–71.
- Ogada, D.L., Torchin, M.E., Kinnaird, M.F. & Ezenwa, V.O. (2012b) Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology*, **26**, 453–460.
- Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. & Martínez-Abraín, A. (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters*, **16**, 1501–1514.
- Pain, D.J., Cunningham, A.A., Donald, P.F., Duckworth, J.W., Houston, D.C., Katzner, T., Parry-Jones, J., Poole, C., Prakash, V., Round, P. & Timmins, R. (2003) Causes and effects of temporospatial declines of Gyps vultures in Asia. *Conservation Biology*, **17**, 661–671.
- Pain, D.J., Cromie, R.L., Newth, J., Brown, M.J., Crutcher, E., Hardman, P., Hurst, L., Mateo, R., Meharg, A.A., Moran, A.C., Raab, A., Taggart, M.A. & Green, R.E. (2010) Potential hazard to human health from exposure to fragments of lead bullets and shot in the tissues of game animals. *PLoS ONE*, **5**, e10315.
- R Development Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Read, J.L. & Wilson, D. (2004) Scavengers and detritivores of kangaroo harvest offcuts in arid Australia. *Wildlife Research*, **31**, 51–56.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie,
 E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M.,
 Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. &
 Wirsing, A.J. (2014) Status and ecological effects of the
 world's largest carnivores. *Science*, 343, 1241484.
- Ruxton, G.D. & Houston, D.C. (2004) Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology*, **228**, 431–436.
- Sebastián-González, E., Sánchez-Zapata, J.A., Donázar, J.A., Selva, N., Cortés-Avizanda, A., Hiraldo, F., Blázquez, M., Botella, F. & Moleón, M. (2013) Interactive effects of obligate scavengers and scavenger community richness on

lagomorph carcass consumption patterns. *Ibis*, **155**, 881–885.

- Segar, S.T., Pereira, R.A.S., Compton, S.G. & Cook, J.M. (2013) Convergent structure of multitrophic communities over three continents. *Ecology Letters*, 16, 1436–1445.
- Selva, N. (2004) The role of scavenging in the predator community of Bialowieza Primeval Forest (Poland). PhD thesis. Universidad de Sevilla, Spain.
- Selva, N. & Fortuna, M.A. (2007) The nested structure of a scavenger community. *Proceedings of the Royal Society B*, **274**, 1101–1108.
- Tella, J.L. (2001) Action is needed now, or BSE crisis could wipe out endangered birds of prey. *Nature*, **410**, 408.
- Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B. & Tylianakis, J.M. (2012) Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, **27**, 689–697.
- Torres-Porras, J., Carranza, J., Pérez-González, J., Mateos, C. & Alarcos, S. (2014) The tragedy of the commons: unsustainable population structure of Iberian red deer in hunting estates. *European Journal of Wildlife Research*, **60**, 351–357.
- US Fish and Wildlife Service (2011) U.S. Department of the Interior, U.S. Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau. 2011 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation.
- Vicente, J., Carrasco, R., Acevedo, P., Montoro, V. & Gortazar, C. (2011) Big Game Waste Production: Sanitary and Ecological Implications. *Integrated Waste Management Volume II* (ed. by S. Kumar), pp. 97–128. InTech, Rijeka, Croatia.
- Weinbaum, K.Z., Brashares, J.S., Golden, C.D. & Getz, W.M. (2013) Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecology Letters*, **16**, 99–111.
- Wenny, D.G., DeVault, T.L., Johnson, M.D., Kelly, D., H. Sekercioglu, C., Tomback, D.F. & Whelan, C.J. (2011) The need to quantify ecosystem services provided by birds. *The Auk*, **128**, 1–14.
- White, C. (2006) Indirect effects of elk harvesting on ravens in Jackson Hole, Wyoming. *Journal of Wildlife Management*, **70**, 539–545.
- Wikenros, C., Sand, H., Ahlqvist, P. & Liberg, O. (2013) Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. *PLoS ONE*, **8**, e77373.
- Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W. & Getz, W.M. (2003) Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA: resource dispersion and consumer dominance. *Ecology Letters*, 6, 996–1003.
- Wilson, E.E. & Wolkovich, E.M. (2011) Scavenging: how carnivores and carrion structure communities. *Trends in Ecol*ogy & *Evolution*, **26**, 129–135.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species names, photo credits and additional references for Tables and Figures.

 Table S1 Main characteristics of the study areas and hunting remains analysed.

Table S2Scavenger species detected consuming huntingremains worldwide.

Table S3 Variables considered to explain global patterns inscavenger communities.

BIOSKETCH

The authors research on ecology and conservation biology of terrestrial ecosystems with a special focus on vertebrates and scavengers and their relationships with human activities.

Author contributions: P.M.T. conceived the initial idea of the manuscript, to whose development further contributed P.P.O. and J.S.Z.; all authors collected data; P.M.T. and P.P.O. performed the analysis and wrote the manuscript; and all authors contributed to revisions.

Editor: David M. Richardson