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Unexpected role of ungulate carcasses in the diet of Golden Eagles *Aquila chrysaetos* in Mediterranean mountains

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Capsule Golden Eagles consumed more carrion than shown by traditional analyses.

Aims To determine whether the traditional methods for diet determination in avian predators are subject to biases in relation to the consumption of carrion.

Methods The consumption by Golden Eagles of ungulate carcasses supplied through sport hunting in a typical Mediterranean area of southeast Spain was monitored by camera trapping through an entire year. We simultaneously analysed the breeding diet of three Eagle pairs by conventional procedures.

Results Golden Eagles regularly used ungulate carrion in the study area, benefiting from 57% of the available carcasses. Ninety percent of the territorial eagles fed on monitored carcasses, and the consumption was similar through the year. However, this source of food comprised only 1.5–9.1% of the prey items identified by traditional methods.

Conclusions Our findings suggest that pellet and prey remains analyses under-represent the role of carrion in the diet of avian predators in Mediterranean ecosystems. The difficulty of quantifying scavenged material in predators' diets have probably contributed to the perception that the scavenging behaviour of species such as Golden Eagles are unimportant in the regulation and functioning of certain ecosystems.

Accurate studies regarding food habits are key for the correct understanding of many animal ecology and life-history traits. However, dietary estimates are subject to several biases when indirect procedures are employed, such as those not based on a direct and continuous observation of the hunting and feeding behaviour of the predator. In predators such as raptors, the most common methods used are the analysis of regurgitated food pellets and/or prey remains (e.g. hair, feathers and bones) (Marti 1987), which are highly dependent on factors such as prey size, environmental conditions, or cleaning behaviour of the predator at nests/roosting sites (Marti 1987, Mersmann *et al.* 1992, Mañosa 1994, Real 1996, Sánchez-Zapata & Calvo 1998, Redpath *et al.* 2001). The errors associated with these procedures can lead to important misinterpretations on the role of a particular prey species in the ecology of the predator.

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Carrion, such as ungulate carcasses, are rich but ephemeral resources extensively used by vertebrates (see a review in DeVault *et al.* [2003]), and their consumption is increasingly recognized as a key ecological process influencing population dynamics, community structure and ecosystem functioning (DeVault *et al.* 2003, Selva 2004, Selva & Fortuna 2007, Cortés *et al.* 2009; Blázquez *et al.* 2009). Carrion availability depends on different sources of death, including disease, malnutrition, parasites, predation and accidents (DeVault *et al.* 2003). In many temperate ecosystems, however, the regulation of ungulate populations through hunting is the main source of carrion for scavengers, particularly where top predators such as Wolves *Canis lupus* are lacking (Wilmers *et al.* 2003). When obligate scavengers are absent, generalist vertebrate predators, which are frequently also facultative scavengers, may account for most of the carcass consumption in terrestrial ecosystems (DeVault *et al.* 2003). However, despite the ecological influence of this source of food, its importance in the diet of facultative

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vertebrate predators has largely been underestimated due to the difficulty of detection of carrion signs by the traditional methods (DeVault & Rhodes 2002, DeVault *et al.* 2003).

Golden Eagles *Aquila chrysaetos* are facultative scavengers, distributed throughout the northern Hemisphere. They are large, highly territorial raptors which have been reported to feed upon medium sized birds and mammals in Mediterranean habitats, European Rabbits *Oryctolagus cuniculus* being the most common prey found in this region (30–65% of the total prey items) (Delibes *et al.* 1975, Jordano 1981, Clouet & Goar 1984, Fernández & Purroy 1990, Fernández 1993, Gil-Sánchez *et al.* 1994, Sánchez-Zapata 1999, Moleón *et al.* 2002a). Although the consumption of carrion in its Mediterranean range has rarely been reported (see previous references), Golden Eagles may employ scavenging frequently in northern latitudes (see a review in Watson [1997]) at least during cold seasons (Halley & Gjershaug 1996, Watson 1997).

Here, we take advantage of a carrion monitoring schedule based on camera trapping to explore if the traditional methods used to assess the species' diet (i.e. pellets and prey remains) are subject to biases related to the consumption of this poorly-studied source of food in a top predator-free Mediterranean area.

MATERIAL AND METHODS

Study area

The study area comprised the Sierra Espuña Regional Park in southeast Spain (2°4′–2°14′N 37°47′–37°57′W) (Fig. 1), and covered 17 800 ha of meso- and supra-Mediterranean habitats ranging from 500 to 1500 m a.s.l. The landscape is dominated by mountain ridges and valleys covered mostly by *Pinus halepensis* woods, scrub and pasture (Sánchez-Zapata & Calvo 1999). Rainfall ranges from 277 mm in the lower part of the mountains to 510 mm in the upper parts of the park. Average annual temperatures also follow an altitudinal gradient ranging from 12.8–18.4 °C. Five Golden Eagle nesting pairs have been recorded during the study (Carrete 2002; Blázquez *et al.* 2009). Four of them were succesful (raised young) during the study and one pair failed. There are no obligate scavengers such as Griffon Vultures *Gyps fulvus*, which have been absent since 1970s and only visit the area occasionally (Sánchez-Zapata & Eguía 2007).

Barbary Sheep *Ammotragus lervia* are large ungulates (40–132 kg), introduced into the study area for hunting purposes in 1970 (González-Candela *et al.* 2004) and which are now subject to culling from June to January. Carcasses from hunters' kills are readily available in the study area (75–100 kg carrion/km^2 per year), but their spatial and temporal arrangement is not homogeneous. Hunter kills take place from summer to winter and hunting kills are skinned and the bodies abandoned in the field (Sánchez-Zapata & Eguía 2007).

Carcass monitoring

We monitored carrion use during a complete hunting period, from November 2005 to October 2006, excluding the spring period from February to May when Barbary Sheep hunting is not permitted (Blázquez *et al.* 2009). Monitoring of carrion consumption was divided into two periods: winter (from November to January) and summer (June to October). In total, we monitored 20 carcasses during winter and 22 carcasses during summer.

Carcasses were monitored with automatic cameras (Blázquez *et al.* 2009) activated by movement (Bushnell Trail Scout 2.1MP) (n = 34 carcasses) or through visual inspections of carcasses with telescopes (n = 8) to assess their use by scavengers. The cameras were hidden close to carcasses immediately after the hunters had left the remains. Cameras were active until carcasses were completely consumed, excluding the skeleton. They were programmed to record one picture every two minutes after being activated and to operate 24 hours day^{-1}. The cameras were attached to trees or shrubs approximately 4 m from the carcass and were camouflaged to avoid conspicuous human signs. Pictures provided information on the species that feed on the carcass, as well as the number of individuals, date and time. Each carcass was visited every 48 hours to download pictures. We assessed scavenging activity (also called feeding time, in minutes) by measuring the time between consecutive pictures. We assigned two-minute scavenging activity to single pictures. However, cameras recorded several faulty pictures and their sensitivity was dependent on the weather conditions (DeVault & Rhodes 2002, pers. obs.), and so we were conservative when assigning a species to a scavenging event (we only did so when an animal was clearly identified). Cameras therefore supplied information about the minimum scavenging activity and minimum number of species at the carcasses. All carcasses available (both monitored and non-monitored carcasses) in the study area during the study period (the days when carcass monitoring was

performed) were global positioning system located to obtain a map of their spatial distribution.

Diet of the Golden Eagle

The diet of three of the Golden Eagle pairs living in the park was studied in 2006 by means of conventional procedures. As is usual in this species (Delibes *et al.* 1975, Jordano 1981, Clouet & Goar 1984, Fernández & Purroy 1990, Fernández 1993, Gil-Sánchez *et al.* 1994, Sánchez-Zapata 1999, Moleón *et al.* 2002a; Whitfield *et al.* 2009), pellets and prey remains were collected from within the nesting areas (under/in the occupied nests and at nearby roosts) at the end of the breeding season (June–August) so avoiding any disturbance to the breeding process, which ended successfully for all three pairs considered. The content of the food pellets were macroscopically analysed (González 1991). Each prey species identified in one pellet was counted as one individual (Real 1996).

The results from pellet and prey remains analyses are shown both combined and separately for each method, in order to ascertain biases associated to each one (Real 1996). For some purposes, prey species were grouped in three different categories: 'mammals', 'birds' and 'reptiles'. Results are compared in terms of frequency of occurrence of each group over the total of prey items, the most common procedure in diet studies for this (Fernández & Purroy 1990, Moleón *et al.* 2002a) and other similar-sized raptors (Donázar *et al.* 1989, González 1991, Gil-Sánchez & Pleguezuelos 2001, Moleón *et al.* 2009).

RESULTS

Carcass consumption by Golden Eagles

Golden Eagles were the most frequently observed birds at carcasses, as judged by presence/absence at all 42 carcasses. Golden Eagles were the main avian scavenger in the study area, benefiting from a large proportion of the available carcasses (57%; at least 24 of the 42 carcasses). Golden Eagles fed on a similar percentage of available carcasses through the year, as they used 13 out of 20 (65%) carcasses in winter and 11 out of 22 (50%) carcasses in summer (see Fig. 1). In addition, Golden Eagles were the first species to arrive at carcasses in most instances (80% of the carcasses). Other diurnal species, such as Common Raven *Corvus corax*, Black-billed Magpie *Pica pica* or Griffon Vulture, were also observed feeding on carcasses (38%, 7%, and 2% of the carcasses, respectively). Red Foxes *Vulpes vulpes* commonly visited carcasses at night and benefited from a large number of carcasses (57%). Other nocturnal scavengers recorded were Wild Boar *Sus scrofa*, Domestic Dogs *Canis lupus familiaris* and Stone Martens *Martes foina* (40%, 12%, and 7%, respectively).

Cameras recorded a total of 2014 pictures. They allowed us to identify, by means of plumage characteristics and the distance to active nests, at least nine different adult Golden Eagles belonging to the five breeding pairs of the Regional Park and at least three different subadult eagles feeding at carcasses. In 677 pictures we identified Golden Eagles feeding on the carcass (33.6% of total pictures, 42.2 ± 61.0 pictures/carcass mean ± sd, n = 16 carcasses) (Table 1). We observed at least 87 visits of Golden Eagles to carcasses and the mean time spent at a carcass (considering all the visits) was 111.5 ± 92.0 min (mean ± sd, n = 16 carcasses) (Table 1).

Diet of Golden Eagles

We obtained a minimum of 99 prey items for the breeding season, 33 of which belonged to prey remains and 66 to the analysis of 36 food pellets. Overall, mammals were the most frequent prey group in the diet Golden Eagles (54.6%), followed by birds (34.3%) and reptiles (11.1%) (Table 2, Appendix 1). However, the diet composition differed significantly between methods (χ^2 = 34.5, df = 2, P < 0.0001), as birds appeared more frequently in prey remains (51.5%, followed by mammals, 42.4%, and reptiles 6.1%), while mammals were more numerous in the pellet contents (60.6%, by birds, 25.8%, and reptiles, 3.6%; Table 2; Appendix 1).

The prey species taken most frequently by Golden Eagles were, and depending on the analysis method, Rabbits (43.6% of the total prey remains and pellets combined, and 56.1% in pellet content) and Rock (Feral) Pigeon *Columba livia* (24.3% in prey remains) (Table 2, Appendix 1).

Ungulate carrion comprised only 1.5% and 9.1% of the total prey items identified by the analyses of pellets and prey remains, respectively (Table 2, Appendix 1).

DISCUSSION

Golden Eagles were the most common diurnal scavenger at ungulate carcasses in the study area, benefiting from at least 50–65% of the carcasses available. This means that eagles might feed upon more than 100 carcasses of Barbary Sheep per year within the limits of

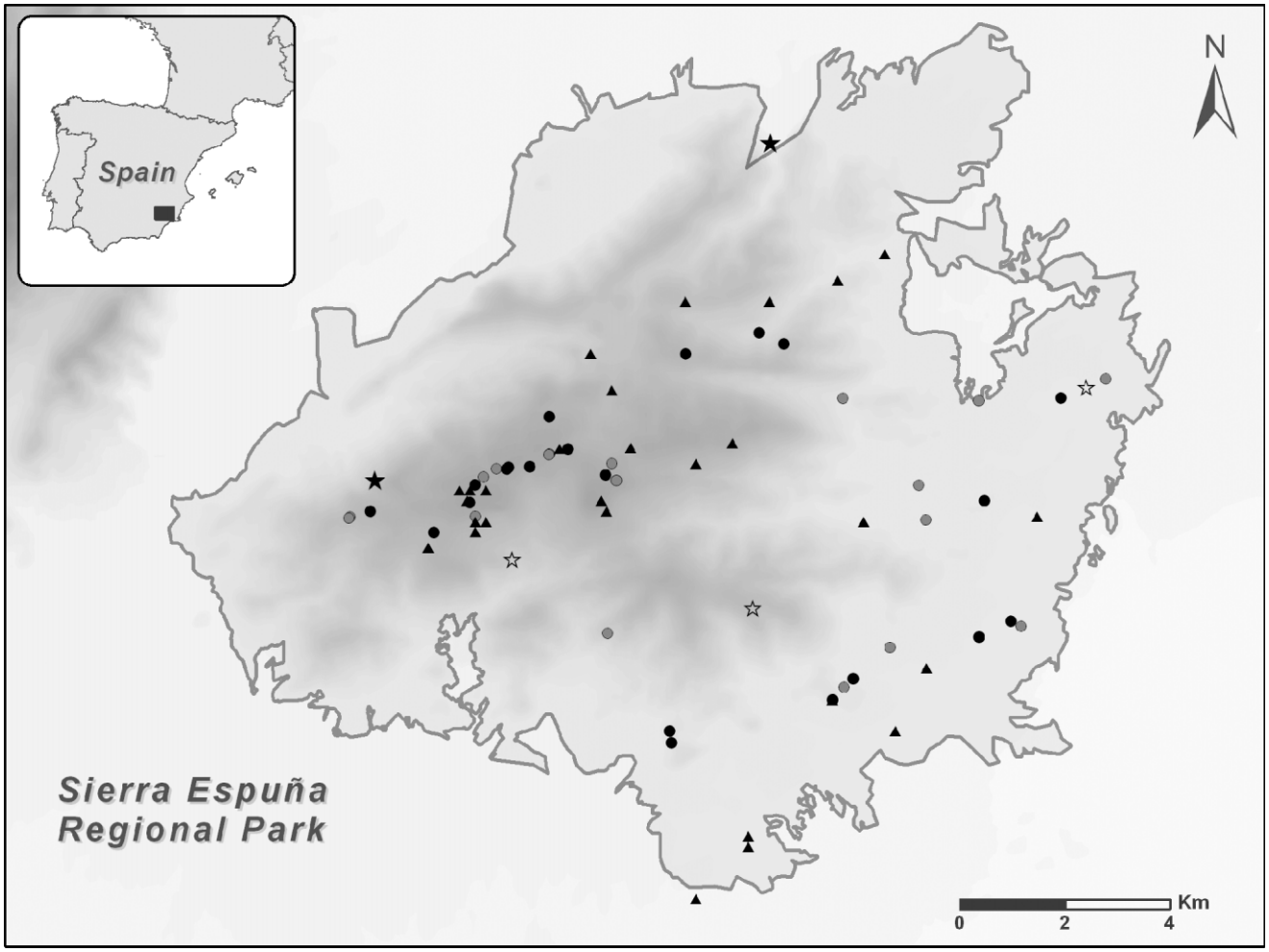

Figure 1. Carcass arrangement and Golden Eagle nests (nest locations have been changed in order to avoid possible disturbances at the breeding sites). ◯, monitored carcasses; ●, carcasses used by Golden Eagles; ▲, non-monitored carcasses; ★, Golden Eagle territories; ☆, Golden Eagle territories with analysed diet.

Table 1. Scavenging activity (minutes) and recorded pictures of Golden Eagles at the camera-monitored carcasses.

	No. pictures		Scavenging activity (min)		
	Pictures/carcass (mean ± sd)	Total pictures	Minutes/carcass (mean ± sd)	Total minutes	No. used carcasses
Adults	35.8 ± 60.5	573	91.7 ± 88.0	1468	16
Subadults	6.5 ± 14.5	104	15.1 ± 34.9	242	4
Winter	27.9 ± 32.9	195	93.0 ± 70.2	651	7
Summer	53.4 ± 77.1	482	125.9 ± 108.6	1059	9
Total	42.2 ± 61.0	677	111.5 ± 92.0	1710	16

the Game Reserve (the total annual availability here is over 200 carcasses; Dirección General del Medio Natural de Murcia, pers. com.). In fact, Golden Eagles were the first species to arrive at a carcass in most instances. Thus Golden Eagles seem to show a very high and important level of scavenging efficiency (Houston 1979) similar to that described for ravens that fed upon hunting kills (White 2005). Golden Eagles might also benefit from the same hunting cues and, although there is no experimental evidence, both

Table 2. Diet of Golden Eagles in the breeding season. Quantity and percentage (in brackets) of prey items detected in pellets and remains from three breeding territories in the study area.

	Prey remains	Pellets	Prey remains and pellets
European Rabbit *Oryctolagus cuniculus*	6 (18.2)	37 (56.1)	43 (43.6)
Iberian Hare *Lepus granatensis*	4 (12.1)	–	4 (4.0)
Red Squirrel *Sciurus vulgaris*	–	1 (1.5)	1 (1.0)
Wild Boar *Sus scrofa*	–	1 (1.5)	1 (1.0)
Barbary Sheep *Ammotragus lervia*	3 (9.1)	–	3 (3.0)
Red Fox *Vulpes vulpes*	1 (3.0)	1 (1.5)	2 (2.0)
Mammals	14 (42.4)	40 (60.6)	54 (54.6)
Red-legged Partridge *Alectoris rufa*	–	1 (1.5)	1 (1.0)
Common Wood Pigeon *Columba palumbus*	1 (3.0)	–	1 (1.0)
Domestic Pigeon *Columba livia*	8 (24.3)	6 (9.2)	14 (14.2)
Wild Pigeon *Columba livia*	1 (3.0)	–	1 (1.0)
Eurasian Jay *Garrulus glandarius*	2 (6.1)	2 (3.0)	4 (4.0)
Red-billed Chough *Phyrrocorax phyrrocorax*	2 (6.1)	–	2 (2.0)
Tawny Owl *Strix aluco*	1 (3.0)	–	1 (1.0)
Common Kestrel *Falco tinnunculus*	–	1 (1.5)	1 (1.0)
Northern Goshawk *Accipiter gentilis*	1 (3.0)	–	1 (1.0)
Unknown bird	1 (3.0)	7 (10.6)	8 (8.1)
Birds	17 (51.5)	17 (25.8)	34 (34.3)
Ocellated Lizard *Lacerta lepida*	2 (6.1)	2 (3.0)	4 (4.0)
Unknown snake	–	7 (10.6)	7 (7.1)
Reptiles	2 (6.1)	9 (13.6)	11 (11.1)
Total	33	66	99

eagles and ravens were frequently observed immediately after sheep were killed in the study area (authors, pers. obs., rangers, pers. obs.). On the other hand, we identified at least 12 different Golden Eagle individuals foraging at carcasses, but we never detected more than two adult eagles feeding on the same carcass, which may support the case for strong intraspecific competition at resources described in previous studies (Carrete *et al.* 2005, 2006).

Carrion has sparsely been considered as a food resource for Golden Eagles in Mediterranean habitats previously (Delibes *et al.* 1975, Jordano 1981, Clouet & Goar 1984, Fernández & Purroy 1990, Gil-Sánchez *et al.* 1994, Sánchez-Zapata *et al.* 1995, Moleón *et al.* 2002a, although see the latter reference). In this study, the results obtained from pellets and prey remains were very similar to those described in the studies mentioned previously, highlighting the role of rabbits as a key prey species, and medium-sized birds and reptiles as complementary food resources. In contrast, by means of carcass monitoring we have assessed that eagles intensively fed on carrion during the big-game hunting season in the study area.

In effect our results have demonstrated notable deficiencies in the estimate of the species' diet when inferred from the traditionally used methods, i.e. the analysis of pellets and prey remains. Neither of these two methods indicated the regular intake of carrion, unlike the carrion monitoring by camera trapping. In fact, only 4 of the 99 prey items identified by these methods probably corresponded to carrion (Table 2). The principal explanation for this strong bias could be related to the practice in the reserve of skinning the carcasses, such that the direct ingestion of the readily digestible flesh and intestines, barely leaves corresponding signs of hair and bones, as has also been demonstrated for other raptor species (e.g., Sánchez-Zapata & Calvo 1998, García 2006). In addition, the carrion is eaten *in situ*, meaning none appears as remains in nests or at perches. Although our results are only directly comparable for the months of June to August (when there were simultaneous data from pellets, remains and carrion use), a diet study from the non-breeding period (September–January) would also probably highlight an underestimation of carrion consumption (Halley & Gjershaug 1996, Watson 1997), due to both the similar carcass consumption found in that season and the lower abundance in Mediterranean environments of the other prey items (Moleón *et al.* 2007) in comparison to the spring–summer season.

The underestimate of the carrion consumption in Golden Eagle diet studies in Mediterranean environments could also be caused in part by the scarcity of this resource in the first half of the breeding season.

Carrion represents an important, but seasonally limited resource given that carrion is principally available during the period of large game culling (Barbary Sheep in our case), which in the Iberian Peninsula generally falls between the end of spring and the beginning of the following winter. Carrion availability should be much scarcer outside these months, and related to natural mortality (disease and accidents) and very occasionally through poaching. If the Golden Eagle diet studies reflect the first part of the breeding season (when there is no ungulate hunting), the resulting biases could be expected to be small. However, the majority of the diet studies for this species are conducted using material collected at the end of the breeding season (a period which temporarily coincides with the beginning of the ungulate hunting season; see aforementioned references). In addition, Fernández (1987) found that this material principally reflected the diet towards the end of the breeding season, given the gradual changes in diet which occur after its onset. Consequently it seems plausible to suggest that the dietary composition revealed by the majority of studies on diet in the Iberian Peninsula published to date, may have genuinely underestimated, to greater or lesser degree, the importance of carrion. Whatever the case, it would be interesting to study Golden Eagle diet during those months of the breeding season with lowest carrion availability (February–May) in those locations where regular carrion consumption is suspected during the hunting season (see concluding remarks).

Additionally, it is possible that the pellets and remains found at perches during the breeding season, and especially those found at nests, may combine those produced by chicks and adults. In a population of Golden Eagles in Idaho, USA, Collopy (1983) found an unbiased relationship between the dietary composition as inferred from direct observations of prey taken to nests compared with that via analyses of the remains together with pellets from the immediate surroundings of the nest (even if the total number of prey was overestimated when combining remains and pellets). This indicates that the diet estimated using pellets and remains could *a priori* be true for the chicks (although at the same time we would continue to support our hypothesis of important biases in the case of adults).

Finally, the results we obtained through conventional analyses were clearly different depending on which source we used (pellets or remains). This may be because of the greater detectability of prey, such as birds, which leave abundant remains (e.g. feathers) in the nest and perch sites, as compared with those prey, such as Rabbits, which are almost completely eaten; in contrast, this last group of prey appears with greater frequency in the pellets. This type of bias in relation to the diet study method employed is well-known in many raptor species (Real 1996, Sánchez-Zapata & Calvo 1998, Redpath *et al.* 2001), with the analysis of pellets being generally recommended as the best method for diet evaluation (Real 1996), especially if comparisons between periods and/or localities is involved (Moleón *et al.* 2009). Even so, we found evident biases in diet as estimated through pellet analysis in the case of a facultative scavenger.

Concluding remarks and conservation implications

Although Golden Eagles in the Sierra Espuña appear primarily to exploit rabbits as its main food source, Barbary Sheep carcasses must act as a highly important dietary complement during the hunting season. Our conclusions can be extrapolated to many other Mediterranean ecosystems within the distribution range of the Golden Eagle, where wild ungulates and hunting are common, and where the skinned carcasses of the quarry are left in the field (either whole, or indeed just the intestines); in contrast, in those areas where carrion derives principally from livestock or the natural deaths of wild animals (i.e. unskinned), the biases would probably be less than those suggested here. Equally, similar results to those found in this study should be expected in other Mediterranean facultative (and even obligate) avian scavengers such as other raptors for example, Spanish Imperial Eagles *Aquila adalberti*, Black Kites *Milvus migrans* and Red Kites *M. milvus*, or corvids.

We also highlight the great importance, both in theoretical and applied fields, for the methodological and diet studies undertaken during different seasons with the aim of obtaining precise data on the frequency of consumption and the relative importance of the different prey of a predator (Moleón *et al.* 2007). In particular, further studies focussing on evaluating in quantitative terms the bias produced (and qualitatively documented here) by conventional methods when Golden Eagles (or any other facultative scavenger) consumes carrion, would be particularly welcome.

In addition, our results are in agreement with the fact that deaths through poisoning (typically administered on carrion baits) are one of the most widespread problems for Golden Eagle in Mediterranean environments (Arroyo *et al.* 1990, Gil-Sánchez 1996, Moleón

et al. 2002b, Arroyo 2004, Bautista *et al.* 2006). We have shown that ungulate carcasses may be consumed regularly by the species, such that it is constantly potentially exposed, at least in our study area to the threat of poisoning. In parallel, the removal of ungulate carcasses from the countryside as a consequence of the sanitary measures imposed in Mediterranean countries as a preventative measure against the transmission of spongiform encephalopathies could negatively affect not only obligate scavengers (Donázar *et al.* 2009), but probably also facultative ones such as Golden Eagles.

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APPENDIX 1. Diet (number of prey items) of Golden Eagles in each of the three breeding territories were prey remains (R) and pellets (P) were collected.

	Territory A		Territory B		Territory C	
Prey item	R	P	R	P	R	P
European Rabbit *Oryctolagus cuniculus*	3	11	2	8	1	18
Iberian Hare *Lepus granatensis*	1		2		1	
Red Squirrel *Sciurus vulgaris*				1		
Wild Boar *Sus scrofa*						1
Barbary Sheep *Ammotragus lervia*			1		2	
Red Fox *Vulpes vulpes*	1	1				
Red-legged Partridge *Alectoris rufa*		1				
Common Wood Pigeon *Columba palumbus*	1					
Domestic Pigeon *Columba livia*	1	2	5	1	2	3
Wild Pigeon *Columba livia*					1	
Eurasian Jay *Garrulus glandarius*	2	2				
Red-billed Chough *Phyrrocorax phyrrocorax*			1		1	
Tawny Owl *Strix aluco*	1					
Common Kestrel *Falco tinnunculus*				1		
Northern Goshawk *Accipiter gentilis*	1					
Unknown bird		3	1	4		
Ocellated Lizard *Lacerta lepida*	1	1	1			1
Unknown snake				1		6
Total	12	21	13	16	8	29