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The role of traditional farming practices in ecosystem conservation: The case of transhumance and vultures

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ABSTRACT

Transhumance is a traditional livestock practice based on the movement of livestock between winter and summer pastures with importance placed on biodiversity conservation. We analyzed the transhumant activity of sheep and cows in the uplands of the Cantabrian Mountains, NW Spain, and its influence on the ecology and management of the griffon vulture, a scavenger with a relevant ecosystem function. For the first time, we provided strong evidence of the close relationship between vultures and transhumance, which was previously only suggested. Vultures occupied roosting sites very close to the summer pastures and often consumed livestock carcasses. There was a strong spatiotemporal adjustment in the use of these mountain areas by transhumant livestock, especially sheep, and vultures. The number of transhumant sheep and cows within 10–12.5 km around the roosts were the best predictors of vulture occurrence and abundance, respectively, in generalized linear mixed models. Our estimates of potentially available food from livestock carcasses for vultures indicated that our study area can maintain important griffon vulture populations through a system based on traditional livestock farming including transhumance. Thus, transhumance is able to influence the top of the ecosystem (scavengers) and could aid in sustainable management of griffon vulture populations. In our study area, transhumant sheep were reduced by 62% in the last 15 years and only 20% of summer pastures are now occupied. The potential impact that the ongoing loss of transhumant activity could have on mountain ecosystem conservation should be assessed and taken into account by the new European Common Agricultural Policy.

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1. Introduction

Many semi-natural ecosystems have resulted from a dynamic equilibrium between wildlife and human activities that have shaped one another over the centuries (Pykala, 2000; Sutherland, 2002). Around half of the European network of Natura 2000 sites are farmed habitats that support a wider range of species than those found in purely natural habitats (MacDonald et al., 2000). However, the rapid changes experienced by agrarian practices (i.e., intensification, mechanization, abandonment) in the last decades have been highlighted as one of the main threats to biodiversity (Luoto et al., 2003; Butler et al., 2007), thereby, altering the composition, structure and function of ecosystems (Vitousek et al., 1997; Kremen and Ostfeld, 2005).

Transhumance is a traditional farming practice that shapes the landscape and benefits ecosystem conservation (Ruiz and Ruiz,

1986; MacDonald et al., 2000; Fortina et al., 2001; Garzón, 2001). This farming system consists of the movement of livestock between winter and summer pastures, maximizing resource exploitation through grazing (Ruiz and Ruiz, 1986). Transhumant systems have been common for centuries in many regions of the Old World (Ruiz and Ruiz, 1986). Today they are still the main livelihood, alleviating rural poverty, in some regions of the world (i.e., Muktan et al., 2008). However, despite this practice being present in many European countries from Balkans to Scotland, it is a currently declining activity in Europe (Ruiz and Ruiz, 1986; Liberatori and Penteriani, 2001). The progressive loss of this land-use model means, besides the decrease of economic and natural capital, the disappearance of an entire culture, which was specially developed over centuries around the wool market (Ruiz and Ruiz, 1986). Many mountain areas in Europe where transhumant livestock spend most of the year have developed highly diverse ecosystems that play a significant role in conserving biodiversity (MacDonald et al., 2000). Interestingly, the adaptation of transhumant livestock practices to resource availability could also provide an optimal way to minimize possible impacts on livestock production derived from climate change (Birch and Grahn, 2007).

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Although recent modifications of the Community Agrarian Policy (CAP; (EC)1698/2005) try to promote sustainable farming systems, several interpretations have been made that encourage very different farming systems that are sometimes not sustainable (Bignal, 2001; Elbersen et al., 2001). Therefore, there is an urgent need to clearly define the relationships between farming and nature conservation in the context of this policy. To manage ecosystems efficiently in a changing human-dominated world, we need to know how human activities influence ecosystem structure and function. The importance that transhumance has in the conservation of natural ecosystems and their biodiversity has rarely been analyzed. Most studies focus on its influence on conservation of plants and invertebrates (Saberwal, 1996; Schmid, 2001; Unusbayev, 2001). However, to our knowledge, no works have described the importance that transhumant activity could have on vertebrate conservation, particularly at the top of the ecosystem, i.e., scavengers. The close relationship between scavengers and transhumant flocks has been suggested previously (Ruiz and Ruiz, 1986; Garzón, 2001; Xirouchakis and Mylonas, 2004) but no formal analyses have been developed. An assessment of the influence that this traditional practice could have on the ecology and conservation of the scavenger guild could be a relevant issue when considering how the ecosystem function of scavengers (i.e., acceleration of nutrient return, limitation of diseases spread from decomposing carcasses or avoidance of an increase in undesirable species) is difficult to replace (Sekercioglu et al., 2004). This is especially important in regard to the context of the current global vulture crisis (Sekercioglu, 2006). The main causes of this crisis are mostly related to important changes in farming practices such as diclofenac use in Asia (Pain et al., 2003; Green et al., 2006), sanitary restrictions derived from bovine spongiform encephalopathy (BSE) in Europe (Tella, 2001; Camiña and Montelío, 2006) and medicated cattle passing antibiotics and affecting vultures in Spain (Lemus et al., 2008). Knowing how farming activities influence scavenger populations is the first step in dealing with the current problems in vulture management. Traditional farming practices, such as transhumance, may be a useful tool in the sustainable management of some vulture populations. This could be especially important in a context based highly on the artificial maintenance of large vulture populations through feeding stations or dumps. This food mainly comes from intensive farming and is generating serious sanitary, social and conservation problems (Lemus et al., 2008; Sánchez-Zapata et al., 2008).

In this work, we analyze the influence of transhumance at the top of the ecosystem. We study the relationship between transhumant livestock and griffon vultures (*Gyps fulvus*) in a mountainous semi-natural ecosystem in NW Spain. In particular, we: (i) analyzed the trend of this practice over the last 15 years and (ii) assessed consumption of livestock carcasses and estimated potential availability of food for vultures through questionnaires given to shepherds and official databases; (iii) studied spatiotemporal patterns of use of highland summer pastures by transhumant livestock and vultures and looked at how one adjusts the other and (iv) took advantage of a natural experiment where recent and rapid changes in the use of some mountain pastures by livestock enabled us to see how vultures respond. Moreover, our study area provides an example of a scavenger community, dominated by the griffon vulture that still acts in a semi-natural way. This is because there were no intensive farming systems or feeding stations in the study area. Finally, we provide information about the potential role that this declining traditional activity has on the management of scavengers' populations and, therefore, on one important part of the structure and function of ecosystems.

2. Materials and methods

2.1. Study system: transhumance and the griffon vulture

2.1.1. Transhumance

The climatic, topographic and anthropological characteristics of Spain enabled the development of transhumance, mainly consisting of sheep. Accordingly, a huge net of tracks (named *cañadas reales*) were created more than seven centuries ago. These tracks were used to move up to 3.5 million sheep each year between wintering areas and summer pastures (Rodríguez, 2004). A major destination on these routes were the Cantabrian Mountains (NW Spain, our study area). Today, this activity in Spain has almost disappeared. The few herds that still move by foot have problems because most of the traditional tracks are occupied by buildings, highways or crops (Gómez, 1991; Garzón, 2001). Today the traditional long movements from the pastures of southern Spain to the mountainous pastures of the north are scarce and most livestock come from nearby locations (Gómez and Rodríguez, 1992). Most of today's transhumant livestock consists of cows and the movement to summer pastures is made by truck. Cows stay at these pastures longer than sheep, from early spring to early winter, while sheep arrive in early summer and depart in early autumn. Nowadays, our study area is one of the few sites in Europe where transhumance still has relative importance (Rodríguez, 2004).

2.1.2. Study species

The community of vertebrates specialized in the consumption of carcasses in our study area is mainly formed by two vulture species: the griffon and Egyptian vulture *Neophron percnopterus*. However, only the first species is totally dependent on medium- or large-sized carcasses of ungulates (Elosegui, 1989). The griffon vulture is a cliff-nesting, large-sized raptor widely distributed from the Mediterranean countries to India, occupying also areas in the north of Africa. Once threatened, now the species is classified as of least concern in both Europe and the world (Birdlife International, 2007). However, the recent collapse of some Asian *Gyps* vulture species as a consequence of diclofenac poisoning (Green et al., 2006) highlights the high vulnerability of this scavenger guild, including the griffon vulture (Swan et al., 2006). Additionally, in the last few years population reductions of griffon vultures have been detected in many parts of Europe, especially in Spain. Such reductions have been related to food shortages produced by sanitary laws derived from the BSE (Tella, 2001; Camiña, 2007). With around 22,700 breeding pairs (Del Moral and Martí, 2001), the Iberian Peninsula holds one of the largest populations of this species in the western Palearctic (Del Moral and Martí, 2001). The griffon vulture is widespread in Spain, but is scarce in wide areas that are not rough or very dry (Fig. 1). The species occupies very different habitats from the plains to the middle and high mountains, with the nests ranging in altitude from sea level to high mountains (above 1700 m.a.s.l.; authors, unpubl. data). The griffon vulture breeds mainly in colonies that number from a few to hundreds of pairs (Donázar, 1993). The breeding season extends from January until July and the brood consists of only one chick (Donázar, 1993). The griffon vulture feeds on the carcasses of large animals, with livestock being its fundamental, or only, trophic resource (Donázar, 1993).

2.2. Study area

The study area extends over a stretch of 3750 km² on the south slope of the Cantabrian Mountains (north of the León province; including Picos de Europa), in the NW of Spain (Fig. 1). The abrupt relief of this area (75% of which is located above 1200 m.a.s.l. and

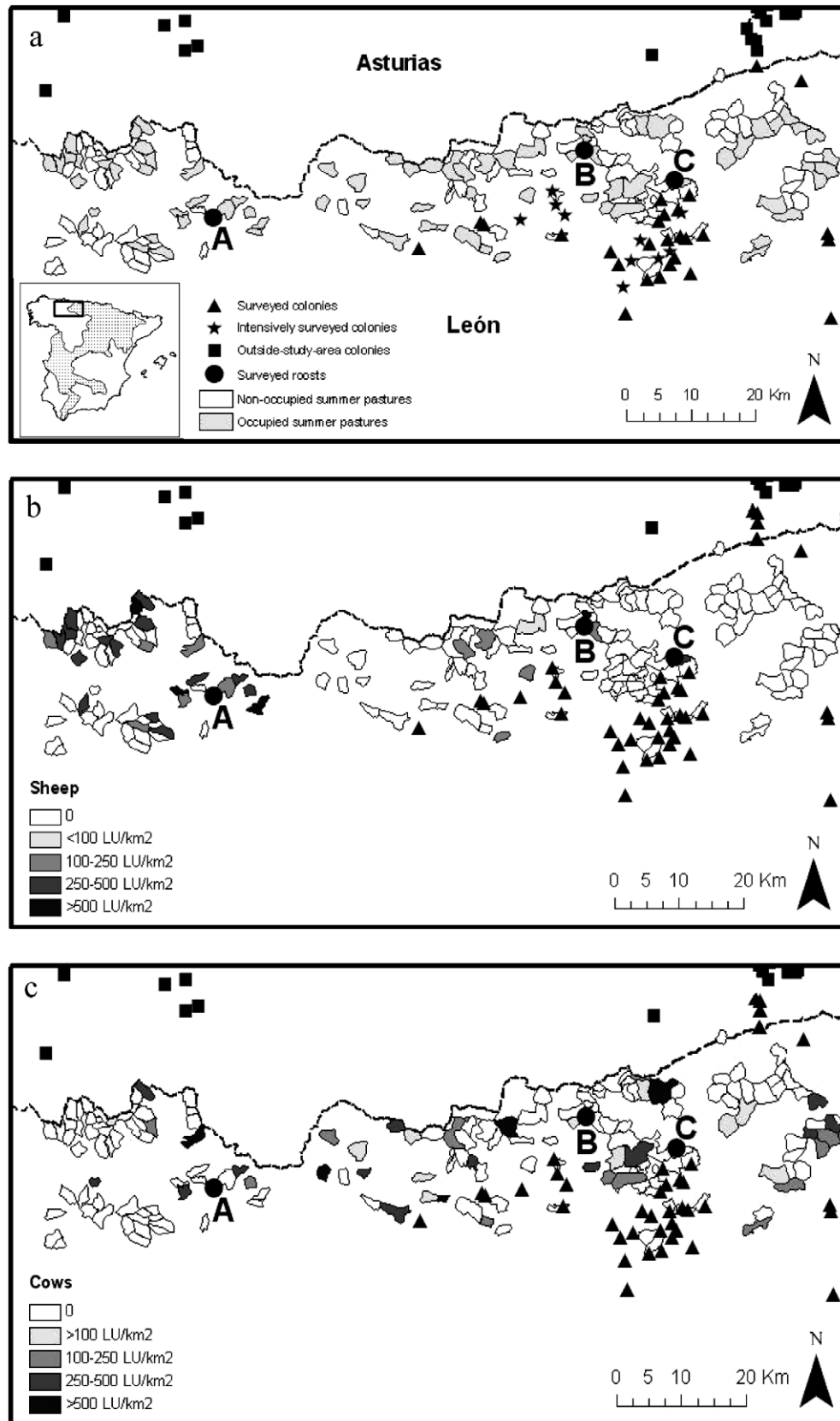


Fig. 1. (a) Study area showing the location of the summer pastures and the colonies and roosts studied. The shaded area in the small map shows the griffon vulture breeding range in Spain (Del Moral and Martí, 2001). Highly surveyed colonies were visited monthly and the rest were surveyed between 4 and 7 times/year (authors, unpubl. data). The black line shows the limit between the northern and the southern slope of the Cantabrian Mountains. (b and c) Show spatial density of LU of sheep and cows, respectively, in the summer pastures of the study area in 2006–2007.

35% above 1500 m.a.s.l.; [Rodríguez, 2004](#)) together with the hard climatic conditions (long cold winters, mean temperature $T_m = 10^\circ\text{C}$, and short cool summers, $T_m = 17^\circ\text{C}$) shapes a landscape mainly consisting of pastures alone or mixed with small shrubs. In fact, more than 50% of the study area consists of pastures ([Rodríguez, 2004](#)). A total of 165 upland summer pastures have been recorded here, located at a mean altitude of 1500 m.a.s.l. (range: 1200–1700 m.a.s.l.; [Gómez and Rodríguez, 1992](#); [Fig. 1](#)). The hard conditions of these pastures, which are covered by snow more than six months per year, make grazing the only production activity possible ([Rodríguez, 2004](#)). Thus, the renting of pastures to transhumant flocks, mainly cows and sheep, during 4–6 months per year (from early spring until late autumn), provides an important economic resource for local residents.

The griffon vulture population in this area has been estimated at 240 breeding pairs (authors, unpubl. data; Parque Nacional Picos de Europa, unpubl. data) and is established at the north-western edge of the distribution range of the species in Spain and Europe ([Fig. 1](#)).

2.3. Surveys of vultures and transhumant livestock

2.3.1. Use of pastures by transhumant livestock

Using ARCGIS 9.2 (Environmental Systems Research Institute Inc.), we identified, mapped and implemented all the summer pastures, those currently used by transhumant livestock and those used in the past for the entire study area ([Gómez and Rodríguez, 1992](#); [Rodríguez, 2004](#) and local authorities; [Fig. 1](#)). To do this, we georeferenced existing maps ([Gómez and Rodríguez, 1992](#)) and added new pastures and modified the former ones using aerial photographs. In order to collect data on the presence of livestock at the pastures, we carried out questionnaires to local and transhumant shepherds ($n = 97$) and to all the veterinary units ($n = 5$) of the study area in 2005–2008. We interviewed 85 sheep shepherds, 15 of which were transhumant (50% of the existing shepherds in the study area) and 70 local shepherds (25%). We also interviewed 12 cow shepherds (five transhumant and seven local). Moreover, we obtained information for all the cow breeders (local, $N = 425$ and transhumant, $N = 200$) through the official databases of the veterinary units. Thus, we obtained the dates of arrival and departure and numbers of transhumant livestock in the summer pastures. Sheep and cow densities were also mapped. We also recorded data on livestock carcasses consumed by vultures.

2.3.2. Vulture surveys

To evaluate the use of mountain pastures by vultures, we looked for cliffs used as roosts or colonies in and around the summer pastures ([Fig. 1](#)). To do this we revised previous censuses ([Olea et al., 1999](#); [Del Moral and Martí, 2001](#)) and carried out intensive field surveys during 2005, following procedures previously reported ([Olea et al., 1999](#); [Mateo-Tomás and Olea, in press](#); [Olea and Mateo-Tomás, submitted](#)). The three roost-sites located were intensively surveyed between 2006 and 2007. Every roost was visited weekly from June to October and monthly for the rest of the year. In addition, two of the three roosts were also monitored in 2008. We performed every visit within the first hour after sunrise or the last hour before sunset. Cliffs were inspected using telescopes 20–60 \times in days with good visibility. At every visit we noted the number of vultures roosting on the cliff and the age of each individual (adult or immature, considering as immature both fledglings of the current year and birds born the previous year), according to physical characteristics ([Elosegui, 1989](#)). We also selected the nine colonies that had the largest size and were the closest to summer pastures for monitoring throughout the year ([Fig. 1](#)). We visited these colonies monthly to count vultures. Censuses of colonies were carried out simultaneously following the same pro-

cedure as for roosts. The rest of the colonies were visited 4–7 times/year on average.

Availability of food was estimated from official databases (veterinary units, JCyL), in which the date and collection/no collection of dead cows is registered. No similar database exists for sheep, so we obtained sheep mortality through interviews with transhumant and local shepherds. However, we could not obtain a detailed temporal distribution of mortality. We found the mean weight of a cow to be 450 kg, with 80% being potentially used by vultures ([Aseava, 2008](#)). The mean weight estimated for sheep was 60 kg, with 40% possible consumption by vultures ([Méndez, 1990](#)). We estimated the minimum daily intake of an adult griffon vulture to be 0.543 kg/day (at $T_m = 17^\circ\text{C}$) based on [Donázar \(1993\)](#). Since the vegetation cover of the pastures is scarce, we considered all carcasses that were not collected from the field as available for vultures (i.e., 100% for dead sheep and 97.2% for dead cows, according to official databases).

2.4. Data analysis

We converted the two types of livestock (cows and sheep) into livestock units (LU; 1sheep = 1LU; 1cow = 5LU; [Olea et al., 1999](#)). Since we did not have precise information about the foraging areas used by vultures around the summer roosts, we considered the number of livestock units within the various nested radii around each roost from roost-site to half the distance to the nearest colony ($\text{NND}/2$) in five intervals of 2.5 km (i.e., within 2.5, 5, 7.5, 10 and 12.5 km radii). Comparisons of livestock medians between roosts and colonies were performed using Wilcoxon tests; P -value < 0.05 was considered significant. We modeled the occurrence and abundance of vultures at the roosts over time using Generalized Linear Mixed Models (GLMMs). The response variables used were presence/absence and number of vultures in the roosts at each visit ($n = 95$), respectively. Roost site and year were fitted as random effects. Roost was fitted as a random intercept to account for vulture counts over time within the same roosts. The year was fitted as a random slope to account for variation between years. Number of sheep and cows (local and transhumant) were included as fixed effects. Presence of sheep and cows (local and transhumant) were also included as fixed effects in the models of vulture abundance. We performed all possible model permutations of the fixed effects for each radius and random structure using a binomial error structure for the response variable of presence/absence and a negative binomial error structure for the abundance of vultures. We built two different sets of models for each response variable. We used the lme4 package ([Bates et al., 2008](#)) for modeling presence/absence of vultures and the glmmADMB package ([Otter Research Ltd., 2008](#)) for abundance using the R statistical software ([R Development Core Team, 2008](#)). The glmmADMB package allows for the simultaneous modeling of random effects and excess zeros for count data (i.e., zero-inflated count data). The resulting models were compared through their AICc (corrected Akaike Information Criterion; [Burnham and Anderson, 2002](#)). The Akaike weight of each model (ω_m) was estimated following procedures by [Burnham and Anderson \(2002\)](#). Akaike weight is the relative likelihood of the model being the Kullback-Leibler best model within a set of n models. We constructed a 95% confidence set of models by starting with the highest Akaike weight and adding the model with the next highest weight until the cumulative sum of weights exceeded 0.95 ([Burnham and Anderson, 2002](#)). A model filtering procedure was applied by removing the more complex models that did not have ΔAIC -values lower than all of its simpler nested models ([Richards, 2008](#); [Burnham and Anderson, 2002](#)). To know the relative contribution of each variable we calculated their Akaike weights. The Akaike weight for each variable (ω_i) was calculated by summing, from the set of models within the 95% probability,

the weights of those containing the variable, with the variables with the highest weight ($\Sigma\omega_m$) being more important relative to the others.

To look for serial correlation in the data collected in the same roost (and year) over time (i.e., temporal autocorrelation of within-group errors), we plotted the within-group residuals of the best models (i.e., those with a $\Delta\text{AICc} < 2$ relative to the model with the lowest AICc) as a function of distance between errors. Significance of autocorrelation values was looked at the level $\alpha = 0.01$ (Supplementary material). Analyses of residuals were performed using SPLUS-8 (Insightful, Seattle, USA; see Olea, 2009 for further details).

3. Results

3.1. Sites used by the griffon vulture

We found 40 breeding colonies and three summer roosts (Fig. 1). Summer roosts were located at higher elevations than colonies and were very close to the main summer pastures used by the transhumant livestock (Fig. 1, Table 1). Importantly, the biggest summer roost in the area (roost A) was located outside the breeding range of the species in the study area, far away from the breeding colonies (Fig. 1; Table 1). The vultures have used this roost for at least 10 years (Olea et al., 1999). The other two summer roosts (B and C) were located inside the griffon vulture breeding area, 8 and 3 km away from the nearest colony, respectively, and 14.7 km from each other (Fig. 1, Table 1). Roost B could also have been used for the last 10 years (Del Moral and Martí, 2001), while roost C was only used for 2007 and 2008 (Olea et al., 1999; Del Moral and Martí, 2001; Fig. 2).

3.2. Transhumance over time

The summer pastures of the study area have been used by transhumant livestock for centuries and most of them have been abandoned in the few last decades (Rodríguez, 2004; pers. obs.; Fig. 1). In 1989–1991, 40% (66 of 165) of these pastures were occupied by transhumant sheep. This number decreased to 19.4% (32 of 165) in 2005–2007. In the same period (1989–2007), the number of transhumant sheep has strongly declined (62%), although the number of cows occupying the summer pastures has risen by 300% (Fig. 3). There is still a relatively high percentage of summer pastures occupied by transhumant livestock around roost A (61% in 2006/07, $n = 23$, within 12.5 km around roost). There are few pastures currently occupied by transhumant livestock, especially sheep, around roosts B and C (Fig. 1).

3.3. Livestock and consumption of carcasses by vultures

The three roosts surrounded by summer pastures were used by cows and sheep (Fig. 1). In 2006/07, the three roosts had a higher

density of LU around them (within 10 km) than that of the colonies. However, only sheep LU were higher (marginally significant, Wilcoxon test: $Z = -1.76$; $P = 0.08$). The differences in LU density between the roosts and colonies responded to transhumant livestock, since local livestock densities were very similar across the study area (mean \pm SE roosts: 68.2 ± 6.6 LU/km² vs. mean \pm SE colonies: 70.9 ± 4.8 LU/km², $n = 3$ and 40, respectively; Wilcoxon test: $Z = -0.79$; $P = 0.44$; note, however, the low test power due to the small sample size). Roost A, with the highest number of vultures (Table 4; Fig. 4), had the highest density of livestock around it (Fig. 1).

From a total of 85 interviews performed to sheep shepherds, both transhumant and local, 65.4% observed griffon vultures feeding on their dead sheep. All the veterinary units interviewed also recorded cases of vultures feeding on dead cows. Additionally, 100% of the transhumant shepherds interviewed ($n = 20$) confirmed the presence of griffon vultures feeding on dead livestock.

3.4. Pattern of use by livestock and vultures

The number of transhumant sheep within 10 km around the roosts was the best predictor of the presence of vultures at roosts ($\omega_i = 0.64$), as shown also by the lower AICc and higher weight of the model, including this predictor (Table 2). This can also be seen in the patterns of use of the study area by vultures and livestock (Fig. 2), where presence of vultures seems to match better with presence of transhumant sheep.

Number of vultures was better explained by number of transhumant and local cows within 10 and 12.5 km around the roosts ($\omega_i = 0.96$ and 0.89, respectively; Table 3). Presence of transhumant sheep within 10–12.5 km around the roosts was also a factor with moderate importance in explaining abundance of vultures ($\omega_i = 0.36$; Table 3). Within-group residuals of both the best occurrence and abundance models did not show significant temporal autocorrelation at the level $\alpha = 0.01$ (Supplementary material).

During our two years of intense study we roughly observed the same spatiotemporal pattern in the use of summer roosts (except when there were changes in use of transhumant livestock in roost B and C, Fig. 2). The pattern of use of vultures at the summer roosts seemed to respond better to the stay of sheep at summer pastures than that of cows, especially in autumn when vultures leave the roost (Fig. 2; Table 2). This relationship between the presence of vultures and transhumant sheep could also be proved for roost B and C in the quasi-experimental situation. After more than 15 years of use, pastures around roost B were not occupied by transhumant sheep in 2007 and 2008, which was followed by the very low use of roost B by vultures (Table 4). Cows followed using pastures around roost B during the same period (Fig. 2). Pastures around roost C were re-occupied in 2006 by transhumant sheep after 10 years without use and in 2007 vultures started to use roost C (Fig. 2). The 1-year lag in occupation of roost C by vultures is probably because roughly the same vulture population occupied roost B and C (Fig. 2).

Table 1

Characteristics of roosts and colonies (mean \pm SE) in the study area. Asterics indicate differences according to Wilcoxon rank test.

Characteristics	Roost A	Roost B	Roost C	Roost mean ($n = 3$)	Colony mean ($n = 40$)	Wilcoxon rank test (Z/W)
Elevation (m.a.s.l.) [*]	1449	1620	1577	1548.7 \pm 51.4	1321.7 \pm 39.1	-1.7749
Height (m)	88	85	60	77.7 \pm 8.9	93.1 \pm 9.5	-0.2048
Length (m)	2416	566	563	1181.7 \pm 617.2	968.0 \pm 127.4	955
Exposure	E	E	NE	E	E	
Substrate	Limestone	Limestone	Limestone	Limestone	Limestone	
Distance nearest colony (m) ^{**}	26550	8194	3433	12725.7 \pm 7047.5	2909.0 \pm 324.4	-2.1618
Distance nearest town (m)	1141	3782	1768	2230.3 \pm 796.7	1705.2 \pm 119.8	-0.6598
Distance nearest road (m)	1244	3263	1788	2098.3 \pm 603.1	1240.3 \pm 128.5	931

^{*} $P < 0.10$.

^{**} $P < 0.05$.

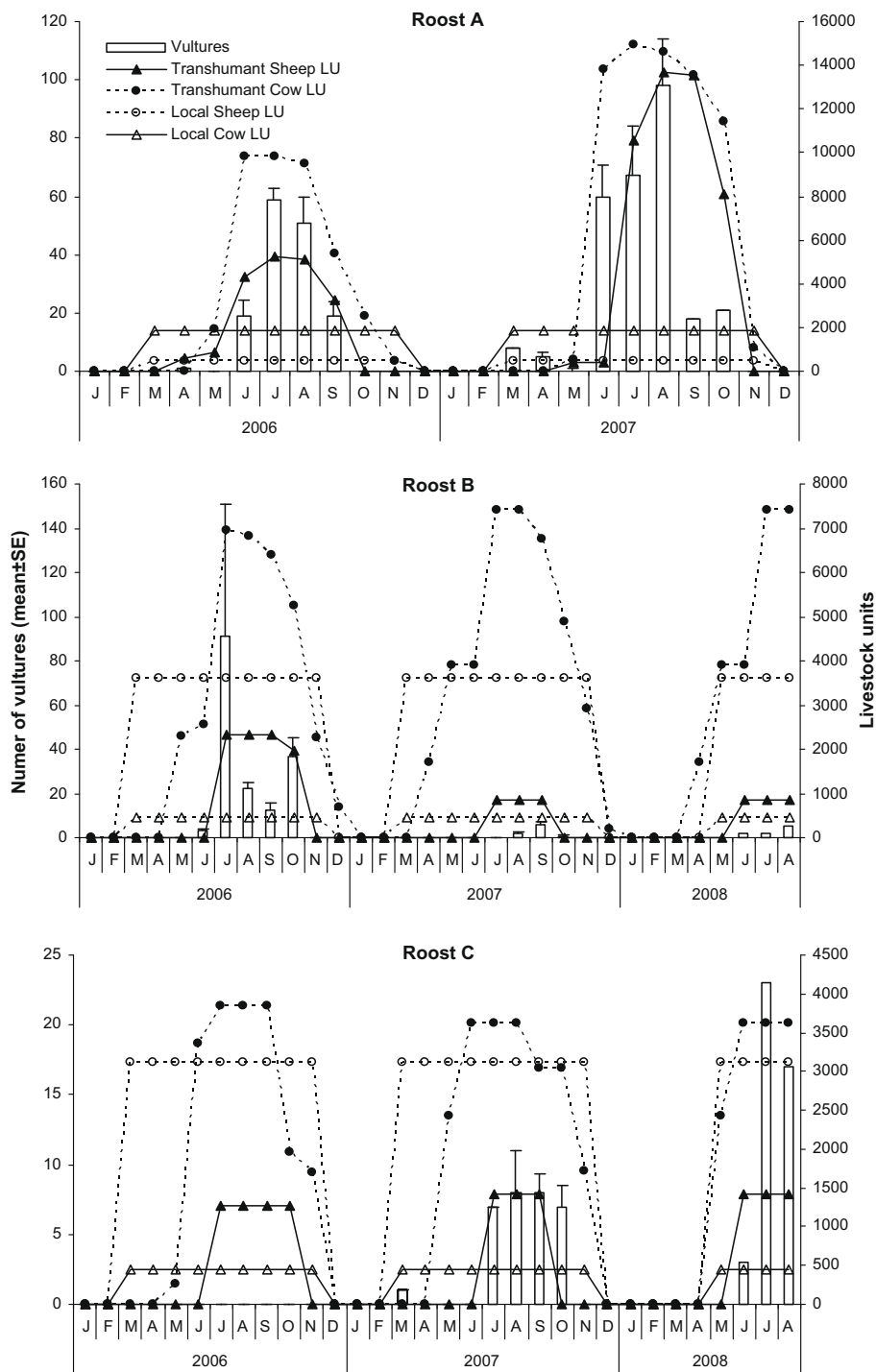


Fig. 2. Number of vultures (mean \pm SE) at summer roosts and number of livestock units of each type within a 10 km radius around every roost, i.e., the distance to which presence of vultures better responded to livestock.

The age of vultures that used the roosts varied across the year. The number of adults was higher than immature vultures during all the periods considered, with the proportion of immature vultures increasing in summer and autumn (Fig. 5). The number of vultures in the colonies fluctuated over time, but either it was roughly constant throughout the year or increased during the summer (Fig. 4).

3.5. Potential food for vultures

Food (kg/year) that was potentially available for vultures within 10 km from the roosts was 1.4–6.5 times higher from transhumant

livestock than that of local livestock (Table 4). The highest amount of potential food available for vultures was found around roost A (Table 4). Potential food availability around roost B considerably decreased (69.6%) during the two years studied (Table 4). With a maximum livestock (local and transhumant) presence of seven months in summer pastures within 10–12.5 km around the roosts, available food could cover the needs of 81–103 vultures/day in roost A and 10–40 vultures/day in roost C. Roost B could maintain 44–81 vultures/day during 2006, and decreased to 13–48 vultures/day during 2007. Number of vultures observed at roosts followed those estimated, but with lower values (Table 4). Total food poten-

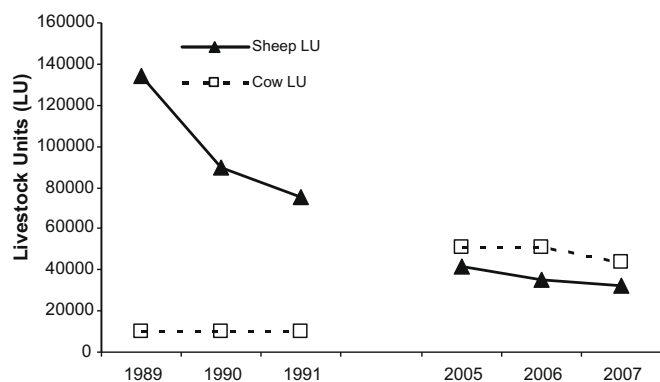


Fig. 3. Numbers of livestock units of transhumant sheep and cows in the study area during the period 2006 and 2007 (this study) and 15 years ago (1989–1991, Gómez and Rodríguez, 1992).

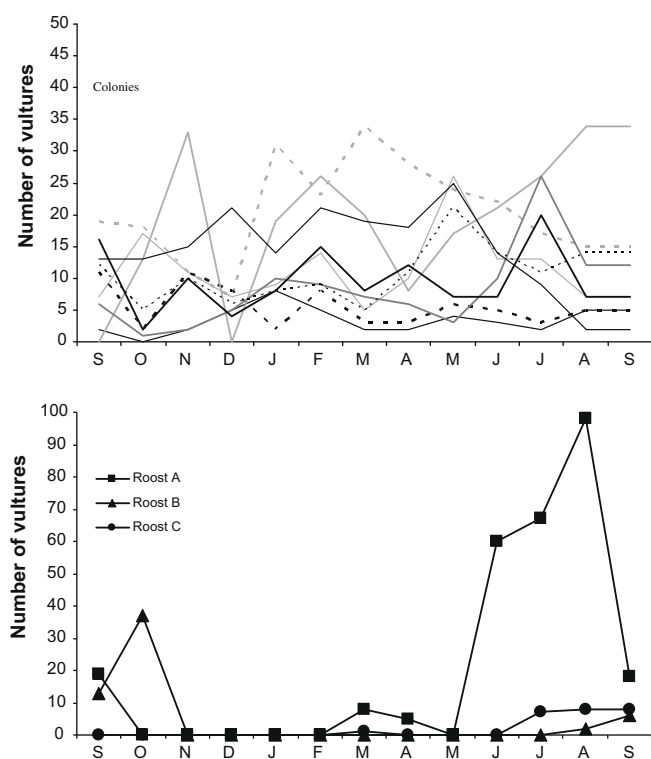


Fig. 4. Variation of the number of vultures at intensively surveyed colonies ($N = 9$) and roosts ($N = 3$) in the study area during a year.

Table 2

AIC values of the set of GLMMs including in the $\Sigma\omega_m = 0.95$ performed for explaining the presence of vultures as functions of livestock units of sheep and/or cow at the different radii considered (from 2.5 to 12.5 km) around the roosts. Equivalent models for each category are shown in bold. AICc-based ranking is also shown. Within parentheses are included random effects. Models including numbers of heads or livestock units were similar, thereby only models fit with numbers of livestock heads are shown.

Model	AICc	Δ AICc	ω	Rank
SheepT10 (year roost)	76.33	0.00	0.643	1
SheepT5 + CowT5 (year roost)	80.51	4.18	0.080	2
SheepT12.5 (year roost)	81.38	5.05	0.052	3
SheepT5 (year roost)	81.50	5.17	0.049	4
SheepT12.5 + CowT12.5 (year roost)	81.51	5.18	0.048	5
SheepT7.5 (year roost)	81.81	5.48	0.042	6
CowT10 (year roost)	82.19	5.86	0.034	7
Null model	123.83	47.50	0.000	20

SheepT: no. of transhumant sheep and CowT: no. of transhumant cows.

tially available for vultures from transhumant livestock in all summer pastures during 2006/07 would be of 49,608 kg/year, which could cover the needs of 755 vultures/day. However, the temporal distribution of carcasses available was not homogenous and also differed between sheep and cows. According to shepherd interviews, the sheep mortality increases slightly at the beginning of the season (July) and is then randomly distributed. The official database available for cows showed that the mortality of cows is mainly concentrated at the end of the season (October–November).

4. Discussion

4.1. Vulture response to transhumance

For the first time, we provided strong evidence of the close relationship between vultures and transhumance, which was previously only suggested (Ruiz and Ruiz, 1986; Garzón, 2001; Xirouchakis and Mylonas, 2004). Firstly, vultures occupied roosting sites very close to summer pastures, especially those most used by transhumant sheep (Fig. 1). In fact, vultures moved their central foraging place relatively far away from their breeding colonies (i.e., roost A; Fig. 1). Secondly, the three surveyed roosts were located in areas with a higher density of transhumant livestock around them than that of the colonies. Statistical models showed that the occurrence and abundance of vultures at roosts was strongly related to the presence and number of transhumant sheep and cows (Fig. 2; Tables 2 and 3), especially within 10–12.5 km around roosts. This suggests that vultures foraged mainly within 10–12.5 km around the roosts. This distance is compatible with observations of griffon vultures in Crete (Xirouchakis and Mylonas, 2004), where vultures mainly used the area within 9 km from a central site (colony) and, when the availability of resources were more than 9 km from the colonies, they used another site (roost site). Therefore, this distance (i.e. 9–12.5 km) could be considered as a threshold for the species in order to maximize the energy gained per round-trip according to the optimal foraging theory (Schoener, 1971). Thirdly, vultures consumed carcasses of transhumant livestock in summer pastures. Finally, sharp and rapid changes in the space use by transhumant sheep, but not by cows, were followed by similar spatial changes by vultures (Fig. 2).

Several reasons could explain the good fit between vulture presence at roosts and number of transhumant sheep, all of them are related to the availability of carcasses for vultures, specifically: (i) after BSE, sanitary norms obligate removal of the dead livestock carcasses, especially cows, from the field, and if not possible, they must be buried. This norm is much more relaxed with sheep, especially in mountain pastures where the access is limited; (ii) the mortality rate of sheep is both higher than that of cow (2% vs. 0.8%) and more constant over time (mortality of cows is mainly concentrated in autumn). This results in a more stable supply of sheep carcasses over time. However, the abundance of vultures in the roosts seems to be better explained by the number of cows (local and transhumant), although the presence of transhumant sheep was also an important predictor. This finding suggests that vultures respond strongly in space and time to the presence and number of transhumant sheep. However, once transhumant sheep are present, peaks of vulture abundance are related to cows. This is probably because cows provide a greater amount of food in each mortality event than sheep, enabling the gathering of higher numbers of individuals.

The formation of communal roosts in vultures is generally related to the presence of regular food supplies (i.e., Donazar et al., 1996; Xirouchakis and Mylonas, 2004). Thus, the observed response of griffon vultures to the presence and number of transhumant livestock highlights its importance as a fundamental

Table 3
AIC values of the set of GLMMs including in the $\Sigma\omega_m = 0.95$ performed for explaining the abundance of vultures as functions of livestock units of sheep and/or cow at the different radii considered (from 2.5 to 12.5 km) around the roosts. Further details in Table 2 caption.

Model	AICc	Δ AICc	ω	Rank
CowT12.5 + CowL12.5 (year roost)	600.09	0.000	0.484	1
PSheepT10 + CowT10 + CowL10 (year roost)	601.10	1.007	0.292	2
CowT10 + CowL10 (year roost)	602.93	2.840	0.117	3
PSheepT12.5 + CowT12.5 (year roost)	605.55	5.458	0.032	4
PSheepT10 + CowT10 (year roost)	605.56	5.464	0.031	5
Null model	651.18	51.091	0.000	54

CowT: no. of transhumant cows; CowL: no. of local cows; and PSheepT: presence of transhumant sheep.

trophic resource for the species. The recent sanitary laws controlling livestock carcasses have considerably reduced the presence of dead animals in the field (Tella, 2001), but the complex topography of the summer pastures makes the collection of carcasses very difficult. In fact, 97.2% of the dead cows and all of the dead sheep are potentially available to scavengers in the field (veterinary units, JCyL). Therefore, food available in these areas from transhumant livestock considerably increases during the summer (between 1.4 and 6.5 times relative to the local one).

The increase in immature presence at roosts during summer and autumn (Fig. 5) may be due to the recruitment of hatching-year vultures as has been observed for other vulture species (McVey et al., 2008). The increased number of vultures in some colonies during summer could be related to the use of the summer pastures occupied by transhumant livestock by vultures from other colonies. Use of these mountain sites by vultures could be greater than simply looking at the number of vultures at the roosts/colonies, since individuals of this population are unmarked and the possible turnover is unknown. High turnover rates of up to 46% have been detected at roosts for other vulture species (Rabenold, 1987). Therefore, the number of vultures we see using these sites could only be a minimal percentage of those that are truly using summer roosts. Further work on this is needed, mainly through marking of individuals, to ascertain real use by vultures.

4.2. Management and conservation implications

We found that one important population of vultures is making use of the food resources from transhumant livestock during at least a third of the year. Therefore, transhumance could be a useful tool for griffon vulture management, especially considering the current situation of the species in Spain (Camiña and Montelío, 2006; Camiña, 2007; Pérez, 2007). The sanitary laws derived from the BSE have created extremely high food shortages in the main griffon vulture strongholds. Most of these vulture populations are artificially fed via feeding stations supplied by intensive farms (Camiña, 2007), and are now rapidly responding to food shortages (Camiña

and Montelío, 2006). In fact, important decreases of up to 40% have been reported for some of these vulture populations of eastern Spain (Camiña, 2007) and productivity has also fallen considerably in the last few years (i.e., from 0.82 chicks/pair in 2001 to 0.41 in 2007; Pérez, 2007). Furthermore, it was found that vultures in Spain are incorporating antibiotics from medicated livestock, mainly pigs from intensive farms, potentially increasing the mortality rate of vultures and bringing important sanitary and conservation problems to light (Lemus et al., 2008). In contrast to this unsustainable scenario, the griffon vulture population of our studied area, which is not feeding-station-dependent, has increased the number of breeding pairs by >30% in the last four years, with relative high productivity rates in the period from 2006–2008 (mean \pm SE: 0.74 \pm 0.04 chicks/pair; $n = 3$ years; authors unpubl. data). Carcass-related sanitary regulations are more difficult to apply under an extensive farming context, especially in mountain areas, making more food available for scavengers. In fact, our estimates show that 140–270 vultures could be feeding during half of one year from livestock carcasses available only within 10–12.5 km around the three studied roosts. This number could rise to 755 vultures if all summer pastures in the study area are included. This indicates that an important griffon vulture population can be maintained through a system based in traditional livestock farming.

Transhumance considerably increases livestock numbers in these mountain areas and, hence, carcass availability and tropic resources. Therefore this practice might have an important role in conservation of other wild species, especially of the scavenger community. In fact, in this same study area, the high importance of extensive grazing of sheep and goats for the conservation of the globally endangered Egyptian vulture has been highlighted (Mateo-Tomás and Olea, in press). Livestock carcasses have also been highlighted as an important resource for the threatened brown bear (*Ursus arctos*; Hartasánchez et al., 2006).

Transhumance of sheep has strongly and rapidly declined in our study area in the last few years, however (Fig. 3). The effect that this could have on scavengers is unknown but it should be taken into account, especially considering the strong vulture-transhu-

Table 4
Total food (kg/year) that is potentially available for vultures from livestock staying at summer pastures within 10–12.5 km around each roost. Note that for roosts A and C only one data is showed because food available was almost the same during the years considered. Data were also similar for roost B in 2007 and 2008. The number of vultures potentially maintained and the number of vultures observed at each roost are also showed.

		Roost A	Roost B		Roost C
			2006	2007–2008	
Sheep	Transhumant	2785–5924	885–4706	105–1009	188–1025
	Local	259–574	177–631	58–505	60–639
Cow	Transhumant	5311–6728	2684	930–1900	479–950
	Local	984–1461	1377–2085	1377–2085	411–1961
Total	Transhumant	8096–12,652	3533–7354	1035–2909	667–1975
	Local	1243–2035	1554–2716	1435–2590	471–2600
Vultures	Predicted	81–103	44–81	13–48	10–40
	Observed median \pm SD (range)	21 \pm 25 (0–98)	20 \pm 56 (3–209)	1 \pm 3 (0–8)	4 \pm 4 (1–15)

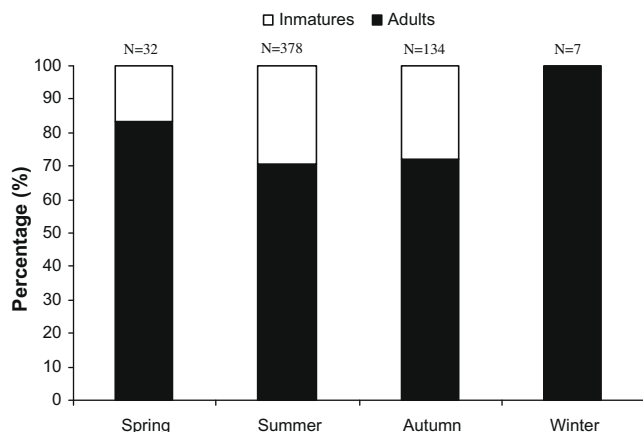


Fig. 5. Percentage of adult and immature griffon vultures present at roosts through the year.

mance relationship shown by our results and the current context of vulture management. This guild has a fundamental role in the ecosystem (Sekercioglu et al., 2004, see Section 1), for this reason its decline could negatively influence ecosystem functions. Because of the great movement ability of vultures, transhumance could also provide benefits (services) to other ecosystems far from the study area. Other effects on the ecosystem derived from changes in transhumant livestock should also be taken into account (Shaoliang et al., 2008). The reduction or disappearance of traditional grazing activities can cause ecosystem degradation through negative effects on vegetation cover (Shaoliang et al., 2007), wild fauna (Tryjanowski et al., 2005) and water availability (Green and King, 1996).

However, the negative impacts of extensive grazing must also be considered. Mismanaged grazing can negatively impact ecosystems through, for example, overgrazing (Shaoliang et al., 2007) or poisoning (WWF/Adena, 2006). The use of poisoned bait in the study area is not a very common practice, with poaching being the most traditional way of predator control (local authorities, pers. comm.). No griffon vultures were found from among the 30 animals that were recorded as poisoned in the study area between 1995 and 2005 (WWF/Adena, unpubl. data). However, at least 14 griffon vultures have been poisoned in the last three years in the study area (2006–2008; local authorities, pers. comm.). Most of these events were related to predator control (especially wolf *Canis lupus*) by farmers (local authorities, pers. comm.). The negative effects of this poisoning practice on wildlife, especially on scavengers (WWF/Adena 2006), makes the design of adequate management actions that minimize conflict between predators and stockbreeders necessary.

Our study assesses the effect of transhumance on vertebrates at the top of the ecosystem, specifically on scavenging birds. The existence of this activity would enable the sustainable management of both vulture populations and the ecosystem. Therefore, ecosystem managers should design integral conservation measures from a holistic perspective. For example, financial support to extensive farming systems, instead of the establishment of artificial feeding points, would not only benefit scavenging birds but other levels of the ecosystem as well. These measures supporting extensive farming practices could decrease the negative attitudes of farmers towards wildlife (such as use of poison). Special attention should be focused on encouraging the conservation of currently declining sheep transhumance (Mateo-Tomás and Olea, in press), both because of the importance for the scavengers (this study) and its benefits to the ecosystem (Gómez, 1991; MacDonald et al., 2000; Garzón, 2001). The European Council Regulation (EC)1698/2005 (European Communities, 2005) provides a good opportunity to

develop specific actions supporting traditional activities, such as transhumance, in the context of its environmental benefits. The recently implemented “Health Check” proposal, which encourages a continuous revision of the CAP (European Commission, 2007), could be useful in streamlining integral actions to support farming systems and species and ecosystem conservation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.03.024.

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