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From Pyrenees to Andes: The relationship between transhumant livestock and vultures

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ABSTRACT

Transhumance is the traditional livestock practice consisting in the seasonal movement of herds between winter and summer pastures. Transhumance have important effects on the ecosystem functions from local to regional scales. Here, we 1) explored the relationship of vultures to transhumant herds, and 2) tested whether there is a shift on the use of space by vultures due to the decline of transhumance. For that, we first assessed whether vultures follow transhumant herds in two mountain areas with transhumant tradition, Pyrenees (Spain) and Andes (Argentina). Second, we compared both systems to determine whether the impact of transhumance on the use of space of vultures is greater in the area where transhumance is still relevant (Andes) than where this activity is in decline (Pyrenees). For this purpose, we analyzed the use of the summer pastures made by 50 griffon vultures (*Gyps fulvus*) and 18 Andean condors (*Vultur gryphus*), as assessed by GPS tracking. Our findings showed that both species respond to transhumance by making greater use of summer pastures when herds are present. A higher proportion of condors made use of summer pastures than griffons, and condors individually made a more intense use of it than griffons. Differences could be explained by the fact that transhumance in the Andes is still important while in the Pyrenees is declining and the amount of carrion provided is lower. Given that the abandonment of traditional activities is a phenomenon underway, it is urgent to evaluate the effects it will have on biodiversity conservation.

1. Introduction

Historically, livestock farming has been one of the main ways in which humans have modified the landscape (Giguet-Covex et al., 2014; García-Ruiz et al., 2020). Traditional livestock husbandry techniques have been based on herds grazing semi-freely which, in many cases, required the transformation of large areas to pasture (García-Ruiz et al., 2020). However, in recent decades, the process of industrialization of livestock farming made stabling and supplementary feeding much more profitable and productive to the detriment of extensive livestock practices. Consequently, large areas of pasture have been abandoned and are undergoing a transition to shrublands and forests (Navarro and Pereira, 2012). These changes in landscape configuration result in a new scenario in which there might be winner and loser species. On the one hand, species that have traditionally competed or come into conflict with livestock such as wild ungulates and large predators might find an opportunity to recover their populations and distributions (Acevedo et al., 2011; Cimatti et al., 2021). On the other hand, species that are positively associated with traditional livestock landscapes, such as open field passerines or pasture plant communities (Olsson et al., 2015),

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would be negatively affected by these landscape changes (Regos et al., 2016). Consequently, the functioning of the entire trophic network might be altered. For example, passive rewilding caused by the disappearance of livestock leads to a slower consumption of carrion because the most efficient scavengers (vultures) are replaced by other species with a lower consumption capacity (Arrondo et al., 2019; Oliva-Vidal et al., 2022).

The decline of extensive livestock has led to the progressive abandonment of traditional practices such as transhumance. This practice consists in the regular movement of livestock between summer and winter pastures following primary productivity gradients, in a mimicry of natural migrations of wild ungulates (Ruiz and Ruiz, 1986). Transhumance appeared almost parallel to the development of livestock (García-Ruiz et al., 2020). Although there are examples of transhumant movements throughout the Old World and on different historical periods (Forbes, 1995), Spain is especially relevant because between XIII and XIX centuries, this country based much of its economy on transhumance (Mier and Tente, 2018). During this period, millions of sheep and cows moved across the Iberian Peninsula with a profound social, economic and ecological impact (Otero-Rozas et al., 2013; García-Ruiz et al., 2020). In addition, until the Spanish colonization of America, transhumance in the New World was a marginal practice focused in camelid species and restricted to certain Andean areas (Westreicher et al., 2007). After Spanish colonization, transhumance spread throughout the continent, from North to South America (Westreicher et al., 2007; de Abreu et al., 2010; Starrs, 2018; Padín, 2019).

Transhumance movements and the feeding of thousands or even millions of ungulates that this practice entails, inevitably produces a transformation of the landscape with consequences for both plant and animal communities. From a vegetation point of view, the deforestation necessary to create pastures in remote mountain areas implies variations in the altitudinal limits of the alpine and subalpine climatic levels (García-Ruiz et al., 2020). For animals, the most direct impacts are on wild ungulates that compete directly with livestock for habitat and food, and may even be excluded from areas with free livestock (Bleyhl et al., 2019). The arrival of thousands of ungulates suppose a large input of possible trophic resources for carnivores that also see their diet affected by the seasonal movements of transhumance (Cozza et al., 1996). For vultures, whose diet is mainly based on ungulate' carrion, transhumance also implies spatial and temporal changes in the availability of food (Olea and Mateo-Tomás, 2009; Margalida et al., 2018; Aguilera-Alcalá et al., 2021) in a similar way that occur with the wild ungulate migrations (Kendall et al., 2014).

The progressive decline of transhumance would inevitably modify the relationship between vultures and livestock. Herds arriving in summer pasturelands are getting progressively smaller. Consequently, the availability of carrion may have been reduced because the natural recovery of wild ungulates cannot quantitatively compensate for the density of ungulates artificially maintained by livestock. Therefore, the attraction exerted by the remaining transhumant herds may not be sufficient for vultures match their movements with those of livestock.

In this work, through extensive GPS tracking projects, we have explored whether vultures respond differently to the presence of transhumant herds depending on the intensity of this traditional livestock activity. First, we assessed whether vultures follow transhumant herds in two mountainous areas with historic transhumant tradition in the Iberian Peninsula and South America (Pyrenees and Andes). Second, we compared both systems to determine whether the attraction caused by transhumance herds is stronger in the site where transhumance is still a relevant activity (Andes) than where this activity is in decline (Pyrenees). For this purpose, we analyzed the use of summer pastures made by 50 griffon vultures (*Gyps fulvus*) and 18 Andean condors (*Vultur gryphus*) tracked by GPS. Our hypothesis is that the response of vultures will be stronger where transhumant activity is higher, so we expect condors to respond more intensely to the arrival of transhumant herds on their summer pastures. Specifically, we predict that in the Andes, a greater proportion of individuals studied will select summer grasslands and will spend more time there than in the Pyrenees.

2. Methods

2.1. Study sites

The Pyrenees is a mountain range between France and Spain with a length of 491 km, a maximum width of 150 km and a maximum altitude of 3404 m (Barnolas and Pujalte, 2004). Transhumance in Spain has been in decline since the XVIII century, but it has been in the last decades when it has reached its lowest levels (Otero-Rozas et al., 2013). In the 1990s, official censuses estimated around 377,300 transhumant sheep and cattle in the study area (MAGRAMA, 1995). However, since then, some areas of the Pyrenees have lost up to 80 % of their transhumant herds and it is estimated that there are currently below 100,000 transhumant sheep and cows left in the whole study area (Lasanta-Martinez et al., 2005; Gartzia, 2017). Traditionally, transhumant movements in this region connects winter pastures in the Ebro valleys (around 100 km to the south) and the high altitude summer pastures in the mountain range (See Fig. S1). These summer pastures are usually above 1500 m of altitude (Fernández-Giménez and Fillat, 2012) but herds may spend the summer at lower altitudes approaching 1350 m (García-Ruiz et al., 2020).

The Andes Mountains are located along western South America, and have a length of approximately 7000 km. This study is focused in central Argentinian Andes including all the west of Patagonia where maximum altitude is 4707 m. Over years, land use has changed throughout the Andes mountain range. However, there are areas where transhumant pastoralism is still a frequent activity and the dominant land-use type (Easdale et al., 2016; Padín, 2019). In Argentina, thousands of transhumant households still exist mainly in Neuquén province (Easdale et al., 2016; Padín, 2019) and their herds could exceed one million sheep (Bendini et al., 2004). During winter, herds stay on plateaus and low valleys, away from snowy areas. During spring, they are moved to the high fields of the mountain slope, mainly located above 1500 m of altitude, although some pastures are under this altitude (Bendini et al., 2004) descending again to wintering pastures in April (Padín, 2019).

2.2. Study species

Our two study species have great flight capabilities that allow them to forage over large areas (Alarcón and Lambertucci, 2018). The griffon vulture is a large bird (6.2–11 kg and 230–265 cm of wingspan) and there are slight sexual morphological differences (Xirouchakis and Poulakakis, 2008). Its diet is mainly based on domestic and wild ungulates (Donázar, 1993). This colonial species breeds in cliffs that also use as communal roost (Donázar, 1993). In Europe, its most important stronghold is the Iberian Peninsula reaching 33,000 breeding pairs, most of them in Spain (Del Moral and Molina, 2018).

The Andean condor is a large soaring bird (7.5–15 kg depending on the sex and age) and 260–314 cm of wingspan (Ferguson-Lees and Christie, 2001; Alarcón et al., 2017; Guido et al., 2020). Currently, they mainly feed on mammal carcasses, particularly livestock and other wild exotic species that replaced the native fauna (Lambertucci et al., 2018). Andean condors roost communally in large cliffs, but do not breed communally (Plaza and Lambertucci, 2020). This species has a clear sexual dimorphism, being adult males up to 50 % larger than juvenile females (Ferguson-Lees and Christie, 2001). The differences between sexes underlie a social hierarchical system dominated by males that produce sex-specific differences in their daily routines and habitat use (Alarcón et al., 2017). The species is distributed along the Andes Mountains range (Ferguson-Lees and Christie, 2001). Its population continues to decline, and is currently classified worldwide as "Vulnerable" and is categorized as "Threatened" in Argentina (Plaza and Lambertucci, 2020).

2.3. Bird tagging

Between December 2015 and March 2016, by means of cannon nets we captured 36 resident adult griffon vultures in Bardenas Reales, a protected area in the Ebro valley where transhumant herds winter. Vultures were tagged with e-obs GPS loggers, which were variably programmed depending on environmental conditions (Table S1). All individuals were monitored from the time of capture until December 2018 except if they died or the device stopped working. In parallel, in May 2018, 15 adult griffon vultures were captured in the North Catalonia and tagged with Ornitela GPS loggers. Loggers were programmed to collect a position every 10 min during light hours and functioned from the time of capture until May 2019. All individuals from this species were molecularly sexed and date by feathers molt and eyes and beak coloration (Wink et al., 1998; Zuberogoitia et al., 2013).

In the Argentinean study site, during the austral spring-summer seasons between 2013 and 2018, 18 immature Andean condors were captured (9 females and 9 males) using cannon net traps in the surroundings of Bariloche city, Río Negro province, Argentina. Of the total Andean condors, 11 were tagged with backpack 100-g solar GPS-GSM CTT NorthStar Science and Tecnology - VektorTek LLC, two birds with backpack 90-g solar CTT®-1090 GPS-GSM Cellular Tracking Technologies, and five of them with backpack 75-g solar CTT®-1000-BT3-Series GPS-GSM 3rd Gen Cellular Tracking Technologies. All individuals were monitored from the time of capture until December 2020 except if they died or the device stopped working. All condors' loggers were duty-cycled to transmit every day from dawn to dusk at the minimum time interval allowed by the tags, i.e. every 15 min. Andean condors were visually sexed based on their clear dimorphism (Ferguson-Lees and Christie, 2001).

2.4. Data processing

GPS data was filtered to obtain one position every half hour. To avoid the inclusion of resting time, we separated flying and perching locations by first establishing 3 ms^{-1} as our ground speed threshold for flying locations in both griffons and condors (Schlaich et al., 2016). To increase our ability to discern between flying and perching locations, we defined a second threshold using altitude (Arrondo et al., 2021). For this purpose, we calculated the cumulative histogram of altitude A.G.L. for both species. We used 1-m breaks, to establish the value after the maximum slope for which cumulative frequency stabilized considering it as the threshold of flying location. To define the stabilization of frequencies, we calculated the relative difference (%) between consecutive cumulative frequencies. We considered a difference of $\leq$0.1 % as stabilization. Therefore, locations with ground speed $\leq$3 ms^{-1} and altitude $\leq$135 m A.G.L. were considered non-flight locations for griffon vultures and in the case of condors, locations with ground speed $\leq$3 ms^{-1} and 85 m A.G.L. of altitude were considered as non-flight locations. Our procedure is very conservative and prone to consider as perching locations where the bird flies slow and very close to the ground. However, given that our objective is to assess foraging intensity within the study area, we believe that these low-speed and low-altitude positions are not particularly relevant since they will not affect significantly the general pattern observed with foraging data. In addition, we focused our analyses on the period of the day when our study species show the highest flight activity. This period was established by visual inspection of the hourly frequency histograms (Fig. S.2). As a result, we used only flying locations between 8:00 A.M. and 16:00 P.M. UTC in the case of griffons, and between 8:00 A.M. and 19:00 P.M. UTC in the case of condors. These periods include the hours where the main foraging behaviors occur for each species (Alarcon et al. 2017; Arrondo et al., 2021). Finally, we discarded those individuals with less than one year of tracking because shorter time periods did not allow for comparison between seasons (i.e., with and without transhumant livestock).

Each flying location was classified as inside or outside the study areas. We define the study areas in Pyrenees and Andes sites as all zones potentially hosting summer pastures. For this, we set a vertical limit of 1300 m. A.S.L., being the study area the zones above this altitude. Although most transhumant herds spend the summer above 1500 m. A.S.L. both, in Pyrenees and Andes (see references above), we set this conservative threshold as a measure to be sure that the number of transhumant herds outside the study area during the summer is as minimal as possible. In a second step flying locations were classified as "summer" if it comes from the time when livestock is in the study area (from June to October in the case of griffons and from December to April in the case of condors; see Fernández-Giménez and Fillat, 2012 and Padín, 2019), or as "winter" for the rest of the year.

2.5. Statistical analyses

In order to test whether our two target species show selection for summer pastures, used by transhumant herds, we performed two sets of GLMM models (generalized linear mixed models, Family = binomial, Function = logit) using the *lme4* package (Bates et al., 2015), one for griffons and the other for condors. In both cases we excluded from the analysis those individuals that never visited the study area. Individual ID and year were included as random effects and in both cases the response variable was the monthly proportion of locations within the study area (i.e. summer pastures). The independent variables were *Season* (summer/winter, being summer the season with livestock presence in the study area; see above) and *Sex* (male/female). Model selection was done by means of the Akaike's information criterion corrected for small sample size (AICc) by using *AICcmodavg* and *MuMIn* packages (Barton, 2009; Mazerolle, 2020). Models with ΔAICc<2 were considered equivalent. We discarded models including uninformative parameters, i.e. parameters whose 85 % confidence interval overlapped with 0 (Burnham and Anderson, 2002).

Finally, in order to compare the strength of the effect of transhumance between our two study areas, the Andes and Pyrenees, we performed two analyses. First, we compared the proportion of individuals that visited the two study areas during summer by means of a chi-square test. Second, we compared the intensity in which individuals use their respective study areas during summer. For that, we calculated the individual proportion of locations inside the study area during summer. Then, we compared both study areas by means of a *t*-test. For this analysis, we only used individuals that had visited the summer pastures at least once and that had data in both seasons. The data processing and analysis were performed entirely with the R software version 3.6.1 (R Development Core Team, 2019).

3. Results

A total of 45 individuals of griffon vultures had enough data to be considered (31 in Ebro population and 14 in North Catalonia). From them, only 14 visited at least one time the study areas and were finally included in the models (4 from Ebro Population and 10 from North Catalonia). Regarding condors, 9 individuals had enough annual data and all of them visited the study area (6 males and 3 females).

The best model structure obtained for griffon vultures (see Table S2) included the random component formed by the additive effect of individual and year. Considering this structure, models including *Sex* as explicative variable resulted non-informative and were not considered. Thus, the only remaining models that could be compared were the NULL and the one that included *Season* as the only explanatory variable (Table S.2). The model including *Season* had a lower AICc value, resulting selected (see Table 1). This means that vultures visited the study area more frequently during the summer, coinciding with the presence of livestock in this area.

The best model structures selected for condors (see Table S2) included individual and year as a random effect. As occurred in the case of griffon vultures, the variable *Sex* resulted non-informative and

Table 1
Results of the models selected to explain the intensity with which Griffon vultures and Andean condors use the study area.

Species	Explicative variable	Levels	Estimate	Std. error	*P*-value	95 % CI	R^2
Griffon vulture	Season	Intercept (Summer)	−4.791	0.353	<0.001	−5.566–4.057	0.11
		Winter	−0.883	0.191	<0.001	−1.264–0.504	
Andean condor	Season	Intercept (Summer)	0.362	0.418	0.039	−0.554 1.274	0.03
		Winter	−0.783	0.047	<0.001	−0.876–0.691	

consequently it was only possible to compare the NULL model and the model including *Season*. The best model was the one that included the variable *Season* (see Table S2) showing that, condors use more frequently the study area during the season when livestock is present (see Table 1).

Regarding the differences between our two study areas and species, we found that a major proportion of Andean condors visited the study area during summer ($\chi^2 = 11.9$; df = 1; $p < 0.001$) and they make a more intense use of the summer pastures than griffon vultures ($t = 6.98$; df = 8.01; p < 0.001; See Fig. 1 and Fig. S.3).

4. Discussion

Our findings show that both Old and New World vultures make a greater use of summer pastures when transhumant herds are present. The availability of carrion in the study areas during winter depends almost entirely on wild ungulates (Bolgeri, 2017; Margalida et al., 2018) and both species typically consume significant amounts of domestic ungulates from extensive farming (Lambertucci et al., 2018; Donázar, 1993). Additionally, both species have wide ranges of movement and breed in mountainous areas (see Methods), so it is not likely that there are physiological impediments limiting their use of the study areas during winter. Therefore, the arrival of large numbers of sheep during the summer seems to makes these areas more attractive to griffon vultures and Andean condors. In contrast, the response of vultures to the natural migration of wild ungulates appears to be based largely on mortality rather than prey density (Kendall et al., 2014), which may be due to the fact that wild and domestic ungulates have a different degree of seasonality in their mortality. Following our predictions, a higher proportion of condors made use of the summer pastures than griffon vultures, and each condor made a more intense use of it. These differences on the strength of attraction generated by transhumant herds could be explained by the fact that transhumance is still an important activity in the Andes, which implies relevant changes in the availability of carrion. In the Pyrenees, on the contrary, this traditional practice is in sharp decline and the amount of carrion provided by transhumant herds is lower (Lasanta-Martínez et al., 2005; Oteros-Rozas et al., 2013; Gartzia, 2017).

Given the difficulty of designing a specific experiment, our work is based on existing data, which undoubtedly has certain limitations. For example, although extensive movements occur at all age-classes in both species (Alarcón et al., 2017; Guido et al., 2020; Arrondo et al., 2021),

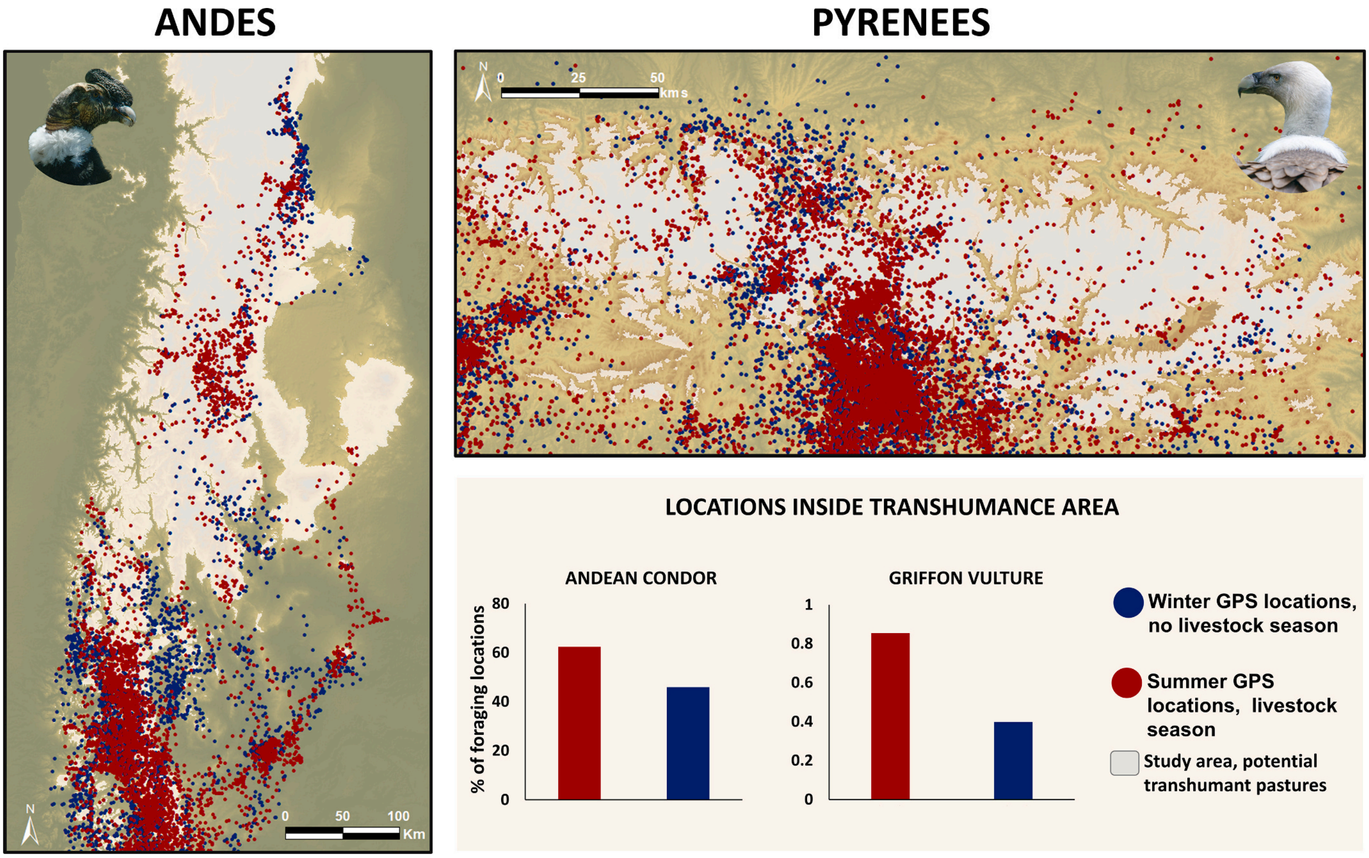

Fig. 1. Maps representing the foraging locations (red during winter and blue during summer) inside the summer transhumance area (white shading) and surroundings. Locations of the Andean condor are on the vertical map and locations of griffon vulture are on the horizontal map. Barplots represent the percentage of locations of each season that were located inside the summer transhumance area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

our interspecific comparison could not be as detailed as we would have liked. For example, the data available for each species were from different age classes. Furthermore, both species show obvious ecological differences, such as the aggregation in colonies in griffon vultures or greater sexual dimorphism in condors. However, the clear patterns found in our models suggest that transhumant livestock remain an attractive resource for large scavengers even in areas where this activity is declining and regardless of the vulture species considered. Thus, our results reinforce the fact that vultures are also able to cope with local and small-scale seasonal changes in food availability associated with traditional human activities such as extensive livestock movements (Aguilera-Alcalá et al., 2021). In this sense, although the available data on herd movement (Fig. S1) did not allow us to test the direct relationship between vulture and livestock movement, it seems clear that our seasonal approach is effective for assessing food availability in the study area.

Our results provide further evidence of the importance for biodiversity conservation of the high nature value of landscapes associated with low-intensity human activities (Lomba et al., 2020). Condors and griffon vultures responded to the altitudinal movements of livestock in large mountain ranges such as the Andes and Pyrenees. Recent research has shown that European savannas (the so called “dehesas”) support vultures from different populations that travel long distances to forage in pastures rich in extensive livestock (Delgado-González et al., 2022). Also, the identification of priority areas for the vulnerable Andean condor could benefit from detailed information on livestock movements (Perrig et al., 2020) and the role of patchy meadows that congregate scavengers and herbivores in Patagonian landscapes (Pérez-García et al., 2018).

5. Conclusions

This work shows that both Old and New World vultures follow transhumant herds on a seasonal scale. This relationship may have deep ecological consequences and evolutionary roots, as transhumance might have replaced somehow the pre-existing link between large scavengers and wild ungulate migrations (Delgado-González et al., 2022). Therefore, the fact that the intensity of the attraction exerted by transhumant herds may depend on the number of transhumant animals raises concerns that the current process of modernization of livestock farming may be affecting the ecological processes associated with transhumance. Altitudinal and latitudinal movements linking scavengers and extensive livestock may provide insights into the sustainability of socio-ecological systems in a context of global change. Seasonal movements of livestock optimize the use of natural grassland productivity and maintain biodiversity, in contrast to the increasing demand for imported feed for intensive farming, and its impacts on ecosystems. It is important to note that the consequences of the disappearance of transhumance would go beyond large scavengers and affect the wider ecological community, with ultimate consequences at the ecosystem and landscape scale, as part of a process of passive rewilding (Navarro and Pereira, 2012; Oliva-Vidal et al., 2022). This process involves a ecosystem changes that, as this article illustrates, is not necessarily positive for the species involved. In this sense, and given that the abandonment of transhumance and other traditional livestock and agricultural activities is a phenomenon currently underway, it is urgent to assess it impacts on biodiversity, especially on those taxa with a precarious conservation status.

CRediT authorship contribution statement

EA, SL and JASZ: conceptualization; EA: analyses; EA: writing original draft. EA, SL, JG and JASZ: writing; JAD; JASZ; AM; JDA and SL: funding; all coauthors contributed equally for review and editing.

Declaration of competing interest

The authors declare that they have no conflicts of interest and that this article is an original manuscript not submitted to any other journal. They also attest to comply with all ethical requirements as well as to have correctly indicated the funding of the work.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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