Moderate sheep grazing increases arthropod biomass and habitat use by steppe birds

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A B S T R A C T

Open semi-natural ecosystems have been historically shaped by anthropogenic land-use, and the abandonment or intensification of these activities implied a detrimental alteration of their landscapes. Extensive sheep grazing has gradually decreased during the 20th century in Mediterranean steppes, triggering changes across all taxa. Here, we address the effect of sheep grazing on both arthropod biomass and space use by insectivorous steppe birds, using an endangered passerine as a model species. We found that biomass of different arthropod groups peaked at intermediate levels of grazing, and that both short-term grazing (affecting arthropod biomass) and long-term grazing (affecting vegetation structure) explain space use by insectivorous birds, whereas only long-term processes are decisive for bird territory establishment. Our results emphasise the role of sustained moderate grazing intensity in the conservation of steppe biodiversity. In the current decline context of extensive sheep grazing, agricultural policies should prioritise these practices to ensure the persistence of open semi-natural ecosystems

1. Introduction

Grazing by domestic livestock is a global, dominant land use covering more than 25 % of the terrestrial surface, and 70 % of the agricultural lands on Earth (FAO, 2018). During the last 30 years, livestock grazing has progressed along two opposing trajectories: intensification in productive areas (increased livestock densities) and abandonment in marginal and less productive ones (Winkler et al., 2021). High livestock densities reduce plant height and biomass, consequently diminishing the abundance of invertebrates and small vertebrates, and ultimately impacting large ones, including predators (Dennis et al., 2008; Evans et al., 2015; Filazzola et al., 2020; Weiss et al., 2013). Overgrazing is one of the most important non-climatic factors behind the degradation of semi-natural ecosystems (IUCN, 2019), because it alters edaphic properties and promotes soil loss by erosion (Podwojewski et al., 2006; Liu et al., 2013; Cai et al., 2020). On the contrary, land abandonment has been described as one of the major drivers of landscape change (Cramer et al., 2008), especially in Europe (Plieninger et al., 2016). In ecosystems shaped by a long and complex

human use, the cessation of grazing favours natural vegetation succession (Debussche et al., 1999), leading to the disappearance of open habitats such as grasslands and shrublands, in favour of woodlands (Sirami et al., 2007). There are both winners and losers from the changes that occur in abandoned areas, ultimately altering species assemblages across all taxa (Russo, 2007). Notwithstanding, the effects of grazing on ecosystem structure and functioning are still relatively unknown, as they strongly rely on local contexts (Maestre et al., 2022). Besides, most of the field studies have focused on presence-absence grazing designs, while studies analysing actual grazing gradients are scarce in the literature (Eldridge et al., 2016).

Extensive livestock grazing is characterised by the use of natural pastures according to their spatial and temporal availability, with low-to-moderate livestock densities of local breeds adapted to the region. Recently, extensive grazing has been put forward as a strategy to preserve semi-natural open ecosystems (e.g., steppes, grasslands, moorlands; Boch et al., 2019) and their avian community (Leal et al., 2019; Skagen et al., 2018). Low-to-moderate grazing intensity reduces plant biomass and avoids woody encroachment (Evans et al., 2015; Filazzola

et al., 2020), but it increases bare ground cover and plant species richness and diversity, as predicted by the intermediate disturbance hypothesis (Boch et al., 2019; Yuan et al., 2016). These changes produce complex responses on higher trophic levels such as arthropods, which serve as prey for open-land birds (Filazzola et al., 2020; Goosey et al., 2019). The abundance of foliar, phytophagous arthropods decreases in moderately grazed areas compared to ungrazed ones likely because of the disruption of direct plant–insect associations (Filazzola et al., 2020). However, the abundance and richness of detritivore and predatory arthropods benefit from the structural changes and spatial heterogeneity introduced by moderate grazing (Filazzola et al., 2020; Goosey et al., 2019). Coprophagous arthropods, which depend on the faeces of herbivorous mammals for both feeding and nesting, are also benefited (Jay-Robert et al., 2008; Perrin et al., 2020). Therefore, moderate livestock densities might increase biotic (i.e., dung and plant diversity) and abiotic (structural complexity) heterogeneity and compensate for the detrimental effects of grazing on arthropods (i.e., incidental predation, direct mortality, or direct competition for resources), ultimately increasing arthropod diversity and abundance (Goosey et al., 2019; Perrin et al., 2019; van Klink et al., 2015). Consequently, moderate levels of grazing can favour open-land birds by two non-mutually exclusive ways (Leal et al., 2019; Malm et al., 2020; Velado-Alonso et al., 2020), either by avoiding vegetation encroachment to which these species respond negatively (Sirami et al., 2007, 2008), or by increasing spatial heterogeneity which favours arthropod diversity and abundance and thus, promoting temporal stability of food resources for insectivorous birds (Goosey et al., 2019; Perrin et al., 2019).

Steppes are illustrative examples of semi-natural open ecosystems where biodiversity has been shaped by historical grazing of low to moderate intensity (Halada et al., 2011). Apart from typical natural grass-steppes of Southern Russia, Ukraine and Kazakhstan, North American prairies, African veldts (treeless and open rural areas), Australian semideserts and Mediterranean steppes are commonly referred as steppes (Sainz Ollero, 2013). They are one of the most extensive terrestrial ecosystems worldwide (Wesche et al., 2016), but also one of the most threatened biomes due to changes in grazing pressures, among other factors (IUCN, 2019). In particular, the abandonment of sheep extensive grazing has become dominant in Iberian steppes since the second half of 20th century (Lepart and Debussche, 1992; Traba and Pérez-Granados, 2022), yet its impact at the ecosystem level has never been quantified.

Here, we address the effect of a sheep grazing intensity gradient on ecosystem functioning in Iberian steppes, focusing on arthropod biomass and on the occurrence and space use of a strictly insectivorous passerine bird as a model species. The study aimed to: (1) estimate the effect of sheep grazing on arthropod biomass (epigeous, coprophagous, and consumer groups: predatory, detritivore, phytophagous and others) as proxies of steppe quality in terms of food availability for insectivorous birds (hereafter, *Goal 1*); (2) evaluate the differences in sheep grazing intensity between areas with and without stable bird territories (i.e., long-term occurrence; hereafter, *Goal 2*); and (3) assess the effect of sheep grazing on the space use by steppe birds (i.e., immediate habitat use; hereafter, *Goal 3*). We quantified the entire sheep grazing intensity gradient ranging from ungrazed areas to heavily grazed areas, i.e., sheep resting sites characterised by low plant cover and heavy foot trampling, by tagging sheeps with collars equipped with Global Positioning System (GPS). We hypothesise that arthropod biomass and space use patterns of insectivorous steppe birds will increase with grazing intensity, due to its role as a driver maintaining a suitable vegetation structure (high cover of short shrubs and bare ground; Leal et al., 2019) and increasing food availability (e.g., coprophagous arthropods; Evans et al., 2015; Perrin et al., 2019; Weiss et al., 2013). The results of this research will provide insights on the importance of sheep grazing on the conservation of steppe biodiversity, and on the potential consequences of the abandonment of this historical land use.

2. Methods

2.1. The study system and model species

Iberian steppes are among the most unique steppe landscapes in Europe (Suárez et al., 2006) and the world, characterised by a great diversity resulted from the complex relief and geomorphology, the geographical and lithological heterogeneity and contrasting climates (Sainz Ollero, 2013). They are dominated by small shrubs, with forbs and grasses, and they have been historically shaped by human action, with a deep importance of extensive sheep grazing (Sainz Ollero, 2013). Traditional land uses were moderate to intensive and balanced between human and wildlife utilisation of the steppes. However, the cessation of these traditional practices has favoured shrub encroachment and the regeneration of native trees, implying a huge transformation of Iberian steppe landscapes. As a consequence, steppes have lost their innate structural simplicity to which the steppe avifauna is adapted (De Juana, 2005), thereby leading to bird population declines (Traba and Pérez-Granados, 2022), as is the case with the Dupont's lark *Chersophilus duponti* (Gómez-Catasús et al., 2018). The Dupont's lark is a threatened steppe passerine listed amongst the 65 priority bird species inhabiting steppes (Burfield and Bommel, 2004) and is one of the scarcest passerine birds in Europe (Gómez-Catasús et al., 2018). It inhabits steppes in Spain and North Africa, and land use changes and the abandonment of extensive sheep grazing, common issues in steppe ecosystems, have been documented as the main threats to the species (Tella et al., 2005). We used it as a model species because its strict habitat-selection habits (Garza et al., 2005) and sensitivity to environmental change (García-Antón et al., 2019) make it an appropriate indicator of the conservation status of Iberian steppes and thus, of the effects of sheep grazing on this ecosystem.

2.2. Study area

The study was carried out in the plateaus of the Iberian System in central Spain (2°26 35.1"W, 41°11 28.9"N; c.1200 m a.s.l., Fig. 1). The landscape is a flat, open and treeless mosaic dominated by continental shrublands and mixed grassland-shrublands such as *Genista pumila*, *G. scorpius*, *Thymus* spp. and *Satureja intricata*, dry perennial grasslands, and terophytic grasslands on carbonate substrates (Zurdo et al., 2021). This area has been historically grazed by sheep. Sheep numbers have experienced a significant decline in the last 20 years in Spain (Traba and Pérez-Granados, 2022). However, the number of herds and their sizes have not varied in the study area during the last decade (J. Esteban, local farmer pers. comm.). Habitat fragmentation associated with anthropogenic activities (e.g., cereal fields, conifer reforestations) is coupled with the natural fragmentation of steppes, resulting in a patchy distribution of this habitat. This study was carried out in five of these patches (hereafter referred to as localities; Fig. 1, Appendix A).

The study area hosts 18 habitat types of Annex I of the Habitats Directive and it harbours 32 bird species included in Annex I of the Birds Directive, such as the Calandra lark (*Melanocorypha calandra*), the Dupont's lark, the Tawny pipit (*Anthus campestris*), and the Thekla's lark (*Galerida theklae*). The study area is located within the 'Altos de Barahona' and 'Páramo de Layna' Special Areas of Conservation (SAC) and Special Protection Area (SPA) of the European Union's Natura 2000 Network (ES4170148 and ES4170120, respectively; Fig. 1).

2.3. Sheep GPS tracking

All livestock farming units in the study area (n = 5 herds) were equipped with GPS collars between April 2018 and June 2019. GPS collars consisted of a GPS CatLog2 device and a 9000 mA h rechargeable lithium battery protected by a PVC tube, and they were provided by Perthold Engineering LLC (www.mr-lee.com; Appendix B). One GPS collar was placed per herd and programmed to obtain a location
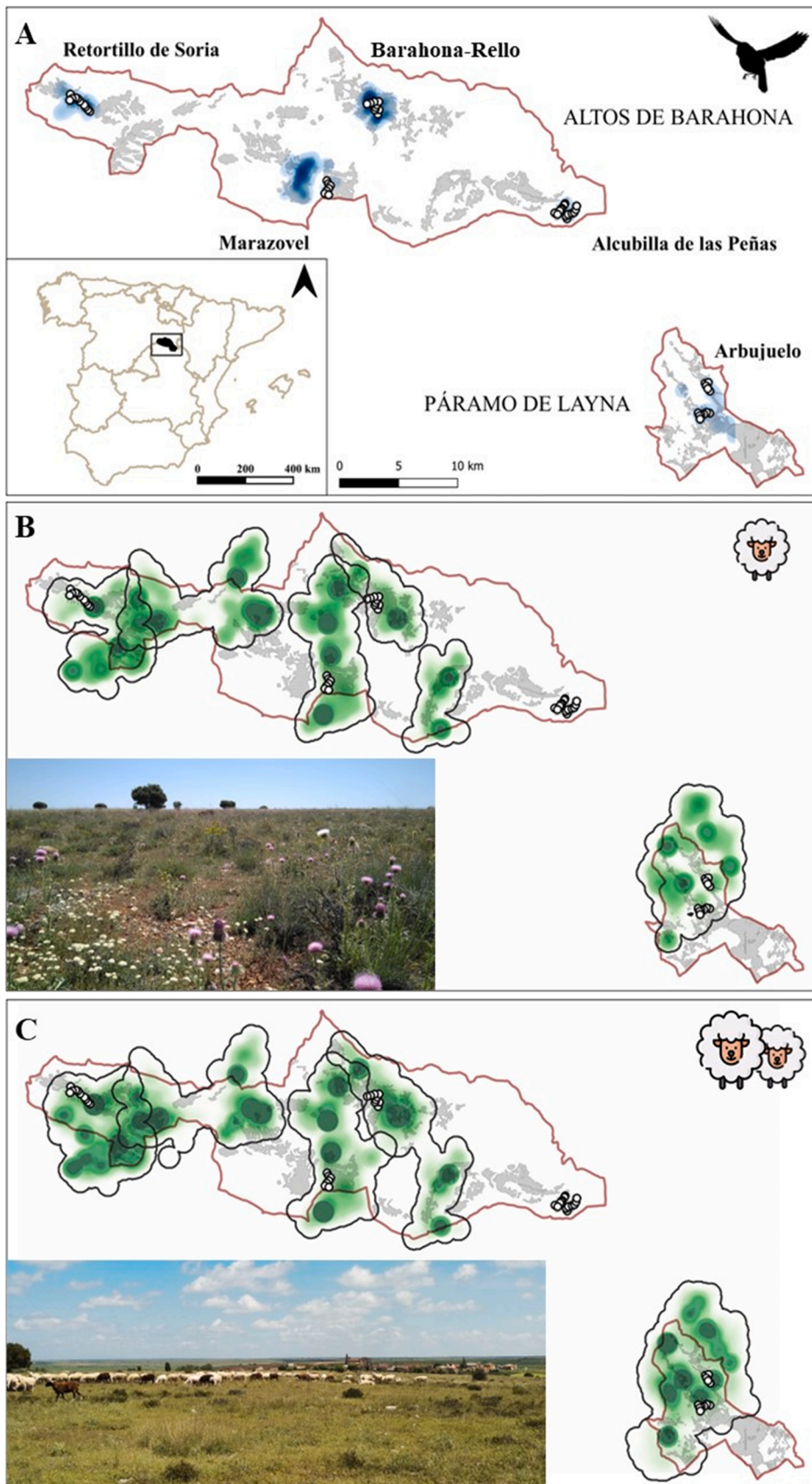
Fig. 1. A) Location of the study area in central Spain (black rectangle), and intensity of space use by the Dupont's lark estimated by the Kernel Density Function (KDF) employing Dupont's lark territories (see text): colour varies from high (dark blue) to low intensity values or absences (white). The name of the Special Protection Area (SPA) and Special Areas of Conservation (SAC; capital letters) and their border (red line) are shown. The name of each sampled locality is depicted (bold letters), as well as the border of steppe patches (grey polygons); B) grazing intensity during the breeding period; and C) grazing intensity during the cumulative period, both estimated by the KDF employing sheep GPS locations and representing from highly grazed (dark green) to ungrazed (white) areas. Black lines in B) and C) are the 100 % kernel density isopleths (i.e., 100 % of the volume of the probability density functions) for each tagged sheep herd. See the text for detailed information about the estimation of the KDF and the differences between the breeding and cumulative periods. White dots in A), B) and C) are the sampling stations.

(accuracy ± 5 m) once every 30 min. Farmers were contacted periodically (once per month) to download the data stored by the GPS device and to record the number of sheep per herd, so that each GPS location could be assigned a weight corresponding with herd size. A detailed description of the GPS data and the cleansing procedure can be found in Appendix B.

2.4. Dupont's lark surveys

We surveyed Dupont's lark by foot transects during the breeding season (April-June) in 2018 and 2019. The number of transects per patch was proportional to patch size (range: 1–5 transects per patch; total of 22 transects) and their length varied between 1 and 3 kilometres. We walked each transect 3 times per breeding season (one per month), alternating the starting point in each visit. Surveys were carried out approximately 1 h before dawn and they lasted around 1 h. Location of singing males was georeferenced with a GPS and territories were delimited by gathering accumulated observations from different surveys and calculating the mean centroid (Pérez-Granados and López-Iborra, 2017).

2.5. Arthropod biomass

We designated 52 field sampling stations to estimate arthropod biomass in 2018 and 2019 (Fig. 1, Appendix A). Sampling stations were separated by a mean distance of 271.7 m (SD = 170.9). Epigeous and coprophagous arthropod biomass was sampled three times (April, May, and June) during each year (2018–2019), and we employed the average value. Epigeous arthropods were sampled using three pitfall traps per sampling station, placed at 5 m intervals. Pitfall traps consisted of a plastic cup of 230 ml, 7 cm diameter and 10 cm depth, with holes at the top to ease rain drainage. Plastic cups were buried and protected by a PVC tube to prevent its collapse and filled with 175 ml of 40 % ethylene glycol and a drop of soap to reduce surface tension. Traps were active for seven days, then being filtered and animals stored in 70 % ethanol. Although flying arthropods also fell into the pitfall traps, we carried out a specific sampling of flying arthropods at the moment of collecting pitfall traps in order to cover all taxa. For that, we walked two 10 m transects per sampling station with an entomological sweep net. Trapped individuals were stored in the same bottle as ground-dwelling arthropods and they were considered together, hereafter referred as epigeous arthropods.

Coprophagous arthropods were sampled at each sampling station placing one baited pitfall trap, consisting of a 20 cm diameter plastic container baited with 200 g of fresh local sheep dung. Traps were active for one day, just after the collection of epigeous pitfall traps and under similar weather conditions in all sampling stations. Coprophagous arthropods were stored in 70 % ethanol and only those individuals with coprophagous habits were identified: order *Coleoptera* family *Scarabaeidae* (*Gymnopleurus* spp., *Onthophagus* spp. and *Scarabeus* spp.) and order *Diptera* suborder *Brachycera*.

We determined arthropods at least to its taxonomic order. Epigeous arthropods were classified into consumer groups (predatory, detritivore, and phytophagous, whereas arthropods with a diverse diet were classified as other arthropods, hereafter referred to as Diptera/Formicidae; Appendix C) because we expected that each consumer group will respond differently to the grazing gradient. Lastly, we calculated the biomass per arthropod consumer group through the specific equations from Hódar (1996). Since three pitfall traps were placed per sampling station, the biomass of epigeous (and consumer groups) arthropods per station was estimated as the mean biomass of the pitfall traps that were active after seven days. Coprophagous arthropod biomass was estimated as the total biomass measured in each sampling station, since only one baited pitfall trap was placed per sampling station. Lastly, as epigeous and coprophagous arthropods were sampled in three occasions (April, May and June) in two consecutive years (2018 and 2019) we calculated

biomass as the mean value over the months and years, so that we would only have one value to relate to the grazing intensity value (see Section 2.3). For a similar methodology for estimation of invertebrate biomass see Gómez-Catasús et al. (2019), Reverter et al. (2021) or Traba et al. (2022).

2.6. Statistical analysis

2.6.1. Kernel density functions

The Kernel Density Function (KDF) was used to estimate grazing intensity by sheep and space use intensity by the Dupont's lark. KDF is a two-dimensional representation of the relative frequency distribution of a spatial pattern of points, which provides higher probability values to those areas with a greater number of points (Worton, 1989). KDFs were estimated using the Kernel Density Estimation function tool of SAGA in the free software QGIS (Quantum GIS Development Team, 2020). For grazing intensity, a smoothing factor of 900 and a cell size of 50 × 50 m was employed, and we assigned each GPS location and date a weighting factor corresponding to the number of sheep per herd (see Section 2.3 and Appendix B). We estimated two KDFs of grazing intensity: (1) one using all GPS locations obtained during the whole study period (April 2018 – June 2019) to estimate the cumulative grazing intensity (hereafter referred to as *cumulative grazing*; Fig. 1C); and (2) a second index using only the GPS locations obtained during April-June (i.e. the breeding period of the Dupont's lark) in 2018 and 2019 (data of both years pooled), in order to obtain an estimate of grazing intensity during the breeding period (hereafter referred to as *breeding grazing*; Fig. 1B). The two KDFs reflect different aspects of grazing intensity. The *breeding grazing* aims to assess the immediate effect of grazing intensity on habitat quality and space use patterns by the Dupont's lark, since there is a temporal overlap between: (i) sheep GPS locations (see Section 2.3 and Appendix B); (ii) Dupont's lark surveys (see Section 2.4); and iii) arthropod biomass sampling (see Section 2.5). In contrast, the *cumulative grazing* aims to find out whether there is a cumulative effect of grazing intensity. Regardless of whether an area is grazed during or outside the breeding period, the effect of sheep grazing may persist over time, in turn affecting arthropod biomass and the intensity of space use by the Dupont's lark during the breeding period.

We also developed a map representing the intensity of space use by the Dupont's lark (i.e., the strength of space use as it relates to the relative frequency of the spatial pattern of Dupont's lark territories) using the KDF and employing all Dupont's lark territories surveyed during the spring of 2018 and 2019 (data of both years pooled, see Section 2.4; Fig. 1A). In this case, we employed a smoothing factor of 600 and a cell size of 50 × 50 m.

2.6.2. General aspects of the statistical procedure

We explored the effect of breeding and cumulative grazing on arthropod biomass, as well as on the occurrence and space use patterns by the Dupont's lark, by means of separate spatial linear regression models (Gaussian error distribution; see below). In all models, we accounted for potential spatial dependencies by incorporating a spatial random effect (i.e., random factor) using Integrated Nested Laplace Approximation with Stochastic Partial Differential Equations (INLA-SPDE; Lindgren et al., 2011). Under this approach, spatial dependency is accounted for using a latent Gaussian random field, which we constructed using two-dimensional irregular grids (meshes; Appendix D) based on the geographic coordinates of the observations (see below) (Gómez-Rubio, 2020; Zuur et al., 2017).

Spatial confounding is another potential problem in our data, which occurs when the covariates or fixed factors are collinear with the spatial random effect, leading to bias and variance inflation of the fixed effects and hence erroneous inference (Hanks et al., 2015). To overcome this problem, the solution is to constrain the spatial random effect to be orthogonal to those fixed effects with a spatial pattern (Adin et al., 2021). We tested for spatial confounding in our models by fitting linear

regression models incorporating the spatial random intercepts for each observation (response variable) and covariates (cumulative and breeding grazing for *Goals 1 and 3*) or fixed factors (Dupont's lark occurrence for *Goal 2*) as predictors (Hanks et al., 2015). We considered the existence of spatial confounding when the 95% Bayesian Credible Interval (95 % BCI) for the explanatory variables under consideration did not contain 0, which means that the spatial random intercepts and the explanatory variables involved are correlated (see Appendix E for results). In the presence of spatial confounding, we fitted spatial linear regression models (Gaussian error distribution) constraining the spatial random effect to be orthogonal to the explanatory variable under consideration (extraconstr argument in INLA; Gómez-Rubio, 2020).

All response and explanatory variables were log-transformed when necessary to achieve linearity, and fixed covariates (i.e., breeding and cumulative grazing intensity) were z-standardised (mean=0 and SD=1). We incorporated both linear and quadratic forms of grazing intensity as predictors to control for non-linear relationships. All models were fitted using the R package INLA (Rue et al., 2009) in the free R software (v.4.0.3; R Core Team, 2020). Parameter estimates were reported as the posterior mean (β), associated standard deviation (SD) and the 95% BCI.

2.6.3. Goal 1: Grazing intensity and arthropod biomass

We calculated the breeding and cumulative grazing as the mean value of both Kernel density maps in a 50-metre buffer around the sampling stations. To assess the effect of cumulative and breeding grazing (explanatory variables) on arthropod biomass (epigeous and coprophagous arthropod biomass, as well as biomass of the four consumer groups; response variables) we fitted separate spatial linear regression models (total of 12 models: two models per arthropod group to assess the effect of breeding and cumulative grazing independently). To account for potential spatial dependencies, we constructed a mesh using a non-convex boundary for the coordinates of the sampling stations (Appendix D; Zuur et al., 2017).

2.6.4. Goal 2: Grazing intensity and Dupont's lark long-term occurrence

We calculated the breeding and cumulative grazing as the mean value of both Kernel density maps in a 50-metre buffer around Dupont's lark territories in 2018 and 2019 (i.e., presences). Similarly, both values of grazing intensity were estimated at an equivalent number of randomly generated points (i.e., 309 points) in areas with optimal habitat for the Dupont's lark (i.e., slope ≤15 %; Garza et al., 2005), where the species has not been recorded during the study period and recent years (i.e., pseudoabsences). We explored the differences in cumulative and breeding grazing (response variables) between localities with presence or absence of Dupont's lark (factor presence/absence) by means of two separate spatial lineal regression models. Following the same procedure explained above, we accounted for potential spatial dependencies using INLA-SPDE and we constructed a mesh using a non-convex boundary and a buffer zone for the coordinates of the presences (i.e., Dupont's lark territories) and pseudoabsences (i.e., generated random points) (Appendix D).

2.6.5. Goal 3: Grazing intensity and space use by the Dupont's lark

To assess the relationship between the intensity of space use by the Dupont's lark and grazing intensity, we generated 1000 random points separated by a minimum distance of 100 m in areas with optimal habitat for the species and where Dupont's lark presence is known. The intensity of space use by the Dupont's lark, and both breeding and cumulative grazing were calculated as the mean value of the corresponding Kernel density maps in a 50 m buffer around each random point. As in the previous analysis, we fitted two spatial linear regression models to assess the effect of breeding and cumulative grazing on space use by the Dupont's lark, independently. For that, we constructed a mesh based on the coordinates of the 1000 randomly generated points (Appendix D).

3. Results

3.1. Grazing intensity and arthropod biomass

The biomass of epigeous arthropods per trapping day ranged from 3.02 to 37.27 g/m^2 (Mean ± SD = 12.19 ± 6.61), while for coprophagous arthropods ranged between 0.21 and 16.66 g/m^2 (3.85 ± 4.28). Among epigeous, predatory, detritivore and phytophagous arthropods accounted for 24.7 ± 12.6% (range= 6.6–72.8 %), 35.7 ± 17.3 % (range= 8.9–77.9 %) and 32.9 ± 16.5% (range= 4.5–74.7 %) of total biomass, respectively. The biomass of Diptera/Formicidae only accounted for 5.1 ± 9.9 % (range= 0.3–69.1 %) of total epigeous biomass.

The total biomass of epigeous arthropods increased with both breeding and cumulative grazing intensity until a threshold from which it decreased (linear and quadratic terms in Table 1; Fig. 2A-B). Similarly, the biomass of coprophagous arthropods reached its maximum value at intermediate levels of grazing intensity during the breeding period (Table 1; Fig. 2G), whereas cumulative grazing did not influence the biomass of this arthropod group (Table 1). Not all arthropod consumer groups showed the same pattern. The biomass of predatory (Fig. 2C-D) and detritivore (Fig. 2E-F) arthropods also increased with breeding and cumulative grazing intensity until a threshold from which the biomass of both consumer groups decreased (Table 1). However, the biomass of phytophagous and Diptera/Formicidae arthropods did not vary with breeding or cumulative grazing intensity (Table 1).

3.2. Grazing intensity and Dupont's lark long-term occurrence

The spatial regression models addressing the relationship between Dupont's lark occurrence and grazing intensity suggested that breeding grazing did not differ between areas in the presence and in the absence of Dupont's lark (β ± SD= −0.027 ± 0.017, 95 % BCI= [−0.061; 0.008]). However, cumulative grazing intensity was higher in areas with

Table 1

Results of the Gaussian spatial models addressing the relationship between the biomass of arthropods (epigeous, coprophagous, and consumer groups: predatory, detritivore, phytophagous and Diptera/Formicidae), and grazing intensity during the breeding (BP) and the cumulative (CP) periods. Models were fitted using data from 52 sampling stations. Posterior mean (β), standard deviation (SD) and 95 % Bayesian Credible interval (95 % BCI) are shown for each predictor. Important predictors are marked with asterisk (*).

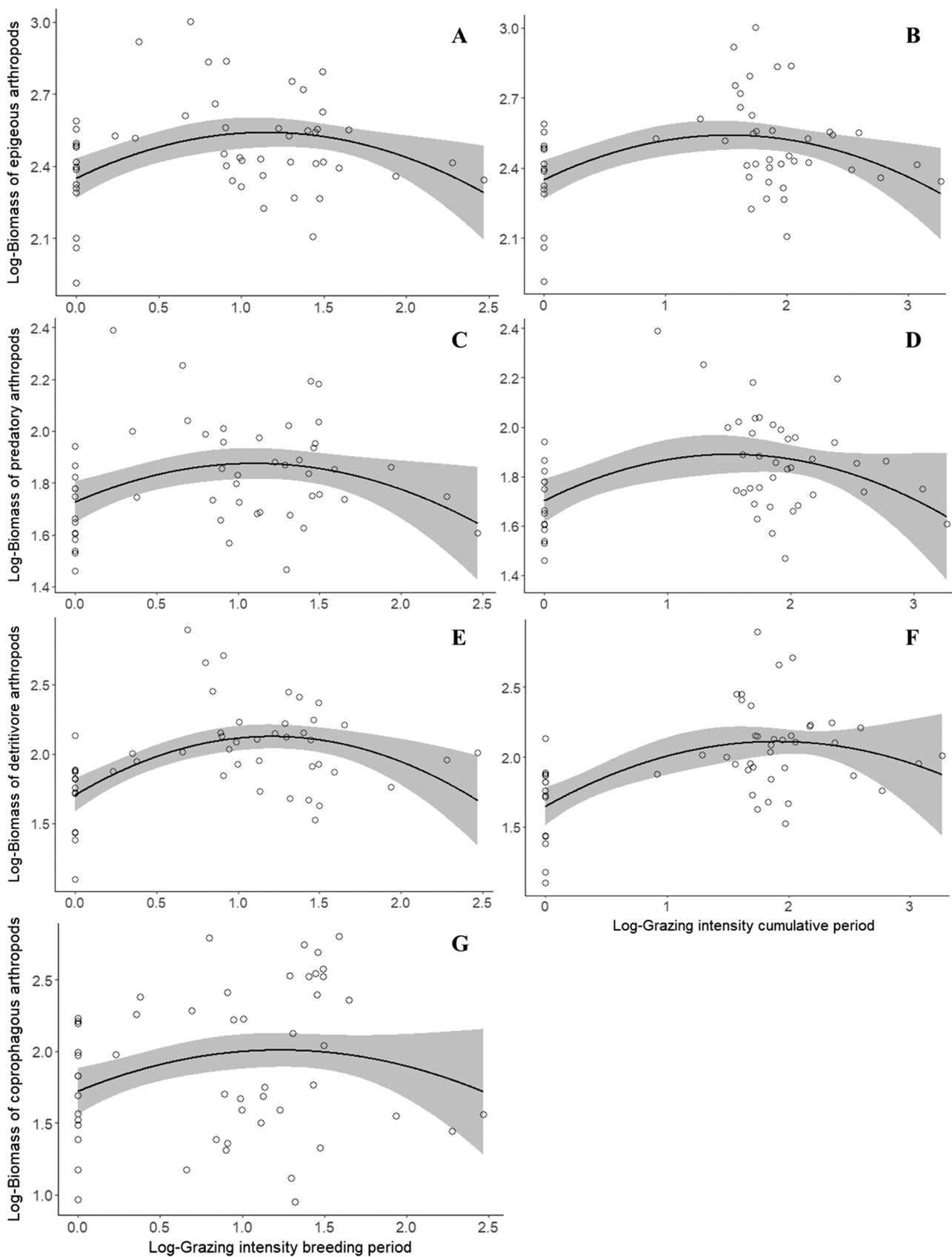|		Grazing BP (linear)	Grazing BP (quadratic)	Grazing CP (linear)	Grazing CP (quadratic)
Epigeous	β	0.196	-0.241	0.234	-0.259
	SD	0.065	0.085	0.063	0.083
	95% BCI	[0.068; 0.323]*	[− 0.401; − 0.074]*	[0.108; 0.360]*	[− 0.422; − 0.096]*
Coprophagous	β	0.33	-0.342	0.094	-0.102
	SD	0.129	0.170	0.451	0.386
	95% BCI	[0.076; 0.584]*	[− 0.677; − 0.008]*	[− 0.868; 0.930]	[− 0.835; 0.697]
Predatory	β	0.192	-0.222	0.232	-0.259
	SD	0.064	0.084	0.086	0.115
	95% BCI	[0.065; 0.318]*	[− 0.389; − 0.056]*	[0.061; 0.401]*	[− 0.487; − 0.029]*
Detritivore	β	0.495	-0.523	0.455	-0.403
	SD	0.095	0.125	0.148	0.2
	95% BCI	[0.307; 0.682]*	[− 0.769; − 0.276]*	[0.163; 0.747]*	[− 0.801; − 0.008]*
Phytophagous	β	0.031	-0.022	0.047	-0.069
	SD	0.169	0.197	0.191	0.211
	95% BCI	[− 0.298; 0.376]	[− 0.419; 0.376]	[− 0.331; 0.437]	[− 0.495; 0.344]
Diptera/ Formicidae	β	-0.029	-0.011	0.11	-0.17
	SD	0.215	0.243	0.226	0.244
	95% BCI	[− 0.491; 0.370]	[− 0.475; 0.491]	[− 0.344; 0.562]	[− 0.656; 0.311]

Fig. 2. Relationship between the biomass of epigeous (A-B), predatory (C-D), detritivore (E-F) and coprophagous (G) arthropods (log-transformed), and breeding (A-C-E-G) and cumulative (B-D-F) grazing intensity (log-transformed). The mean (black line) and 95% BCI (grey surface) of the values predicted by the quadratic models, are depicted. Moreover, the observation values for each sampling station (empty points) are shown.

Dupont's lark territories (β ± SD= 0.183 ± 0.008, 95 % BCI= [0.167; 0.199]; Fig. 3). These differences in cumulative grazing intensity were mainly related to non-grazed areas which were more abundant in localities without Dupont's lark territories (16.8% of the sampling points) as compared to areas with species territories (3.23 %; χ^2= 31.62, p-value < 0.001).

3.3. Grazing intensity and space use by the Dupont's lark

The intensity of space use by the Dupont's lark increased with grazing intensity during both the breeding and cumulative periods (linear terms in Table 2) until a threshold from which the use of space by the Dupont's lark decreased (quadratic terms in Table 2; Fig. 4).

4. Discussion

Our study emphasises the key role of sustained moderate intensity of livestock grazing in the conservation of Iberian steppes. Intermediate levels of grazing had a consistent positive effect on arthropod biomass, but also on the space use and territory location by an insectivorous specialist bird linked to this ecosystem, the Dupont's lark. However, the positive effect of grazing intensity turned negative when grazing intensity exceeded a certain threshold, which seems to support the intermediate disturbance hypothesis that has also been supported by previous studies of plants (Boch et al., 2019; Yuan et al., 2016), arthropods (Filazzola et al., 2020; van Klink et al., 2015) and birds (Leal et al., 2019). Previous studies have addressed the impact of grazing on open semi-natural habitats, but typically under regimes of livestock inclusion and exclusion. The novelty of our research lies in the coverage of a complete grazing intensity gradient, which allowed us to demonstrate that grazing must be maintained within certain thresholds, avoiding very low and high grazing intensity, in order to preserve steppe ecosystems. We were unable to unravel the possible effect of historical grazing in our results. However, the number of herds and their size has remained stable since 2015 (J. Esteban, local farmer personal communication), which suggests that the grazing intensity measured during the study was also representative of the historical grazing regime in the study area.
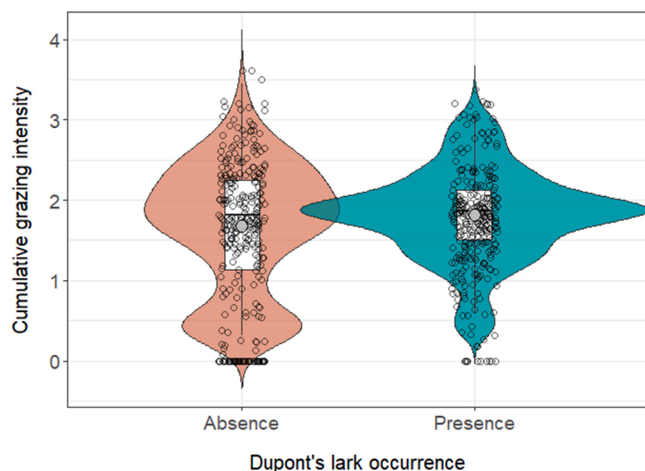

Fig. 3. Cumulative grazing intensity (log-transformed) in areas with (n = 309) and without Dupont's lark territories (n = 309) are shown with empty points. Median (black line), mean (grey dot), and 25th and 75th percentiles (box) are depicted. The violin plot (surfaces) represents the distribution (kernel probability density) of the cumulative grazing intensity predicted by the model at areas in the presence (blue) and absence (red) of Dupont's lark.

Table 2

Results of the Gaussian spatial models addressing the relationship between the intensity of space use by the Dupont's lark, and grazing intensity during the breeding (BP) and the cumulative (CP) periods, respectively. Models were fitted using data from 1000 random points in areas with Dupont's lark territories. Posterior mean (β), standard deviation (SD) and 95% Bayesian Credible interval (95% BCI) are shown for each predictor. Important predictors are marked with asterisk (*).

	β	SD	95% BCI
Grazing BP (linear)	0.354	0.008	[0.339; 0.370]*
Grazing BP (quadratic)	-0.435	0.010	[− 0.454; − 0.416]*
Grazing CP (linear)	0.348	0.007	[0.334; 0.363]*
Grazing CP (quadratic)	-0.319	0.009	[− 0.337; − 0.301]*

4.1. Effects of grazing on arthropod biomass

We have found a positive effect of extensive grazing on epigeous arthropod biomass, peaking at intermediate values of grazing intensity, for both cumulative and breeding grazing periods. This result is in accordance with previous studies based on a factorial design of livestock inclusion and exclusion but, to our knowledge, this is the first study evaluating grazing effects on arthropods across a gradient of grazing intensity (Filazzola et al., 2020; Goosey et al., 2019). In general, low-to-moderate livestock densities have been associated with increasing micro-scale heterogeneity, via dung depositions and disturbances (Goosey et al., 2019; van Klink et al., 2015). This heterogeneity could offset potential negative effects of grazing on arthropods (van Klink et al., 2015), such as accidental predation or competition for nutritious plants that could diminish the resources available for phytophagous arthropods. As a result, previous studies have reported a decrease in the abundance of phytophagous arthropods in grazed areas (Dennis et al., 2008; Filazzola et al., 2020), but an increase in detritivore and predator arthropods (Filazzola et al., 2020; Goosey et al., 2019). In our case, phytophagous arthropod biomass showed little response to grazing, perhaps due to the dominance of woody plants encroaching the studied communities, which resulted in decreasing prevalence of herbaceous plants usually consumed by sheep (Zurdo et al., 2021). On the contrary, detritivore, coprophagous and predator arthropod biomass, as well total epigeous biomass, were positively related to intermediate levels of grazing, which might be explained by the beneficial effects of the structural changes induced in the plant community by sheep grazing (Dennis et al., 2008; Goosey et al., 2019). Future studies should address the direct effect of grazing on vegetation structure and floristic composition in steppes, as well as the indirect effects on the arthropod biomass through the changes induced in the plant community.

Sheep might also benefit coprophagous arthropods through dung depositions, since they are directly dependent on the faeces of herbivorous mammals for both feeding and nesting (Perrin et al., 2020). In this study we report a positive relationship between coprophagous biomass and grazing intensity during the breeding season, which reached a maximum at intermediate levels and decreased thereafter. This result suggests that even in a direct relation like this, intermediate levels of grazing may provide better conditions for coprophagous than intensive areas. In our case, areas with increased grazing use coincide with resting sites characterised by low plant cover and heavy foot trampling, which ultimately could exacerbate the positive impacts of sheep on coprophagous arthropods (i.e., dung deposition), but without offsetting the increase in negative impacts (i.e., high accidental predation, foot trampling). Lastly, we did not detect an effect of the cumulative grazing intensity on coprophagous arthropods, highlighting the relevance of immediate effects of grazing on this arthropod group, likely through dung depositions, and suggesting that cumulative effects alone (i.e., structural changes on vegetation) may not be enough. In our study we captured a limited set of points with high grazing intensity. This suggests that in our study system, grazing intensity is generally below the maximum thresholds above which relationships between grazing and
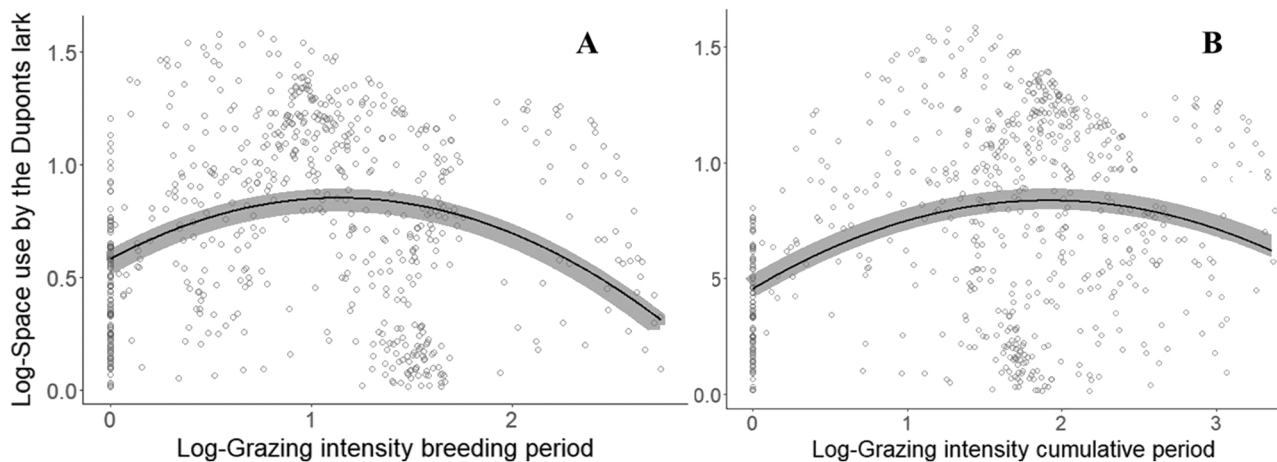
Fig. 4. Relationship between the intensity of space use by the Dupont's lark (log-transformed) and breeding (A) and cumulative (B) grazing intensity (log-transformed). The mean (black line) and 95 % BCI (grey surface) of the values predicted by the models, are depicted. Moreover, the observation values for each sampling station (points) are shown.

arthropod abundance are negative. Future studies should better cover this part of the gradient to define optimal grazing thresholds.

4.2. Effects of grazing on Dupont's lark long-term occurrence

The relationship found between Dupont's lark occurrence and cumulative grazing intensity, but not with breeding grazing, points to the effect of grazing on long-term ecosystem processes, probably linked to changes on vegetation structure. Dupont's lark, as several other steppe birds, nests under small shrubs with a significant proportion of bare ground (Yanes and Suarez, 1995; Herranz et al., 2004; Barrero et al., 2023), which is a plant structure clearly linked to grazed steppes. This way, moderate cumulative grazing intensities may facilitate ideal vegetation structure for nesting. Our results also emphasise the importance of maintaining moderate grazing on a long-term management (see also, van Klink et al., 2015), as effects on territory establishment are observed through the cumulative effect of grazing over two years. This result suggests that the application of relatively cheap and rapid management measures as dung sown may have short-term positive effects on food availability (Reverter et al. in prep.) and thus, on bird populations, but may fail on achieving stable territories and nesting conditions if they are not accompanied by actual and continuous grazing. Overall, our results reveal that the effective area of habitat available for the Dupont's lark and other steppe species might be subjected to grazing levels, being lower than previously expected. Considering the optimal grazing values for the occurrence of Dupont's lark territories (Fig. 3), the effective area of available habitat as compared to the total area of steppe would be reduced by 23.35 % (SD= 38.46; see Appendix F).

4.3. Effects of grazing on space use by an insectivorous model species

Space use by the Dupont's lark was positively associated with intermediate levels of both the long-term (cumulative) and short-term (breeding season) grazing intensity, which could reflect delayed effects on plant structure (see below) and immediate ones on food availability (e.g., coprophagous arthropod biomass). The most immediate effect of sheep grazing is the supply of dung, which increases the abundance of coprophagous arthropods and other invertebrates (see Section 4.1). Increased in arthropod biomass may improve habitat quality for the Dupont's lark and other bird species, especially during the breeding period when fledglings are extremely dependent on protein supply (Herranz et al., 1994; Jiguet, 2002). Recent research on the diet of Dupont's lark found that this species prefers coprophagous arthropods in general (Talabante et al., 2015) and insects of the orders

Coleoptera, *Julida* and *Araneae* (Zurdo et al., 2023). Other positive but not instantaneous effects of grazing on space use by steppe birds are related with increasing foraging efficiency by easing movements in open habitats (Buckingham and Peach, 2005; Leal et al., 2019; Murray et al., 2016; Zbyryt et al., 2020), while predation risk diminishes in sparser vegetation (Whittingham and Evans, 2004). Overall, a trade-off must exist between foraging efficiency, shelter, food availability and nesting requirements, as has been reported for other species (Meadow pipits Evans et al., 2015; but see effects for food availability Leal et al., 2019; for breeding success Malm et al., 2020). High grazing intensity seems to address overconsumption of plants and high fertilisation, being disadvantageous for many farmland and steppe birds (Fuller, 1996). This also highlights the need to keep grazing below levels that avoid impacts on soil and plants, but above certain values to provide adequate microhabitat characteristics (Jay-Robert et al., 2008).

5. Recommendations and future directions

Extensive sheep grazing is decreasing in Spain (37.6 % decline from 1992 to 2020), and in other European countries, and steppe bird numbers are also in a resounding decline (Traba and Pérez-Granados, 2022). Steep decrease in sheep numbers has been related to inefficient EU's Common Agricultural Policy (CAP) subsidies and explained by the uncoupling of sheep subsidies that started in 2006 and became permanent in 2010 (Mújica et al., 2015). In addition to decline of sheep numbers, livestock husbandry has drastically been intensified in Spain and Europe in the last decades, diminishing free-ranging grazing and enlarging herd size, thus increasing the risk of overgrazing in some areas, and abandonment in many others (Martínez-Valderrama et al., 2021), ultimately leading to habitat quality degradation and modified habitat-use by steppe birds (Oro et al., 2004; Zengeya et al., 2014). This is specially worrying in the Mediterranean basin where most avian species of high conservation concern depend on open semi-natural landscapes (Burfield, 2005; Burfield and Bommel, 2004), raising concerns about their persistence in the future (Sirami et al., 2007). Our results suggest that not only extensive sheep grazing is needed to maintain steppe habitat quality, but also that this has to be managed between certain thresholds, avoiding very low and high grazing intensity (Tonelli et al., 2019). In our study system average annual livestock density was estimated between 0 and 0.18 livestock units per hectare (LSU/ha; Appendix A), which is well below the threshold suggested by current Spanish regulations (0.2–0.3 LSU/ha; Urivelarrea and Linares, 2020). Extensive grazing should be prioritised in the agricultural policies, especially in the upcoming European CAP reform to

preserve steppe habitats and birds. Future studies should consider direct and indirect effects of sheep grazing on vegetation structure, together with the study of ecosystem processes, such as carbon storage or organic matter decomposition, to provide a more comprehensive picture of how sheep grazing shapes Iberian steppes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Authorship

JT conceived the original idea and supervised the project. JG-C curated and analyzed data. MR and JG-C prepared original data bases. JG-C, MR, DB-R, AB, CPG, and JZ carried out field work, and MR and JZ carried out lab work. JG-C took the lead in writing the manuscript in consultation with MR and JT. All authors provided critical feedback and contributed to the final manuscript.

Publication Ethics

This work was approved by the Local Ethical Committee for Animal Experiments of the Universidad Autónoma de Madrid (CEI80–1468-A229).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108556.

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