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ORIGINAL PAPER

Changes in management shape the spatial ecology of wild ponies in relation to habitat conservation

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Abstract

Large herbivores are key regulators of open habitats across the world. Free roaming ponies have a prominent ecological role in many Atlantic landscapes, where different habitats with conservation interest are linked to ponies' occurrence. The traditional management of wild ponies, which implies minimum human intervention, is declining in Galicia, NW Spain. Changes in the management regimes include the confinement of ponies in fenced areas, the use of improved pastures (IPs) and rotation between fields. Indirect effects of these changes are expected on the ecological condition of important habitats for conservation such as dry and wet heathlands and bogs. We studied social structure, spatial ecology and habitat use in 29 mares fitted with global positioning system (GPS) collars and field observations in two areas of Galicia dominated by wet heaths and blanket bogs (Xistral), and dry heaths (Sabucedo). We used spatial location and field observations to identify each band, and calculated band size, sex ratio, home range (HR) and core areas size and overlap, and habitat use. We addressed differences and adjusted Generalized Linear Models (GLMs) for these variables as functions of the type of management: free roaming vs rotation, use of IPs, fencing, and available ranging area. Larger bands were found in smaller commons, fenced and with rotation management. Home ranges, but not core area, varied as a function of the available ranging area. Bands overlap more on fenced areas with rotation management. Increasing management may concentrate grazing pressure by reducing HR and increasing bands overlapping areas, and this may have a long-term effect on habitat quality and conservation.

Keywords Atlantic wet heathlands · Blanket bogs · Dry heathlands · Semi-feral horses · Spatial ecology · *Ulex*

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Introduction

Large herbivores are key elements of open ecosystems across the world (Van Wieren 1995; Gordon et al. 2004; Ripple et al. 2015). They exert multiple influence on their habitat, directly via feeding and travelling, and indirectly through dispersal of seeds (Mouissie et al. 2005), nutrient recycling by urination and defecation (Hobbs 1996), influx of nutrients from carcasses (Towne 2000; Melis et al. 2007), and interactions with other fauna (Van Wieren 1995; Hobbs 1996). Impacts of herbivores depend on the grazing species, population density, spatial use pattern and social organization (Augustine and McNaughton 1998; Boissy and Dumont 2002; Gordon et al. 2004).

Galician wild ponies are small size equids that live in the low mountain ranges of western and northern Galicia, NW Spain. They have a prominent role in natural habitats conservation (López-Bao et al. 2013; Fagúndez 2016; Fagúndez et al. 2021), wildfire risk reduction (Celaya et al. 2012; Rigueiro-Rodríguez et al. 2012), or trophic interactions (Lagos 2013; López-Bao et al. 2013; Lagos and Bárcena 2018). Moreover, wild ponies and their management represent a cultural heritage of Galicia, and a link between the Atlantic European regions that still hold free-roaming ponies with similar management regimes (Nuñez et al. 2016; Fagúndez et al. 2021). Last census of Galician wild ponies (Iglesia 1973) estimated c.22,000 ponies as the overall population that had already suffered a significant reduction in some areas of the region. At present day, we roughly estimate a general loss of about one half of the ponies since the 1970's due to restrictive regulations, rural abandonment, and conflicts with other land uses (Lagos et al. 2019, 2020; Fagúndez et al. 2021).

In Galicia, the current population of wild ponies is found in mountain areas mainly covered by heathlands, which are semi-natural habitats maintained by different forms of human management such as mowing, burning and grazing by herbivores (Webb 1998). Heathland conservation requires setting appropriate management regimes, including selection of grazers and stocking rates (Grant and Armstrong 1993; Bullock and Pakeman 1997; Rupprecht et al. 2016). High grazing pressure may cause a strong loss of shrub cover, and absence of herbivores may boost shrub encroachment (Bullock and Pakeman 1997; Fagúndez 2013). Heathlands and bogs, another important habitat present in Galician mountain ranges, are open habitats characteristic of the Atlantic European landscapes considered as of conservation importance under EU Habitats Directive 92/43/ EEC. Specifically, it has been suggested that wild ponies have a noteworthy influence on natural grasslands and heathlands in the European Atlantic region (Fraser et al. 2019). Wet heaths grazed by ponies show a heterogeneous vegetation structure with shrub mats and open gaps which holds higher levels of rare species (Fagúndez 2016, 2018).

Management of Galician wild ponies follows a traditional system: The ponies are owned by locals, but they free roam in the mountains, and human intervention is generally limited to a drift once a year (Iglesia 1973; Lagos 2013; Nuñez et al. 2016). The traditional management of Galician wild ponies is changing towards a stronger intervention in some cases, or abandonment of the activity in others (Lagos et al. 2019). For example, in the Xistral mountains in the north of Galicia, the land ownership is arranged in commons as in many other Galician mountain areas. In these commons, the traditional pastoral system deeply changed in the 1980's and 90's. At that time, large areas of heath and blanket bogs were transformed into improved pastures (IPs) by ploughing, liming, fertilizing and seeding. Goats, sheep and local breeds of cattle were substituted with more productive cattle breed including the "rubia gallega" breed, improved for meat production (Sánchez García 1978). In some Commons, the existing free roaming ponies started to be used to restrain gorse

encroachment within IPs, as ponies are known to include large amounts of gorse in their diet (Putman et al. 1987; Aldezabal et al. 2013; Ferreira et al. 2013; López et al. 2017). Ponies are either allowed to use IPs for short periods of time, mainly in winter, or are temporarily moved to IPs (Lagos et al. 2019). This rotation system causes gorse encroachment in the heathlands that are consequently less used, reducing habitat quality (Muñoz-Barcia et al. 2019).

Recently, perimeter fencing of the commons and construction of unpaved roads has led to a higher control over ponies. In addition, the available ranging area decrease as consequence of fencing, and ponies are restrained to move seasonally in search for shelter and food. In some commons, drifting has changed from once to several times a year to remove foals or move ponies to IPs in winter. In the last twelve years, strict EU rules on equids identification by microchipping has also promoted higher control levels (López-Bao et al. 2013; Nuñez et al. 2016; Fagúndez et al. 2021). Finally, traditional management generally includes annual removal of the majority of male foals which biases the sex ratio toward females. Sex ratio is different in each common, and may have implications for ponies' social organization and use of the territory.

Herbivore density, sociability and gregariousness constrain the use of vegetation by herbivores (Gordon et al. 2004). Here, we used GPS collars and field observations to study the social structure and spatial ecology of Galician wild ponies in two study areas and different commons under different management levels and environmental conditions. We aimed to describe the changes in spatial behaviour of ponies in an increasing gradient of management intensification, and in two contrasting habitats of dry and wet heaths. If present day trends of strong management constraints and higher intervention are maintained, we predict these changes in behaviour will generalize in ponies' populations throughout the region.

Material and methods

Study area

We selected two study sites in two mountain ranges of Galicia which represent two different scenarios of land management and climatic constrains (Fig. 1, Table 1): The "Serra do Xistral" Special Area of Conservation belonging to Natura 2000 Network (hereafter Xistral), and the unprotected ranging area of the "Rapa das Bestas de Sabucedo" society (hereafter Sabucedo). Xistral comprises eleven commons, in three different municipalities, with approximately 11,000 ha. These commons are managed mainly for cattle grazing, but restrictions apply for protecting the habitats and species of Natura 2000. There is a population of about 1500–2000 ponies which belong to 163 commoners. The majority of the commons are fenced. Sabucedo study site is c.3000 ha and comprises seven commons and multiple small private properties in four different municipalities. The area is not fenced and a population of c.230 ponies can move freely. Forestry and cattle grazing are marginal activities in the area, and land abandonment is increasing.

Strong differences are found between the two areas regards climate and the main vegetation types (Table 1). Annual precipitation is high in both areas. However, the mountains of Xistral (maximum altitude 1,056 m a.s.l.) are extremely wet and foggy, with relative humidity above 80% through the year, while Sabucedo (maximum altitude 798 m.a.s.l) has less relative humidity and lower values for summer precipitation and higher temperatures

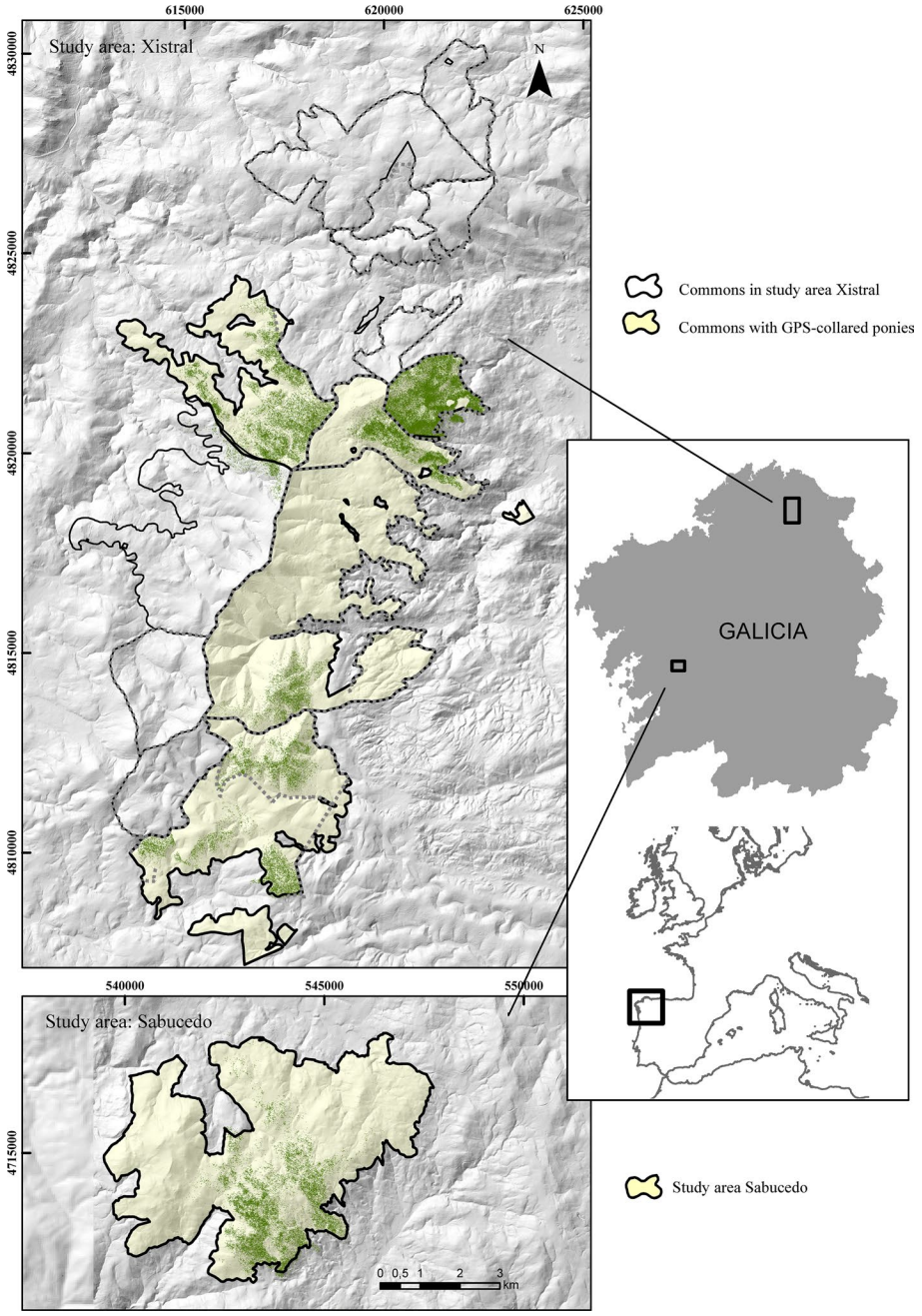

Fig. 1 GPS-telemetry locations of wild ponies, from June 2018 through July 2019 (in green) in the two study areas of Xistral and Sabucedo, Galicia, NW Spain (inset). The boundaries of the different commons are marked in black and fenced boundaries in dashed grey

Table 1 Climatic, geographic, environmental and management data of the two study areas and the five commons in Xistral area

Main area	Climate	Common	Geography		Environmental	Management					
			Elevation range (m)	Area (ha)	Main vegetation types	Ponies/ha	Num. of ponies	Sex ratio	Livestock	% of IP	Management details
Xistral	Mean T = 10.56 (5.94–15.56) Total P = 2,105 mm Summer P = 192 mm Mean RH = 85%	Miñotos	246–933	956.25	Wet heathlands (38%), blanket bogs (19%) and forest (27%)	0.17	160	0.08	Cattle (> 200)	-	Partly fenced: East and Northeast limit
		Montouto	670–1,023	1,561.59	Wet heathlands (30%), blanket bogs (25%) and improved pastures (15%)	0.10	160	0.04	Cattle (600–700) Sheep/goat (140)	15%	IP for cattle, not available for ponies. Common divided in 2 areas: 1 totally fenced around and other not fenced
		Recaré	396–791	325.19	Wet heathlands (44%), other shrublands (19%) and improved pastures (16%)	0.22	70	0.08	Cattle (70)	16%	IP available for ponies in winter
		Cadramón	364–1,056	2,298.52	Wet heathlands (29%), blanket bogs (29%) and improved pastures (9%)	0.13	300		Cattle (1,000)	9%	Ponies moved to IP and lowland meadows in winter. Land available to ponies > 500 ha
		Frexulfe	145–931	572,36	Wet heathlands (20%), improved pastures (24%), other shrublands (17%)	0.17	100	0.03	Cattle (300)	24%	Rotation between heathlands-bogs and IP. Common divided in areas and totally fenced around. Land available to ponies < 500 ha

Table 1 (continued)

Main area	Climate	Common	Geography		Environmental	Management					
			Elevation range (m)	Area (ha)	Main vegetation types	Ponies/ha	Num. of ponies	Sex ratio	Livestock	% of IP	Management details
Sabucedo	Mean T = 12.67 (7.23–18.67) Total P = 2,178 Summer P = 190 Mean RH = 81%	–	339–798	2,963.32	Dry heathlands (32%), other shrublands (35%) and forest (27%)	0.07	204–231	0.05	Cattle (unknown)	–	

Mean T (°C) = mean annual temperature (mean temperature of the coldest month (January)—mean temperature of the warmest month (July), Total P (mm) = annual precipitation, Summer P (mm) = precipitation in the period June–August. RH = relative humidity in air. IP = Improved Pastures. Number of ponies = number of adult ponies (> 3-year-old). Sex ratio = number of adult males between number of adult females. Wild pony population was estimated through total counts and through interviews to owners which also provided management regime. Numbers of livestock were retrieved from interviews to commoners. % of IP is the percentage cover of improved pastures in the common

leading to moderate hydric stress in summer. Wet heaths and blanket bogs (habitats of conservation importance under Habitats Directive) are dominant in Xistral, while dry heaths, bracken and broom communities cover most of the Sabucedo mountains with some patches of wet heaths and confined bogs.

Management of wild ponies

Pony owners at Xistral belong to different commons and many are professional farmers whose incomes come mainly from cattle breeding. Ponies are mainly used for maintaining mountain pastures in good condition, and marginally for meat production (Lagos et al. 2019; Fagúndez et al. 2021). In turn, Sabucedo ponies are managed by an association of the village neighbours who keep the traditional management mainly for the annual drift, a local fest and a touristic attraction (Nuñez et al. 2016; Hartigan 2020). Emotional attachment and tradition are the main reasons for pony ownership in general in Galicia (Fagúndez et al. 2021).

We described management of the bands of ponies using five dichotomous variables: (1) Type of management, which was classified as (a) year round free roaming, or (b) ponies rotated between fenced areas (heathlands/bogs to IP or to lowland meadows); (2) Availability of IP to ponies, classified as (a) IP not available to ponies, (b) IP available to ponies; (3) Fencing of the common, classified as (a) common not fenced around, or (b) common fenced around; (4) Available roaming area, which was classified as (a) >500 ha, vs (b) ≤ 500 ha; (5) Sex ratio, classified as high (≥ 0.05) or low (<0.05). We calculated sex ratio (number of adult males divided by number of adult females per common) as an additional variable, as this is mainly a management decision, although predation and other factors may have an influence (Lagos 2013). Management practices on each studied common are shown in Table 1 and the five dichotomous factors considered are in Table 2.

Spatial data management

Between April and October 2018 we fitted 40 mares with GPS collars manufactured by Digitanimal (https://digitanimal.com) 40 mares that inhabited five different Commons in Xistral, and in Sabucedo (Table 1 and Fig. 1). Mares were selected to wear collars to ensure there was at least one collared mare per band. Collars were scheduled to record one GPS position every hour. Several collars failed for different reasons such as battery loss, and data from five GPS collars that failed before 6 months were discarded. We discarded another six mares in Sabucedo, because they were confined in a fenced field outside their normal ranging area for a certain period. The final dataset included 133,451 locations recorded form June 2018 to June 2019 for 29 mares, from which 23 were from Xistral and six from Sabucedo (Table 2).

Home ranges (HR) for each mare were calculated using the GPS locations recorded (range 1,591–7,163) using the minimum convex polygon method and the kernel density estimation method (fixed bandwidth = 100) (Powell 2000). We considered HR as 95% of adaptive kernels (White and Garrott 1990) and core areas as 50% (Linklater 2000) (Fig. 2). We calculated HR overlap of tracked mares calculating the HR overlap index (HROI) and the Utilization Distribution Overlap Index (UDOI) (Fieberg and Kochanny 2005). The HROI is the proportion of an individual home range that is overlapped by the home range of another individual, so it is calculated as the area of overlap between individuals i and j divided by the area of the home range of the individual i. The UDOI quantifies HR

Table 2 Spatial ecology variables of the ponies in the different commons and classification of the commons according to their management parameters

Area	Common	N	Management factors					Home Range KDE (ha)		Core areas (ha)		Overlap indexes	
			Man. type	IP	Fencing	Available area	Sex ratio	Mean (SD)	Range	Mean (SD)	Range	HROI	UDOI
Xistral	Miñotos	7	FR	no	no	> 500 ha	≥ 0.05	308.52 (35.10)	248.92–356.33	69.38 (11.36)	56.76–89.276	0.28 (0.22)	0.11 (0.15)
	Montouto	4	FR	no	no/yes	> / ≤ 500 ha	< 0.05	210.78 (54.60)	130.07–247.87	53.64 (8.87)	44.87–65.95	0.10 (0.26)	0.06 (0.15)
	Recaré	7	FR	yes	yes	≤ 500 ha	≥ 0.05	221.88 (45.52)	127.44–256.10	52.31 (11.26)	30.67–65.98	0.53 (0.23)	0.28 (0.28)
	Cadramón	3	R	yes	yes	> 500 ha	< 0.05	216.99 (61.14	147.20–261.09	51.60 (12.46)	39.56–64.44	0.66 (0.21)	0.60 (0.11)
	Frexulfe	2	R	yes	yes	≤ 500 ha	< 0.05	199.59 (14.93)	183.42–212.86	51.79 (6.65)	45.06–58.36	0.85 (0.06)	0.89 (0.18)
Sabucedo	–	6	FR	no	no	> 500 ha	≥ 0.05	290.28 (106.57)	214.32–498.72	59.42 (17.33)	35.89–78.65	0.10 (0.13)	0.02 (0.06)

N is the number of mares fitted with collars in each common. Management factors include: type of management (Man. Type), classified as year round free roaming (FR), or ponies rotated between fenced areas as heathlands/bogs to IP and to lowland pastures (R); availability of improved pastures to ponies (IP); fencing; available area; and sex ratio. When management factors varied in the Common, as in Montouto, different values were used for each band for the analysis. Spatial ecology variables include home range size estimated with the kernel density estimation (KDE) method, core areas size, overlap indexes estimated using the HR method (HROI) and the utilization distribution overlap index (UDOI)

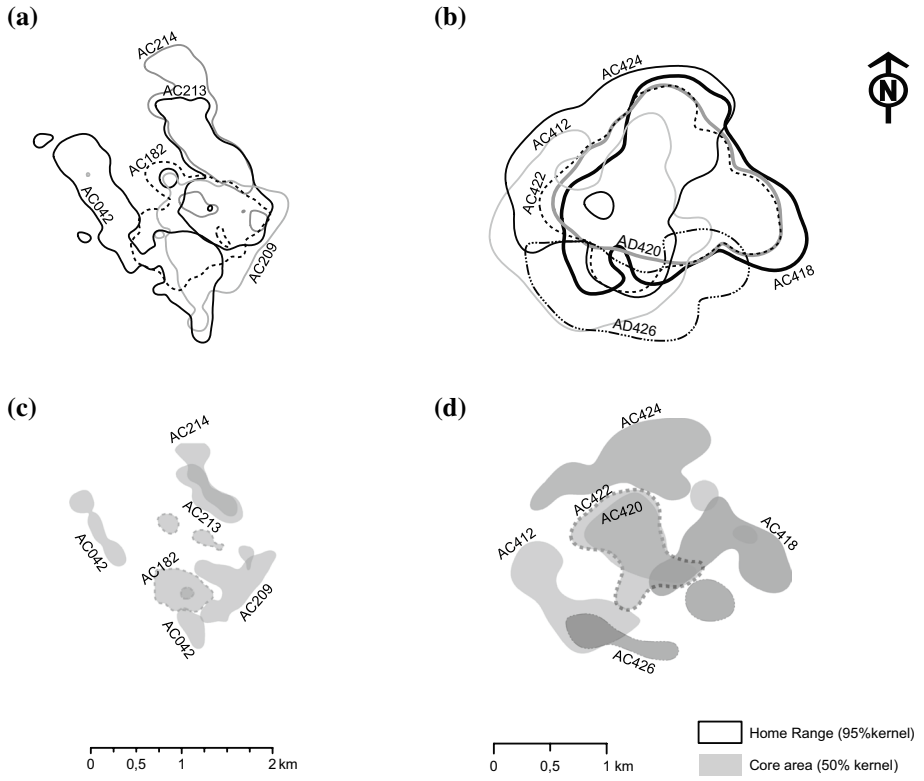

Fig. 2 Bands' home ranges represented as the 95% utilization distribution contour (**a**, **b**) and core areas, as the 50% utilization distribution contour (**c**, **d**), of 11 GPS collared mares in two Commons in Xistral. Miñotos (HR in a, core areas in **c** as an example of a Common no fenced, with no IP, > 500 ha available, and where ponies are free roaming. Recaré (**b**, **d**) as an example of a Common fenced, with IP, ≤ 500 ha available and free-roaming management

overlap incorporating information about shared space use considering the utilization distribution of the animals, so is defined as the product of the average probability of encounter and the amount of area shared between the two HR. The UDOI equals zero when two home ranges do not overlap, equals 1 if both UDs are uniformly distributed and have 100% overlap, and can be > 1 if the 2 UDs are no uniformly distributed and have a high degree of overlap (Fieberg and Kochanny 2005). For the core areas overlap we used the same function as for the HROI due to potential issues with low overlapping values of the Utilization Distribution. Therefore, we calculated the core areas overlap index (CAOI) as the proportion of an individual core area that is overlapped by the core area of another individual (Fieberg and Kochanny 2005). Overlap indexes for each collared mare were calculated as the mean of its overlap index with mares of other bands in the same common. These analyses were done using the package adehabitatHR (Calenge 2006) on R (R Core Team 2013).

Field observations

We performed field observations of collared ponies on monthly or bimonthly visits from August 2018 to June 2019, to address their social characteristics and description of the

group to which they belong. To assess the social characteristics of mares, data consisted of 167 observations of 29 collared mares. We recorded an average of six observations per mare (90% ≥ 4 observations, range 2–8 observations). For each observation of the collared mares we recorded: (i) group ages composition (adults: > 3 year, sub adults: 1–3 year, foals: < 1 year), (ii) size of the group (adults plus sub adults), (iii) band membership. Mares were considering as belonging to a band if they were located within the same band (recognized by the stallion and other mares) in more than 50% of the visits and were never located in other band (with other stallion). Mean band size was calculated from size of the group associated to each collar across field visits.

Habitat selection

To acknowledge the use of the different vegetation types, we modified the study area land cover data map in Xistral (Blanco et al. 2019) into 11 general cover classes: (1) blanket bogs; (2) raised bogs; (3) wet heathland; (4) other shrubland communities; (5) improved pastures; (6) forest; (7) other, including rocks, rivers, and artificial covers. In Sabucedo, we considered one single cover class, which is a matrix dominated by different types of shrubland communities including dry heaths with *Ulex europaeus* and *Erica* spp., tall shrubs dominated by brooms (*Genista* spp., *Cytisus* spp.), and other vegetation types with less than 5% cover such as rock pavements, forests or wet heaths. We only assessed habitat use in Xistral, where habitats protected under Habitats directive are dominant on the landscape.

We analysed third-order habitat selection (selection within HR) following Johnson (1980). For each band, habitat use data were compared with habitat availability using Ivlev's Electivity Index (Ivlev 1961). We estimated habitat use as the proportion of the GPS locations on the target habitat to available area. In the three bands with more than one GPS collars in Xistral we selected the one with the larger number of records. Availability of each habitat was calculated as the proportion of the area occupied by the habitat on the whole HR. Previously, we estimated the available area by mapping the existing fences where ponies have free access. In unfenced areas, we delineated a boundary line around the GPS locations. The GPS collars use GSM system, so we delimitated areas with no GSM signal using the available maps of cover (Vodafone España S.A.U. 2020). From the map of accessible area, locations in those areas with poor GSM or outside the common boundary were removed from the dataset.

Data analysis

We analysed the effects of management on ponies' performance by fitting the five management factors described in the *Management of wild ponies* section (type of management, availability of IP, fencing, size of the available roaming area) into Generalized Linear Models (GLMs) for each response variable including social (band size) and spatial variables (HR size, core area size, UDOI and CAOI) using normal distribution with the identity link function. Intercept alone was used as the null model, and all models were compared to the null model by means of a Chi-square test (Supplementary material 1). Models that did not significantly improved the null model at $\alpha = 0.05$ were discarded, and the best alternative model was chosen using lowest Akaike information criteria (AIC).

We used the Wilcoxon-Mann–Whitney U test to address differences in the habitat selectivity index of the mares according to the management factors (type of management, availability of IP, fencing, available roaming area) and for differences in the band size and HR

size according to the sex ratio of the bands. To evaluate seasonal differences of use of altitudinal ranges, we used Kruskall-Wallis (Dytham 2003) to test for each common separately for differences in elevation of the GPS location using month as the group factor. Statistical analyses were conducted using SPSS Statistics 25.0 (IBM 2017).

Results

Social structure

We identified 24 different bands that included at least one of the 29 adult mares fitted with GPS collars. Two collars from one common showed weak social structure (i.e. non clear aggregation between individuals due to intensive management) and bands could not be identified. Bands had a mean of 12.7 individuals (range = 2–36, SD = 5.3). Bands included one stallion, 11.3 mares (range = 2–27), 1.2 sub-adults (> 1 and ≤ 3 years; range = 0–4) and a variable number of foals born in the foaling season. Band size decreased with increasing sex ratio in the common (i.e. with less mares per stallion). Bands were larger where sex ratio was low (< 0.05) in comparison with commons with higher sex ratio (mean = 22.85, SD = 10.52 for commons with sex ratio < 0.05 and mean = 11.35, SD = 4.19 for higher values; Mann–Whitney U = 25.00, $P = 0.033$, $n = 29$). The predictive model for band size showed that type of management (χ^2 Wald = 46.546, $P < 0.001$) and size of the available roaming area (χ^2 Wald = 20.51, $P < 0.001$) negatively affected the size of the bands. Larger bands are found in small commons with rotation management. Fencing had a positive but weaker effect (χ^2 Wald = 5.249, $P = 0.022$). Availability of improved pastures did not improve the model.

Spatial ecology of ponies

The mean range size (HR) of the collared mares was 253.27 ha (SD = 72.5, range = 127.44–498.72), similar for the two areas (Mann–Whitney U = 69.0, $P = 0.618$, $n = 29$). The GLM for the HR was weakly improved by including the selected predictors. Only size of the available roaming area was statistically significant (χ^2 Wald = 4.962, $P = 0.026$), and ponies maintained greater home ranges when available roaming areas was larger. In turn, the model built for size of the core area with the selected predictors did not improve the resolution of the null model. In addition, HRs were larger when total sex ratio was ≥ 0.05 males per female (i.e. with smaller bands) (median = 255.04, range = 127.44–498.72 for sex ratio ≥ 0.05; median = 219.13, range = 130.07–247.87 for sex ratio < 0.05; Mann–Whitney U = 22.00, $P = 0.021$, $n = 29$,). Core areas (CA) (mean = 57.75 ha, SD = 13.54) showed little variation among commons (Kruskall-Wallis H = 8.080, $P = 0.152$, $n = 29$, $df = 5$, Table 2). Looking at ponies with minimum management, and thus comparing only Miñotos and Sabucedo, we did not observe differences in HRs (Mann–Whitney U = 10.00, $P = 0.116$, $n = 13$), neither in core areas (Mann–Whitney U = 16.00, $P = 0.475$, $n = 13$) between these areas with wet and dry heaths (Table 2).

The overlapping index UDOI varied between 0.00 and 0.98, with significant differences between commons (Kruskall-Wallis H = 20.758, $P = 0.010$, $n = 29$, $df = 5$, Table 2). The GLM for UDOI, was improved by including management type (χ^2 Wald = 91.23, $P < 0.001$) and fencing (χ^2 Wald = 12.873, $P < 0.001$), but not size of the available roaming area, nor availability of improved pastures. Lower values of UDOI and small home range

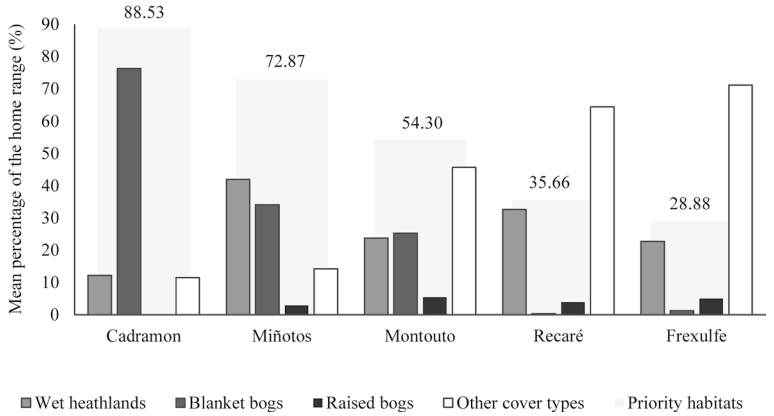

Fig. 3 Percentage cover of the different habitats in each common in Xistral. Other types include forest, dry heaths, improved pastures, rocks, rivers and artificial. The light grey bars represent the total percentage of priority habitats

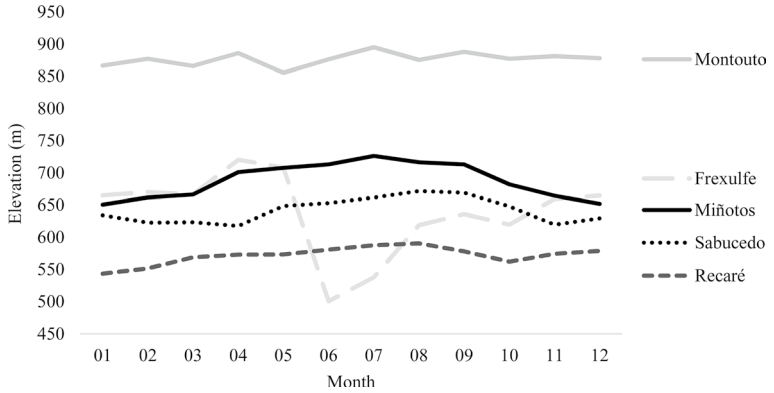

Fig. 4 Seasonal altitudinal range of 29 mares from Xistral commons and Sabucedo

sharing among bands are predicted for bands living in not fenced commons and free roaming management. Core areas barely overlapped (CAOI index ≤ 0.10, mean $= 0.04$, Fig. 2) and, according to the GLM, management did not have any effect on the CAOI (Supplementary material),

Habitat use

Wild ponies in Xistral included between 28.9% and 88.5% of priority habitats (wet heaths and bogs) in their HR (Fig. 3). We observed significant differences in the elevation range of the areas used by ponies through the year on all the different commons (H Kruskall-Wallis: Montouto $H = 504.75$, $P < 0.001$; Frexulfe $H = 4{,}292.74$, $P < 0.001$; Miñotos $H = 2{,}529.92$, $P < 0.001$; Sabucedo $H = 1{,}755{,}77$, $P < 0.001$; Recaré $H = 2{,}258.62$, $P < 0.001$; Fig. 4). In commons where ponies are free-ranging and not

artificially moved to IPs in winter (Miñotos, commons in Sabucedo), the mean height of GPS positions was higher between April/May and September, while in October ponies move to lower altitudes. Use of priority habitats was consistent with habitat availability for wet heaths and blanket bogs (D = − 0.04, D = − 0.08 respectively), but raised bogs were used in a lower proportion (D = − 0.24). Magnitude of selection of the different priority habitats did not change significantly according to management variables, but a lower selection of blanket bogs was observed for free roaming management in comparison with rotation, although not statistically significant (Mann–Whitney U = 9.0, $P = 0.072$ $n = 19$, Fig. 5, Supplementary material 1).

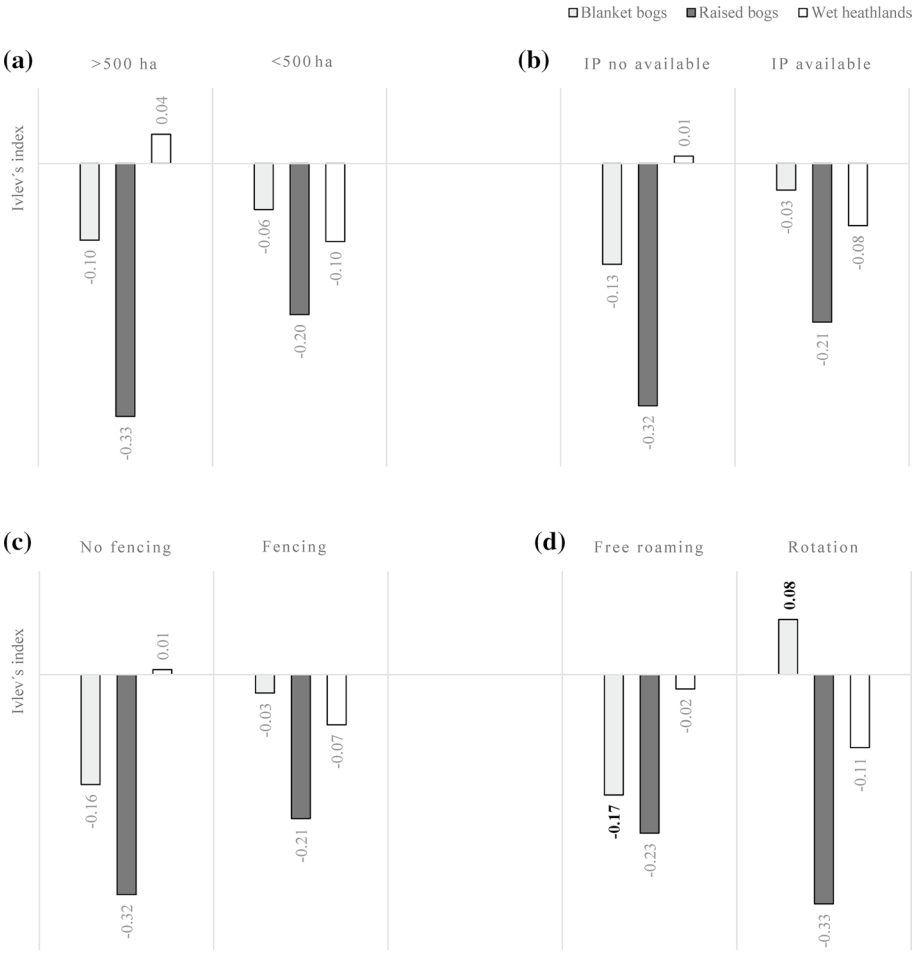

Fig. 5 Ivlev's selectivity index of ponies for wet heathlands, blanket bogs and raised bogs for bands according with their management variables: **a** available area, **b** availability of improved pastures (IP), **c** fencing of the common, **d** degree of management. Values range from 1 (complete positive selection) to − 1 (complete avoidance)

Discussion

The ecological role of wild ponies in Galician mountain areas has recently been highlighted, especially in relation to semi-natural habitats conservation (López-Bao et al. 2013; Fagúndez 2016; González-Hernández et al. 2020). However, increasing human intervention in management may constrain the ponies' performance and indirectly affect the target habitats. Our results suggest an effect of management intensification, represented by smaller available ranging areas, fencing and rotation on features of ponies' social structure, spatial ecology and habitat use. The main effects of management intensification observed were an increase in band size, decrease in the home range size and an increase in the overlapping of home ranges, with could have negative implications on ponies' performance as conservation grazers or browsers. We also found that in traditionally managed populations these parameters were similar between two different vegetation types dominated by dry or wet heathlands, which suggest management has a higher relevance than environmental variability in shaping the ponies' performance in the region.

Social structure and spatial ecology

The predictive model for the spatial ecology included size of the available roaming areas as the main explanatory factor for the HR, while the core area size model did not incorporate any of the management variables as significant predictors. At the same time, we observed that HR size was not significantly different among areas. This suggest that ponies concentrate their activities when the available roaming area is limited, therefore grazing pressure on the habitat increases. Increase of grazing and browsing pressure on the habitat may have different effects depending on the initial conservation status. Atlantic ponies are able to feed on gorse in considerable amounts, especially in winter (Tyler 1972; Putman et al. 1987; Aldezabal et al. 2013), which has meaningful implications for the conservation status of the habitat, as gorse encroachment is a clear indicator of low habitat quality (Alonso et al. 2003; Fagúndez 2016; Lagos et al. 2019; Muñoz-Barcia et al. 2019). Therefore, in closed heaths with high gorse cover this increased browsing pressure may be desirable, especially in winter. However, well-preserved heaths are traditionally managed, including large grazing areas.

The influence of available roaming area on the ponies HR size means that in the smaller commons the movement of the ponies could being constrained. Previous works have observed that feral horses home ranges are constringed by geological features as rivers our mountain ridges, as well as by human-made infrastructures (Rubenstain 1981). The observed seasonal variations in the pony use of different altitudes, with heavier use of higher lands in spring–summer and lowlands in autumn–winter on those commons with no roaming area limitations may suggest that this seasonal patterns may be also constrained by the size of the commons. Therefore, in small fenced commons (< 500 ha in our work) ponies may not find all the resources necessary for their survival, in terms of different types of food depending on the season, or shelter. This may require more management from their owners, having to feed them or move them to pasture in times of scarcity, that did not happen under traditional management since they migrate seasonally to low heathlands in winter and higher areas with bogs in summer.

The HRs found in our study are comparable to other Atlantic ponies in similar conditions (Gates 1979), but smaller than other horses inhabiting less productive environments

(e.g. Miller 1983; Berger 1986; Girard et al. 2013; Zabek 2015; Henning et al. 2018) suggesting an inverse correlation between HR and habitat productivity (Winnie et al. 2008; Naidoo et al. 2012). In our system, use of IPs may provide a higher nutritional value to ponies (López et al. 2019), restricting their needs for wider HRs and specially for larger core areas. At the same time the confinement of the ponies on certain moments of the year on fenced pastures artificially limit the mobility of ponies and may reduce de size of HRs. However, we did not find influence of the use of IP on bands HR neither core areas.

Core areas are not strictly determined by home range size. Animals with home ranges of equal size can have different core areas due to different patterns of spatial use behaviour (Powell, 2000). Biologically, core areas represent areas of concentrated space use within the home range (Fieberg and Börger 2012), areas used more frequently than any other areas (Samuel et al. 1985), or areas of intense use within which an animal spends a maximum amount of time (Vander Wal and Rodgers 2012). We analysed the influence of management factors on both spatial ecology variables due to the importance of what core areas represent for large mammals as horses and because this is a variable usually used specifically to describe spatial ecology of horses (Berger 1986, Linklater 2000, Zabek 2015, Hennings et al. 2018). The concept of core areas is related to critical resources (Powell 2000) and therefore can be understood as the minimum space and resource requirements of a band. Our results show that management affect the home range size, while core areas remain similar independently of the existing changes in the management of ponies, suggesting that changes in management did not constrained the basic needs of ponies. This concept however may leave out specific resources such as shelter in unusually adverse weather conditions.

We also found larger HRs when the sex ratio was higher, i.e. less mares per stallion, and sex ratio negatively correlated with band size. This contradicts the statement that HR positively correlates with band size (Berger 1986; Linklater et al. 2000; Girard et al. 2013). In our study, management factors and specifically small size of available roaming area and the rotation of ponies among fenced areas determines the presence of larger bands and, at same time, small size of available roaming area constrain the HR size. It could be related to the fact that higher sex ratios (smaller bands) are found in commons with low human intervention in coincidence with other factors that may result in larger HR as for example larger available areas. However other authors have also observed lack of correlation between band size and HR size, which seem to be more related to availability and distribution of key resources on the habitat (Tyler 1972). Moreover, Rubenstain (1981) also observed larger groups where available area was limited, in the island of Shackleford Banks, in comparison with groups that live inland, with less spatial limitations. Larger bands on smaller home ranges constrained by small available area could increase as well pressure on habitats in comparison with the traditional management that have maintained the heathlands from millennials.

A large overlap of bands home range results in a higher grazing pressure in those areas used by several bands. The predictive model showed management type and fencing had an influence on UDOI, with rotation and fencing resulting in higher overlap of HRs. In the traditionally managed commons of Miñotos and Sabucedo, overlapping of HRs (UDOI) was as low as 10% suggesting exclusive use of the home ranges and coinciding with the studies that reported home range or core areas exclusivity (Gates 1979; Kerekes et al. 2021 at the beginning of the study for Przewaslki horses; Rubenstein 1981), but raised to 85% in more intensively managed areas, reaching the proportion usually observed in horses (e.g. Berger 1986; Linklater 2000; Zabek 2015). Furthermore, we observed very low overlap of core areas, indicating exclusive use of core areas

by bands of wild ponies in these areas as it was described for Exmoor ponies by Gates (1979), but contrary to what has been observed for other free roaming horses (Tyler 1972; Berger 1989; Linklater 2000). Previous studies reflect that free roaming horses in large open areas live in bands that largely or entirely overlap their HRs (Berger 1986, Linklater 2000; Zabek 2015) and a similar pattern was observed for Przewalski horses (King and Gurnell 2005; Kerekes et al. 2021). However, exclusive use of HR and core areas has been described as an atypical spatial behaviour of dense populations of feral horses confined artificially (Linklater et al. 2000). Our results show the opposite trend, with traditionally managed populations (i.e. closer to natural grazing) in unfenced areas with no rotation showing the lowest overlapping values (Fig. 2). Within this traditional management, the pony bands selectively use the territory with a HR that has little overlap with that of neighbouring bands. Thus, grazing pressure is low, and there are limited areas shared by two or more bands where grazing pressure could increase. This would explain the lack of an effect of pony density on heathlands vegetation and biodiversity parameters observed by Fagúndez (2016) and confirm his hypothesis that social and spatial behaviour allows for a natural shelf control of their densities and, therefore, their grazing pressure on vegetation. Then, when ponies are managed traditionally, the heathlands grazed by ponies show higher values of plant richness and diversity regardless of the density of ponies (Fagúndez 2016) and the soil condition is unaffected (Fagúndez and Pontevedra-Pombal 2022). This behaviour of exclusive use of the home range, together with the light pony type largely explain this low-intensity grazing regime that has been highlighted as important for heathland conservation (Fagúndez 2016; González-Hernández et al. 2020). Changes in this management that increase overlap may have implications such as overgrazing in certain areas. However, areas of extensive overlap may have a positive impact on the habitat, mainly in heathland with an unfavourable status due to lack of grazing (Muñoz-Barcia et al. 2019.

Habitat selection

We did not find a correlation between management intensity and habitat selection, except for a weak negative selection for blanket bogs in free roaming ponies in Xistral. This could mean ponies prefer wet heathlands, as they provide a variety of plants including gorse, a plant very consumed by Atlantic ponies (Tyler 1972; Putman et al. 1987; Aldezabal et al. 2013) which is mostly absent in bogs (Muñoz-Barcia et al 2019). This selection may be lost when ponies are constrained by higher managing pressure, and it could have a negative impact on conservation of blanket bogs. The high negative value of habitat selection for raised bogs (Fig. 5) could be due to the small patch size of this habitat. This can make them more sensitive to small variations in the use of these patches.

We observed seasonal movements of ponies, from higher altitudes on spring–summer to lower altitudes in autumn–winter. Fencing of their range constrain these movements, with implications for their performance on free roaming conditions and habitat use. Commonly, fencing is associated with rotation to IPs in winter. Confinement of ponies in IP in winter, the time of the year when they mostly use heathlands at lower altitudes, may constrain gorse consumption by ponies, and thus favour gorse encroachment. The ecological condition of the wet heathland will be lowered, and quality of pasture for cattle will also be degraded (Muñoz-Barcia et al 2019).

Main conclusions

Previous studies have shown the positive impact of wild ponies in the conservation of Atlantic European habitats like heaths and bogs, and environmental issues if they are removed (López-Bao et al. 2013; Fagúndez 2016; López-Bao et al. 2013; Fraser et al. 2019; González-Hernández et al. 2020, Fagúndez et al. 2021). Their selective grazing pressure enhances heathers and limits the growth of gorse (Putman 1987; Aldeazabal et al. 2013; López et al. 2017), increases plant diversity especially for rare species (Fagúndez 2016; González-Hernández et al. 2020), improves conditions for cattle grazing (Lagos et al. 2019), reduces the risk of wild fires (Celaya et al. 2012; Rigueiro-Rodríguez et al. 2012) and restrains the understorey in forest plantations (Rigueiro-Rodríguez et al. 2012) while have a null impact on soil condition (Fagúndez and Pontevedra-Pombal 2022). According to our results, changes in pony management may constrain their grazing performance and indirectly affect habitat conservation. For example, rotation and use of IPs can counteract the positive effects of pony grazing (López et al. 2017; González-Hernández et al. 2020). Management seems to affect grazing performance more than habitat type, either dry heaths or mosaics of wet heaths and bogs. Thus, if the present trend of management intensification continues in the region, we predict negative consequences for habitat conservation in the long term.

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Data availability The datasets generated during and/or analysed during the current study are not publicly available due to the fact that they are sensible information about the location of animals privately owned roaming free on private land, but are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

Ethical approval We conducted the present study in adherence to regulations and guidelines about animal care and use following the Spanish and European regulations (Spanish law 32/2007 and Directive 2010/63/EU of the European Parliament).

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