



Article

Habitat Use of the Hen Harrier (*Circus cyaneus*) during the Breeding Season in Spain

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Simple Summary: This study examined Hen Harriers' breeding habitat use in Spain using GPS/GSM data from 17 individuals. Harriers used agricultural lands and natural vegetation scrubs. Nest location influenced habitat selection, with northern harriers favouring natural vegetation and southern harriers using agricultural fields, likely due to habitat availability across Iberia.

Abstract: Raptors usually show use for a particular habitat to settle during the breeding period. In this study, we aimed to study the habitat use of the breeding populations of Hen Harrier (*Circus cyaneus*) in Spain, which represents the southern distribution limit of the species. We used GPS/GSM data from 17 individuals during 21 breeding periods. We analysed space and habitat use using 95% kernel density estimators to obtain home ranges during the breeding period. Then, we performed a third-order habitat selection analysis, extracting the percentage of locations on each land use and comparing it with random points generated within each home range. Furthermore, an Agricultural Use Index was created to classify harriers with agricultural or forest use depending on habitat. The results showed that harriers had a general use for agricultural land and, to a lesser extent, habitats with natural vegetation scrubs. Nest location was key to habitat selection, and these uses varied with latitude, with natural vegetation being chosen as the nesting habitat in the north and agricultural fields in the south, probably due to the availability of habitats in different parts of Iberia.

Keywords: behaviour movements; harriers; GPS/GSM; Iberian Peninsula; satellite tracking; habitat analysis



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1. Introduction

Raptors occupy practically all types of habitats. There are species typical of mountainous and forest ecosystems, species of steppe or cereal areas and those that develop even in urban areas. Habitat selection is a behaviour based on innate or acquired uses by which raptors choose a certain habitat in which to settle, feed and/or breed [1], which will be determined by biotic and abiotic factors [2]. Of relevant importance are breeding habitats, places with certain characteristics to hide their nests and provide security for chicks to develop until they become independent, maintaining populations [3–5]. Meanwhile, for example, hunting territories must be open so that harriers can see and catch their prey with ease of manoeuvre [6]. Habitat uses may change according to species and their specific reproductive needs, and thus, habitat functions as a limiting factor in reproduction [7]. But thanks to the higher mobility of raptors, they are able to traverse large areas of potential territories and assess the quality of these, allowing them to select the most beneficial for their reproductive success [8].

The Hen Harrier (*Circus cyaneus*) is a widely distributed raptor that occupies a wide variety of habitats, generally open or with little vegetation cover [9]. They usually nest in shrub or low vegetation ecosystems, such as heathland, moorland, grassland or gorse, although they may also nest in cereal fields, such as wheat or barley [10,11]. A peculiarity of harriers is that they nest directly on the ground in dry areas, crops or in dense vegetation rather than building nests in trees or elevated spaces [12,13]. For this reason, this species can be very sensitive to changes in the habitat where it breeds [14]. In Spain, Hen Harrier nesting habitats have been recorded as scrublands and agricultural fields, the second most frequent as we move southwards [15].

The Spanish breeding population of Hen Harriers usually performs itinerant movements around the Iberian territory or short migrations during the non-breeding period [12,15,16]. However, we also found sedentary individuals [9,17] due to their location in the south of their distribution [18] where seasonal changes are not as noticeable. Although the distribution of Hen Harriers in the Iberian Peninsula is quite widespread, their breeding area is concentrated in the northwest of the Iberian Peninsula [15].

From a conservation point of view, the study of habitat allows us to identify the species' breeding uses and to establish measures to mitigate possible threats to its survival [19]. The conservation status of the Hen Harrier in Spain was established as *Endangered* (EN) due to declines in breeding pairs in recent decades, mostly caused by the loss and transformation of breeding and feeding habitats [20].

This study aims to find out for the first time in a comprehensive way the habitat uses of the Hen Harrier breeding population in Spain. Using high-precision global positioning system (GPS) telemetry, the main objectives were as follows: (1) to study and define the habitat uses of Hen Harriers at the breeding stage; (2) to analyse whether the used habitat differs according to the nest site; (3) to compare the breeding area between the majority habitat uses.

2. Materials and Methods

2.1. Capture and Tagging

The data used in this study belong to 21 breeding periods of 17 Hen Harriers, 12 females and five males, which were marked at the beginning of the breeding seasons between 2019 and 2021. The tagged harriers were distributed in the following provinces: Álava (4), Madrid (2), Toledo (2), Valladolid (2), Asturias (1), La Rioja (1), León (1), Ourense (1), Palencia (1), Salamanca (1) and Segovia (1).

Birds were tagged with GPS–GSM satellite transmitters (9 g Milsar u9 and 10–12 g OrniTrack-10/E10 3G model) fitted with Teflon harnesses; the combined weight of which did not exceed the recommended limit of 3% of the body weight of any harrier (mean percentage \pm SD = $2.30 \pm 0.19\%$, range = 1.90–2.62%; [21]). GPS position, date and UTC time data were programmed to broadcast at a frequency between every 5 and 15 min. Adults were trapped with a dho-gaza net with an eagle owl (*Bubo bubo*) lure due to its proven efficacy in raptors [22,23]. Handling time until the release of the individual was less than one hour to minimise the animals' stress experienced.

2.2. Habitat Analysis

We conducted a habitat analysis using the European Environment Agency's (2018) CORINE 2018 land cover map (raster resolution = 100) to determine the type of habitat used by Hen Harriers during the breeding period. We organised the original land cover classes ("CLCs") into nine categories proposed by García-Macía et al., 2022 [24]: artificial surfaces (CLC codes: 111–142), non-irrigated arable land (CLC code: 211), permanently irrigated land (CLC code: 212), permanent crops and pastures (CLC code: 221–231), heterogeneous agricultural areas (CLC codes: 241–244), forests (CLC codes: 311–313), scrubland and/or herbaceous vegetation associations (CLC codes: 321–324), open spaces (bare rocks or sparsely vegetated areas; CLC codes: 331–335) and wetlands and water bodies (CLC codes: 411–523).

2.3. Home Range and Statistical Analysis

For the spatial calculations, we homogenised the GPS data at a transmission frequency of 15 min for all specimens with R Statistics v. 4.0.5 [25]. Subsequently, the locations included in the reproductive period were delimited, obtaining 100,449 total locations, with an average of 5165 ± 2285 locations for each individual and reproductive season. A series of measurements were calculated to analyse space and habitat use.

First, we calculated the overall breeding season home range of each individual using Kernel density estimators (KDE) [26]. We calculated the 95% kernel (95% KDE) considered the home range [27,28]. We defined the onset of breeding as when individuals settle in a relatively small and unchanging area and drastically reduce their daily movements, coinciding with the reproductive literature of the species in the peninsula [15,18,29]. On the other hand, we consider the end of breeding when individuals leave the breeding area and begin to make dispersals and post-breeding movements typical of the species to other territories [30–32]. KDEs were calculated using R software through the statistical packages *amt* [33] and *adehabitatHR* [34].

Second, we visualised the spatial behaviour of Hen Harriers during the breeding season by inserting the 95% kernels into the geographic software QGIS 3.28.1, creating maps of their breeding areas. We analysed in which habitat type the nest locations of the different individuals were found during the different breeding periods. Nest location was estimated by calculating centroids in QGIS from the weekly 95% kernel with the smallest area found throughout the breeding period.

Third, we calculated percentages from the number of locations within the 95% kernel of the 17 individuals in each of the nine land cover categories and saw which are most used by harriers (Figure 1). We then performed a Pearson correlation analysis between these percentages and the latitude of the locations with the basic R stats package. The centroid of the breeding home range was taken as a reference point to measure the latitude of each individual. Then, we performed a third-order habitat selection analysis [35] to evaluate whether Hen Harriers used habitats more frequently than expected by their availability, comparing the observed values against a set of random samples [36]. First, we generated a number of random points within the home range (95% KDE) equivalent to the number of GPS fixes collected for each breeding season, which represents the potential area used by the harriers. Then, we assigned the corresponding habitat type to every random point and to every real location recorded during the breeding season. We calculated the percentage of GPS fixes and random points within each habitat type and the difference between both of them (positive values mean a higher percentage of habitat use with respect to potential use).

Fourth, to simplify the predisposition of harriers to one habitat or another, we created an Agricultural Use Index (AUI), dividing the sum of all locations on *Agricultural* landscapes (grouping: non-irrigated arable land; permanently irrigated land; permanent crops and pastures; heterogeneous agricultural areas) by all locations on *forest* soils (grouping: forest; scrub and/or herbaceous vegetation associations). Locations in wetlands and water bodies, artificial surfaces and open spaces were ignored for this calculation. We compared the size of the home range of individuals with land use using the Agricultural Use Index (AUI) and explored a possible relationship between the territory efficiency of harriers. Then, a non-parametric Mann–Whitney U test was performed (as the data did not show a fit to a normal distribution), comparing the predominant habitats (grouped into agricultural and forest) to test for a possible relationship with the size of home ranges.

Finally, we performed both the Linear Mixed Model (LMM) and General Mixed Model (GLM) with a Gaussian-type error distribution and the LMM, which showed very similar results to the previous one. In fact, when we performed the GLM, we obtained the same results as in the previous with LMM. Then, we chose the simplest GLM. “Habitat type” was set as a fixed effect and the response variable was the difference between potential and real use of habitat (%).

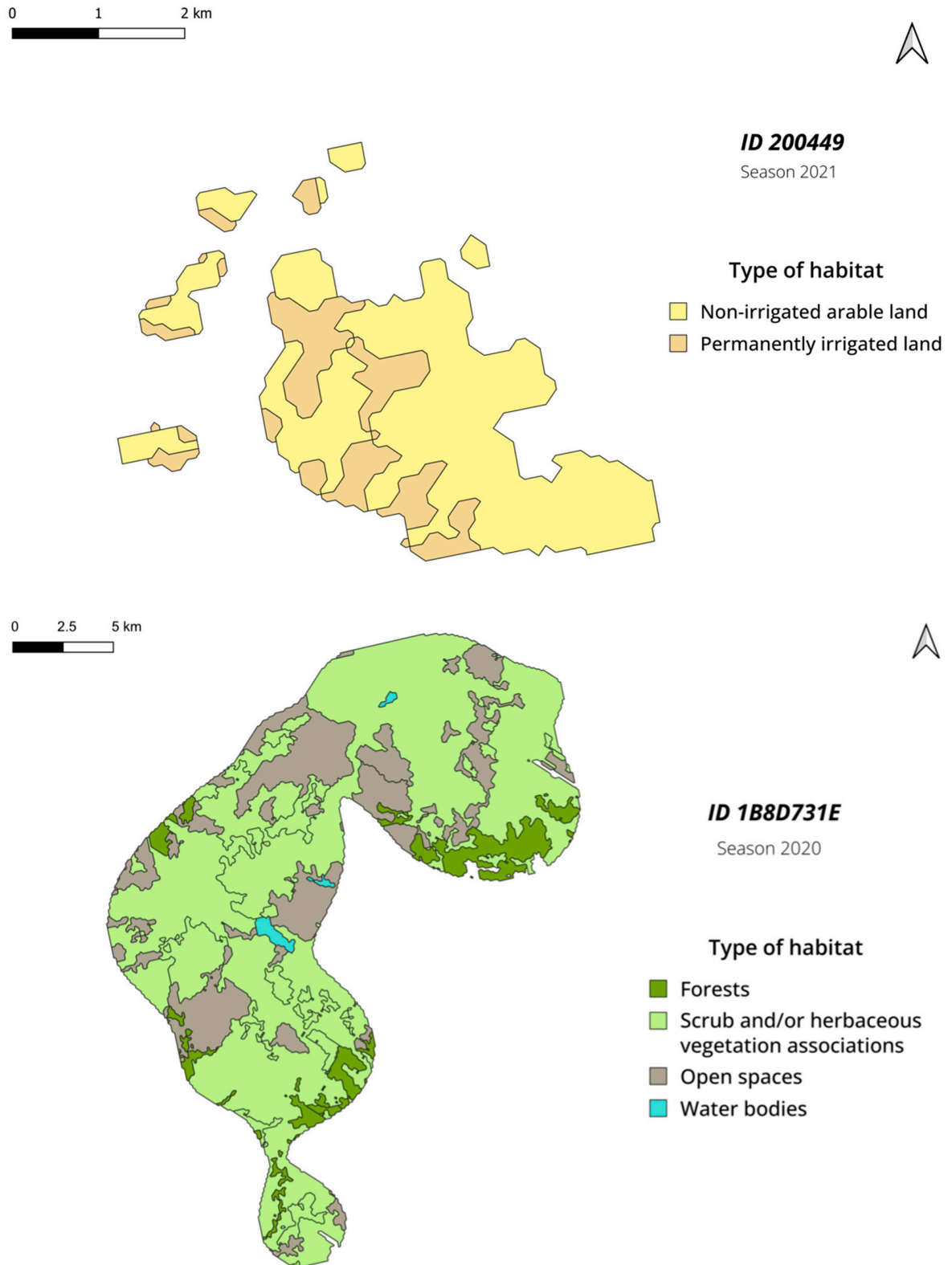


Figure 1. Examples of an individual with agricultural habitat use (ID 200449 in 2021) and with forestry habitat use (ID 1B8D731E in 2020).

We achieved sample independence in this analysis, as the percentages of use in a particular territory are related; however, here, we compared the percentages of actual habitat use (using the locations of harriers within each habitat type in their home range) versus the sample of potential use (using the same number of random locations in the

same home range). If the percentage of actual locations is greater than the number of random locations, then the habitat is positively used, and the difference is significant in the GLM analysis. The actual values are weighted with the random values, measuring in our study the greater or lesser habitat use of the different habitat types available in the home ranges of each individual. We used the *lme4* [37] and *jtools* [38] R packages to perform the statistical analyses.

3. Results

The average number of habitats overflown by harriers during their breeding period was 5.09 ± 1.58 with a range of between two and seven habitat types (Figure 1; Table 1). The highest percentages of locations were in non-irrigated arable land habitat (ID 5690B91E in 2020: 99.94% and in 2021: 99.79%; ID 200426: 99.67% and ID 211270: 98.86%; Figure 2A; Table 2). Although in shrub and/or herbaceous vegetation associations, habitats with two individuals showed very high percentages (ID 1B8D731E: 96.9% and ID 200438: 95.5%; Figure 2A; Table 2), along with another individual showing most of its locations in permanently irrigated land (ID 190217: 77.31%; Figure 2A; Table 2). Wetlands and water bodies and artificial surfaces are the habitats with the lowest number of locations and number of individuals (ID 1B8D731E: 0.06% and ID 200445: 0.04%; Figure 2A; Table 2).

The General Linear Model showed that harriers tended to select non-irrigated arable lands and scrub and/or herbaceous vegetation associations (Figure 2B, Table 3), while the rest of the habitat types were negatively selected or no significant trends were detected.

Table 1. Metadata from the 21 reproductive periods of the 17 tagged Hen Harriers. ID: Individual. AUI: Agricultural Use Index. M: male. F: female. * The specimen presented 0 locations on forest soils, so it was assigned a value of 1.

ID	Sex	Province	Season	No. of Used Habitats	Nest Site Surface	Habitat Use	AUI	Home Range (km ²)
1B8D731E	F	Orense	2020	4	Forestry	Forestry and scrub surface	0	264.75
5C90B91E	M	Álava	2021	6	Agricultural	Agricultural systems	3.45	30.66
5690B91E	F	Álava	2020	4	Agricultural	Agricultural systems	4998	1.25
			2021	3	Agricultural	Agricultural systems	554.55	1.09
180225	F	León	2022	6	Forestry	Forestry and scrub surface	0.24	97.33
190217	F	Palencia	2021	3	Agricultural	Agricultural systems	45.08	12.96
200424	F	Madrid	2021	7	Agricultural	Agricultural systems	171.23	55.09
			2022	7	Agricultural	Agricultural systems	327.13	44.56
200425	M	Toledo	2021	6	Agricultural	Agricultural systems	47.15	51.52
200426	F	Salamanca	2021	4	Agricultural	Agricultural systems	1999	6.79
200428	M	Segovia	2021	6	Agricultural	Agricultural systems	15.02	41.89
200434	F	Madrid	2021	4	Agricultural	Agricultural systems	1 *	0.74
			2022	6	Agricultural	Agricultural systems	4969	1.54
200435	F	Valladolid	2021	4	Agricultural	Agricultural systems	2499	13.50
200438	F	Asturias	2021	6	Forestry	Forestry and scrub surface	0.01	34.09
200445	M	Álava	2021	7	Agricultural	Agricultural systems	40.76	80.52
200447	F	La Rioja	2022	7	Agricultural	Agricultural systems	150.29	159.14
200449	F	Valladolid	2021	2	Agricultural	Agricultural systems	9999	10.82
200452	F	Toledo	2021	6	Agricultural	Agricultural systems	145.90	33.87
			2022	6	Agricultural	Agricultural systems	713.21	169.91
211270	F	Álava	2022	3	Agricultural	Agricultural systems	86.72	15.32

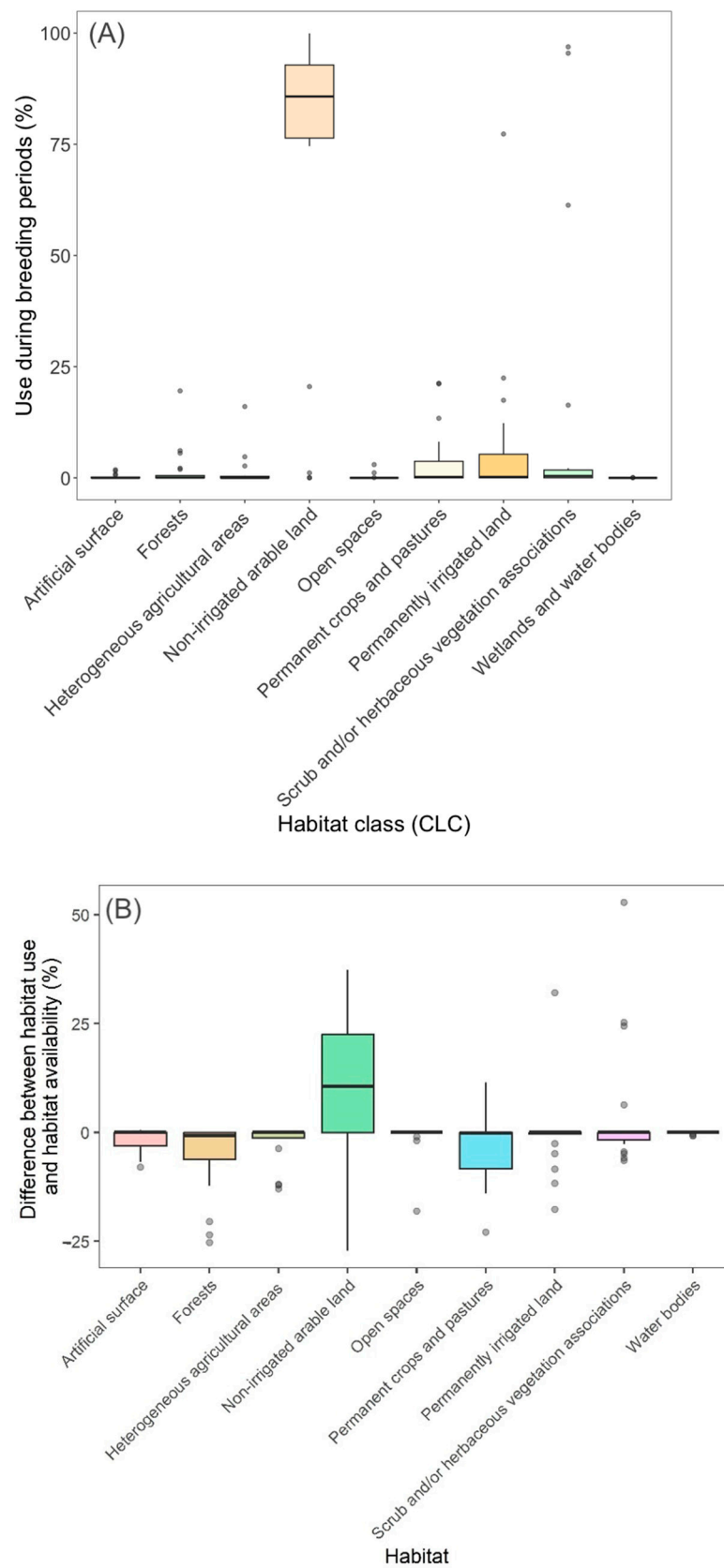


Figure 2. Average of use percentages by the 17 Hen Harriers of the nine habitats during breeding season. (A,B) Difference between habitat use (GPS fixes) and habitat availability (random points within home ranges).

Table 2. Habitat use percentages of the 17 Hen Harriers during the 21 breeding seasons in the nine habitat categories.

ID	Season	Artificial Surface (%)	Non-Irrigated Arable Land (%)	Permanently Irrigated Land (%)	Permanent Crops and Pastures (%)	Heterogeneous Agricultural Areas (%)	Forests (%)	Scrub and/or Herbaceous Vegetation Associations (%)	Open Spaces (%)	Wetlands and Water Bodies (%)
1B8D731E	2020	0	0	0	0	0	0.06	96.90	2.98	0.6
5C90B91E	2021	0.02	76.40	0.15	0.98	0	6.11	16.34	0	0
5690B91E	2020	0.02	99.94	0.02	0	0	0	0.02	0	0
5690B91E	2021	0	99.79	0.03	0	0	0.18	0	0	0
180225	2022	0	1.12	17.45	0.20	0.37	19.56	61.30	0	0
190217	2021	0	20.52	77.31	0	0	0	2.17	0	0
200424	2021	1.83	82.72	1.04	13.39	0.45	0.27	0.30	0	0
200424	2022	1.56	74.58	1.98	21.27	0.31	0.06	0.24	0	0
200425	2021	0.82	85.75	0	6.64	4.73	0.3	1.76	0	0
200426	2021	0	99.67	0.25	0.03	0	0	0.05	0	0
200428	2021	0.01	86.99	6.74	0.02	0	5.56	0.68	0	0
200434	2021	0.27	91.50	0.10	8.13	0	0	0	0	0
200434	2022	0.60	78.15	0.08	21.13	0.02	0	0.02	0	0
200435	2021	0	77.49	22.44	0	0.03	0.04	0	0	0
200438	2021	0	0.05	0	0.81	0.35	2.18	95.47	1.14	0
200445	2021	0.15	92.07	5.31	0.04	0	1.91	0.48	0	0.04
200447	2022	0.1	96.84	1.33	1.02	0	0.25	0.41	0.05	0
200449	2021	0	87.67	12.33	0	0	0	0	0	0
200452	2021	0.11	92.82	0	3.72	2.67	0.07	0.61	0	0
200452	2022	0.01	80.74	0.21	2.87	16.03	0	0.14	0	0
211270	2022	0	98.86	0	0	0	0.52	0.62	0	0

Table 3. Results of the General Linear Model (GLM) to explore differences between real and potential use of habitat. Positive values mean higher use of habitat with respect to habitat availability. Estimates, standard error (SE), confidence intervals (CI), degrees of freedom (df) and statistics are shown. Significant values ($p < 0.05$) are highlighted in bold.

Habitat Type	Estimate	SE	Statistic	Lower CI	Upper CI	<i>p</i> -Value
(Intercept)	-1.659	1.860	-0.892	-5.305	1.987	0.374
Forests	-3.702	2.631	-1.407	-8.859	1.454	0.161
Heterogeneous agricultural areas	-0.414	2.631	-0.157	-5.571	4.743	0.875
Non-irrigated arable land	12.140	2.631	4.614	6.984	17.297	<0.001
Open spaces	0.667	2.631	0.254	-4.490	5.824	0.800
Permanent crops and pastures	-1.807	2.631	-0.687	-6.964	3.350	0.483
Permanently irrigated land	1.029	2.631	0.391	-4.128	6.185	0.696
Scrub and/or herbaceous vegetation associations	5.440	2.631	2.068	0.284	10.597	0.040
Water bodies	1.573	2.631	0.598	-3.583	6.730	0.551

On the other hand, different trends in land use linked to latitude were observed (Figure 3). Breeding areas in southern latitudes show a tendency to use more non-irrigated arable land ($R = -0.351, p = 0.118$), permanent crops and pastures ($R = -0.650, p = 0.001$) and heterogeneous agricultural areas ($R = -0.376, p = 0.092$) (Figure 3). In the northernmost breeding areas, the opposite is true. The used habitats are shrub and/or herbaceous vegetation associations ($R = -0.444, p = 0.043$); in low-latitude breeding territories, there are few locations for this type of habitat, and with increasing latitude, the locations increase. However, the remaining habitats do not show a clear latitude-related trend in Hen Harrier land use. In general, greater variability in Hen Harrier land use is found in the more northerly breeding areas (Figure 3).

The average home range size of harriers during breeding was $53.68 \pm 68.25 \text{ km}^2$, with a range of $0.74\text{--}264.75 \text{ km}^2$ according to the 95% KDE. We can see that our values are grouped into two types (Figure 4A), harriers with a habitat use distribution over agricultural fields or forest soils. The mean home range size of agricultural harriers was $40.62 \pm 50.44 \text{ km}^2$, while that of forest harriers was $132.06 \pm 119.19 \text{ km}^2$. Hen Harriers with forest floor uses ($n = 3$ periods) had very different home range sizes (ID 1B8D731E: 264.75 km^2 ; ID 180225: 97.33 km^2 ; ID 200438: 34.09 km^2 ; Figure 4A; Table 1). Agricultural Hen Harriers were higher

in number ($n = 18$ periods) and also had very different home range sizes, with the smallest home ranges being found with values close to 1 km^2 (ID 5690B91E in 2020: 1.25 km^2 and in 2021: 1.09 km^2 ; ID 200434 in 2021: 0.74 km^2 and in 2022: 1.54 km^2 ; Figure 4A; Table 1). The statistical result was non-significant for differences between kernel size 95% in harriers with agricultural uses and harriers with forestry uses ($W = 9$; $p = 0.080$).

Harriers nesting in agricultural soils spent most of their breeding period in this same habitat, just as individuals nesting in forest habitats showed most of their locations in these natural vegetation territories (Table 1).

When we compare breeding area size with AUI, we can observe that harriers with very high affinities for agricultural soils (higher indices) have very small home ranges, whereas harriers with part of their locations on agricultural and forest soils (intermediate index values) or with most of their locations on forest soils (low indices) generally tend to have larger home ranges (Figure 4B; Table 1).

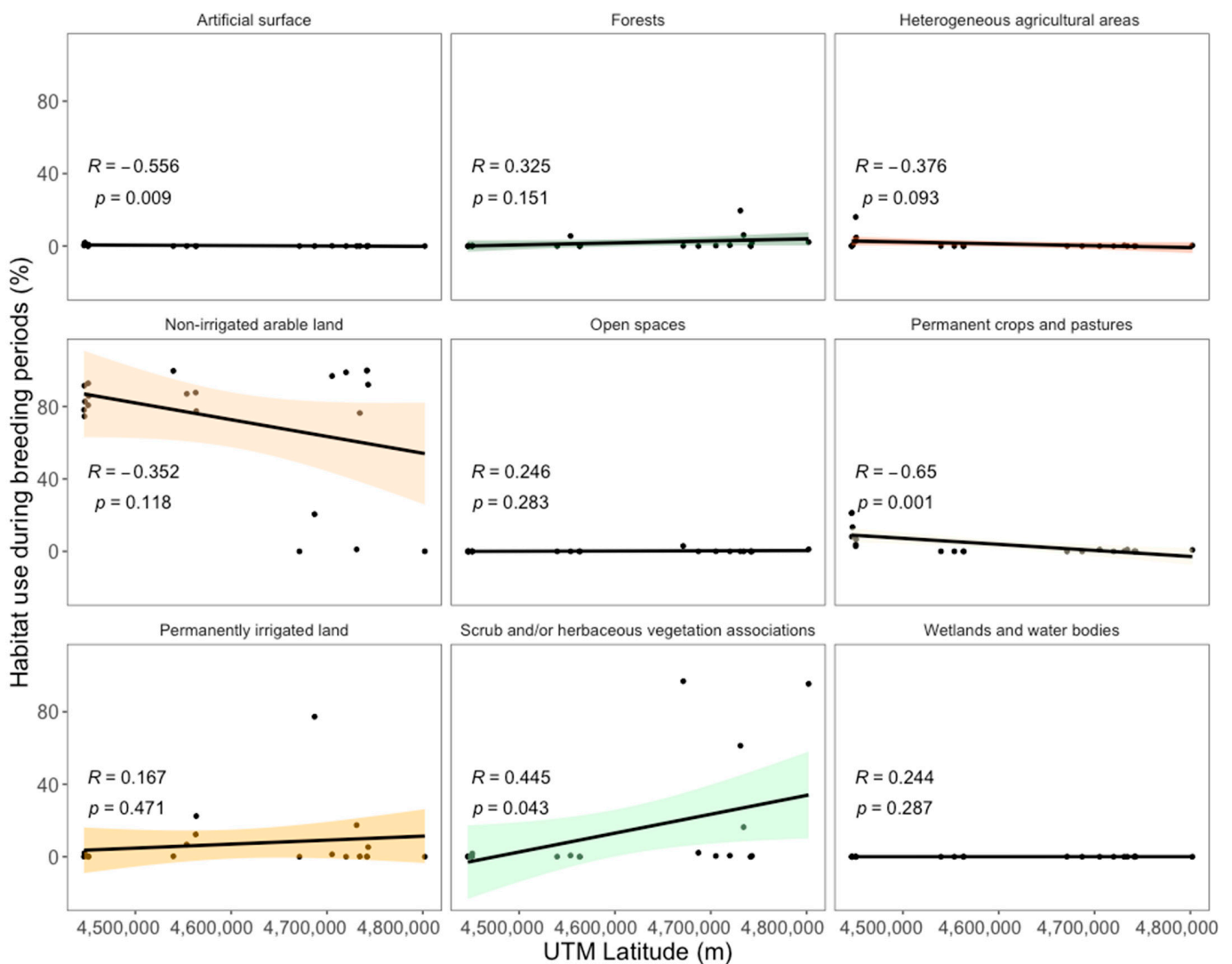


Figure 3. Linear adjustments between the habitat use percentages and latitude. Each type of habitat is represented with a different colour.

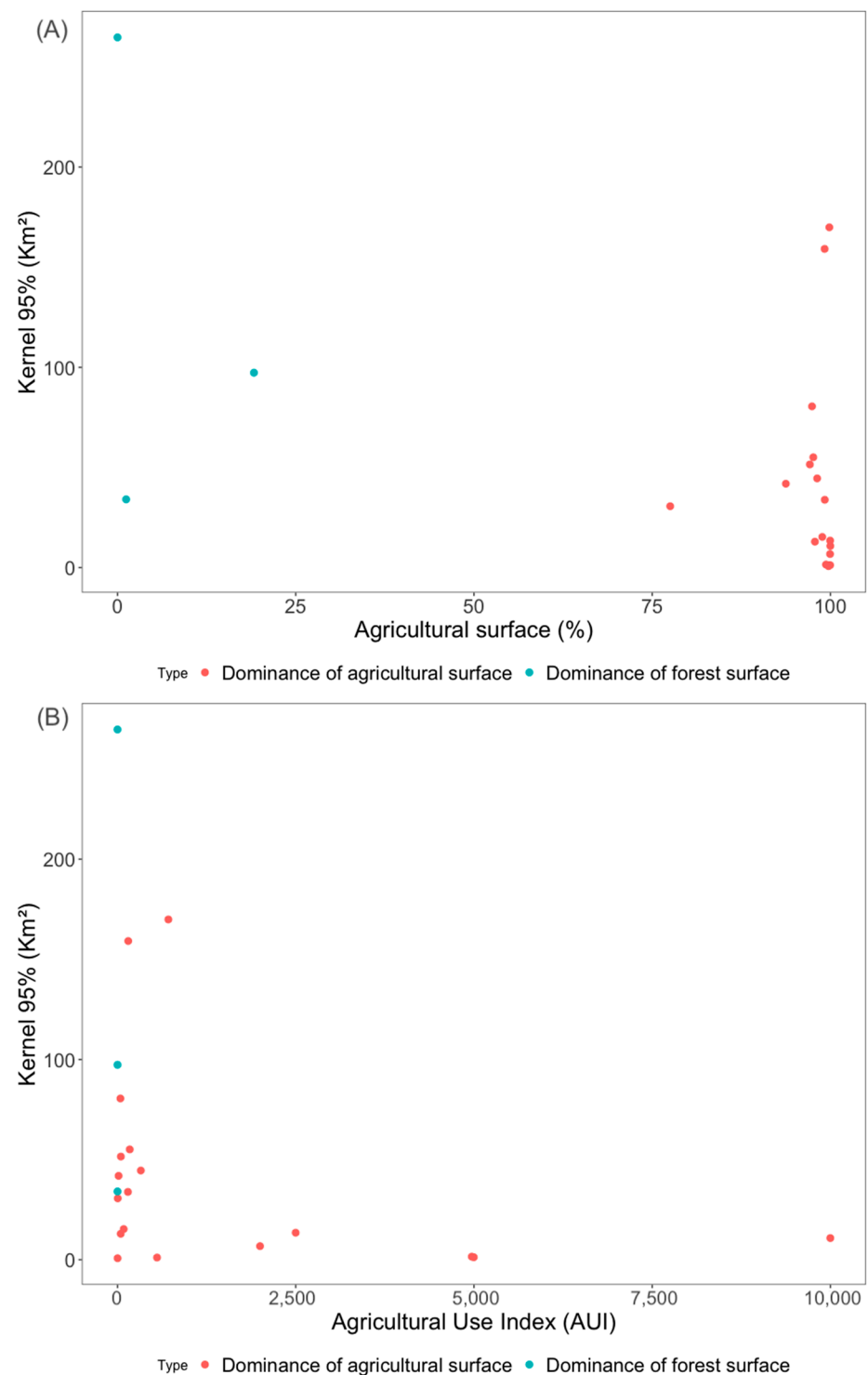


Figure 4. (A) Correlation between home range by the 95% kernel and the agricultural surface (grouping: non-irrigated arable land, permanently irrigated land, permanent crops and pastures and heterogeneous agricultural areas). (B) Correlation between home range by the 95% kernel and the Agricultural Use Index.

4. Discussion

Although Hen Harriers in the Iberian Peninsula were known to occur in agricultural areas [39], this is the first time that land use types and sizes during the breeding season have been studied in depth in this species using GPS data.

The two breeding habitats with higher uses by Iberian Hen Harriers found in this study are mainly agricultural fields and to a lesser extent natural vegetation scrubs. In some habitat types, we did find a significant trend when comparing habitat uses with latitude, with agricultural habitats being found further south and those with shrub and/or herbaceous vegetation further north. These results are consistent with previous studies of this species where populations in the south and north of its distribution have been studied [15,40,41]. On the one hand, these studies explain that in colder territories, usually located in northern areas, this species breeds in open habitats such as scrublands and unenclosed forests [17].

In the northern United States, harriers nest in territories dominated by scrubland [42,43] and are common in cornfields and wetlands [44]. Moorland, heathland and scrub in the UK and Scotland [45–47] as well as young pre-scrub woodland and peatland in Ireland [48,49] are some of the typical habitats of Hen Harriers, as we found in harriers breeding in northern Spain. Furthermore, in France, harriers breed in cereal croplands [10,50] as our results show for southern harriers, where the most frequent habitat overflowed was agricultural systems.

This study shows how, in Spain, this latitudinal differentiation is seen at a finer scale, following a general tendency for agricultural land, but finding some individuals with higher use of scrub and grasslands of natural vegetation further north. The Hen Harrier has a slow, low-altitude flight, and wooded vegetation would impede these movements [6,51], so it is expected to be found in this type of habitat. In Figure 3, we find the utilisation relation to the latitude and as latitude increases, the percentage of non-irrigated arable land decreases and the percentage of herbaceous and/or shrubland associations increases, probably due to the availability of these habitats.

We observed a selection in nesting habitat with the latitude of the species in Spain, where nests are generally found in natural vegetation in the north and in the south in agricultural areas, being the dominant habitat in the centre of the peninsula, near Castilla la Mancha [15]. Hen Harriers are frequent in cereal crops throughout most of the Iberian Peninsula [39]. Of all the seventeen Hen Harriers studied, only three nested and spent most of their breeding period in areas of shrub–scrub vegetation, which were found in northern Spain. In Galicia, northwestern Spain, Hen Harriers tend to occupy heathland—forest vegetation [52]. These ecosystem types tend to be more abundant than in the south; forest and agricultural habitats differ in their dominance due to climatic differences within the Iberian Peninsula [53].

All harriers showed habitat use for the type of ground on which they nested. These results show a tendency not to move away from the nest, at least the females [54], which were the majority in this study. Males, however, hunt independently of the nest [54] and in general obtained larger home ranges, although they also followed this trend where habitat use is linked to nest location. Therefore, we can say that nest location and the most abundant vegetation in the different zones are probably determining factors in Hen Harrier use for breeding habitat.

Differences in home range size between harriers with agricultural uses and harriers with forest uses were not significant, although the p -value ($p = 0.080$) was close to the established limit. This result is probably influenced by the small number of harriers showing a higher use of forest land as opposed to the numerous Hen Harriers on agricultural land.

Habitat uses related to vegetation structure have been found in other raptors, such as the Northern Goshawk (*Accipiter gentilis*), the Eurasian Buzzard (*Buteo buteo*) and the Eurasian Sparrowhawk (*Accipiter nisus*) [55]. In addition, previous habitat studies of other species of the genus *Circus*, such as the Western Marsh Harrier (*Circus aeruginosus*), show the adaptability of the species to both natural and human-disturbed environments [56–58], as in our study. In this study, we found a higher habitat use or specific search on rain-fed arable land in the behaviour of harriers during the breeding period. We believe that this higher use is a reflection of the habitats close to the nest site that were more abundant in each region. In other studies, nest proximity was considered a nuisance variable for habitat

analysis [6]. This supports our view of the results obtained. Although there is evidence of a selection of certain habitats and avoidance of others for nesting by harriers [47], in other studies, this higher use did not result in better breeding success [45].

This study has some weaknesses. One of them may be the lack of representation of harriers in the north of Spain and with a greater tendency to nest in forest or herbaceous habitats, as we only have three out of seventeen individuals studied. Statistical analyses would be more powerful by increasing the sample size. On the other hand, the lack of field monitoring of harriers makes it difficult to monitor breeding behaviour, forcing us to use methodologies to know the location closest to the nesting area, and the breeding periods. For future studies where the size of the home range is much more important, we will use more novel methods such as Autocorrelated Kernel Density Estimators.

Ultimately, this study of Hen Harriers in the Iberian Peninsula is the first to use satellite data to analyse in detail the types and sizes of land use during the breeding season. We found that the two habitat uses are generally agricultural fields and, to a lesser extent and located to the north, natural vegetation thickets. Nest location is key to habitat selection, and habitat uses vary with latitude, probably due to habitat availability in different parts of Spain.

Author Contributions: S.M. (Sara Morollón), J.G.-M. and V.U. conceived the ideas and designed the methodology; S.L. collected the data; S.M. (Sara Maeso), S.M. (Sara Morollón) and J.G.-M. analysed the data; S.M. (Sara Maeso), S.M. (Sara Morollón), J.G.-M. and V.U. wrote the manuscript; S.M. (Sara Maeso), S.M. (Sara Morollón), J.G.-M., S.L. and V.U. and contributed critically to the drafts; S.L. and V.U. gave final approval for publication. All authors have read and agreed to the published version of the manuscript.

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