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Home Range and Habitat Selection of Feral Horses (*Equus ferus* f. *caballus*) in a Mountainous Environment: A Case Study from Northern Greece

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Abstract: The spatial ecology of feral horses (*Equus ferus* f. *caballus*) in Greece has never been studied before, including home range size and habitat selection. We tracked two mares fitted with global positioning system collars between September 2020 and August 2021 in a portion of Mount Menoikio in Central Macedonia, Northern Greece. We used K-select analysis to assess habitat selection for the study period by combining location data with several environmental variables. The mean home ranges for horses varied from 26.72 km^2 (95% Minimum Convex Polygon; SE = 0.442) to 27.84 km^2 (95% Kernel Density; SE = 1.83). Both horses selected areas with flat and smooth topography near natural grasslands with high green productivity. Conversely, they avoided areas near broadleaved forests and pastures, as well as at north-facing aspects. Overall, suitable habitats corresponded to a small portion (15.1%) of the available habitat. Our findings could assist land managers in mapping primary horses' habitat in the wider region and implement management regimes that will aid in preserving natural grasslands.

Keywords: equids; Mount Menoikio; movement ecology; resource selection; habitat suitability; GPS

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1. Introduction

Understanding how animals use their geographic [1] and environmental [2] space has long been a central topic in ecology [3,4] with important implications for the conservation and management of wildlife populations [5–7]. A key characteristic of an animal's space use is its individual home range size [8], which results from its movement patterns [3]. However, most individuals do not move at random [9,10] but instead move in response to changes in the environmental space [11] in order to fulfill their ecological and biological requirements [12–14].

Feral equids (*Equus ferus* f. *caballus*) illustrate a variety of movement and habitat selection patterns that differ across populations and landscapes [15,16] or even temporally within populations [17–19]. However, topography [19–21], food [19,20,22,23], and water availability [22,24–26] are among the strongest factors influencing habitat selection and hence movement patterns of feral horses. In addition, habitat selection has been found to be influenced by predation risk [27], thermoregulation [28], and population density [29]. In general, equids are considered to be very adaptive and may occupy a variety of habitats and ecosystems [30–33]. Based on the characteristics and availability of resources in these ecosystems, their home range size may vary considerably and may be as small as 2.6 km^2 or as large as 110 km^2 [19,34–37].

Studies of feral equids' ecology have been focused on specific regions for management purposes as a result of their negative impacts on the environment [30–33,38,39]. Conversely, while equids have established feral populations in many parts of Greece, there are no published studies investigating their ranging behavior and habitat requirements. Feral populations are believed to have originated from work-horse releases in the 1970s. In addition, during the previous decade and in an attempt to preserve local breeds, the Greek government subsidized their breeding. This resulted in many feral foals being captured by local livestock farmers for breeding purposes. However, once the subsidies came to an end, additional horse releases were made, enriching the already established feral population. Despite their domestic origin, feral populations form herds and maintain group cohesion and bonds similar to their wild counterparts. Unfortunately, basic information regarding their population size, distribution, and behavior is unavailable. This may be partly explained by the illusive nature of equids and the remote and rugged territories that they occupy, both of which pose logistical and methodological challenges in studying them. Fortunately, in recent times, wildlife monitoring devices, such as satellite GPS collars, have allowed for the tracking of individual animal movements even in the most remote of areas [40,41]. Modern devices not only collect an extensive and accurate amount of animal location data, but they do so over large spatial and temporal extends without the need of exhausting fieldwork from researchers [40–42]. However, this type of technology is seldom utilized to study feral horses' spatial ecology [43].

In this context, the objective of this study was twofold: to quantify the home range size, and to investigate the habitat resource selection of a feral (wild) horse population established in Mount Menoikio in Central Macedonia, Northern Greece, in an attempt to fill the existing knowledge gaps that would otherwise aid in managing or conserving this iconic species.

2. Materials and Methods

2.1. Study Area

The study was carried out in Mount Menoikio (Figure 1), which is located at the border of Serres and Drama Prefectures in Central Macedonia, in Northern Greece. It covers an area of 27,542 ha, with a maximum altitude of 1963 m. Meadows and rocky outcrops compose one-third (31.3%) of the area, followed by shrubs (19.8%), partially forested land (19.6%), and forests (19.2%) [44]. The main economic activity of the region is animal husbandry, which to a great extent follows traditional free-range grazing and includes beef and dairy cattle production.

2.2. Location Data

Between September and October 2020, two randomly selected mares (identified as H1 and H2, respectively) were captured using a baited corral trap. Handling was performed by ungulate experts, under the supervision of a veterinarian who was there to ensure the animal's safety and welfare at all times. Once they were fitted with Lotek Wireless Litetrack Iridium TL-500 GPS collars (Lotek Wireless Inc, Newmarket ON, Canada), both mares were immediately released back into the wild. The collars were programmed to record GPS locations at 1 h intervals for a duration of two years following deployment. Each collar included 2-way communication, allowing a daily download of horse locations. The collars recorded the date, time, location (latitude and longitude), elevation, ambient temperature, type of fix status, and dilution of precision (DOP). In addition, the collars were furnished with a remote drop-off mechanism, which allowed collar removal without recapture and ensured the welfare of the animals after the completion of the study [45]. Mares were chosen over stallions as they are more likely to remain within the same harem in relation to the latter [34]. Prior to any analyses, location fixes with DOP values of > 5 were considered inaccurate and were therefore removed [46,47]. All procedures carried out in this study were conducted in accordance with the Greek animal welfare legislation and conducted under the authority of the project (BIO—INNOVATE/5047319).

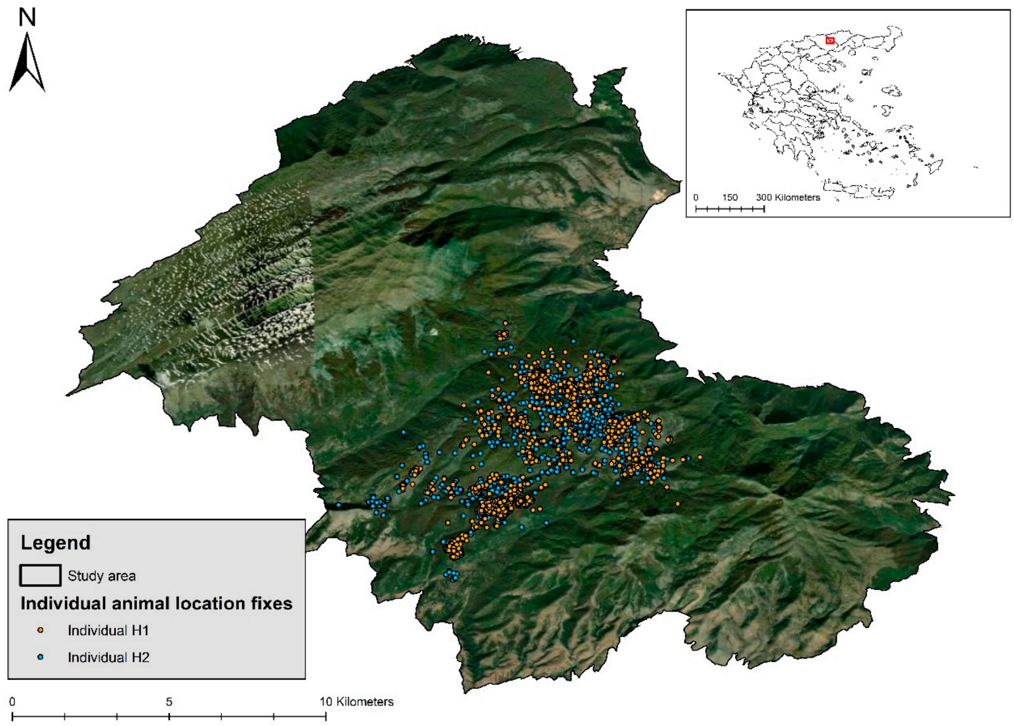


Figure 1. Map of the study area and location fixes of individual feral horses in Mount Menoikio, Central Macedonia, Northern Greece.

2.3. Home Range Size

Home ranges exhibited little interannual variation; thus, a single home range was developed for each individual mare for the entire study period. The home range size of each collared horse was defined using two different methods: the Minimum Convex Polygon (MCP) method and the Kernel Density (KD) method. Both these methods are among the most widely used in calculating home ranges, allowing comparisons with similar studies. The home range size for each horse was calculated in R version 4.3.0 [48] using the adehabitatHR package version 0.4.21 [49] and the resulting outputs were screened in ArcMap version 10 [50] for visualization purposes. In addition, we used the adehabitatLT [49] package version 0.3.27 to calculate the daily distance traveled by each individual mare.

2.4. Habitat Selection

2.4.1. Environmental Variables

Environmental variables for the study area were available with a spatial resolution of 100 × 100 m pixels. Each pixel was characterized by 11 variables related to land-use type and topography (Table 1). The CORINE Land Cover map (CLC18) [51] was used to calculate the Euclidean distance from each land-use type. A digital elevation model (DEM) was available for the entire study area with a spatial resolution of 25 × 25 m pixels, from which we also calculated the slope and aspect, a topographic ruggedness index (TRI), and an index of solar radiation (SR). Finally, we calculated the Normalized Difference Vegetation Index (NDVI), using Landsat 8 images from the USGS Earth Explorer for each season and for the entire study area. We then calculated the mean NDVI at a spatial resolution of 100 × 100 m pixels. All variables were created in ArcMap [50].

Table 1. Description of the environmental variables used to estimate habitat selection (K-select) and habitat suitability (Mahalanobis D^2) of feral horses in Mount Menoikio, Greece.

Variable	Abbreviation	Description
Topographic ruggedness index *	TRI	Amount of elevation difference between adjacent cells of the Digital Elevation Model (DEM) [52]
Solar radiation *	SR	Amount of incoming solar radiation
Elevation *	DEM	Digital elevation data (ASTER)
Slope *	Slope	Slope in degrees calculated from the DEM
Aspect *	Aspect	Aspect values identifying the compass direction that the downhill slope faces for each location (pixel)
Normalized Difference Vegetation Index ***	NDVI	The NDVI is a dimensionless index that describes the difference between visible and near-infrared reflectance of vegetation cover and can be used to estimate the density of green on an area of land [53]
Distance to broadleaved forests **	BR	Euclidean distance from broadleaved forests
Distance to pastures **	P	Euclidean distance from pastures
Distance to sparsely vegetated areas **	SP	Euclidean distance from sparsely vegetated areas
Distance to natural grasslands **	G	Euclidean distance from natural grasslands
Distance to sclerophyllous vegetation **	SC	Euclidean distance from sclerophyllous vegetation

* Variable derived from DEM. ** Variable derived from CLC18. *** Variable derived from Landsat 8 images.

2.4.2. K-Select Analysis

Habitat selection by feral horses was investigated by means of a K-select analysis. This approach allows the identification of subtle disparities in habitat selection among individuals of a group, instead of averaging the variation across individuals [49]. The K-select analysis generates marginality vectors for each individual, thereby highlighting those environmental variables that drive habitat selection [49]. The vectors extend from the centroid of an available resource space to the centroid of a used resource space. Each vector's direction denotes the selected variables, with its length indicating the strength of selection by an individual animal. Hence, disparities in marginality vectors reflect individual variations in habitat selection [49]. The "Available habitat" was defined as a single large area enclosing the entire 100% MCP home range of both horses, expanded by a 500 m buffer area to allow for the inclusion of border effects [54]. Similarly, we defined as the "used habitat" all fixes that were obtained for each individual mare. Prior to the K-select analysis, we performed randomization tests (n = 10,000 steps) using the first eigenvalues to determine the influence of each environmental variable on the marginality of each individual and, if observed, use differed significantly from what was expected under a random habitat use hypothesis [54,55]. Analyses were performed using the adehabitatHS package version 0.3.17 [49] in R [48].

2.5. Habitat Suitability

A habitat suitability map was generated using the Mahalanobis distance (D^2) statistic [56]. The Mahalanobis distance statistic measures the contrast between the average habitat characteristics at each resource unit (100 × 100 m pixel), and the mean of habitat characteristics calculated from aggregated horse relocations. According to Hellgren et al. [57], habitat quality is inversely proportional to D^2; therefore, smaller Mahalanobis distance values indicate more favorable habitat conditions. We used the mahasub function in the adehabitatHS package version 0.3.17 [49] to produce a map with a continuous gradient of habitat suitability (ranging from 0 to 1) from D^2. The resulting output was screened in ArcMap [50] for visualization purposes in five suitability classes (unsuitable: 0–0.2; marginal: 0.2–0.4; moderately suitable: 0.4–0.6; suitable: 0.6–0.8; and optimal: 0.8–1) [58].

2.6. Sample Size and Model Inferences

Home range and habitat selection estimates may be subject to several sources of potential bias such as the accuracy, precision, and frequency of location data, the duration of the study, individual behavior, and a lack of representativeness [34,36,59,60]. In this study, we used high-end GPS collars producing high fix rates over a significant time period. As such, individual-level home range estimates are considered robust, especially in relation to similar studies in which estimates were based on individual sightings [37]. In addition, habitat selection was investigated at the individual level, so as to capture variance resulting from behavioral differences between the two tracked mares. On the other hand, our small sample size may not adequately represent the variability in home range size and habitat selection at the population level. Despite the rapid advancements in GPS technology, its use in tracking equids is still lacking [43]. While some studies report their findings based on relatively large sample sizes [24,35,61], others make inferences based on a limited number of individuals [34,62] or by including less precisely sampled data [37]. However, in all these cases, individual harems were previously identified, and horses were selected to represent different harems. In our study, individual harems or groups were not identified prior to collar fitting. While based on drone footage taken during the course of this study, we believe that both our tracked mares were part of the same group, this conclusion must be treated with caution since we did not follow a standardized protocol when utilizing the drone [63]. Consequently, our results of home range and habitat selection may not be representative at the population level, and the ability to generalize our findings may be limited to equids occupying mountainous areas. Nonetheless, similar to other published work with a limited sample size [62], our study offers valuable insights into feral horses' spatial ecology, which up to now has remained largely unstudied, especially in Greece and in Europe in general. The results presented below should be treated as those of a pilot study, on which future work should be built.

3. Results

3.1. Home Range Size

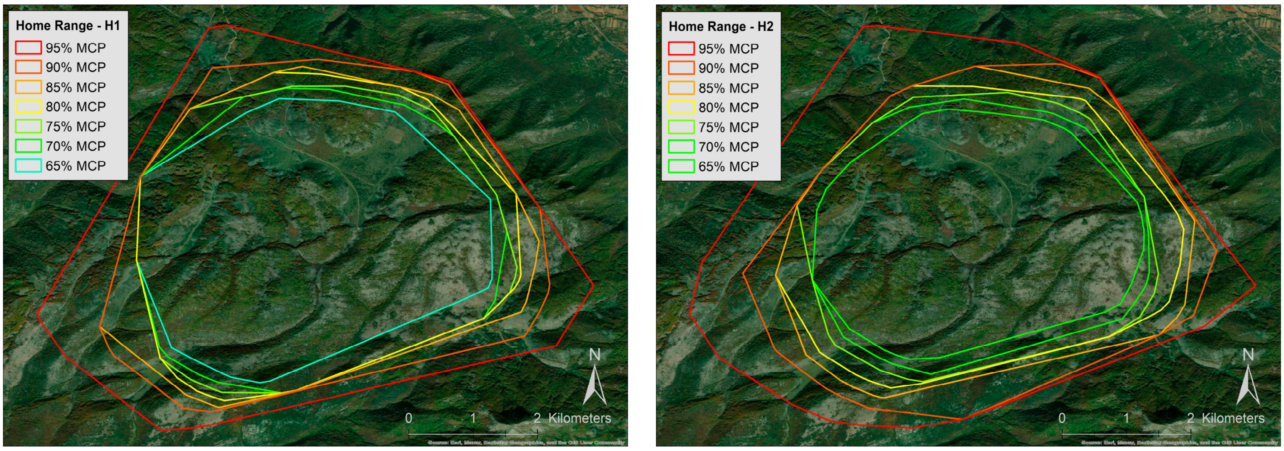
The home range size for H1 and H2 was calculated from a total of 1182 and 2800 relocation points, respectively (Table S1). While both horses were tagged with a time difference of about 3 weeks, the fewer relocation points of H1 were due to mortality caused presumably by wolves on 10 February 2021, as indicated by bite marks on the retrieved collar. Home range analysis based on the MCP methodology indicated that both horses illustrated very similar movement patterns. More specifically, the 95% MCP for H1 and H2 was 26.27 km^2 and 27.16 km^2, respectively (Table 2, Figure 2a,b). Similarly, the 95% KD for H1 and H2 was 29.68 km^2 and 26.01 km^2, respectively (Table 2, Figure 3a,b). H1 and H2 shared 94.91% of their 95% MCP home range, and 82.55% of their 95% KD home range respectively (Figure 4a,b). Finally, the mean daily distance traveled by H1 was estimated at 4507.13 m (Standard error: ±172.19 m), whereas H2 traveled a mean daily distance of 3995.23 m (Standard error: ±109.45 m).

Table 2. The home range size (km^2) for H1 and H2 according to the Minimum Convex Polygon (MCP) and Kernel Density (KD) methodologies. Home range sizes are given in increments of 5%, ranging from 65% to 95%.

Home Range Size	H1		H2	
	MCP	KD	MCP	KD
95%	26.27	29.68	27.16	26.01
90%	21.19	23.91	20.88	20.34
85%	19.05	20.21	18.20	16.71
80%	17.34	17.49	16.38	14.06

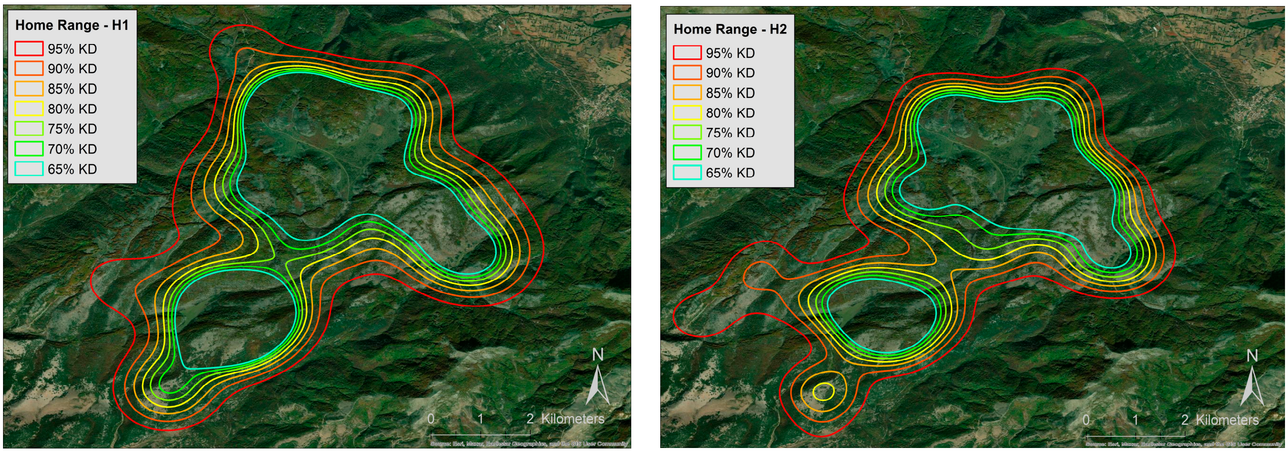
Table 2. *Cont.*

Home Range Size	H1		H2	
	MCP	**KD**	**MCP**	**KD**
75%	16.45	15.29	14.40	12.01
70%	15.68	13.39	13.21	10.33
65%	13.46	11.72	11.32	8.92



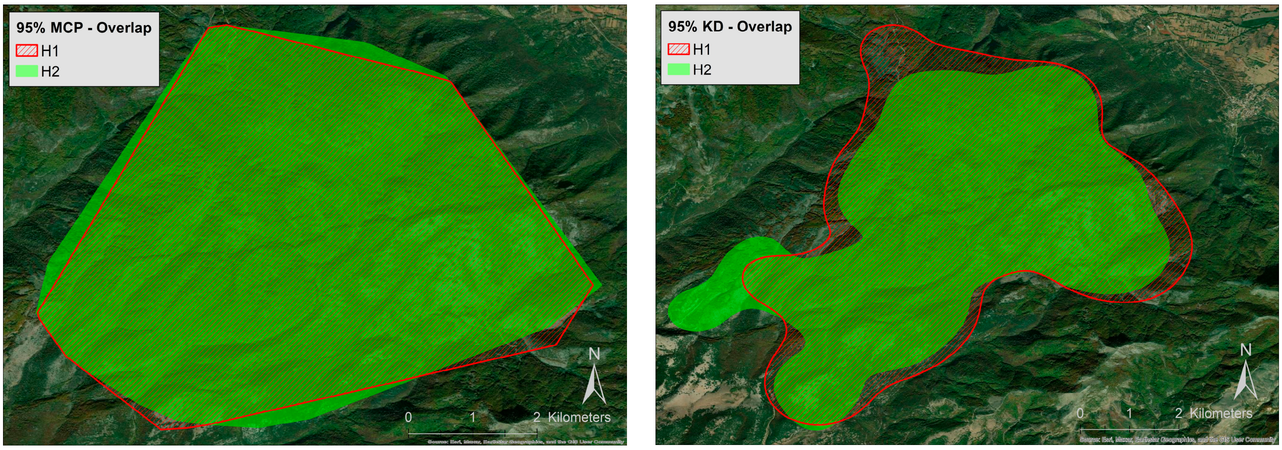
(**a**) (**b**)

Figure 2. Map depicting the home range size of (**a**) individual H1 and (**b**) individual H2, based on the Minimum Convex Polygon (MCP) methodology. Home ranges are illustrated in increments of 5%, ranging from 65% to 95%.



(**a**) (**b**)

Figure 3. Map depicting the home range size of (**a**) individual H1 and (**b**) individual H2, based on the Kernel Density (KD) methodology. Home ranges are illustrated in increments of 5%, ranging from 65% to 95%.



(**a**) (**b**)

Figure 4. Map depicting the overlap between individual H1's and H2's home range size, calculated from (**a**) the 95% Minimum Convex Polygon (MCP) and (**b**) the 95% Kernel Density (KD) methods.

3.2. Habitat Selection

Randomization tests carried out on marginality vectors showed that habitat selection was significantly non-random ($\lambda_1 = 1.231$, $p < 0.001$), making further analysis on habitat selection patterns informative. K-select analysis identified two major axes (Figure 5). The first axis explained 98.3% of the marginality (i.e., the difference between availability and use of resource units by horses) and was related positively to the distance from sclerophyllous vegetation (SC) and negatively to aspects (Aspect). The second axis explained 1.7% of the marginality and corresponded negatively to slopes (Slope) and to distance to natural grasslands (G). Marginality was non-random for both individuals (Table 3; Figure 5). The high proportion of variance described by the two axes, as well as the relative length and direction of re-centered marginality vectors (Figure 6) indicate that both individuals had similar habitat selection patterns to one another. More specifically, both horses showed a selection for gentle slopes (Slope), less rugged terrain (TRI), and lower aspects (Aspect; avoidance towards north-facing slopes) (Table 3). In addition, both horses selected areas with higher green productivity (NDVI), within or in close proximity to natural grasslands (G), but away from broadleaved forests (BR) and pastures (P). One horse (H1) showed selection for areas with higher solar radiation (SR), as well as areas away from sparsely vegetated areas (SP) and sclerophyllous vegetation (SC). On the other hand, individual H2 showed selection for higher altitude (DEM) areas.

Table 3. The results of the randomization tests for the K-select analysis on habitat selection by horses. Tests were based on 10,000 randomization steps, at which the first eigenvalues of observed data were compared to those from randomized datasets.

Test of Marginality	**Individual**	
	H1	**H2**
Marginality value	1.108	1.312
p-value	<0.001 *	<0.001 *
Selection of environmental variables (marginality vectors)		
TRI	−0.240 *	−0.294 *
SR	0.209 *	0.070
DEM	0.057	0.149 *
Slope	−0.587 *	−0.683 *
Aspect	−0.260 *	−0.221 *

Table 3. *Cont.*

Test of Marginality	Individual	
	H1	**H2**
NDVI	0.405 *	0.396 *
BR	0.091 *	0.132 *
P	0.137 *	0.209 *
SP	0.161 *	0.060
G	−0.571 *	−0.679 *
SC	0.214 *	0.003

* Significant at the 5% level after Bonferroni correction (Bonferroni α level = 0.05/2 = 0.025).

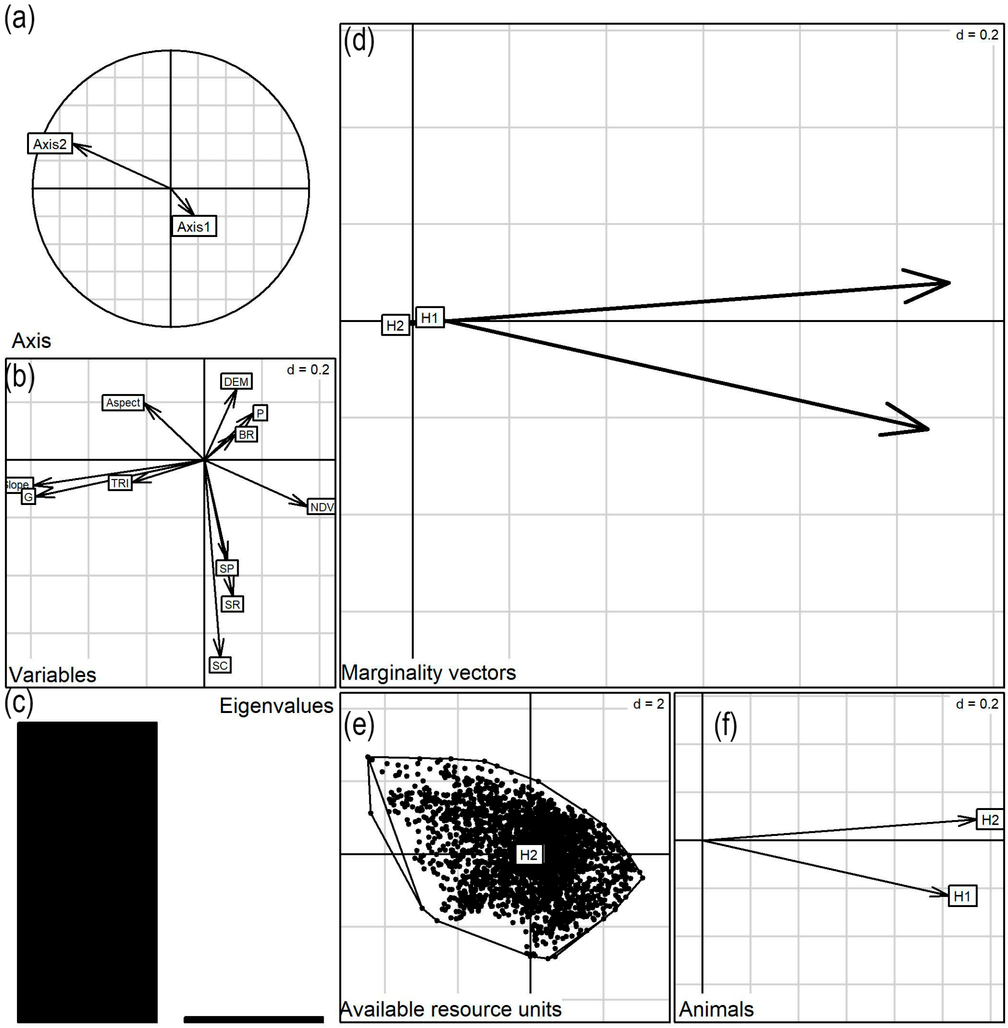


Figure 5. Results of the K-select analysis carried out on the radio-tracking data collected on the feral horses in Mount Menoikio, Central Macedonia, Northern Greece. The graphs are as follows (**top** to **bottom**, **left** to **right**): (**a**) the correlation between the first two axes of the K-select analysis, (**b**) the scores of the environmental variables on the axes of the K-select analysis, (**c**) the eigenvalues of the analysis, (**d**) the uncentered vectors of marginality (the origin of the arrow indicates the centroid of the cloud of available points and its end indicates the centroid of the cloud of used points), (**e**) scores of the available resource units on the axes of the analysis, and (**f**) scores of the recentered marginality vectors on the first axes of the analysis. The notation "d" indicates the distance of each grid cell.

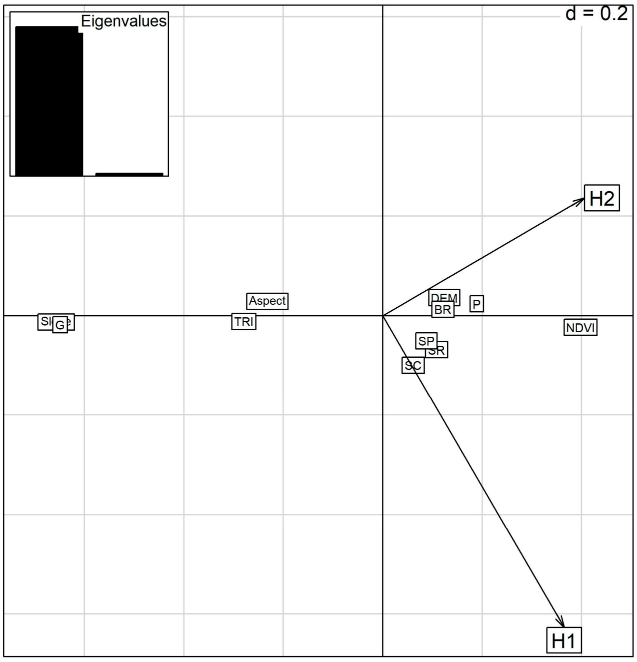


Figure 6. Scores of the recentered marginality vectors on the first axes of the K-select analysis. The notation "d" indicates the distance of each grid cell.

3.3. Habitat Suitability

The habitat suitability map based on the Mahalanobis distance (D^2) statistic (Figure 7) revealed that optimal and suitable habitats represented 8.3% and 6.8% of the entire "available habitat", respectively. The most suitable habitats (suitability value > 0.6) were located in the plateau, in the north part of the area, as well as in the southeast and southwest. These areas are dominated by natural grasslands and are relatively flat compared to other available locations. Moderately suitable and marginal habitats accounted for 5.5% and 6.7% of the area, respectively, whereas unsuitable habitats covered 72.7% of the area.

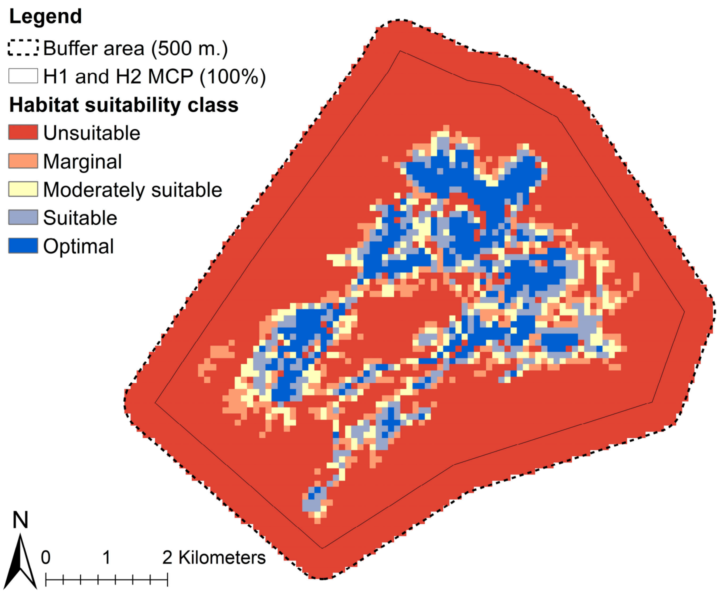


Figure 7. Map depicting the habitat suitability for feral horses in Mount Menoikio, Central Macedonia, Northern Greece. Suitability values are based on the Mahalanobis distance (D^2) statistic and are classified into five suitability classes. The area corresponds to the 100% MCP of both horses, plus a buffer area of 500 m.

4. Discussion

Our study provides the first-ever account of space use and habitat selection by feral equids in Greece, using accurate telemetry data from GPS transmitters. From a broader perspective, our results provide a better understanding of the habitat ecology and behavioral biology of feral equids, which may contribute to conserving and/or managing this iconic species. In addition, estimates of home range size found in our study, as well as habitat selection can be compared to those found in similar studies in other parts of the world.

The home range size of free-ranging equids may vary considerably as a result of resource availability, exposure to disturbance, and study methodology [34]. For example, the mean home range size of 26.72 km^2 found in our study was almost double the size of that reported by Salter et al. [37], according to which the mean home range size of feral horses did not exceed 15 km^2. Conversely, our estimates of the mean home range size were almost half of that reported by Girard et al. [34] and Hennig et al. [35], who found mean home range sizes of 48 km^2 and 40.4 km^2, respectively. Finally, our estimates were much smaller than those reported by Schornrcker et al. [19] (103–117 km^2) for feral horses and by Kaczensky et al. [22] for Przewalski's horses (*Equus ferus przewalskii*) (471 km^2) and Asiatic wild assesses (*Equus hemionus*) (5860 km^2). While the home range estimates reported by Schornrcker et al. [19], Kaczensky et al. [22], and Girard et al. [34] were based on relocation points taken at 1–2 h intervals, those reported by Hennig et al. [35] and Salter et al. [37] came from sightings of marked individuals. As such, the latter may not be suitable for comparison with our findings [59]. Interestingly, both of our tracked individuals shared a high proportion of their 95% MCP (94.91%) and 95% KD (82.55%), and their location fixes illustrated significant spatial overlap, suggesting that they were part of the same group. Based on aerial footage taken during the implementation of this study, we believe that Mount Menoikio is home to several groups of feral horses which often, and due to the topography of the area, come together and form a large herd that consists of up to 80 individuals. However, the social structure and organization of equids should be more thoroughly investigated in the future, taking advantage of drone technology [63]. In addition, our study revealed that horses may travel up to 4.5 km per day in search of resources. Similar results were reported for Przewalski's horses in Mongolia, with a mean daily distance of 3.5 km [22]. On the other hand, the daily distance traveled by horses in our study was much lower than that reported by Hampson et al. [64] for feral horses in Australia (15.9 km), and by Hennig et al. [35] in the United States (9 km), as well as by Kaczensky et al. [22] for Asiatic wild assesses in Mongolia (8.3 km). As in the case of the home range estimates, a comparison of daily distances traveled by horses may not be suitable when different fixed rates are used for their calculation [65]. In addition, while there is evidence supporting that horses usually stay in close proximity to water sources [66], water was not included as a variable in our analysis. However, within our study area, there were several troughs, suggesting that water availability may not pose a limiting factor. Conversely, space use by horses was found to be driven by food availability and limited due to the rugged landscape.

Despite the small sample size (two mares), our results of habitat selection are consistent with those of feral horses in other parts of the world. Both horses showed similarities in habitat selection, favoring flatter areas within or in close proximity to natural grasslands and higher green production. Grassland habitats have favorable herbage production [34] and are often sought out by foraging horses [23]. Similar results have been reported in previous studies [34,67]. However, according to van Beest et al. [29], as the local carrying capacity is reached, the selection of grasslands may be weakened, and the selection for other habitat types may increase. In our case, this finding suggests that, within our study area, horse density has not yet reached its carrying capacity, allowing individuals to select habitats with higher-quality vegetation. While our data did not exhibit interannual variation in habitat selection, other studies have shown that grasslands may be less favored during fall due to the depletion of available forage in habitats selected during summer by the combined grazing pressure from both horses and domestic cattle [20,34], as well as due to seasonal fluctuations in forage quality [68]. While domestic cattle use our study area during summer months for grazing, their spatial and dietary overlap with horses occupying the area is not known, but could perhaps be an interesting subject for future research.

In addition to food availability, the horses illustrated a strong selection for flatter, less rugged areas. This finding is consistent with the findings of [20,54,69]. The terrain has been found to influence habitat selection by horses, as steep slopes prevent access and distribution across the landscape. In rugged topography, accessibility may be limited or may be associated with increased energy expenditure [70]. However, in the presence of corridors (roads and trails), topography may not pose a limiting factor [34].

We did not find any evidence supporting that horses select forested areas for thermoregulation purposes or for shelter from weather extremes (wind, snow, or cold) [28]. On the contrary, both horses avoided areas in close proximity to broadleaved forests, horse H1 selected areas with higher solar radiation, and both horses avoided north-facing aspects. The above-combined pattern suggests that both horses followed similar strategies for maximizing sun exposure, therefore achieving thermoregulation. Moreover, both individuals' aversion towards forested areas may have been an adaptive strategy for minimizing predation risk [27].

The habitat suitability map revealed that only a small part (15.1%) of the available habitat is considered suitable for feral horses and underlines the need to conserve all natural grasslands within the plateau of Mount Menoikio, in an effort to preserve horses' presence in wider the area. While all suitable areas fall within the Natura 2000 network, management actions need to be implemented if horses are to be maintained.

Overall, our findings suggest that in mountainous areas in Northern Greece, feral horses tend to select certain habitat characteristics, primarily distance to natural grasslands and areas of high green productivity, with gentle slopes and smooth terrain. While our study included relocation data from only two mares, their similarities in habitat selection patterns, as well as home range size and daily distance traveled suggest that these findings may be considered representative of the whole feral herd that occupies the area. Our findings may assist land managers in mapping primary habitats in the wider mountainous region that are likely to be used by feral horses. In addition, and in order to maintain free-ranging equids within the broader area, management regimes are required to preserve natural grasslands and promote green biomass productivity. In this context, grassland declines due to woody plant encroachment [71] should be halted, whereas future studies should focus on understanding the possible impacts of shared grazing by equids and cattle. Moreover, future research should be built upon the groundwork established by this preliminary study, increasing the sample size and including a range of feral horses' environments.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land13081165/s1, Table S1: Duration of individual horse (H1 and H2) tracking and number of relocation data collected.

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