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Seasonal habitat preference by the flagship species *Testudo hermanni*: Implications for the conservation of coastal dunes

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A B S T R A C T

In this study, we explored if, how, and when the European Union habitats (EU *sensu* Habitats Directive 92/43/CEE) are used by the flagship species *Testudo hermanni* in a well-preserved coastal dune system of the Italian peninsula. Radio telemetry data and fine-scale vegetation habitat mapping were used to address the following questions: (a) is each EU habitat used differentially by Hermann's tortoises? (b) is there any seasonal variation in this utilization pattern? (c) how does each habitat contribute to the ecological requirements of the tortoises? Nine tortoises were fitted with transmitters and monitored for the entire season of activity. The eight EU habitats present in the study area were surveyed and mapped using GIS. The seasonal preferential use or avoidance of each habitat was tested by comparing, through bootstrap tests, the proportion of habitat occupied (p_iTh) with the proportion of available habitat in the entire landscape (p_iL). The analysis of 340 spatial locations showed a marked preference for the *Cisto-Lavanduletalia* dune sclerophyllous scrubs (EU code 2260) and a seasonal selection of *Juniperus macrocarpa* bushes (EU code 2250*), wooded dunes with *Pinus* (EU code 2270) and mosaic of dune grasslands and sclerophyllous scrubs (EU codes 2230, 2240, 2260). Seasonal variation of habitat preference was interpreted in light of the different feeding, thermoregulation and reproductive needs of the tortoises. Our results stress the ecological value of EU coastal dune habitats and suggest prioritization of conservation efforts in these ecosystems.

1. Introduction

Coastal dunes represent extremely interesting environments both from an ecological and a landscape perspective [1], but at the same time, they are among the most fragile and threatened ecosystems worldwide [2]. Coastal ecosystems are particularly vulnerable to climate variability and to coastal erosion, and in recent years, they have undergone consistent transformations due to urban expansion, agricultural and afforestation spread, and industrial and harbour development [3]. The degradation and loss of the littoral landscape has concerned all coastal countries of the European Union and is particularly striking in the Mediterranean [4]. For this reason, sandy coastal vegetation types are of most concern among EU directive habitats [5], and most of the sand dune coastal fauna is included as threatened or endangered in the IUCN Red List [6]. Some of these endangered species could act as flagship species, driving public awareness on conservation issues of the coastal dunes. Among these, the tortoises (family *Testudinidae*) are the best candidates for coastal dune conservation, as they are charismatic and appealing to the target audience (e.g., EU Life Projects), are often endemic [7], and symbolize the uniqueness of the coastal dunes to foster a sense of local pride [8].

Specifically, we focused on the Hermann's tortoise *T. hermanni* (Gmelin 1789), endemic to the northern

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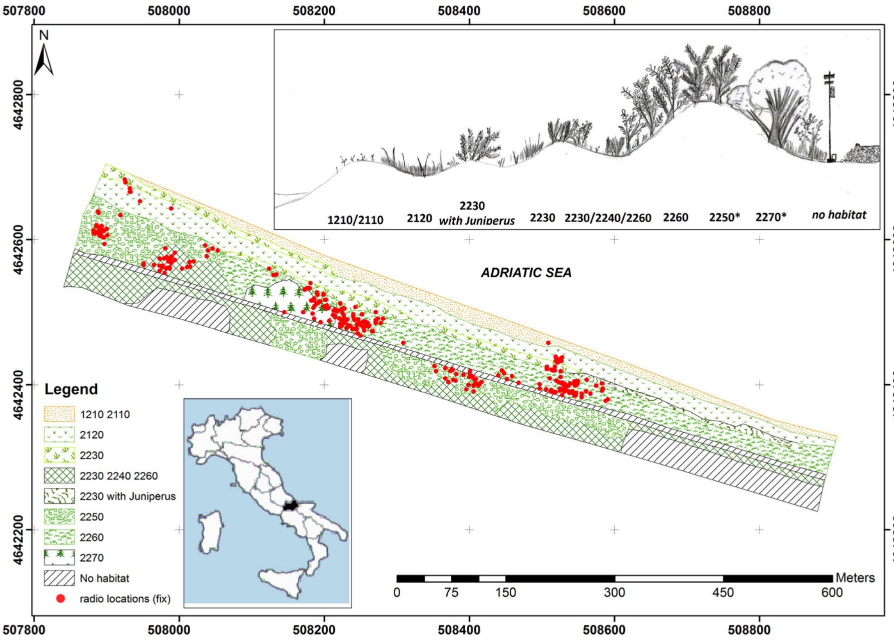


Fig. 1. (Color online.) Detailed vegetation map of the study area and radiolocations. The profile diagram indicates the sequence along the sea inland gradient of the mapped EU habitats. For codes, see Table 1.

coastal Mediterranean region, and the only indigenous species of Testudinidae found in Italy. The subspecies *T. hermanni hermanni* is listed as endangered in the IUCN Red Data Book [6] and is threatened by the degradation and destruction of its habitat, especially in coastal areas [7,9]. This species is strictly protected by the Bern Convention and the European Habitat Directive (92/43 EEC, Annex II, IV), while the international trade of the species is regulated by the Washington Convention (CITES, App. II, C1). It is common in coastal areas of western central Italy; it is less common in the eastern coast and hilly landscapes [7].

The Hermann's tortoise occurs in Italy with two subspecies: *T. h. boettgeri*, mostly found along the northern Adriatic coast, and *T. h. hermanni*, prevailing along the Tyrrhenian coast. Hermann's tortoises are located in the xeric areas of the Mediterranean region, characterized by thermo- and meso-Mediterranean climate [9], mainly in the littoral pinewoods, coastal dunes, Mediterranean scrub, and garrigues [10–13]. Most studies regarding the eco-ethology of *T. hermanni* have been conducted in Spain, southern France [14,15], Greece [16,17], and Italy [18,19].

The habitat preferences of this species have been investigated in a variety of habitats, from coastal dunes [8,20,21] to rural landscapes [22], while habitat preference studies taking into account the seasonal utilization of the different vegetation types are still necessary [23].

In this study, we explored if, how, and when the EU coastal dune habitats (*sensu* Habitats Directive 92/43/CEE) are used by Hermann's tortoises in a well-preserved coastal dune system of the Italian peninsula. Radio telemetry data and fine-scale vegetation habitat mapping were used to address the following questions:

(a) is each EU habitat used differentially by Hermann's tortoises?
(b) is there any seasonal variation in this utilization pattern?
(c) how does each habitat contribute to the ecological requirements of the tortoises?

We assumed that the utilization by tortoises of the EU habitat dune mosaic is not homogeneous, but varies through space and time. By linking the EU coastal habitats to the survival of the flagship Hermann's tortoise, we contribute to the prioritization of the conservation in this fragile and highly vulnerable ecosystem.

2. Method

2.1. Study area

The study area is part of the eastern coast of southern Italy (Molise region, Fig. 1). The Molise coast stretches for 30 km along the Adriatic Sea and is mainly composed of sandy beaches. Recent dunes (Holocene) occupy a narrow strip along the seashore. They are not very high (less than 10 m high) and are relatively simple in structure (usually only one dune ridge) [24]. In the dune profile, abiotic conditions vary greatly, moving along the sea inland gradient. Under natural conditions, the vegetation zonation follows this ecological gradient, ranging from pioneer annual communities on the beach to Mediterranean macchia on the landward fixed dunes [24–26]. The Mediterranean macchia can be considered the most mature vegetation type on fixed dunes. The climate of the area is typically Mediterranean, with dry summers, mild and rainy winters, and frequent precipitation

Table 1
Detailed description of vegetation types along with the relative information concerning EU habitat types, cover (percent of the landscape), vegetation shading capacity (percent of vegetation ground cover), and vascular plants dominant phenology (budding, presence of soft leaves, growing and flowering periods).

Description	EU code	Cover (%)	Shading capacity	Phenology
Annual vegetation of drift lines and embryonic shifting dunes (mosaic)	1210/2110	11.9	3.5	May–June
Shifting dunes along the shoreline with *Ammophila arenaria* (white dunes)	2120	2.22	15	May–June
Dune grasslands of *Malcolmietalia*	2230	4.45	0	April–June
Dune grasslands of *Malcolmietalia* with burned Mediterranean macchia	2230 (with Mediterranean macchia)	2.54	20	April–June
Dune grasslands and sclerophyllous scrubs mosaic: *Malcolmietalia* dune grasslands; *Brachypodietalia* dune grasslands with annuals and *Cisto-Lavanduletalia* dune sclerophyllous scrubs	2230/2240/2260	22.87	40	April–August
Dune sclerophyllous scrubs of *Cisto-Lavanduletalia*	2260	4.94	50	Evergreen
Coastal dunes with *Juniperus macrocarpa* bushes	2250*	22.08	70	Evergreen
Wooded dunes with *Pinus pinea* and/or *Pinus pinaster*	2270*	3.93	80	Evergreen
No habitat		25.07	0	

* EU priority habitats.

[25]. The mean annual temperature is 15.9 °C, the mean minimum temperature is 13.2 °C, the mean maximum temperature is 18.6 °C, and mean precipitation amounts to 356.8 mm/year (Termoli meteorological station, 1971–2000).

Despite the fact that dune vegetation has been severely damaged and reduced along the whole Adriatic coast [26], the coastal dunes of Molise still host many EU Directive 92/43 habitats [27,28]. The study area is included in the SCI IT7222217–Foce Saccione–Bonifica Ramitelli, and is part of the Long-Term Ecological Research Sites (LTER_-EU_IT20_003_T) [29,30].

2.2. Vegetation map

Based on high-resolution panchromatic aerial photographs (dated 2008) and an extensive field survey (Spring 2013), we produced a detailed map at a scale of 1:1000 of the coastal dune habitats in the study area. Particular attention was given to natural dune cover types that, according to Acosta et al. [31] and Malavasi et al. [32], were mapped in nine different types that enclose eight habitats of European conservation interest according to Annex I of the European Council Directive 92/43/EEC (1992, Table 1). All artificial areas were classified as *no habitat*. The vegetation map was verified through several field surveys (performed from 2010 to 2012 using a GPS) and presented a global accuracy of 0.77. For each vegetation, type ecological information, such as shading capacity and vegetation phenology, was also reported. Shading capacity summarizes the plant community physiognomy [5] and differentiates densely vegetated dunes, offering shadowed and cool microhabitats, from open areas, offering sunny hot habitats, all habitats that can help tortoises with thermoregulation activities. Phenology describes budding and flowering periods [33], thus, a temporal supply of trophic resources.

2.3. Radio telemetry

A radiotelemetric study of Hermann's tortoise was performed between October 2012 and January 2014. A total of nine specimens (five males and four females) were captured through visual encounters by random walking across the coastal zonation from the drift line to the foredunes. An ongoing study on the population dynamic indicates that the number of specimens was representative of the whole population of 20 resident individuals/year (personal observations). Tortoises were equipped with a VHF radio transmitter (Very High Frequency, SOPR 2380 Transmitters–Wildlife Materials Inc.). Animals were located by means of a receiver (model R-1000 Telemetry Receiver 148–152 MHz w/220 of the Communications Specialist) connected to a Yagi or Adcock antenna. The tortoises were immediately released at the capture site and were monitored once a day for 7–8 consecutive days from April to October (one radiotelemetric fix location per day). During the hibernation period (from November to March), each animal was located once a month. Each monitoring session lasted 2 h and was shifted during the 7–8 days to cover the whole daily activity period (maximum duration of 15 h).

2.4. Data analysis

According to the most common definition, habitat corresponds to the resources and conditions present in an area that produces occupancy by a given organism [34]. Thus, the aim of habitat selection studies is to identify the environmental characteristics that make a place suitable for a certain species. A series of techniques have been developed for habitat selection, including compositional analysis [35], Jacobs' index [36], and selection ratio [37].

In this paper, habitat selection was performed by comparing the proportion of habitat occupied by *T. hermanni* (p_iTh) with the proportion of available habitat in the entire landscape (p_iL) (i.e. first-order selection) through a bootstrap procedure [37,38]. In particular, to calculate the proportion of habitat occupied by *T. hermanni* (p_iTh) within each habitat type, we overlapped the radiolocations map with a buffer radius of three meters on the habitat type map. We obtained a nine-dimensional habitat type compositional vector for each radiolocation (i.e., the distribution of the area of each fix location within

Table 2
Description of radio tracked tortoises. For each animal, information concerning sex, number of radiolocated points and dates of the first and last radiotelemetric locations are reported.

Tortoise code	Sex	Date of the first location (Day/month/year)	Date of the last location (Day/month/year)	Number of location points
1	M	18/09/2012	9/01/2014	45
2	F	18/09/2012	9/01/2014	44
3	M	19/09/2012	9/01/2014	43
4	M	25/04/2013	9/01/2014	46
5	F	28/04/2013	10/10/2013	22
6	M	28/04/2013	9/01/2014	44
7	M	28/04/2013	9/01/2014	45
8	F	28/04/2013	9/01/2014	45
9	F	26/04/2013	1/05/2013	6

the nine habitats). The choice of this radius was based both on the consideration of the visual field of the tortoises, their movement speed (personal observations), and the scale of the habitat map. Then, a vector of the occupied habitat type composition for the whole study area was obtained as a sum of the single-fix compositional vectors. For a given habitat *i*, p_iTh was calculated as the ratio between the total area occupied by radiolocations in the said habitat and the sum of the single-location compositional vectors (i.e., total area occupied by all the fixes in the whole habitats). Finally, we tested whether the proportional area of a given habitat *i* that has been occupied by *T. hermanni* (p_iTh) is significantly different from the proportional area of the habitat *i* in the entire landscape p_iL. In particular we compared *S*, that is the absolute difference between the occupied and available habitat proportion, $S = |p_iTh - p_iL|$, with SB the bootstrapped value of *S*. $SB = |p_iB - p_iTh|$, where p_iB is the bootstrapped proportional area of a given habitat type (*i*) occupied by *T. hermanni* obtained by resampling with replacement (999 times) the nine-dimensional compositional vectors (see [39] for details).

If the actual value of *S* is sufficiently extreme in comparison to the bootstrap distribution (SB), the null hypothesis (random selection) is rejected. *P* values were computed as the proportion of bootstrapped values SB that were greater than the actual values of *S*. After identifying a habitat for which the null hypothesis was rejected (random selection, $P < 0.05$), we investigated whether a specific habitat was positively ($p_iTh/p_iL > 1$) or negatively ($p_iTh/p_iL < 1$) selected by tortoises [39]. The analysis was performed on pooled data of males and females for the whole activity season (April–October), and for each monthly session.

3. Results

3.1. Vegetation map

The map included eight vegetation types, some of them characterized by a mosaic of EU habitats. Table 1 reports the correspondence of vegetation types with EU habitats and a detailed description in terms of cover, phenology, and shading capacity. The mosaic of dune grasslands and sclerophyllous scrubs (*Malcolmietalia* dune grasslands-cod. 2230, *Brachypodietalia* dune grasslands with annuals-cod. 2240, Cisto-*Lavanduletalia* dune sclerophyllous scrubs-cod. 2260) was the most represented vegetation type, covering 23% of the study area. The least represented type was the shifting dunes along the shoreline with *Ammophila arenaria* (white dunes, cod 2120), which covers 2% of the study area.

Unfortunately, the easternmost sector of the study area was recently burned (July 2007) and vegetation regrowth proceeded fairly slowly. In particular, the large shrubs typical of coastal dunes, such as *Juniperus* sp. bushes (cod. 2250*), have not grown back [40].

3.2. Radio telemetry

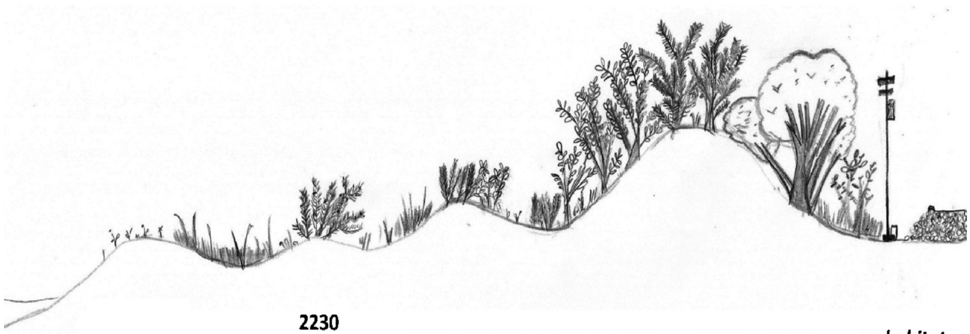
The detailed description of dates and total locations for each of the nine tortoises (five males and four females) are shown in Table 2. Seven of the nine animals were tracked for the entire period of activity, i.e. from the end of hibernation to the new hibernation period and were monitored for at least seven days per month (codes: 1–2–3–4–6–7–8). Two female tortoises were lost after one and three months (codes: 9–5). We obtained a total of 340 radiolocations from October 2012 to January 2014. The distribution of the three buffered locations is shown in Fig. 1. In 2013, all tortoises were active from late April to early July as well as from late August to early November.

3.3. Habitat selection

According to the bootstrap tests, most vegetation types were used differently by *T. hermanni* (Table 3). The results obtained for the entire cycle of activity showed a marked preference for the dune sclerophyllous scrubs (EU cod. 2260), *J. macrocarpa* bushes (EU cod. 2250*), wooded dunes with *Pinus* spp (EU cod. 2270*), and for shifting dunes along the shoreline (EU cod. 2120) (Table 3).

A marked preference for the dune sclerophyllous scrubs (EU cod. 2260) was also evident throughout the activity period, with the only exception of the session run in June, when tortoises selected the annual dune grasslands (EU cod. 2230), the dune grassland and sclerophyllous scrubs mosaics (EU cod. 2230, 2240 and 2260), and the no habitat class. Moreover, we identified a preference for some habitats during specific periods. While shifting dunes along the shoreline (EU cod. 2120) were selected in April,

Table 3
Vegetation types and their degree of selection by the *Testudo hermanni*. For each type (see Table 1 for a description of vegetation), the absolute differences between the occupied and available habitat proportions $S = |piTh - piL|$, and the P values are reported. Values of $piTh/piL$ ratio > 1 indicate a positive selection; values of $piTh/piL$ < 1 indicate negative selection. NS: not significant at P values > 0.05.



	1210/2110	2120	2230 with Juniperus	2230	2230/2240/2260	2260	2250*	2270*	no habitat	
Cycle of seasonal activity (April–October)	0.113	0.019	0.019	0.015	0.125	0.326	0.112	0.05	0.237	S = |piTh – piL|
	< 0.001	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*P values*
	0.04	**1.88**	**0.22**	**0.66**	**0.45**	**7.61**	**1.51**	**2.31**	**0.05**	*piTh/piL* ratio
Session I (April) (16 °C)	0.089	0.072	0.0251	0.003	0.157	0.520	0.117	0.049	0.250	S = |piTh – piL|
	< 0.001	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*<0.001*	*< 0.001*	*P values*
	0.2	**4.2**	**0.009**	**0.9**	**0.312**	**11.5**	**0.466**	**NS**	**0**	*piTh/piL* ratio
Session II (May) (19 °C)	0.119	0.004	0.025	0.014	0.103	0.267	0.169	0.040	0.238	S = |piTh – piL|
	< 0.001	*0.641*	*< 0.001*	*0.574*	*0.009*	*< 0.001*	*< 0.001*	*0.229*	*< 0.001*	*P values*
	0	**NS**	**0**	**N.S.**	**0.54**	**6.402**	**1.765**	**NS**	**0.044**	*piTh/piL* ratio
Session IV (June) (24 °C)	0.119	0.022	0.025	0.370	0.161	0.317	0.241	0.030	0.223	S = |piTh – piL|
	< 0.001	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*< 0.001*	*0.272*	*< 0.001*	*P values*
	0	**0**	**0**	**5.960**	**3.402**	**0.134**	**0.477**	**NS**	**9.502**	*piTh/piL* ratio
Session IV (July) (26 °C)	0.119	0.022	0.051	0.044	0.086	0.303	0.083	0.084	0.250	S = |piTh – piL|
	< 0.001	*< 0.001*	*0.281*	*< 0.001*	*0.187*	*0.001*	*0.297*	*0.206*	*< 0.001*	*P values*
	0	**0**	**NS**	**0**	**NS**	**7.136**	**NS**	**NS**	**0**	*piTh/piL* ratio
Session V (August) (24.4 °C)	0.119	0.034	0.025	0.022	0.114	0.266	0.126	0.087	0.232	S = |piTh – piL|
	< 0.001	*0.309*	*< 0.001*	*0.061*	*0.018*	*0.001*	*0.047*	*0.044*	*< 0.001*	*P values*
	0	**NS**	**0**	**NS**	**0.499**	**6.374**	**1.572**	**3.216**	**0.071**	*piTh/piL* ratio
Session VI (September) (24 °C)										
	0.119	0.006	0.025	0.021	0.08	0.259	0.139	0.063	0.222	
	< 0.001	*0.77*	*< 0.001*	*0.242*	*0.125*	*< 0.001*	*0.017*	*0.141*	*< 0.001*	*P values*
	0	**NS**	**0**	**NS**	**NS**	**6.257**	**1.631**	**NS**	**0.109**	*piTh/piL* ratio
Session VII (October) (22 °C)	0.119	0.073	0.025	0.007	0.123	0.268	0.139	0.044	0.249	S = |piTh – piL|
	< 0.001	*0.075*	*< 0.001*	*0.767*	*0.006*	*< 0.001*	*0.026*	*0.297*	*< 0.001*	*P values*
	0	**NS**	**0**	**NS**	**0.458**	**6.434**	**1.629**	**NS**	**0.002**	*piTh/piL* ratio

J. macrocarpa bushes were selected in May as well as from August to April, and wooded dunes with *Pinus* sp. (EU cod. 2270*) were preferred in August.

Generally, tortoises showed a preference for natural land cover types, as *no habitat* areas were negatively selected in all seasons, with the only exception of the session run in June, when most radiolocations were recorded near the railroad tracks. Another negatively selected vegetation type was the mosaic of annual vegetation of drift lines and embryonic shifting dunes (cod.1210–2110). Finally, wooded dunes with *Pinus* sp. (EU Cod 2270*) were used in proportion to their availability without any significant tendency based on habitat availability (P values > 0.05), with the exception of August, when they were positively selected.

4. Discussion

Radio telemetry and fine-scale habitat mapping provided an accurate framework of habitat preference and avoidance by the Hermann's tortoises in the Adriatic costal dunes, through accurate and replicable selection functions (HSFs).

The habitat preference analysis suggested that the Hermann's tortoises operate both a positive and a negative selection of the different coastal dune vegetation types and that this pattern varies according to the season.

The tortoises used most of the coastal dune EU habitats throughout their activity period, except for those characterized by low shading capacity (code 1210–2110 in Fig. 1) or recent disturbance (e.g. burned). They also avoid artificial and agricultural areas (no EU habitats). Avoidance of the mosaics of annual vegetation of drift lines, embryonic shifting dunes and anthropogenic areas is most likely related to the scarcity of edible herbaceous vegetation and low density of shading plants. These habitats are, in fact, characterized by the prevalence of perennial graminoids with coriaceous leaves [41]. The target species avoided burned juniper macchia (2230 with *Juniperus*), although edible vegetation is expected to increase after fire (new buds and young leafs) [42]. Thus, avoidance could be due to the low availability of shrubs providing shelters against thermic stress and predators.

The most widely used EU habitats were the dune sclerophyllous scrubs (EU cod. 2260) and the *J. macrocarpa* bushes (EU cod. 2250*). These habitats are characterized by evergreen woody vegetation types growing on fixed dunes and quite sheltered from the harsh drift line conditions. Dune sclerophyllous scrubs are located in an intermediate position along the gradient from sea to inland and are characterized by a high richness of herbs and low bushes [24]. These habitats have a medium shading capacity and are rich in herbaceous edible species, thus, they are likely used by tortoises for both feeding and thermoregulation. Similar preferences for clumped shading vegetation alternating with open areas were observed in both *T. hermanni* and *T. graeca* living in rural landscapes [22,43] and in the Tyrrhenian coastal dunes of Tuscany [21]. Our results are also consistent with Blouin-Demers and Weatherhead [44,45], who postulated a general effectiveness of ecotones with patchy vegetation in providing optimal habitats for the thermoregulation of ectothermic species.

The observed seasonal utilization pattern of the different EU habitats by Herman's tortoises may be related to the capacity of each vegetation type to satisfy temporal variations in the thermoregulation, feeding, reproductive and breeding requirements of the species. For instance, the preference for the shifting dunes along the shoreline with *Ammophila arenaria* (2120) in the early spring likely corresponds to the thermoregulation requirements of tortoises at the onset of activity after winter hibernation. Indeed, during the first period of the activity cycle after hibernation, tortoises spend much of their active time basking to reach their optimal temperature [14]. This hypothesis is supported by local climatic data that indicate an average temperature of 16 °C in April, corresponding to the minimum temperature of activation for tortoises [46].

During the early summer, the Hermann's tortoise reaches the maximum peak of its activity [14]. The preference for both annual dune grasslands (cod. 2230) and the mosaic of dune grassland with sclerophyllous scrubs (cod. 2230, 2240 and 2260) in June is likely linked to the various activities performed in this season, such as feeding, egg laying, and mating [14,17].

The need to escape the high summer temperatures at the onset of the pre-estivation phase [14–16,47,48] is the main factor that most likely influenced the exclusive preference for the close vegetation of sclerophyllous scrubs (EU cod. 2260) observed in July. From this period onwards, the open foredune habitats (Eu cod. 1210/2110; 2120; 2230 with *Juniperus*, 2230; 2230/2240/2260) were no longer positively selected due to both the heat and the reduced food availability, as the growing and flowering stages are over and the plants are dry and leathery [41].

The increased need for protection from heat and the reduced metabolism during the estivation phase may explain the exclusive preference for the sclerophyllous scrubs (EU cod. 2260) and the *J. macrocarpa* bushes (EU cod. 2250*) from August onwards. Only during August did tortoises select the wooded dunes (cod. 2270*), most likely in search of coolness provided by the high shading capacity of the pinewoods. Moreover, in the late summer, occasional rainfalls allow the growing of low herbs in the small gaps among the evergreen bushes, providing additional trophic resources within these habitats.

4.1. Final remarks and conservation implications

This work contributed to our knowledge of coastal dune ecological processes and functioning. We focused on the relationships between the flagship species *T. hermanni* and the coastal EU habitats. Our results confirmed that climate and behavioral patterns play a crucial role in habitat use and preference by ectothermic species, especially tortoises [15,16,21,47–51]. Hermann's tortoise broadly selected patchy areas [21] where close vegetation alternates with open areas with a specific seasonal pattern that was assessed here for the first time. The sustainable management of sclerophyllous scrubs (EU cod. 2260) and the *J. macrocarpa* bushes (EU cod. 2250*) may play a predominant role in the conservation of the Hermann's tortoise. Indeed, these habitats could act as a type of "umbrella habitat", as their protection triggers a sort of "chain protection" from the individual habitat to the entire landscape [52].

These habitats should be preserved not only for their intrinsic floristic value [24,27], but also as providers of critical resources for the endangered tortoises. Conservation efforts toward these habitats could benefit from the presence of tortoises as a flagship species that could drive public interest and awareness toward these often neglected vegetation communities [52,53]. In addition, as tortoises are seed dispersers, their conservation contributes to the preservation of local flora [54].

Our analyses also revealed a seasonal utilization pattern of the EU habitats by tortoises across the coastal dune zonation. This temporal pattern is likely related to the specific capacity of each vegetation type to satisfy the thermoregulation, feeding, reproductive and breeding needs in different periods of the year. These outputs stress the importance of preserving the complete sequence of natural dune habitats, whose functionality is ensured by the integrity of its vegetation mosaic [29].

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