Nesting habitat characteristics and predation patterns in the European pond turtle *Emys orbicularis* (L., 1758): Implications for management and conservation measures

Mirko Liuzzo [a],[*], Arianna Spada [a], Chiara Facca [a], Stefano Borella [b], Stefano Malavasi [a]

[a] *Dipartimento di Scienze Ambientali, Informatica e Statistica, Università Ca' Foscari di Venezia, Campus Scientifico, Venezia, Italy*
[b] *WWF Oasi Società Unipersonale, Roma, Italy*

ABSTRACT

Integrating knowledge regarding habitat characteristics and animal behaviour into conservation programs has the potential to impact the results of management and conservation efforts. This study aimed to explore the relationship between spatial and environmental data on the nesting activity of the European pond turtle, *Emys orbicularis*. Additionally, it sought to analyse the abundance, activity pattern, and behaviour of potential nest predators of *E. orbicularis*. Natural predated nests of the European pond turtle were utilized to characterise nesting habitat features, while artificial nests and camera traps were deployed to identify potential predators and their behaviour. Artificial nests and camera traps were established in areas with evidence of track detection or historical observations indicating past instances of nest predation. The nest site distribution of the European pond turtle showed a positive relationship with north-south oriented canals, the presence of vegetative components on embankments (shrubs, grass, emergent vegetation), finer-grained soil components (silt and clay), and soil moisture. Camera trapping of artificial nests revealed mammals (*Meles meles* and *Vulpes vulpes*) and a bird (*Pica pica*) as predators engaging in digging and destroying behaviour. *P. pica* detection was notably higher in mowed vegetation areas. Results indicate that natural nest distribution and predation on artificial nests may be influenced by their distribution concerning human-controlled vegetation and foraging activities of common nest predators. Protecting nesting sites in predator-frequented habitats, combined with landscape management targeting vegetation control along embankments, could mitigate nest predation and enhance hatchling recruitment.

1. Introduction

Currently freshwater chelonians face multiple threats due to their long-term life cycle. Alongside population declines resulting from the destruction and degradation of their wetland habitats, they confront heightened mortality risks from predation, road networks, pollution, non-indigenous species, rising sea levels, genetic fragmentation, and diseases (Agha et al., 2018; Lovich et al., 2018; Vecchioni et al., 2020; Vecchioni et al., 2022). During the first life stage, the survival of eggs and hatchlings is jeopardized by increased

levels of nest predation, a consequence of heightened nest-detection abilities among predators. This heightened ability is often a result of human-induced changes, such as habitat loss and alteration, which lead predators to concentrate their activities on the narrow nesting areas (Mitchell and Klemens, 2000; Prugh et al., 2009).

Wetland-associated species, such as *Emys orbicularis* (L., 1758), commonly known as the European pond turtle, have suffered negative impacts due to the regulation of major rivers and the drainage of marshes and wetlands (e. g., Italy: Bonato et al., 2007; Slovakia: Horváth et al., 2021b; Hungary: Purger et al., 2023). Extreme water flow modification, such as channelization and dam building, is known to have harmful ecological and demographic effects, especially on small, isolated populations, leading to the disruption of the population structure of species and their recovery requires long periods (Anthonysamy et al., 2013; Keevil et al., 2018; Mullin et al., 2020). The alteration of the water flow and terrestrial sedimentation directly affects the egg-laying of *E. orbicularis* and indirectly influences the nesting behaviour of females. Due to the lack of a suitable nesting habitat near the water bodies, juveniles are exposed to higher risks of predation (Tetzlaff et al., 2020). The presence of potential predators, such as mammals or bird's species (Chelazzi et al., 2000; Rössler, 2000; Zuffi, 2000), is generally prevalent within natural and semi-natural environments. It was hypothesized that these predators may impact approximately 75–95 % of undisturbed nesting sites (Rovero and Chelazzi, 1996; Zuffi and Odetti, 1998; Rössler, 2000). For instance, various mammalian species, such as the red fox (*Vulpes vulpes*), renowned for their egg's predation behaviour, engage in burrowing activities on the embankments. In 2017, the predominant egg predation pressure in a protected marshland area of Hungary was exerted by the red fox. Its relative frequency along the embankments bordering the wetland areas was estimated equal to one individual every 2 km (Purger et al., 2023). Moreover, the embankments, serving as linear structures, might act as ecological traps for nesting turtles within that specific vicinity (Battin et al., 2004; Hale and Swearer, 2016).

The presence of *E. orbicularis* and the high rate of predation on the eggs have also been reported in similar habitat along the inland boundaries of the Venice lagoon, the largest Mediterranean lagoon (Beggiato et al., 2019; Liuzzo et al., 2021). However, notwithstanding recent investigations and conservation initiatives leveraging the legal frameworks (e.g., Habitat Directive 92/43/CE, Bern Convention, Ramsar Convention) and ecological strategies (e.g., flagship or sentinel species) that designate this species as a management tool for safeguarding freshwater fauna and habitat (Ficetola et al., 2004; Ottonello et al., 2014; Burkart et al., 2021; Merleau et al., 2024). Up to date, there remains a paucity of clear information concerning the relationship between spatial and environmental data on nesting activity in the European pond turtle. Moreover, the limited published data differ in methodology (Zuffi et al., 2006; Purger et al., 2023). This lack of fundamental ecological knowledge produces an unobjective approach to conservation planning
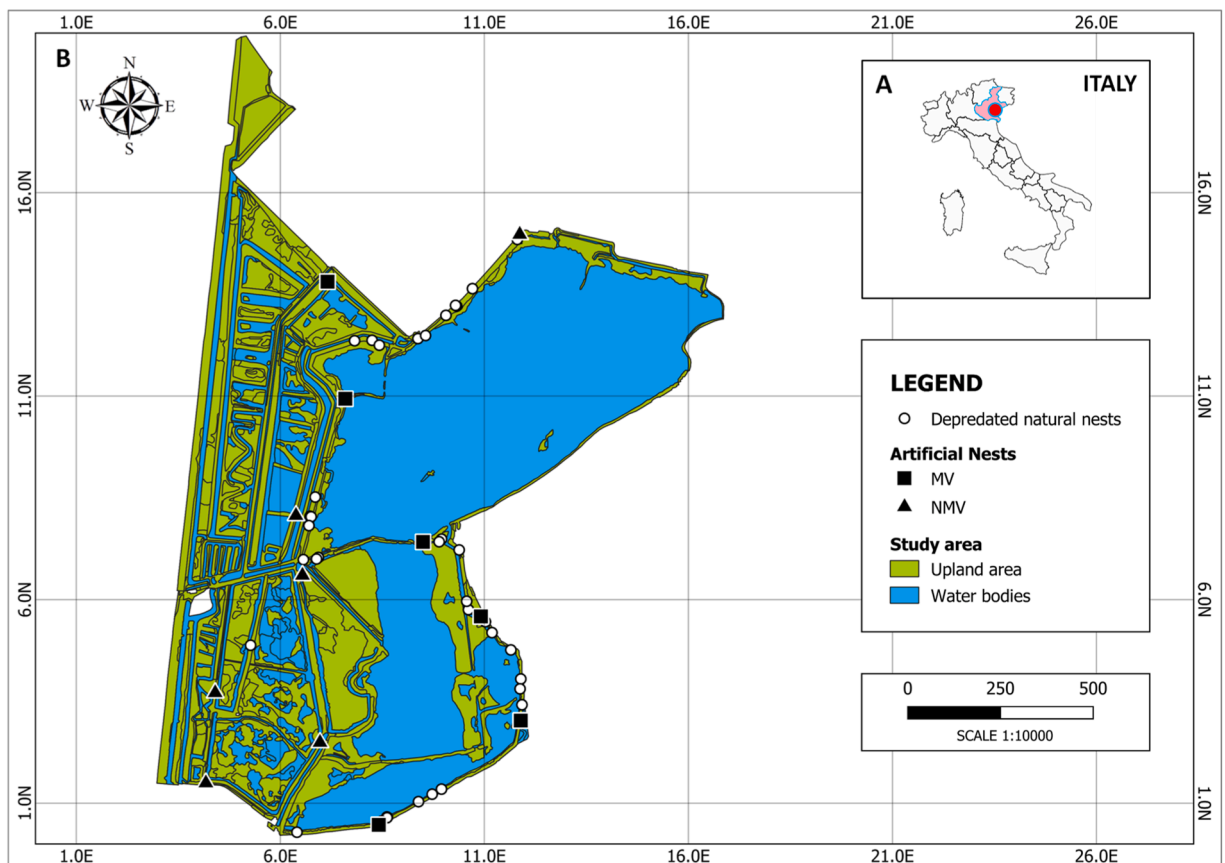

Fig. 1. (A) Geographic locations of the study area within the Veneto region, Italy. (B) Map of study area focused on artificial (black) and depredated natural (white) turtle nests. The artificial nests were placed in Mowed Vegetation (MV, squares), and Non-Mowed Vegetation (NMV, triangles).

strategies. Research programs based on quantitative data and statistical approaches are crucial to better assess environmental management avoiding a potential enhancement of nest-detection abilities among predators of these threatened populations. This research has been planned i) to assess the nest sites distribution and habitat features immediately surrounding the predated *E. orbicularis* nests; ii) to identify nest predators and their behaviour, using camera trapping and artificial nests, and comparing human altered habitat types (i.e., mowed vegetation vs non-mowed vegetation); iii) to provide new data on the ecology and life history of pond turtles to assess opportunities for enhancing habitats for *in-situ* conservation and wetland management efforts.

2. Materials and methods

2.1. Study area

The Valle Averto Oasis is a designated conservation zone situated in the meridional basin of the Venice lagoon, formally established in 1988 and presently under the stewardship of the Italian Association for the World Wildlife Fund (WWF Italy Ong – ONLUS). The site is officially recognized as an internationally relevant wetland under the Ramsar Convention. It is situated within the Special Conservation Area designated for the intermediate and lower reaches of the Venice Lagoon (ZSC IT3250030) and the Special Protection Area covering the entire lagoon basin (ZPS IT3250046) under European Directives (92/43/CE; 2009/147/CE). This Oasis is geographically situated within the municipal boundaries of Campagna Lupia, in the province of Venice, Italy (45°21'N, 12°09'E), encompassing a total expanse of 500 ha. Of this expanse, approximately 78 ha are under the ownership of WWF and encompass emerging lands, freshwater wetlands, two brackish lakes and saltmarshes (Fig. 1). The salinity levels within this area exhibit a dynamic range between 0.5 and 17‰, contingent upon the seasonal variation and proximity to the shoreline, with highest values predominantly during the summertime in the aquatic environments adjacent to the lagoon (Liuzzo et al., 2023). The Valle Averto site is characterised by a blend of natural habitats and an abandoned fishing valley, distinguished by a prevailing flora composition comprising *Phragmites australis* and *Typha latifolia*, along with the *Lolio-Plantaginetea* association within the wetland areas, and the presence of *Nymphaea alba*, *Potamogeton natans*, and *Myriophillum spicatum* in aquatic habitats. The upland section of the area is demarcated by diverse habitat categories, which include linear structures of hedges and tree spots, bushy or herbaceous vegetation with *Rubus ulmifolius* and dense reed vegetation with the association of *Puccinellio festuciformis-Phragmitetum australis* (Padoan and Caniglia, 2004). In this territory framework, the upland area near the embankments is frequented by turtles for travelling and laying their eggs (Liuzzo et al., 2023). The incidence of human presence within the study area is rather scarce, characterised primarily by activities related to habitat conservation and water management (e.g., LIFE18 NAT/IT/001020 Life forestall).

2.2. Characterisation of predated nests

Surveys were conducted between the latter part of May and the latter part of July in 2022 to encompass most of the turtles' nesting season. The research area (Fig. 1) was systematically sampled by visual encounter survey that focused along canals or around lakes where past sightings showed old nest predation event (Liuzzo et al., 2021). Given the limitations on survey effort and the challenge associated with detecting nests that were not predated (e.g., Zuffi et al., 2006; Schindler et al., 2017), only depredated nests were employed to record turtles' nesting activity. Explorations were conducted daily by two observers walking back and forth throughout the entire study site for about 60 days throughout the nesting season. These nest inspections were executed during the hours between 08:00 and 15:00 each day. Nests were categorised as predated when discernible remnants of eggshell were evident on the surface, coupled with indications of excavation. The positioning of nests in relation to primary environmental elements, such as canal boundaries, foliage, or nearby nests, was considered. Given the complexity of the environment, numerous variables were directly

Table 1
Variables recorded at each predated nest (cont, continuous variables; ord, ordinal variables).

Variables (Type)	Units	Code
Week (Ord)	Number of weeks	Week
Nest width (Cont)	Millimeters (mm)	NW
Nest depth (Cont)	Millimeters (mm)	ND
Nest clutch size (Cont)	Number of eggshells	NCS
Soil obscured by vegetation (Ord)	0: 0–25 %; 1: 25–50 %; 2: 50–75 %; 3: 75–100 %	OG
Bare ground/dirt (Ord)	0: 0–25 %; 1: 25–50 %; 2: 50–75 %; 3: 75–100 %	BG
Surrounding grass (Ord)	0: 0–25 %; 1: 25–50 %; 2: 50–75 %; 3: 75–100 %	GRASS
Surrounding shrub (Ord)	0: 0–25 %; 1: 25–50 %; 2: 50–75 %; 3: 75–100 %	SHRUB
Emergent vegetation (Ord)	0: 0–25 %; 1: 25–50 %; 2: 50–75 %; 3: 75–100 %	EM_VEG
Leafy detritus (Ord)	0: 0–25 %; 1: 25–50 %; 2: 50–75 %; 3: 75–100 %	LEAF
Sun exposure (Ord)	0: 0–25 %; 1: 25–50 %; 2: 50–75 %; 3: 75–100 %	SUN_EXPO
Distance to nearest water (Cont)	Meters (m)	WATER
Clay (Cont)	Micrometer (μm)	CLAY
Silt (Cont)	Micrometer (μm)	SILT
Sand (Cont)	Micrometer (μm)	SAND
Soil (Cont)	Millimeters (mm)	SOIL
Soil moisture (Cont)	Percentage (%)	SM
Organic matter (Cont)	Grams (g)	OM

assessed in the field, while the distance to the nearest water body, were inferred through calculations using local topographic maps plotted into QGIS version 3.4.9-Madeira software. For each detecting nest, 14 environmental variables were recorded (Table 1). Soil obscured by vegetation, bare ground/dirt, grasses, shrubs, emergent vegetation, leafy detritus, and sun exposure were extracted as the percentage of approximately 10 m side transversal strip of the embankments that surrounding the nest. The maximum dimensions of the nest chamber pavement, encompassing its width and depth were measured. In addition, the tally of eggs/eggshell and the week collection period were recorded (Table 1).

Eggshells might have broken in the centre or at one end or split into two or even multiple fragments. Single eggs were determined solely by the presence of pairs of halved egg portions (Zuffi et al., 2006. The granulometric analysis of the soil type surrounding depredated nests and the determination of the percentage of organic matter were conducted following the protocols outlined by Loring and Rantala (1992) as well as Allen and Thornley (2004) (refer to supplemental materials).

2.3. Nest predator identification and behaviour

To identify current nest predators, a total of 12 camera traps (Scout Guard BG590-K2–45mHD, Bushnell 30MP Trophy Cam and Bushnell Trophy Cam Aggressor) were distributed at 200–250 m from each other during 390 camera trapping-days (Fig. 1). Camera stations were positioned in areas where historical events of nest predation and the potential presence of predators have been documented or indicated in previous studies (e.g., Liuzzo et al., 2021; unpublished data). In each camera station artificial nests were strategically placed (Fig. 1). In order to minimize the anthropogenic disturbance, and/or to assist the wildlife managers in the management plans for the long-term survival of *E. orbicularis* habitat and populations, the artificial nests were positioned in two distribution patterns: near edge of the water body with Mowed Vegetation (MV) (n = 6) and near edge of the water body with Non-Mowed Vegetation (NMV) (n = 6) (Fig. 1). The control of vegetation (e.g., *Phragmites*) involved cutting at the terrestrial shore by the wildlife managers to maintain the well-trodden tourist paths in the Valle Averto Oasis. The artificial nests were made utilizing a mallet and a perforated iron pipe with a diameter of 10 centimetres. The depth of the chamber ranged from 10 to 13 centimetres, emulating the dimensions of a European pond turtle nest (Novotný et al., 2004; Rogner, 2009; Purger et al., 2012). The turtle-scented water was used as a bait to attract predators. This bait was preferred as it was considered the most effective triggering in the potential predation of the European pond turtle nests (Horváth et al., 2021a; Geller et al., 2022). The camera placement, the housing and spraying of turtle-scented water were performed following the protocol by Horváth et al. (2021a). Specifically, the bait was deployed at intervals of 12 ± 5 days, and the camera traps were checked on 10 ± 5 days cycle.

2.4. Data analysis

2.4.1. Characterisation of predated nests

All considered parameters to assess the nest sites distribution and habitat features immediately surrounding the predated natural nests underwent Shapiro-Wilk tests for normality and were subsequently analysed using either parametric or non-parametric statistical methods. In particular, differences in the allocation of predated natural nests and the number of eggshells on opposite sides of the canal system (North-South (NS) or East-West (ES)) were analysed using a χ^2 test with Yate's correction and the Mann-Whitney U test. Moreover, the Principal Component Analysis (PCA, Lenk and Wüster, 1999) were employed to reduce the quantity of variables associated with depredated nesting habitats. PCA was carried out after Varimax rotation of all the considered variables. Component extraction was conducted on data featuring eigenvalues larger than one, and it was employed to verify the extent to which environmental variables indeed contributed to the description of depredated nesting habitats.

2.4.2. Nest predator identification and behaviour

To identify nest predators, through camera traps on artificial nests, two observers examined all images and videos and annotated all relevant metadata automatically (date, time, etc.) and manually (species, behaviour) into the dataset. The potential predators were

Table 2
Ethogram of behaviours for potential predators observed on the artificial nests indicating the keys behaviours (in grey): fast approach (M2), slow approach (M3), digging the artificial nest (M4) and interaction with artificial nest (U3).

ID	Behaviour	Description	
M1	Passing By	Movements past the artificial nest with no interaction	
M2	Fast Approach	Move rapidly towards the artificial nest without pausing	
M3	Slow Approach	Move slowly and tentatively towards the artificial nest or sprayed turtle-scented water, pausing looking and sniffing around	Mammals
M4	Digging the artificial nest	Destroy the artificial nest by raking	
M5	Marking	Mammalian scent marking in the proximity of the artificial nest	
M6	Other	Any behaviour that deviates from the previously defined-behaviours	
U1	Inspecting	The bird is focused on looking at something. Generally accompanied by walking/hopping with no interaction with the artificial nest	Birds
U2	Feeding	The bird is taking food on the ground	
U3	Interaction with artificial nest	The bird pecks or lay down on the artificial nest	
U4	Other	Any behaviour that deviates from the previously defined-behaviours	

identified using fauna guides (Boitani et al., 2003; Svensson et al., 2012; Paolucci and Bon, 2022) and consultation with experts. All the images collected were processed with dedicated open-access software, Wild.ID (Fegraus and MacCarthy, 2016). The minimum time interval between two independent photographic events was defined as 1 h, thereby largely preventing the scoring of multiple events for images depicting the same individual pausing in front of the camera trap (e.g., O'Brien et al., 2003; Rovero and Spitale, 2016). The camera trapping rate, or Relative Abundance Index (RAI), was calculated for each detected species by dividing the number of photographic events by the sampling effort (camera days) and multiplying the result by 100 (i.e., events per 100 days of camera trapping; e.g., Rovero and Spitale, 2016).

To assess the behaviours of species, videos were recorded and analysed for each interaction with the artificial nest. This assignment followed an ethogram used in previous behavioural studies on nest and burrow (Table 2) (Dziadzio and Smith, 2016; Aya-Cuero et al., 2017; White and Tuberville, 2017).

Individual behavioural events were discerned by a behavioural change in a focal organism. The total number of behavioural events was quantified based on species, behaviour, and distribution patterns (NMV vs MV). The percentages of the number of behaviours were also compared to the total species count. Since not all visits were of equal duration, the time spent by each potential predator was measured across three key behaviours: fast approach, slow approach, digging the artificial nest (for mammals) and interaction with artificial nest (for birds) (Table 2). To assess potential predators, the detection rate was calculated only for species exhibiting key behaviours. Additionally, differences in the detection rate were tested between two distribution patterns (NMV vs MV). The detection rate was inferred by dividing the total count of detections of each species by the total duration of video taken by the camera (detections/hours) in each key behaviours (Parsons et al., 2018; Kays et al., 2020). Significant differences in the detection rate between MV and NMV were tested with the independent samples t Test. Differences in the total duration of digging behaviour in the mammals and birds were also analysed, using the Mann-Whitney U and the Kruskal-Wallis's test.

To estimate the daily activity patterns, only potential predators were selected, defined as such by their nest excavation activity and any documented tracks and signs from past studies or observations (Zuffi et al., 2006; Horváth et al., 2021a; Purger et al., 2023; unpublished data). In line with other similar studies, the approach developed by Ridout and Linkie (2009) was executed to estimate the daily activity patterns of each potential predator involved in three key behaviours, using kernel density analysis (Bu et al., 2016; Ikeda et al., 2016; Porfirio et al., 2016; Marcon et al., 2017; Lazzeri et al., 2022). This is a non-parametric method for assessing the probability density function of a random variable (Worton, 1989), time of capture in the present research. Moreover, the overlap between the two estimated distributions was measured using a coefficient of overlapping Δ, which varies from 0 (no overlap), to 1 (complete overlap) (Ridout and Linkie, 2009). The coefficient was determined as the area under the curve which is generated by selecting the minimum of the two density functions at each time point (Linkie and Ridout, 2011). The Dhat4 estimator was utilized due to the number of samples exceeding 50 (Meredith and Ridout, 2017). The 95 % confidence intervals (CI) of the overlap were obtained by 10, 000 bootstrap samples from the estimated probability density functions of each potential predator. All procedures were implemented in SPSS Statistics 26.0 software and R v. 4.0.2 software (IBM Corp, 2019; Core Team, 2020) with the "overlap" package (Meredith and Ridout, 2014).

Table 3
Rotated Factor matrix: Principal Component Analysis with Varimax rotation to verify which potential environmental variables that may contribute to the description of nesting habitats (above). Eigenvalues and variance of the overall components (below). For interpretation regarding the code variables, please refer to Table 1.

	Component				
	1	**2**	**3**	**4**	**5**
SAND	-0.972				
SILT	0.862				
CLAY	0.726				
SM	0.648				
SUN_EXPO		-0.852			
SHRUB		0.814			
OG		0.779			
WATER			0.796		
SOIL			0.793		
GRASS				0.773	
OM				0.711	
BG					
EM_VEG					0.745
LEAF					
Eigenvalues	3.407	2.627	1.628	1.371	1.302
% of Variance	24.336	18.762	11.629	9.794	9.3
Cumulative %	24.336	43.097	54.726	64.521	73.82

3. Results

3.1. Characterisation of predated nests

A total of 246 predated eggs were obtained from 41 clutches during the 2022 nesting season (Fig. 1). Out of the examined depredated nests, 36.6 % were collected in the week 8–14 June 2022. Predated nests had an average width chamber of 100.8 ± 36.8 mm (range 11–191.5 mm) and a depth chamber of 101.4 ± 27.7 mm (range 59.3–165.1 mm). The average estimation of nest clutch size was 6 ± 1.7 (range 1–9). The number of eggshells and nests differed in the canal orientations, being 109 NS, 61 EW and 20 NS, 10 EW, respectively. Nonetheless, significant differences in the numbers of eggshells were not observed between canal orientation ($W = 96.5$, $P = 0.925$). Conversely, significant differences were detected in their relative distribution ($\chi^2 = 29$, $P < 0.001$). Average untransformed distance to the nearest water body for predated nests was 3.5 ± 2.3 m (range 0.6–8.8 m).

Principal Component Analysis (PCA) revealed that components such as sand, soil moisture, clay, silt, and sun exposure explained more than 70 % of the observed variability in nesting area characteristics (Table 3). The rotated factor matrix suggested that depredated nests were positively associated with silt, clay, soil moisture, shrubs, soil obscured by vegetation, shortest distance to the nearest water source, soil fractions with granulometry greater than 1 mm, percentage of organic matter, percentage of emergent vegetation and negatively related to sand and the percentage of sun exposure (Table 3).

3.2. Nest predator identification and behaviour

The 12 camera traps set gathered 390 camera days (mean per station 32.5). Sampling yielded 891 independent events overall, of which 568 were of birds, 320 of wild mammals and 3 of reptiles. Fourteen species of birds, six of wild mammals and three reptiles were recorded. The checklist (Table S1) matched the expectations based on knowledge of the local fauna, with no species representing new records in the area. The most frequently observed birds were pheasant *Phasianus colchicus* (273 events; 70.00 RAI) and magpie *Pica pica* (198 events; 50.77 RAI). Among mammals, the most common species in the area were in descending order red fox *Vulpes vulpes* (186 events; 47.69 RAI), nutria *Myocastor coypus* (73 events; 18.72 RAI) and badger *Meles meles* (40 events; 10.26 RAI).

The most frequently observed behaviours between mammals and birds were M1 and U1 ($\Sigma_{M1} = 82$, 40.59 %; $\Sigma_{U1} = 219$, 54.48 %), whereas the least recorded behaviours were M5 and U4 ($\Sigma_{M5} = 8$, 3.96 %; $\Sigma_{U4} = 11$, 2.74 %). The key behaviours were documented per 50 % among taxa recorded by video (8 species) (Fig. 2). Specifically, the digging/destroying behaviour of the artificial nest were
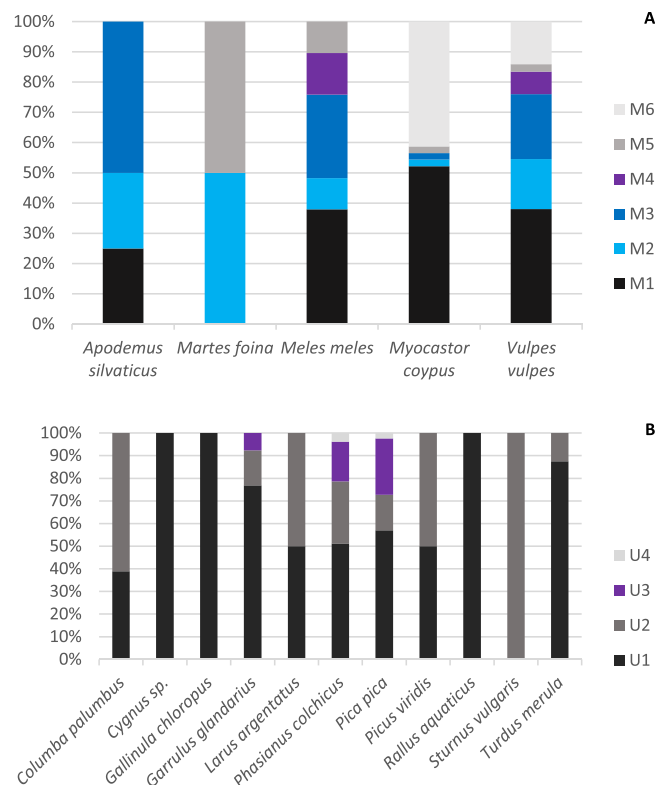

Fig. 2. Percentage variation in the quantity of behaviours between mammals (A) and birds (B) expressed during the nesting period of the European pond turtle (season 2022). Key behaviours have been highlighted with light blue, dark blue, and violet (digging behaviour). For interpretation regarding the legend, please refer to Table 2.

detected in 2 mammals (*M. meles*, *V. vulpes*) and 3 birds (*G. glandarius*, *P. colchicus*, *P. pica*) (Fig. 2). The duration of digging behaviour was significantly different across birds ($K = 34.10$, $P < 0.001$), showing a descending order of *P. colchicus*, *P. pica*, and *G. glandarius*, respectively. Conversely, no significant differences were observed in terms of duration among mammals ($W = 17.5$, $P = 0.864$). Considering the key behaviours, the most represented species for detection rate were *V. vulpes*, *M. meles* for mammals whereas were *P. colchicus* and *P. pica* for birds. Significant differences in detection rate were not observed between MV and NMV for mammals (*V. vulpes*: $t_{5.21} = 1.041$, $P = 0.334$; *M. meles*: $t_8 = 0.388$, $P = 0.708$). On the contrary, significant differences in detection rate were detected between the two distribution patterns for birds (*P. pica*: $t_5 = 5.025$, $P < 0.05$; *P. colchicus*: $t_5 = -21.897$, $P < 0.001$). The frequency of magpie occurrence was higher in MV areas ($t = 5.99$, $P < 0.05$) whereas the pheasant has been significantly more frequent in NMV areas ($t = 22.096$, $P < 0.001$) (Fig. 3).

Taking the day as a 24-h period allows us to illustrate activity patterns through density plots. Among the potential turtle nest predators red foxes and badgers showed an activity pattern predominantly nocturnal, whereas magpie was primarily diurnal (Fig. 4A). Additionally, the two mesocarnivores exhibited a temporary niche with moderate overlap in the *E. orbicularis* egg-laying period ($\Delta_4 = 0.47$, $CI = 0.34$–0.48) (Fig. 4B).

4. Discussion

The present research has significantly contributed to the initial establishment of a relatively comprehensive information repository regarding European pond turtle nesting habitat characteristics and the identification of current nest predators. However, due to the complicated task of identifying intact nests and the diversity of methodologies employed in other studies (Zuffi et al., 2006; Purger et al., 2023), assessing the nesting habitat of *E. orbicularis* is extremely challenging without a sustained sampling effort and a multi-disciplinary approach that is currently not standardized in the field. Therefore, a mix of naturally predated nests of the European pond turtle and artificial nests was utilized to identify current nest predators, describe nesting habitat characteristics, and assess new strategies for predation control in human-altered habitats. These results from artificial nests can replicate the predation pattern of natural nests (Pärt and Wretenberg, 2002). Although this idea has been considered controversial (Burke et al., 2004), it has received support from many authors (Marchand and Litvaitis, 2004; Thompson and Burhans, 2004; Purger et al., 2023).

4.1. Characterisation of predated nests

Our findings highlight that the nesting site distribution in the European pond turtles can be influenced by a combination of factors, including hydrological condition, vegetation cues, sunlight exposure, and substrate quality. These characteristics can serve as indicators of optimal conditions for incubation and can significantly impact nest site success (Wood and Bjorndal, 2000). In line with previous studies female turtles displayed a tendency for nesting sites in proximity to water bodies as opposed to locations selected randomly (Congdon et al., 1987; Marchand and Litvaitis, 2004; Zuffi et al., 2006).

This nesting distribution is a determining factor in the success of embryo's life as increase moisture within the incubation environment. The Principal Component Analysis (PCA) highlighted a discernible pattern wherein finer-grained soil components (such as silt and clay) and soil moisture exhibited a positive correlation with nest positioning. Generally, in moister soil, survival is higher in wetter soils, leading to reduced mortality compared to drier substrates (Cagle et al., 1993; Packard et al., 1987; Packard et al., 1991).
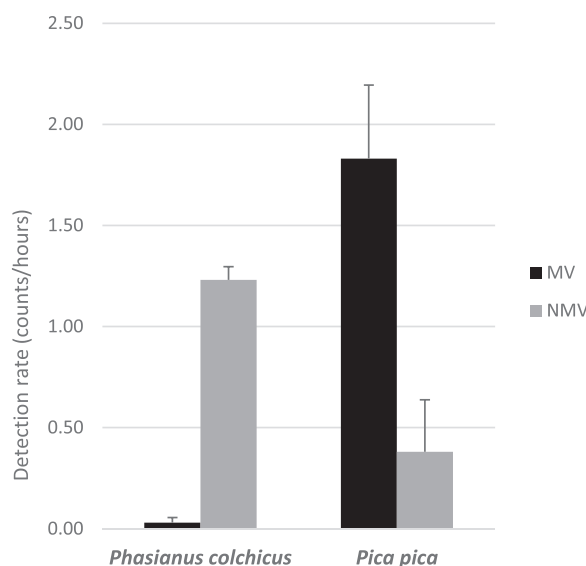

Fig. 3. Mean ($+$ 1 SD) differences in the relative detection rate of bird species detected by camera traps during the exhibition of key behaviours between mowed (MV) and non-mowed habitat type (NMV).
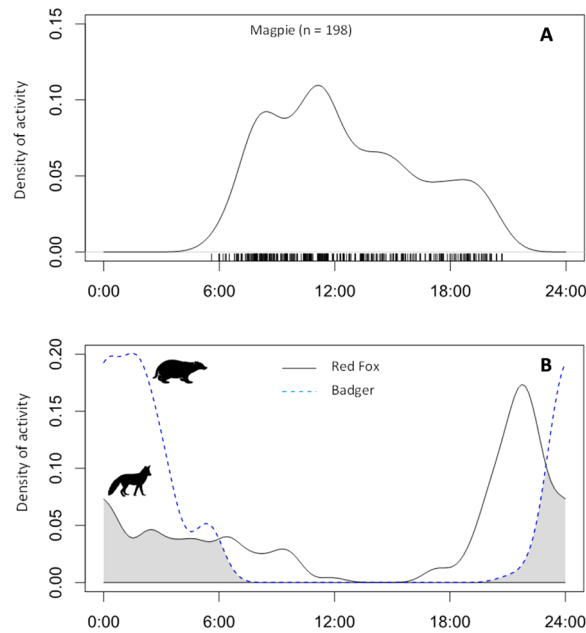
Fig. 4. (A) Kernel density of daily activity of *P. pica*, magpie. (B) Daily activity overlaps estimated between *V. vulpes*, red fox (n = 186) and *M. meles*, badger (n = 40). Coefficient of activity overlap is represented by shaded area.

Moisture levels can also influence the survival of turtles beyond the hatching phase. Increased water potential generally results in amplified egg mass, incubation duration, yolk consumption, and dimensions and weight of hatchlings (Cagle et al., 1993; Packard et al., 1987; Packard et al., 1991). Additionally, the granulometry of the nesting substrate has been verified to have a direct effect on the survival of hatchlings. Finer-grained substrates may create cooler and wetter incubation conditions, whereas coarser grain sizes result in warmer and drier surroundings (Rasmussen and Litzgus, 2010; Tornabene et al., 2018; Mitchell and Janzen, 2019; Saito et al., 2019). The nest sites distribution showed a positive and significant correlation with the presence of organic matter and canopy cover, including surrounding grass, shrub, and emergent vegetation. Organic matter is a feature that influences almost all soil characteristics (Brady and Weil, 2008) and is positively linked to water retention capacity, and therefore, conductivity, especially in sandy soils (Hudson, 1994; Minasny and McBratney, 2018). Previous research has demonstrated reduced survival rates in nesting areas with higher levels of organic material, possibly due to the decreased soil drainage in these sites (Thomasson, 1978; Mui et al., 2015). Our results indicate overall low levels of organic matter on the predated nests, with 100 % of locations containing less than 15 % organic matter, and an average of 11.8 %. Hence, it appears that soil organic matter content is not a constraining factor in terms of its influence on the soil's hydrological properties within the inland water of the Venice lagoon. As observed by Zuffi et al. (2006), in the current study, the distribution of predated nests of the European pond turtle showed a positive relationship with the north-south oriented canals and the presence of vegetative components on the embankments, such as shrubs, grass, and emergent vegetation. Moreover, in the frame of the sampling activities aimed at investigating the depredated nests of *E. orbicularis*, one adult female was observed while laid eggs along the north-south shore of the canals. Conversely, our results deviate from those of Zuffi et al. (2006), as the predated nests were predominantly distributed in areas with soil obscured by vegetation, and they were infrequently found in sunny areas (Table 3). The arrangement of predated nests might be attributed to the behaviour of the predators. At a more localized level, predators tend to concentrate their activity in specific areas where crucial resources for their survival, including prey, water, perches (i.e., magpie), and suitable den sites (i.e., the badger), are abundant. This difference might also result from a sampling bias as sun exposure can be influenced by time of day or by wetland features such as bank morphology (Ficetola et al., 2004). Remarkably, these specific locations also happen to be chosen as nesting sites by turtles, increasing the likelihood of unintended encounters with turtle nests (Vickery et al., in, 1992. Hamilton et al., 2002).

4.2. Nest predator identification and behaviour

Camera trapping has revealed that exclusively two mammals (*M. meles* and *V. vulpes*) and three bird species (*G. glandarius*, *P. colchicus*, and *P. pica*) exhibited digging and destroying behaviour in relation to the artificial nests within the inland basin of the Venice lagoon. The identification of the potential egg predators on the Italian peninsula was deduced by examining the signs left by predators on *E. orbicularis* eggs (e.g., *G. glandarius*, *Corvus corone* (birds), *Rattus* sp., *Microtus* sp. (rodents), *Sus scrofa* (ungulates) and *Mustela nivalis*, *V. vulpes* (carnivores)) (Zuffi et al., 2006). In this study, the badger (*M. meles*), the red fox (*V. vulpes*), and the magpie (*P. pica*) were observed with a preying behaviour on artificial nests. This finding has also been reported in other European nature reserves (Kahlke et al., 2015; Purger et al., 2023). More specifically, three individuals of *P. pica* were sporadically documented (via

videos and photos) engaging in predation upon three natural nests. Notably, this is the first documented instance of such behaviour (Fig. S2A). Although the pheasant (*P. colchicus*) was observed digging up and destroying the artificial nests, no artificial or natural nests were preyed upon in the 273 positive camera events that were examined. It appears that this species utilizes the artificial nest coverage as a substrate for dust-bathing activity (Fig. S2BD). Moreover, the detection rate among predators to verify predation in nesting areas was tested, as has been employed in the management of several threatened species (e.g., Butler et al., 2004; Marchand and Litvaitis, 2004). A significant difference in the detection rate of *P. pica* was observed between two habitat types: MV and NMV. Numerous factors might contribute to variations in corvids' likelihood to prey on turtle nests, including differences in their external environment. Within this context, if the magpie habitat offers less natural concealment for nests, possibly due to extensive and sparse cutting of emergent vegetation, this predator may have a higher probability of detecting and preying on turtle nests. Comparable observations have been documented regarding the predatory activity of *P. pica* on songbird nests (Dunn et al., 2016; Capstick et al., 2019).

The daily activity patterns of the potential nests' predators observed in the Valle Averto Oasis are in line with similar behavioural studies (Obermueller et al., 2021; Lovell et al., 2022). The moderate overlap in the temporal niche between the badger and the red fox observed along the embankments at the artificial nesting sites and historical deposition areas is stimulating (Fig. 4B). Future studies should concentrate on the trophic niche overlap of these animals in areas where a high density of turtles has been confirmed as in this study site. If it's confirmed during the turtle nesting periods, this could highlight an adaptation of these mesocarnivores to feeding on turtle eggs, exerting selective pressure on the recruitment of the juveniles. This might be an additional explanation for the low number of juvenile turtles that are frequently recorded in population structure studies of protected areas (Vamberger and Kos, 2011; Fediras et al., 2017; Romanato et al., 2020; Liuzzo et al., 2021).

4.3. Management and conservation implications

As the European pond turtle is listed in the Habitat Directive 92/43/CE of the European Commission (Annexes II and IV) and in the Bern Convention (Annexe II), it's crucial to identify potential management and conservation measures for the critical life stages of this species inhabiting the inland wetlands of the largest Mediterranean lagoon. Turtles are known to utilize human-altered environments for egg-laying (Joyal et al., 2001; Purger et al., 2023), making them vulnerable to generalist predators. Some researchers have attempted the nest transplantation to reduce predation rates. Specifically, nests were relocated from natural to artificial sites to minimize visual and olfactory cues. Although this approach has shown promise among sea turtles (Stancyk et al., 1980), its use in freshwater turtle species has been limited (Marchand and Litvaitis, 2004). Mesh enclosures have also been employed to protect turtle nests, especially those of rare and/or threatened species like *E. orbicularis*, from predators (Butler and Graham, 1995; Kiviat et al., 2000; Schindler et al., 2017). Despite yielding positive results, these methods may require a considerable economic effort, both in terms of man hour and in the construction mesh enclosures. In contrast, another strategy involves active landscape management, aiming at both controlling tourist use and mitigating the effects of predators. Our research indicates that local environmental modification could potentially reduce nest predation. For instance, controlling vegetation on tourist paths might be particularly advantageous at the local level in areas with limited nesting opportunities and consistently high levels of nest predation, such as the Valle Averto Oasis. To minimize threats to the life cycle of *E. orbicularis*, cutting should occur in early March (before mating activity) and mid-October (after the breeding season). The initial cutting would prevent the presence of bare tourist pathways during the peak egg-laying period, reducing nest detectability by predators like the magpie, while the latter would avoid disturbing brumation and hibernation sites (Thienpont et al., 2004; Liuzzo et al., 2023). Our findings emphasize the importance of nesting site placement. When designing suitable habitats for turtle nesting sites, distribution across the landscape must be assessed. It has been confirmed that nest predation typically increases near the edges of wetlands (within 50 m) and vegetation boundaries (Kolbe and Janzen, 2002; Marchand and Litvaitis, 2004; Strickland et al., 2010; Thompson et al., 2017; Braga-Pereira et al., 2024). Such predation could result in reduced recruitment, potentially impacting population growth, even in healthy populations with high densities (Browne and Hecnar, 2007). Therefore, it's advisable to place nest sites within 50–300 m of wetlands (to minimize predation) and avoid vegetation edges, such as those along tourist paths (Burke and Gibbons, 1995; Semlitsch and Bodie, 2003; present research). The concentration of nests could also influence predation levels, and potential nesting areas should be evenly distributed across the terrain instead of being clustered (Kolbe and Janzen, 2002; Marchand and Litvaitis, 2004). To guarantee optimal recruitment into turtle populations, nesting environments should align with the habitat preferences of turtles (Ficetola et al., 2004; Beggiato et al., 2019; Liuzzo et al., 2023), enhance embryo survival (Cagle et al., 1993), and reduce predation risks (Purger et al., 2023).

CRediT authorship contribution statement

Mirko Liuzzo: Writing – review & editing, Writing – original draft, Visualization, Software, Resources, Methodology, Investigation, Data curation, Conceptualization. **Arianna Spada:** Writing – review & editing, Software, Methodology, Data curation, Conceptualization. **Chiara Facca:** Writing – review & editing, Supervision, Software, Project administration, Methodology, Funding acquisition. **Stefano Borella:** Resources, Project administration, Funding acquisition. **Stefano Malavasi:** Writing – review & editing, Supervision, Project administration, Investigation.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02975.

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