

The importance of aquatic and terrestrial habitat for the European pond turtle (*Emys orbicularis*): implications for conservation planning and management

G.F. Ficetola, E. Padoa-Schioppa, A. Monti, R. Massa, F. De Bernardi, and L. Bottoni

Abstract: The European pond turtle, *Emys orbicularis* (L., 1758), is threatened throughout its distribution, prompting management of habitats and populations for conservation. Quantitative data on habitat requirements for this species are needed to better evaluate which areas are the most suitable, or what actions can improve habitat suitability. We studied relationships between the distribution and abundance of *E. orbicularis* and the environment by analysing water quality and features of 39 wetland and upland habitats in the Po River delta of northern Italy; visual transects and point counts were used to determine turtle presence and relative abundance. *Emys orbicularis* occurs more frequently and abundantly in permanent wetlands surrounded by woodlands, and its presence does not appear to be related to water eutrophication. Woodlands strongly influence adjacent wetland features and may be important for turtles' terrestrial activities such as nesting and dispersal. Habitat management and conservation plans for *E. orbicularis* should include protection of extensive terrestrial woodland habitat containing diverse wetland systems, to support turtle survival at different life-history stages. The requirements for wetlands and natural terrestrial habitat are difficult to meet in the currently human-dominated European lowlands; nevertheless, conservation plans for this species should take a broad-scale approach.

Résumé : La cistude, *Emys orbicularis* (L., 1758), est menacée dans toute son aire de répartition, ce qui a suscité l'aménagement d'habitats et de populas dans un but de conservation. Il nous faut des données quantitatives sur les besoins en habitat de cette espèce afin de mieux évaluer les sites les plus appropriés et les actions qui peuvent rendre les habitats propices. Nous avons étudié la relation entre la répartition et l'abondance d'*E. orbicularis* et le milieu au moyen d'analyses d'eau et de caractérisations de 39 habitats de terres humides et de terres hautes dans le delta du Pô dans le nord de l'Italie; des transects visuels et des décomptes ponctuels nous ont servi à déterminer la présence et l'abondance relative des tortues. *Emys orbicularis* se retrouve plus fréquemment et en plus grand nombre dans les terres humides entourées de boisés et sa présence ne semble pas reliée à l'eutrophisation de l'eau. Les boisés affectent considérablement les caractéristiques des terres humides adjacentes et peuvent être d'importance pour les activités terrestres des tortues, telles que la nidification et la dispersion. L'aménagement des habitats et les plans de conservation d'*E. orbicularis* devraient comprendre la protection de grands habitats terrestres boisés qui contiennent divers réseaux de terres humides, afin de favoriser la survie des tortues aux diverses étapes de leur cycle biologique. Ces besoins en terres humides et en habitats terrestres naturels sont difficiles à satisfaire dans les terres basses d'Europe actuellement dominées par les humains; néanmoins, les plans de conservation pour cette espèce devrait suivre une approche à large échelle.

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Introduction

Many turtle species are of conservation concern worldwide, as they are threatened by human exploitation for food, the pet market, and the shell trade, habitat deterioration and loss, and competition with exotic species (Klemens 2000).

These problems are worsened because turtles have limited capability for rapid demographic recovery after decline, owing to the relatively long time required to attain sexual maturity, the low reproductive output, and high rates of nest predation and juvenile mortality (Iverson 1991; Congdon et al. 1993). Therefore, many turtle species are protected, and

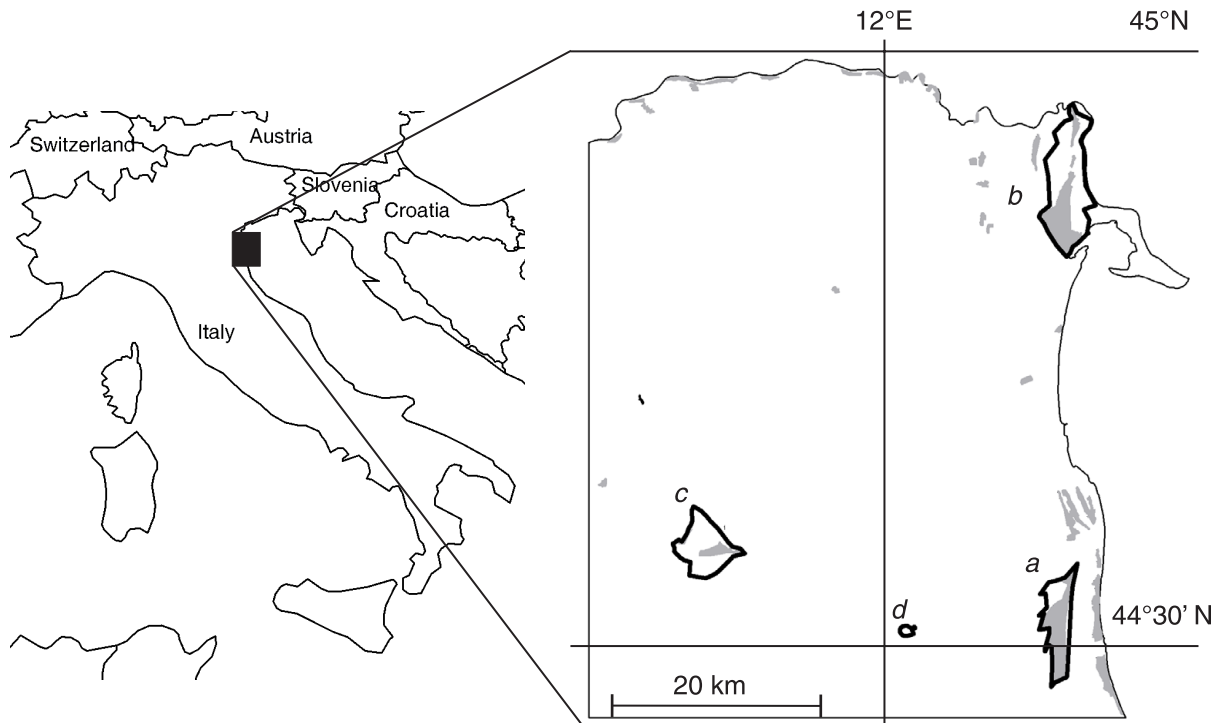
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Fig. 1. Study area in Italy, showing four reserves. (a) Punte Alberete – Valle Mandriole. (b) Bosco della Mesola. (c) Campotto di Argenta. (d) Fornace Violani. Shaded areas are woodlands.



conservation plans are being implemented for some species. However, because financial resources for conservation are intrinsically limited, there is need for improved understanding of turtle ecology to optimize conservation using currently available resources (Dalton 2003).

The European pond turtle, *Emys orbicularis* (L., 1758), has the largest geographic range of any freshwater turtle in Europe, but it has become rare in most of the countries where it occurs. *Emys orbicularis* is rigorously protected in the European Union, and the designation of special areas is required for its conservation (Council Directive 92/43/CEE of 21 May 1992 on the conservation of natural habitats and wild fauna and flora). Thus, there is growing interest in the conservation of this species, as evidenced by several international symposia held in recent years (see Fritz et al. 1998; Buskirk and Servan 2000; Fritz et al. 2002). The decline of *E. orbicularis* is well documented but there is ongoing debate over the causes. The most widely suggested causes include hunting for food; habitat loss due to wetland drainage for agriculture; the declining quality of residual habitats; water pollution; and competition with the introduced North American red-eared slider, *Trachemys scripta elegans* (Wied-Neuwied, 1839) (Schneeweiss et al. 1998; Ballasina and Lopes-Nunes 2000a; Quesada 2000; Cadi and Joly 2003). Conservation actions to counteract the decline of *E. orbicularis*, including recovery of individuals confiscated from poachers, relocation plans, and habitat preservation and management, are ongoing in several European countries (Gariboldi and Zuffi 1994; Delevaud et al. 1998; Ballasina and Lopes-Nunes 2000a; Lacomba and Sancho 2000; Schneider 2000). However, to our knowledge, studies of *E. orbicularis* ecology have dealt with only one or few biotopes at a time, and frequently lack statistical analysis

(Fritz et al. 1998; Buskirk and Servan 2000 and references therein). It is difficult to generalize the results of such studies to obtain conservation indications; thus, it is difficult to evaluate relationships between habitat features and turtle distribution solely on the basis of these analyses. For example, no clear data exist on the relationships between *E. orbicularis* distribution and water quality or the availability of terrestrial habitat, despite the generally acknowledged importance of upland habitat for freshwater turtles (Naulleau 1992; Semlitsch and Bodie 2003).

In the absence of quantitative data on the habitat requirements of *E. orbicularis*, most conservation planners have used "expert judgement" to decide which areas are most suitable for reintroductions, or what management actions should be taken to improve habitat suitability for existing populations (e.g., Ballasina and Lopez-Nunes 2000a; Schneider 2000). However, a more objective approach based on quantitative data and statistical models can provide more accurate management indications (Lecis and Norris 2003 and references therein). In turn, these indications could have value in optimizing conservation efforts by concentrating funding on management areas and improving landscape features that are most important to the species.

We studied the distribution of *E. orbicularis* in the Po River delta, a large protected wetland system in northern Italy (Fig. 1). Our aim was twofold. First, to assess the habitat requirement of the species, we evaluated habitat features related to the presence and abundance of *E. orbicularis* at the regional scale. We monitored turtle presence in a much greater number of biotopes than in previous studies, across more than 3000 ha of protected land. We measured environmental characteristics at the water, wetland, and landscape levels, since influences on turtle distribution could occur at

Table 1. Environmental features measured.

	Code
Wetland surface (m ²)	Area ^a
Maximum water depth (cm)	Wat depth ^a
Water permanence between February and October (yes/no)	Wat perm
Bank slope (mean of 4 measures on north-, south-, east-, and west-facing banks)	Banks
Wetland covered by floating vegetation (%)	Float veg
Presence of deadwood or tree trunks emerging from the wetland surface (yes/no)	Trunk
Sun exposure (%) ^b	Sun expos
Surrounding grass (%) ^b	Grass%
Surrounding scrub (%) ^b	Scrub%
Surrounding trees (%) ^b	Tree%
Wood cover within a radius of 250 m (%) ^b	Wood250m
Presence of <i>Trachemys scripta elegans</i> (yes/no)	Trachemys
Nitrate concentration (mg/L)	Nitrates
Sulphate concentration (µg/L)	Sulphates
Phosphate concentration (µg/L)	Phosphates
Water conductivity (µS)	Conductivity
Macrobenthos (number of taxa)	Macrobenthos

^aVariable was log-transformed prior to analysis.

^bSee the text for a definition.

all three of these levels. Our second aim was to integrate our data with the existing literature on the ecology and life history of pond turtles to evaluate possibilities for improving habitat for in-situ conservation of threatened *E. orbicularis* populations and the habitat requirements that must be met prior to turtle relocations.

Material and methods

Study area

Our study area was located in the Po River Delta Natural Park, one of the most important wetland systems in Italy. In past centuries, the pristine delta was largely reclaimed for agriculture and only a fraction of it remains unconverted. The most natural remnant wetlands, distributed across an agricultural matrix, are protected. We surveyed 39 wetlands in four reserves (Fig. 1): Bosco della Mesola (1922 ha), Campotto di Argenta (1011 ha), Fornace Violani (3 ha), and Punte Alberete – Valle Mandriole (480 ha). All four reserves are partially bordered by the agricultural landscape, and are composed of a complex mosaic of flooded broadleaf forest, mixed coniferous and broadleaf forest, ditches, ponds, swamps, and slow-flowing canals and rivers.

Turtle census

We used visual transects and point counts to assess turtle presence in 39 wetlands (Heyer et al. 1994; Quesada 2000; Joyal et al. 2001). Most censuses were performed by slowly driving a car (5 km/h) around the border of the wetland. Census crews consisted of the driver and one or two observers searching for basking or swimming turtles. If bank morphology did not allow us to perform transects by car, two or three observers walked around the wetland to conduct the survey. In large wetlands we also used a spotting scope (30×) to observe the farthest zones. If a wetland was >250 m across, we restricted our observations to fixed-array point counts of 250 m to reduce the risk of not detecting turtles. We performed transects by car because during preliminary

trials we observed that turtles did not flee even though a car moved near them, possibly because they are accustomed to the passing of vehicles. We performed all transects on sunny days between 0900 and 1500, since during this period 40%–60% of *E. orbicularis* present in wetlands are on basking sites (Cadi and July 2000; Dall'Antonia et al. 2001) and are easily detectable. We conducted census sessions in April, May, and early October (2002), since these are the periods of maximum activity for *E. orbicularis* (Lebboroni and Chelazzi 1991). Each wetland was visited at least once during each census session, and most were visited twice, on different days.

Habitat features

We recorded 17 environmental features for each wetland (Table 1). We collected a 0.5-L water sample from each wetland in April for chemical and physical analysis.

Freshwater turtles feed primarily on aquatic invertebrates, and invertebrate diversity is frequently used as an indicator of freshwater health. Thus, in May we evaluated macrobenthos richness within each wetland. Benthic macroinvertebrates were collected using a long-handled dip net to sample submerged vegetation, banks, and the bottom for at least 3 min. If the bottom was covered mainly by sand or silt, we also collected 1 L of sediment that was subsequently sieved using a series of metal sieves (mesh size 2, 0.5, and 0.25 mm). We stored macrobenthos organisms in 70% ethanol and identified them to the most specific taxon possible using a stereomicroscope.

We recorded morphology (surface, water depth, and bank slope) and vegetation in the field during May; percentages were approximated to the nearest 10%. Vegetation was recorded visually estimating the percent cover in a 30 m wide strip surrounding the wetland. Sun exposure was recorded as the percentage of the entire wetland surface exposed to direct sunlight, measured in June during sunny days between 1100 and 1300. We also recorded the presence of *T. s. elegans*, which has been introduced in many European wetlands and

is a possible competitor of *E. orbicularis*. The percentage of surrounding woodlands within a radius of 250 m was evaluated in the field, and measured with a Geographic Information System (ArcView 3.2) on the basis of 1 : 25 000 maps and CORINE land-cover maps. We chose a radius of 250 m because 150–300 m is the proposed extent of terrestrial buffer zones for amphibians and reptiles (Semlitsch and Bodie 2003). Moreover, we measured woodland cover also at a radius of 100, 500, 1000, 1500, and 2000 m to evaluate the importance of forested habitat at different distances from the wetland.

Assessment of census effectiveness

Our census method was mainly based on observation of basking turtles. Basking behaviour could be influenced by time of day or by wetland features such as bank morphology, sun exposure, or the availability of basking logs (Di Trani and Zuffi 1997; Cadi and Joly 2003). For example, it is possible that in sunny wetlands turtles bask earlier in the day, and are therefore active during the hottest hours, while in shaded wetlands turtles could also bask during the central hours of the day. Such behavioural differences between wetlands could lead to underestimation of turtle presence in sunny wetlands surveyed during the hottest hours, and should be detected from a significant interaction effect between time of survey and sun exposure on turtle observation. To determine if differences in wetland features resulted in differences in timing of basking behaviour, we tested whether interaction between habitat features and time of census caused differences in detectability of turtles. First, we subdivided the census time into three intervals (before the hours of 1100, 1100 to 1300, after 1300) and regarded time as a factor (Hour). Next, we calculated turtle abundance in each survey as (number of basking turtles divided by wetland area). Finally, we used a multifactorial ANOVA to test the effect of month of sampling, hour, bank slope, sun exposure, presence of tree trunks, and the interactions between month of sampling, hour, and these three habitat features (Table 2) on the observed abundance of basking *E. orbicularis* in each survey. For this analysis, we only used data from surveys of the 22 wetlands occupied by *E. orbicularis* (see Results).

Relationship between turtle distribution and habitat

We considered a wetland to be occupied by *E. orbicularis* if we observed at least one individual in one survey. Since pond turtle occurrence did not differ between wetlands in the four reserves (likelihood ratio: $\chi^2 = 1.770$, $df = 3$, $p = 0.621$), all data were pooled for subsequent analysis. We used multiple logistic and linear regression models to relate *E. orbicularis* distribution to environmental variables, testing for multicollinearity using the correlation matrix between variables (Table S1):² if $|r| > 0.7$, the regression may be biased (Berry and Feldman 1985). All correlations with $|r| > 0.7$ involved four variables: sun exposure, grass%, tree%, and woodland%. These variables were strongly correlated (Table S1; wetlands surrounded by woods had low grass

Table 2. Effects of survey month and hour, wetland features, and interactions between them on observed abundance of basking European pond turtles, *Emys orbicularis* (multifactorial ANOVA).

Factor	<i>F</i>	df	<i>p</i>
Month	6.583	2	0.002
Hour	0.677	2	0.511
Month × hour	1.542	3	0.210
Banks	0.928	1	0.338
Sun expos	1.353	1	0.248
Trunk	0.052	1	0.820
Month × banks	5.640	2	0.005
Month × Sun exp	1.131	2	0.328
Month × Trunk	2.417	1	0.124
Hour × Banks	0.295	2	0.745
Hour × Sun exp	0.383	2	0.683
Hour × Trunk	1.011	1	0.317
Error		84	

Note: Significant results are in boldfaced type.

cover, low sun exposure, and high tree cover: $|r| \geq 0.63$ in all pairwise correlations), thus they could not be included together in the analysis. Therefore, prior to logistic and linear regression analyses, we performed a principal components analysis on these variables, and replaced them with the extracted factor(s). Principal components analysis extracted only one component (eigenvalue >1 rule: eigenvalue = 3.215) explaining 80.37% of the variance of the four factors. The extracted factor was negatively correlated with sun exposure ($r = -0.912$) and grass% ($r = -0.894$) and positively correlated with tree% ($r = 0.936$) and woodland% ($r = 0.841$). We called this factor Woodedness and added it to all the models as an environmental characteristic in lieu of the four original factors. After replacement of the collinear variables with the factor Woodedness, no pairwise correlations were ≥ 0.7 .

Logistic regression was used to relate presence/absence of *E. orbicularis* to environmental characteristics. A forward stepwise procedure was used to assess which variable should be added to the model: we used the likelihood ratio to select the variables that further reduced the log-likelihood of the model (Menard 1995), until any new variable did not reduce it by any significant value. A variable was retained in the final model if remove p on the last step was < 0.05 . We used Hosmer and Lemeshow's r^2 (R_L^2) to evaluate the percentage of variance explained by our model (Menard 1995). We inspected residual deviance to check for overdispersion. Since the residual deviance (32.816) was not greater than the residual degrees of freedom (35), data were not overdispersed, suggesting that the error structure was appropriate for the data and the predictors are adequate to describe our data set (Rushton et al. 2004). We calculated *E. orbicularis* abundance in each wetland as a ratio (the maximum number of *E. orbicularis* seen in a wetland at one time divided by the wetland area). We are aware that our estimate of *E. orbicularis* abundance could be inaccurate, since we did not vali-

²Table S1 is available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 3631. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Table 3. Logistic regression model explaining the distribution of *E. orbicularis*.

Term in the model	<i>B</i>	χ^2	Remove <i>p</i>	Model χ^2	Model <i>p</i>	Model R_L^2	Correctly classified (%)
Wat perm	+4.369 (4.043/6.356)	10.408	0.0013				
Woodedness	+2.894 (2.700/4.055)	14.758	0.0001				
Area	+0.795 (0.715/0.990)	8.418	0.0037				
Constant	-8.913 (-11.416/-8.414)			20.607 (df = 3)	0.0001	0.386	74.4

Note: *B* values are logistic regression coefficients; values in parentheses show minimum and maximum *B* values estimated using the jackknife procedure. Correct classification (%) was calculated using the jackknife procedure (df = 1 unless specified).

date it using capture–mark–recapture methods. However, it could be considered a reliable estimate of relative abundance among wetlands. We performed a forward stepwise multiple linear regression on the subset of wetlands occupied by turtles to determine whether environmental characteristics cause variation in turtle abundance among occupied wetlands.

We evaluated the performance of the logistic and linear multiple regression models using a jackknife procedure. Each wetland was removed from the data set in turn, and the model of *E. orbicularis* distribution was evaluated with the remaining data. We calculated the predicted occupancy of the removed wetland using the resulting model parameters. We then compared predicted and observed distributions to evaluate the percentage of wetlands that were correctly classified (logistic regression model) and the relationship between predicted and observed *E. orbicularis* abundances (linear regression model).

To evaluate how much upland habitat is necessary for *E. orbicularis* to be present, we repeated the logistic regression analysis by considering the woodland cover at several distances from the wetland (100, 250, 500, 1000, 1500, and 2000 m). In turn, woodland cover at each of these distances was added to a logistic regression model including as independent variables wetland surface and water permanence (see Results). The importance of woodland cover at these six distances was evaluated as the likelihood ratio of the variable, with the largest value of the likelihood ratio indicating that a variable is more strongly related to turtle presence. In a similar fashion, the importance of each of these six variables for the abundance of *E. orbicularis* was evaluated by using Pearson's correlation coefficient between woodland cover at a given distance and turtle abundance.

We used Cook's distances to evaluate the presence of influential cases in the model (Cook and Weisberg 1982). Since all Cook's distances were <1, we assumed that no influential cases were present in our models. To meet assumptions of residual normality, *E. orbicularis* abundance, wetland area, and water depth were transformed using natural logarithms. All residuals were normally distributed after the transformations.

Results

Twenty-two water bodies (56.4%) were occupied by *E. orbicularis* and 17 (43.6%) were unoccupied. We observed *E. orbicularis* in all four reserve areas. The highest observed abundance was 286 individuals/ha in a small canal (210 m²).

We found a higher abundance of basking turtles in April and May than in October ($F_{[2,84]} = 6.583$, $p = 0.002$), but found no significant differences in basking turtle density in

relation to sampling hour, sun exposure, presence of basking logs, or bank slope (Table 2). We found a significant interaction between bank slope and sampling month: we rarely observed *E. orbicularis* in wetlands with low bank slope in October ($F_{[2,84]} = 5.640$, $p = 0.005$). However, in October we never observed turtles in wetlands where they had not been previously observed, or at higher abundances than previously recorded. We found no significant interaction effects between sampling month and either sun exposure or presence of basking logs, or between sampling hour and any habitat feature (Table 2). Therefore, we assumed that basking behaviour was consistent across wetlands.

Presence of *T. s. elegans*

We observed *T. s. elegans* in only 6 of the 39 wetlands. They were associated with wetlands having a large area (likelihood ratio test: $\chi^2 = 4.431$, df = 1, $p = 0.037$), rich macrobenthos communities ($\chi^2 = 7.124$, df = 1, $p = 0.008$), and low Woodedness ($\chi^2 = 4.071$, df = 1, $p = 0.044$). No pairwise relationships between *T. s. elegans* presence and the other environmental features were significant (all $p > 0.1$). We also found no significant relationship between the presence of *T. s. elegans* and *E. orbicularis* ($\chi^2 = 0.118$, df = 1, $p = 0.732$).

Water characteristics

Wetlands occupied by *E. orbicularis* showed slightly lower mean conductivity than unoccupied wetlands ($t_{37} = 0.218$, $p = 0.036$). Univariate *t* tests showed no differences between occupied and unoccupied wetlands in nitrate, sulphate, or phosphate concentration or in macrobenthos richness (all tests: $p > 0.5$). We observed *E. orbicularis* in wetlands with high concentrations of nitrates (range 66.37–773.93 mg/L), sulphates (2.57–19.22 µg/L), and phosphates (26.55–201.56 µg/L), with a wide range of conductivity (2.03–1388 µS), and with very poor macrobenthos communities.

Presence and abundance of *E. orbicularis*

Emys orbicularis presence was related to water permanence, Woodedness, and wetland area (Table 3). This model suggests that *E. orbicularis* prefers large permanent wetlands surrounded by mature woods, and therefore having low sun exposure and minimal adjacent grass cover. All but two occupied wetlands had permanent water. No physical–chemical wetland characteristics were entered in the model. Using the jackknife procedure, the model correctly predicted *E. orbicularis* distribution in 74.4% of the cases.

Emys orbicularis abundance in occupied wetlands was positively related to water permanence and Woodedness ($F_{[2,19]} = 19.279$, $p < 0.0001$, $r^2 = 0.670$; see Table 4). *Emys*

Fig. 2. Relationship between woodland cover within at 250 m from the wetland and abundance of the European pond turtle, *Emys orbicularis* (log-transformed).

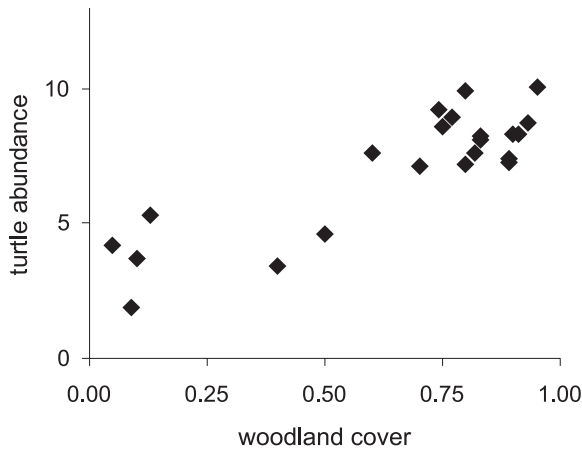


Table 4. Multiple regression model showing the effects of habitat features on the abundance of *E. orbicularis*.

Variable	<i>B</i>	<i>t</i>	<i>p</i>
Woodedness	+1.674 (1.593/1.762)	6.204	<0.0001
Wat perm	+1.962 (1.823/2.112)	2.413	0.026
Constant	+0.885 (0.790/0.973)		

Note: *B* values are multiple regression coefficients; values in parentheses show minimum and maximum *B* values estimated using the jackknife procedure.

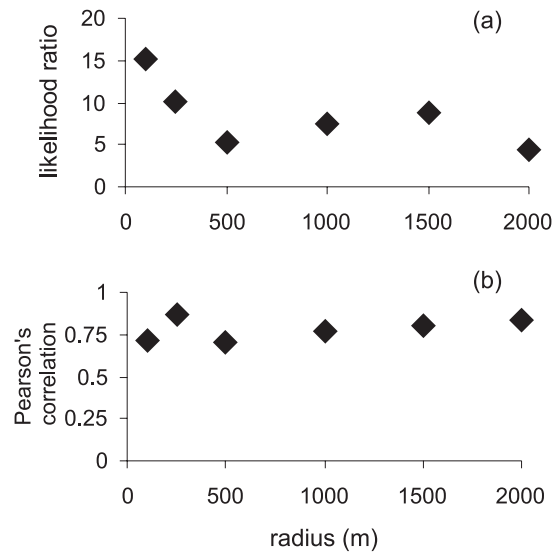
orbicularis abundance predicted using the jackknife procedure was strongly related to observed abundance ($F_{[1,20]} = 31.932, p < 0.0001, r^2 = 0.615$); coefficients calculated using the jackknife procedure were consistent across the overall data set (Table 4). Woodedness seems to be the most important variable in explaining *E. orbicularis* abundance. If used as the sole independent variable in a linear regression model, it explains 57% of variance ($F_{[1,20]} = 26.378, p < 0.0001, r^2 = 0.569$). The highest *E. orbicularis* abundances were observed in wetlands with more than 60% of woodland cover within a radius of 250 m (Fig. 2).

The percentage of woodland cover at all the six distance measured was positively related to the presence and the abundance of *E. orbicularis* (all $p < 0.04$). Woodland cover at the shortest radius (100–250 m) was the most strongly related to turtle presence (likelihood ratio = 15.146 and 10.101, respectively; see Fig. 3a). *Emys orbicularis* presence was strongly related also to woodland cover at a radius of 1500 m (likelihood ratio = 8.871). Woodland cover at a radius of 250 m was the most strongly related to turtle abundance, but strong relationships were observed also for radii of 1000, 1500, and 2000 m (Fig. 3b). All six concentric measures of woodland cover were strongly correlated with each other (in all pairwise correlations, $r \geq 0.720, p < 0.0001$).

Discussion

Our results show that the features of both wetlands and the habitat surrounding wetlands are important for the presence of *E. orbicularis*. Interestingly, the two habitat features

Fig. 3. Relationship between the percentage of woodland cover at six concentric distances from the wetlands and the presence (a) and abundance (b) of *E. orbicularis*. Higher values of the likelihood ratio and Pearson’s correlation indicate that the variable is more strongly related to turtle distribution.



most important for *E. orbicularis* presence in the 39-wetland data set (water permanence and Woodedness) were also the most important for abundance of the species among the subset of 22 occupied wetlands. Therefore, we conclude that these two variables should be considered crucial habitat characteristics for *E. orbicularis* in habitat-management actions aimed at protecting this species. We are aware that our study dealt with only one geographic area and a limited sample of wetlands. However, because the existing literature supports our findings (see below), we believe that our results could be useful for conservation planning across the entire range of *E. orbicularis*. Moreover, our conclusions are strengthened by the observation that the factors related to species presence are also related to species abundance, no cases strongly influenced the models, and all jackknife models yielded very similar results (Tables 3 and 4). Therefore, we assume that our model results are at least partially applicable to other landscapes for assessing *E. orbicularis* conservation plans (see Whittingham et al. 2003). Further research in other landscapes could lead to better understanding of the ecology of *E. orbicularis* across its range.

Habitat requirements of *E. orbicularis*

Water permanence is an important habitat feature for many freshwater turtle species (Bodie et al. 2000); our study confirms its importance for pond turtles (Tables 3, 4). The variable Woodedness, a factor positively related to the percentages of surrounding woodlands and riparian trees and negatively related to the percentages of surrounding grass and wetland sun exposure, has great importance for *E. orbicularis* presence and abundance. This factor depends mainly upon the terrestrial habitat surrounding the wetland, since water bodies surrounded by woodlands are intrinsically shaded. *Emys orbicularis* frequently use upland habitats for many activities (Semlitsch and Bodie 2003). Female turtles sometimes move long distances for egg laying, and can

choose nesting sites several hundred metres from their residential ponds, often in open areas near woodlands (Rovero and Chelazzi 1996; Jablonski and Jablonska 1998; Schneeweiss and Steinhauer 1998; Andreas 2000; Meeske 2000; Utzeri and Serra 2001), likely because the choice of nesting site at both the micro- and the macro-habitat level can be critical for turtle breeding success (Spencer and Thompson 2003). Woodlands surrounding a wetland allow turtles to move relatively long distances and find suitable nesting sites. The presence of woodlands reduces sun exposure during migration, thereby reducing the risk of dehydration, and provides a more open understory that allows easier movement of turtles. A wooded landscape could also be favourable for hatchlings when they move from nest to wetland. Moreover, terrestrial habitat and leaf litter provided by woodlands can be used during aestivation and hibernation (Naulleau 1992; Fritz and Gunther 1996; Utzeri and Serra 2001).

Woodlands are frequently the preferred upland habitat for terrestrial movements (Naulleau 1992). Therefore, we hypothesize that a more natural, wooded terrestrial landscape increases connectivity between wetlands, allows greater movement of individuals among populations and the existence of a metapopulation, and therefore enhances the likelihood of long-term *E. orbicularis* persistence in the landscape (Bennett 1999; Joly et al. 2001; Ficetola and De Bernardi 2004). Finally, the environment surrounding wetlands strongly influences the aquatic habitat. For example, the presence of trunks and dead wood in wetlands is positively associated with Woodedness (likelihood ratio: $\chi^2 = 22.473$, $df = 1$, $p < 0.0001$), and is very important for turtles. The presence of tree trunks favours aerial basking (Cadi and Joly 2003), and dead wood in the water can be used as shelter or as a source of prey (Meeske 2000).

We observed *E. orbicularis* in wetlands with high concentrations of nitrates and phosphates and with poor macrobenthos communities, which indicates that this species can also live in eutrophic water. Studies of other freshwater turtle species have shown that they also can survive in water with high levels of organic pollution (Souza and Abe 2000). Therefore, water eutrophication does not appear to be limiting factor for the presence of *E. orbicularis*. However, it is possible that chemical pollution has contributed to the decline of this species in disturbed landscapes; further studies are required to test this hypothesis. The absence of *E. orbicularis* from the wetlands with highest conductivity ($>1400 \mu\text{S}$) is likely caused by the presence of brackish water in these wetlands, which are near the coast.

Management implications

By integrating our results with data from the literature, we are able to make several suggestions for use in plans for managing *E. orbicularis* habitat. First of all, to ensure the persistence of this species, it is important to preserve large areas of natural habitat, including both wetland and terrestrial habitat. Scientists and conservation planners have frequently overlooked the importance of upland habitat for semi-aquatic vertebrates (Gibbons 2003). Several recent studies outline the pivotal role of the terrestrial environment, not only in the protection of water resources and aquatic

ecosystems (Kiffney et al. 2003 and references therein), but also in permitting several critical life-history functions of semi-aquatic species, allowing long-term survival of populations (Burke and Gibbons 1995; Nolet and Rosell 1998; Joyal et al. 2001; Gibbons 2003; Semlitsch and Bodie 2003; Schabetsberger et al. 2004). 250–300 m has been reported as the buffer zone encompassing most terrestrial activity for many freshwater turtles (Burke and Gibbons 1995; Semlitsch and Bodie 2003). However, we showed that *E. orbicularis* presence and abundance are also strongly related to woodland cover at larger radii. Our data do not allow us to unambiguously evaluate how much terrestrial habitat is enough for *E. orbicularis*, since all the six measures of woodland cover are strongly intercorrelated and not independent. Furthermore, *E. orbicularis* frequently moves 1000–2000 m or more from wetlands during terrestrial activities (e.g., a distance of over 4 km is reported by Jablonski and Jablonska 1998), distances much greater than those recorded for many other freshwater turtles (see data on 28 turtle species reported by Semlitsch and Bodie 2003). Thus, the extent of terrestrial buffer zones proposed for other turtles species may not be adequate for *E. orbicularis*; we suggest protecting a terrestrial area extending at least 1000–1500 m from wetlands. Ideally this area should include open areas with soft soil and good sun exposure (i.e., south-facing slopes) for nesting (Rovero and Chelazzi 1996; Schneeweiss et al. 1998; Andreas 2000; Ballasina and Lopez-Nunes 2000b; Chelazzi et al. 2000).

Moreover, turtles at different life-history stages may utilize different types of wetlands. For example, hatchlings require shallower wetlands than adults do, to avoid the risk of drowning; temporary wetlands may be used for hibernation; ditches and ponds can be used during migration as stepping stones or to move across the landscape (Rovero and Chelazzi 1996; Schneeweiss and Steinhauer 1998; Andreas 2000; Rossler 2000; Utzeri and Serra 2001). Therefore, the presence of a protected complex system of water bodies as well as upland habitat should be ensured for *E. orbicularis* to persist, with some large permanent wetlands to support the aquatic life of adults, and smaller and (or) semipermanent wetlands for other life-history stages. The presence of multiple wetlands could also facilitate the existence of metapopulations, thus increasing the likelihood of long-term survival of populations (Hanski and Gilpin 1997).

At the wetland level, one useful and relatively inexpensive way of improving habitat for freshwater turtles is to provide basking logs, such as tree trunks and dead wood (Spinks et al. 2003). Because the presence of mature woodlands in uplands surrounding wetlands naturally leads to wood falling into the water, from a long-term wetland-management perspective, priority should be placed on upland habitat preservation.

We did not analyse the effects of shoreline vegetation because in almost all the analysed wetlands it was quite abundant, covering 75%–100% of the banks. However, several studies describe the importance of shoreline vegetation to *E. orbicularis*: it provides shelter, abundant food items, and easier access to upland habitat than is allowed by steeply sloping bare banks (Lebboroni and Chelazzi 1991; Andreas 2000; Meeske 2000). Therefore, for the improvement of tur-

the habitat suitability in wetlands, another important goal is to ensure the presence of natural banks with abundant vegetation.

Trachemys scripta elegans were not abundant in our study area, probably because human exploitation of this area remains low. Therefore, *T. s. elegans* are limited to wetlands surrounded by the most human-modified landscapes (i.e., areas with low Woodedness), and we did not observe a negative effect of the presence of *T. s. elegans* on *E. orbicularis*. However, in many areas in Europe, *T. s. elegans* is now much more common than *E. orbicularis*, and this introduced species can successfully compete with *E. orbicularis* for basking sites and other resources (Arvy and Servan 1998; Cadi and Joly 2003). The problem of competition between *E. orbicularis* and *T. s. elegans* could become more severe in the future because new *T. s. elegans* continue to be released in natural wetlands, and because some populations of introduced *T. s. elegans* breed successfully in southern Europe. Therefore, *T. s. elegans* should be removed immediately from all wetlands, to avoid further cases of acclimatization and competition with the native fauna (Martínez-Silvestre et al. 1997; Quesada 2000; Cadi and Joly 2003; Ficetola et al. 2003).

Our study suggests that habitat-management plans for *E. orbicularis* conservation should protect many features of wetlands and the landscapes surrounding them. The habitat requirements of this species are not easily satisfied in the now human-dominated lowlands of Europe that were once pristine *E. orbicularis* habitat. In particular, this species requires relatively large wetlands and (or) wetland systems for different life-history stages, and quite large, natural, wooded terrestrial habitats to allow interwetland movements, reproduction, and other terrestrial activity. Therefore, conservation plans for *E. orbicularis* should focus not only on wetland features but also on features of upland habitat surrounding wetlands. Planning should take a broad "landscape level approach" (Joyal et al. 2001) to allow population persistence, and also a long-term approach, since these animals have a long generation time and require many years for demographic growth.

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