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Demographics and Survivorship in the European Pond Turtle (*Emys orbicularis*): a 31–Year Study

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Abstract.—**Two populations of the European Pond Turtle (*Emys orbicularis*) separated by a distance of 4 km were studied in the tributaries of the Tordera River in northeast Spain. One population was observed from 1987–2018 (Zone 1) and the other from 2008–2018 (Zone 2). We captured turtles using baited funnel traps and we marked turtles individually. We used capture-recapture and radio-tracking techniques to determine population structure and dispersal movements. The sex ratio favored females in Zone 1 (males/males + females = 0.25) and males in Zone 2 (males/males + females = 0.57). The sex ratio remained stable for 21 y in Zone 1. Using a capture-recapture model, we found a high probability of turtle survival in Zone 1 and 2 (females 0.91–0.92; males 0.84–0.86). The population growth is fundamentally supported by a low adult mortality in both zones. We estimated the adult population size as 148 in Zone 1 and 155 in Zone 2. In Zone 1, we recaptured one female 31 y after being first marked and one male and another four females after 30 y. The recaptured turtles showed an important fidelity to the capture sites, and only 19% of the females and 30% of the males moved between successive recaptures. The mean displacement distances were 0.09 km for females and 0.15 km for males**.

Key Words.—capture-recapture; Emydidae; long-term study; population size; radio-tracking

Introduction

The European Pond Turtle (*Emys orbicularis*) is one of three species of native freshwater turtles found in Europe and occupies a wide geographical region (Speybroeck et al. 2016). Despite this, in Western Europe, a large part of the population is fragmented, has a low number of individuals, or has become extinct in some countries (Hofer 2001; Keller and Andreu 2002; Vamberger and Fritz 2018). This species shows high longevity, estimated to reach or exceed 50 y (Gibbons 1987; Schneeweiss 2004); however, previous studies carried out in Europe encompassed comparatively short periods of time: e.g., Cordero-Rivera and Ayres (2004) in Galicia, northwest Spain (6 y); Mitrus and Zemanek (2004) in central Poland (13 y); Schneeweiss (2004) in northeast Germany (8 y); Mazzotti (1995) in northeast Italy (3 y); and Vamberger and Kos (2011) and Vamberger et al. (2017) in central Slovenia (2 y). Although studies of this type could be suitable to evaluate the population structure at a single time point, they are clearly insufficient to evaluate demographic trends in long-lived species. Long-term studies have been carried out with other turtle species, involving study periods between 20 and 38 y (Wilbur 1975; Stickel 1978; Williams and Parker 1987). These long-term studies allow the evaluation of temporal fluctuations in turtle populations and have important implications for conservation, such as detecting factors that could negatively influence survival (Stickel 1978; Williams and Parker 1987).

We analyzed a temporal series of data obtained over 31–y in the upper Tordera River system. We used capture-recapture and radio-tracking methods to study population structure, dispersal patterns, and survivorship. This population is considered the most important for the species in the northeast of Spain given the population size and the expanse it occupies (Mascort and Budó 2017); however, it could be threatened due to the loss of habitat quality and the increasing presence of invasive species in the fluvial systems of the region (Escoriza 2018). We measured several population parameters collected from 1987–2018 and placed special emphasis on survival rates and population size trends, which are difficult to discern from short-term studies. These analyses allowed us to estimate demographics and patterns of space use to define better management and conservation strategies for this regionally threatened species.

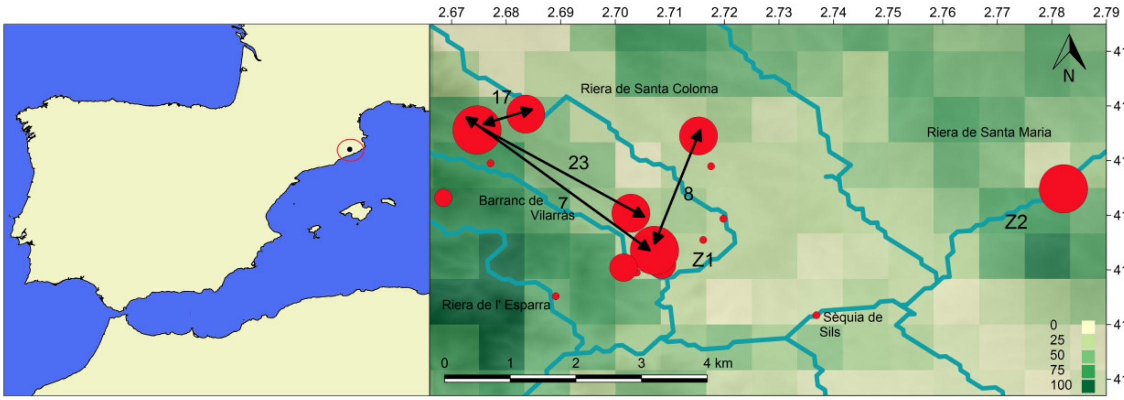

Figure 1. Map of the study area in Spain, showing the main hydrographic network (blue lines), sampling points (red circles, size is proportional to the number of specimens found) and dispersal movements (black bidirectional arrows, numbers indicate the number of dispersion events greater than five). The green background represents forest cover per km^2 according to Tuanmu and Jetz (2014). The abbreviations Z1 = Zone 1 and Z2 = Zone 2.

Materials and Methods

Study area.—The study area included the Riera de Santa Coloma and its tributaries: Riera de Santa Maria, Riera de l'Esparra, and Sèquia de Sils. This network of intermittent streams flows into the Tordera River (Riba et al. 1980). The climate of the basin is Mediterranean (Csa; Köppen-Geiger classification), with an average annual temperature of 15.5º C and average accumulated rainfall of 741 mm y–1. The landscape consists of forest patches (mean cover = 39.7% km^2; Tuanmu and Jetz 2014) alternating with fields and small villages. In the Girona area, *E. orbicularis* occurs in small and isolated populations, with the population of the Riera de Santa Coloma completely isolated (Mascort and Budó 2017).

In the study area, *E. orbicularis* occurs in two disjunct populations: one occupies a system of permanent and temporary ponds structured around several seasonal streams (Riera de Santa Coloma, Barranc de Vilarràs, and Riera de l'Esparra; hereafter Zone 1) and the other in the Riera de Santa Maria and Sèquia de Sils (Zone 2; Fig. 1). These two zones are geographically separated by 4 km (Fig. 1); therefore, they were studied as independent units because this range of distance is only covered rarely by this turtle (Gariboldi and Zuffi 1994; Mitrus and Zemanek 2004).

Sampling procedures.—We captured turtles using nets and floating baited net traps (110 × 50 cm; McDiarmid et al. 2012). We placed the traps in all available types of aquatic habitats including permanent (natural and artificial) ponds, temporary ponds, and seasonal streams. Depending on the size of the aquatic habitat, we placed one to five traps separated by 10 m at each station. We conducted surveys between 1987 and 2018 in Zone 1 and between 2008 and 2018 in Zone 2; however, sampling could not be carried out continuously throughout this period for reasons unrelated to the design of the study. In 1995, 2001, and 2004, we did not sample Zone 1, and in 2010, 2013, and 2014, we did not sample Zone 2. We performed surveys twice a year in spring (April-June) and early autumn (October), coinciding with the periods of maximum activity of *E. orbicularis* (Ramos et al. 2009). We marked turtles using unique combinations of holes drilled in the marginal scutes of the carapace (Plummer 1979). Once the pattern was established, we determined the sex of a turtle and measured total carapace length. We determined sex of adult individuals based on external dimorphic traits, such as plastron morphology, color of the irises and the head, relative size of the tail, and the presence of a precloaca (Zuffi and Gariboldi 1995), although we did not determine sex of turtles from 1987–1997. We classified most individuals that did not show secondary sexual traits and with an axial carapace length of < 103 mm as juveniles (Mazzotti 1995; Ramos et al. 2009). After handling, all the captured turtles were released at the capture spot.

Additionally, we assessed terrestrial movement by radio-tracking the specimens in Zone 1. We attached radio tags (model TW3 10/28 and TW4 Ag 391/357; Biotrack Ltd., Wareham, UK) to the carapace of 11 individuals (two juveniles, seven females, and two males). The weight of the radio tags represented 2–4% of the weight of the individuals. We determined the location of a turtle by triangulation, and we followed individuals for 12 mo (autumn 1999 to autumn 2000), taking one location per month.

Data analyses.—We evaluated demographic parameters based on capture-recapture methods (Mazzotti 1995) and dispersal patterns based on the distances covered between successive recaptures

(Gariboldi and Zuffi 1994). Demographic parameters included indexes directly calculated from the recapture data (sex ratio and relative frequency of population groups: females, males, and juveniles) and other data derived from statistical models. We calculated sex ratio as the relative male proportion (male/male + females), following similar studies in Spain (Keller 1997; Cordero-Rivera and Ayres 2004). To assess whether the sex proportion differed from parity, we used a Single Proportion test (Julious 2005). This test evaluated whether an observed proportion differed from a theoretical one and determined statistical significance on the basis of the sample size (Julious 2005). Differences in the proportion of females and males between the two study zones were estimated by a Chi-square test. The range of sizes according to population groups was visualized by violin plots using the package PAST v3.26 (Hammer et al. 2001).

We used a Pradel model to analyze the capture-recapture data (Pradel 1996). This population model assumed that the size of the study area remains constant throughout time and the probability of capture was equivalent among the different individuals that constitute the target population, that the marking code is correctly identified, and that the life trajectory of individuals is independent (Williams et al. 2002). We performed the analysis independently for the two study zones. The Pradel model allows estimating several demographic parameters: the probability of capture (p) for each capture episode, the apparent probability of survival (phi) and the seniority probability between subsequent capture episodes (γ). The seniority probability is the probability that a specimen present at the capture event i +1 was already present in the population at the immediate capture event i (Pradel 1996). If $\gamma > 0.5$, adult survivorship is the factor that contributes most to population growth (Nichols et al. 2000). The model estimated these parameters depending on a sampling occasion (t) or along the entire sampling period (.). The best model fitting our data was determined using the Akaike Information Criterion corrected for small sample sizes (White and Burnham 1999). Population size (N) was calculated based on the formula N = n/p, where n is the number of specimens captured during a particular sampling period, and p is the probability of capture (White and Burnham 1999). We used the package MARK v9.0 (White and Burnham 1999) to analyze these data.

We also evaluated dispersal movements in Zone 1 (Fig. 1) based on the distances covered per year: $\Sigma d / t$ (Gariboldi and Zuffi 1994), where d is the distance (km) and t the recapture interval (years). We calculated the distances between different points of recapture from geodetic coordinates using the Great Circle Distance Method (WGS84 ellipsoid). We estimated the differences in the proportion of sexes that dispersed by a Chi-square test, and in the covered distances per year by a Mann-Whitney test, after evaluating that this variable is not normally distributed. We set the alpha level at 0.05 and made these calculations using the package sp (Pebesma et al. 2018) in R (R Development Core Team 2018).

Table 1. Survey and demographic statistics (mean and standard deviation) of the European Pond Turtle (*Emys orbicularis*) in Riera de Santa Coloma (Girona, north-eastern Spain). Variables are Total unique specimens = total of specimens marked during the sampling period and Specimens year–1 = mean number of specimens captured per year. Interzone dispersal is the percentage of unique specimens that migrated from Zone 1 to Zone 2 (first box) and from Zone 2 to Zone 1 (second box). Sex ratio year–1 is the mean sex ratio (males/males+females) per year. Group year–1 is the mean relative frequency (group/total captures) per year. The total of specimens marked of the Mediterranean Stripe-necked Terrapin (*Mauremys leprosa*) and the Red-eared Slider (*Trachemys scripta*) is also shown.

	Zone 1	Zone 2
Survey period	1987–2018	2008–2018
Surveyed years	28	7
Total captures	2348	433
Total unique specimens	517	253
Specimens year^{-1}	52.8 ± 30.7	46.0 ± 20.6
Interzone dispersal	0.58%	0.00%
Sex ratio year^{-1}	0.25 ± 0.07	0.57 ± 0.19
Females year^{-1} (%)	58.90 ± 11.43	36.52 ± 14.65
Males year^{-1} (%)	19.75 ± 7.95	52.11 ± 20.91
Juveniles year^{-1} (%)	21.18 ± 16.41	11.37 ± 10.42
Mauremys leprosa	9	37
Trachemys scripta	0	4

Results

We captured 770 unique turtles, with 517 in Zone 1 and 253 in Zone 2. We also found two other species of freshwater turtles: the native Mediterranean Stripe-necked Terrapin (*Mauremys leprosa*) and the invasive Red-eared Slider (*Trachemys scripta*; Table 1). Recaptures indicated that interzone dispersal was rare and unidirectional (from Zone 1 to Zone 2), involving 0.58% of the total specimens in Zone 1 (Table 1). Therefore, both zones, as expected, can be considered independent populations.

The sex ratio significantly favored females in Zone 1 (mean = 0.25; range, 0.08–0.38) most years, except in 2003, 2015, and 2016 (Tables 1, 2). The sex ratio favored males in Zone 2 (mean = 0.58; range, 0.31–0.78) but only differed significantly between 2015 and 2018 (Tables 1, 2). There were significant differences in the sex ratio between Zone 1 and Zone 2 in 2008 (χ^2 =10.05, df = 1, P = 0.004), 2011 (χ^2 = 8.23, df = 1, P = 0.005), 2015 (χ^2 = 32.12, df = 1, P < 0.001), 2016 (χ^2 =

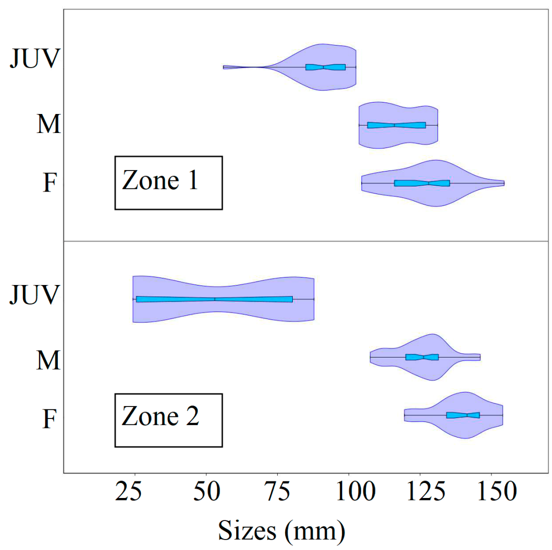

Figure 2. Violin density-plot (from the minimum to the maximum value) showing the population structure of the European Pond Turtle (*Emys orbicularis*) in Riera de Santa Coloma (Girona, north-eastern Spain). The plots show the two studied zones (2017 period) and the range of sizes (carapace length). The box plot represented the 95% confidence interval for the mean. Abbreviations are F = females, M = males, and JUV = juveniles.

35.99, df = 1, $P < 0.001$), 2017 ($\chi^2 = 36.98$, df = 1, $P < 0.001$) and 2018 ($\chi^2 = 29.17$, df = 1, $P < 0.001$). In Zone 1, juveniles accounted for 21.18% of the specimens, and in Zone 2, they accounted for 11.37% of the specimens (Table 1). We found that females can attain larger sizes than males, in the two zones evaluated (Fig. 2). The mean carapace length of the adult males in Zone 1 was 115. 2 mm ± 1.4 standard error (maximum size 145.7 mm) and in Zone 2 was 126.4 mm ± 1.2 (maximum size 196.4 mm) and of the females in Zone 1 was 127.4 mm ± 1.0 (maximum size 174.0 mm) and in Zone 2 was 134.5 mm ± 2.4 (maximum size 154.0 mm).

The best candidate model to estimate the demographic parameters was phi(.) p(t) in both zones and for both sexes, in which apparent survival remained constant during the sample period but the probability of capture was time-dependent (Tables 3 and 4). The apparent probability of survival of the recaptured specimens in Zone 1 and 2 was high for both sexes, during the entire sampling period (Tables 3 and 4). In females, the apparent probability of survival estimated by the best candidate model was 0.91 (Zone 1) and 0.92 (Zone 2) and the seniority probability was 0.89 (Zone 1) and 1.00 (Zone 2). In males, the apparent probability of survival estimated by the best candidate model was 0.86 (Zone 1) and 0.84 (Zone 2) and the seniority probability was 0.91 (Zone 1) and 0.80 (Zone 2). The capture-recapture model also allowed an estimation of the adult population size for the Zone 1 (N = 147.6) and Zone 2 (N = 154.5). In Zone 1, one female was recaptured after an interval of 31 y, another four females and one male after 30 y, and other two males after 28 y.

Table 2. Parity of sexes for the European Pond Turtle (*Emys orbicularis*) in Riera de Santa Coloma (Girona, north-eastern Spain) estimated per year and area. The sex ratio (males/males+females) and total number of adults (n) are shown. Statistically significant results ($P \leq 0.05$) indicated that the observed ratio differed from parity.

	Sex ratio	n	*z*	*P*
Zone 1				
1997	0.21	29	-3.12	0.002
1998	0.24	42	-3.37	< 0.001
1999	0.20	70	-5.02	< 0.001
2000	0.17	36	-3.96	< 0.001
2002	0.25	20	-2.24	0.025
2003	0.38	13	-0.87	0.387
2005	0.32	44	-2.39	0.017
2006	0.08	13	-3.03	0.002
2007	0.24	99	-5.17	< 0.001
2008	0.22	109	-5.85	< 0.001
2009	0.17	30	-3.62	< 0.001
2010	0.23	60	-4.18	< 0.001
2011	0.23	62	-4.25	< 0.001
2012	0.23	53	-3.93	< 0.001
2013	0.30	27	-2.08	0.038
2014	0.21	48	-4.02	< 0.001
2015	0.33	27	-1.77	0.078
2016	0.36	28	-1.48	0.138
2017	0.29	76	-3.66	< 0.001
2018	0.26	66	-3.90	< 0.001
Zone 2				
2008	0.43	53	-1.02	0.308
2011	0.42	33	-0.92	0.358
2012	0.31	13	-1.37	0.171
2015	0.73	26	2.35	0.019
2016	0.78	41	3.59	< 0.001
2017	0.72	53	3.20	0.001
2018	0.64	61	2.19	0.029

The analysis of movement patterns in Zone 1 showed that 18.95% of the females and 29.92% of the males were recaptured at different surveillance points. The comparison between both sexes showed no significant difference ($\chi^2 = 3.4$, df = 1, $P = 0.066$). The average distance (km y–1) traveled between recapture points was slightly higher in males (0.15 km) than in females (0.09 km), and this difference was significant ($z = -2.31$, $P = 0.021$). The results of the radio tracking showed that the tagged specimens dispersed throughout terrestrial habitats mainly in spring, with distances reaching 110 m for some females looking for an egg-laying site or 450 m to visit temporary pools.

Table 3. Capture-recapture model candidates used to estimate population parameters of the European Pond Turtle (*Emys orbicularis*) in Zone 1. We include a group (Nsx) for which sex could not be determined, encompassing the 1986–1996 period. Abbreviations are phi = apparent survival probability, p = probability of capture, γ = seniority probability, AICc = Akaike Information Criterion corrected for small sample sizes, and np = number of parameters included in the model. For simplicity, only the first three best models of the eight possible candidates are shown.

Zone 1	phi	p	γ	AICc	Delta AICc	AICc weight	np
Nsx							
phi(.)p(t)γ(.)	0.95	0.17	0.92	1175.45	0.00	0.863	10
phi(.)p(t)γ(t)	0.93	0.23	0.83	1179.39	3.94	0.122	15
phi(t)p(t)γ(.)	0.95	0.19	0.91	1183.66	8.21	0.011	15
Females							
phi(.)p(t)γ(t)	0.91	0.44	0.89	3238.44	0.00	0.994	39
phi(t)p(t)γ(t)	0.90	0.45	0.89	3250.93	12.49	0.002	56
phi(.)p(t)γ(.)	0.90	0.39	0.91	3282.94	44.50	0.000	22
Males							
phi(.)p(t)γ(.)	0.86	0.38	0.91	1036.75	0.00	0.991	22
phi(.)p(t)γ(t)	0.86	0.43	0.88	1056.22	19.47	< 0.001	39
phi(t)p(t)γ(.)	0.87	0.39	0.90	1064.46	27.72	< 0.001	39

Discussion

We analyzed the population structure, survival, and demographic trends of two separate populations of *E. orbicularis* in the northeast Iberian Peninsula. Our long-term series in Zone 1 (31 y) showed a population that contained a significant proportion of juveniles, was dominated by long-lived adult females, and was mostly philopatric. *Emys orbicularis* is known to be a long-lived species, with a lifespan < 50 y (Gibbons 1987). Our data also indicated that this species can live for prolonged periods of time (at least 31 y in females and 30 y in males), although few turtles survived more than 25 y. The longevity of our oldest turtles is possibly > 31 y as three of them surviving at the end of the study were marked in 1987, and their carapace lengths were then > 105 mm (meaning they were already adult sized). Schneeweiss (2004), using indirect estimators (shell wear and morphology), observed that a wild population in northeastern Germany included individuals with lifespans > 30 y.

In our study populations, the proportion of juveniles was relatively high (mean of 21% in Zone 1 and 11% in Zone 2), reaching 55% in some years (in Zone 1). Similar proportions of juveniles were observed in other populations in the Mediterranean region, including 18.9% in northeast Italy (Mazzotti 1995) and 19.7% in southwest Spain (Keller 1997); however, this proportion varied significantly over time when a sufficiently long interval was considered. This pattern could be explained by stochastic variation in breeding success and nesting microhabitat availability (Spencer and Thomson 2003; Schwanz et al. 2010; Bayrakci and Ayaz 2014).

Population parameters modeled according to capture-recapture data indicated that adult survival, both female and male, is constant over time and is relatively high. The population growth is fundamentally supported by low adult mortality, as indicated by the high seniority probability for both zones and both sexes. These estimations mirror those described in other studies of long-lived vertebrates, like tortoises and elephants (e.g.,

Table 4. Capture-recapture model candidates used to estimate population parameters of the European Pond Turtle (*Emys orbicularis*) in Zone 2. Abbreviations are phi = apparent survival probability, p = probability of capture, γ = seniority probability, AICc = Akaike Information Criterion corrected for small sample sizes, and np = number of parameters included in the model. For simplicity, only the first three best models of the eight possible candidates are shown.

Zone 2	phi	p	γ	AICc	Delta AICc	AICc weight	np
Females							
phi(.)p(t)γ(t)	0.92	0.09	1.00	466.77	0.00	0.993	13
phi(t)p(t)γ(.)	0.92	0.09	1.00	481.28	14.51	< 0.001	19
phi(.)p(t)γ(t)	0.90	0.17	0.87	485.79	19.01	< 0.001	21
Males							
phi(.)p(t)γ(.)	0.84	0.17	0.80	592.96	0.00	0.694	13
phi(.)p(t)γ(t)	0.82	0.21	0.79	594.68	1.72	0.292	17
phi(t)p(t)γ(.)	0.80	0.20	0.80	601.74	8.78	0.009	19

Freilich et al. 2000; Moss 2001).

The analysis of dispersal movements by means of recaptures showed a highly philopatric population, with a relatively small proportion of individuals moving among aquatic habitats. The males showed a slightly higher proportion of dispersal, with this difference marginally significant. A greater proportion of dispersing males associated with a sex-ratio biased towards females could be attributed to agonistic interactions among breeding males (Rovero et al. 1999). The mean distances covered by both sexes showed slightly higher values than those observed by Gariboldi and Zuffi (1994). These authors found mean distances of 44 m in females and 33 m in males, whereas in this study, we found 90 m in females and 150 m in males. The movements were mainly conducted between ponds connected by a seasonal stream (i.e., Barranc del Vilarràs or Riera de Santa Coloma).

The sex ratio significantly favored females in most years in Zone 1 and males in Zone 2, although only at the end of the survey period (2015–2018). In populations located in the southwest Spain, northwest Spain, and central Slovenia, sex ratio favoring males were observed (0.61, 0.64 and 0.84, respectively; Keller 1997; Cordero-Rivera and Ayres 2004; Vamberger and Kos 2011). A sex ratio favoring females (0.30) was also reported in a population of the northeast Italy (Mazzotti 1995), with a proportion relative to the total captures (57.5%) very similar to that we found in Zone 1 (i.e., 58.9%). The differences observed in the sex ratio interzones were significant, except in 2012. These differences could be attributable to the environmental conditions. The habitat in Zone 2 is a stream section subject to summer low flows and autumnal floods and is therefore intrinsically less stable than the network of permanent ponds that constitute Zone 1. This fact could explain the lower probability of capture compared to the same period in Zone 1, attributable to dispersal associated with fluctuations in habitat quality (Mazzotti 1995). Additionally, in this habitat, we found invasive aquatic species (i.e., Eastern Mosquitofish, *Gambusia holbrooki*, American Mink, *Neovison vison*, Louisiana Crawfish, *Procambarus clarkii,* and *Trachemys scripta*) and higher densities of the native turtle *Mauremys leprosa*. These species can act as potential competitors or predators, acting as an additional environmental stressor to this population (Cabral et al. 1998; Pérez-Santigosa et al. 2011; Dupuis-Désormeaux et al. 2017; Escoriza and Ben Hassine 2017).

This study highlighted the critical importance of adult survival to maintain population stability, as previously indicated in other chelonian species (Doak et al. 1994). In the Zone 1 the conservation of this population would greatly benefit from actions aimed at increasing the availability of suitable habitats and their connectivity. In Zone 2, the removal of invasive species must be prioritized as they serve as a major threat to *E. orbicularis* (Cadi and Joly 2004).

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