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Growth patterns of *Emys orbicularis* across a range of aquatic habitats: a long-term study

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Emys orbicularis is a semi-aquatic turtle with great longevity being able to reach 50 years. In this study, we estimated the growth rates (in carapace length and body mass) in a population of *E. orbicularis* from the northeastern Iberian Peninsula over a period of 23 years**.** We compared their growth rates among age groups, sexes, and years and across different types of habitats (small forest ponds, large forest ponds, and slow-flow streams). We hypothesized that the subpopulation that inhabits the small forest ponds may show slower growth rates because these habitats have lower solar exposure and lower water temperature. The study population showed sexual dimorphism in size, with females being larger and heavier than males. The analyses confirmed that the individuals from small forest ponds are smaller and grow at slower rates. Our results also revealed significant inter-annual variability in the growth rates of *E. orbicularis*, emphasizing the importance of conducting long-term studies of species with great longevity.

Key words: forest pond; freshwater turtles; growth rates; longevity; long lived species; stream.

The European pond terrapin *Emys orbicularis* (Linnaeus, 1758) is the most widespread freshwater turtle in Europe, occurring throughout the circum-Mediterranean region and the temperate regions of central Europe, reaching southern Lithuania and Poland (Vamberger & Fritz, 2018). This species is very long-lived, reaching 50 years of age, although few individuals exceed 25 years (Gibbons, 1987; Escoriza *et al*., 2020). The growth patterns of this species have been little studied and, despite the great longevity of this species, it has been usually studied only during relatively short periods (Mitrus & Zemanek, 2004; Zuffi *et al*., 2007; Zuffi & Foschi, 2015). In semi-aquatic turtles, body growth may show important inter-annual variability (Tucker *et al*., 1995); therefore, it may be useful to evaluate growth rates over longer periods to obtain results robust to episodic oscillations of climate.

The growth rates of temperate reptiles are highly influenced by the thermal quality of their habitats (Cadby *et al*., 2014). Thus, within the same species, the size of adults in one population can be twice as large as that in other populations (Niewiarowski & Roosenburg, 1993). In freshwater turtles, the role of habitat properties, such as the environmental temperature, hydrological dynamics and habitat productivity, in growth rates has been demonstrated (e.g., Kennet & Georges,

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1990; FRAZER *et al*., 1991; BROWN *et al*., 1994; ROWE, 1997; KAGAYAMA, 2020). For this reason, differences among lentic and lotic habitats, the structure of riparian habitats, and water body size can be expected to be relevant, as suggested by broad variations in the physicochemical conditions of the water, faunal assemblage composition (i.e., competitors or trophic resources), and biological productivity (WANG *et al*., 2008; GRATTON & ZANDEN, 2009; BISCHOF *et al*., 2013).

In this study, we evaluated the growth rates (in carapace length and body mass) of *E. orbicularis* using capture-recapture data obtained over 23 years. This population occupies various types of aquatic habitats, such as small forest ponds, large ponds, and slow-flowing streams (ESCORIZA *et al*., 2021). In turn, the studied aquatic habitats also differ in their thermal quality, because streams and larger ponds have greater sun exposure and water temperature (mean value 12.9ºC small ponds, 17.7ºC large ponds, and 20.9ºC for streams during the mid-spring season, 2016–2017; SUNYER-SALA, 2018; SUNYER-SALA, unpublished data). These differences in habitat properties are important enough that the small forest ponds are not inhabited by other species of turtles that also occur in the area but have greater thermophilic requirements (*Mauremys leprosa* and *Trachemys scripta*; ESCORIZA *et al*., 2021). Given that semi-aquatic turtles thermoregulate by sun basking, it can be expected that the occupancy of habitats with less solar exposure could have effects on their foraging efficiency, assimilation of nutrients, and growth (COMPTON *et al*., 2002; CARRIÈRE *et al*., 2008; CADBY *et al*., 2014). Our hypothesis was that the populations that occupy small forest ponds (with low sun exposure) would display smaller sizes and lower growth rates than populations inhabiting other sites with more suitable features.

MATERIALS AND METHODS

Study area and surveys

The study region is the upper Tordera basin (Girona, northeastern Iberian Peninsula) (Fig. 1). In this region, the demographic evolution of *E. orbicularis* has been followed since the late 1980s, based on seasonal captures with baited traps (RAMOS *et al*., 2009; ESCORIZA *et al*., 2020). In the upper Tordera basin, *E. orbicularis* inhabits a complex network of slow-flowing streams and interconnected permanent ponds surrounded by dense broadleaved forests of *Quercus pubescens* and *Q. ilex* and patches of open farmlands (Fig. 2). The study population occurs in three types of aquatic habitats: small forest ponds (< 900 m^2), large forest ponds (> 900 m^2), and slow-flowing seasonal streams (Fig. 1).

Here, we evaluated the growth rates of freshwater turtles captured in one seasonal stream (surface area of 2400 m^2), two large ponds (surface area ranging from 950 to 1200 m^2 mean = 1075 m^2), and four small permanent ponds (surface area ranging from 70 to 550 m^2, mean = 205 m^2) (Fig. 1). The turtles were captured using baited traps (110 × 50 cm) between 1997 and 2020. The traps were placed partially submerged to avoid accidental suffocation, and the turtles were removed from the traps every 24 hours. The surveys were conducted during spring (April-June) and early autumn (October), coinciding with the activi-

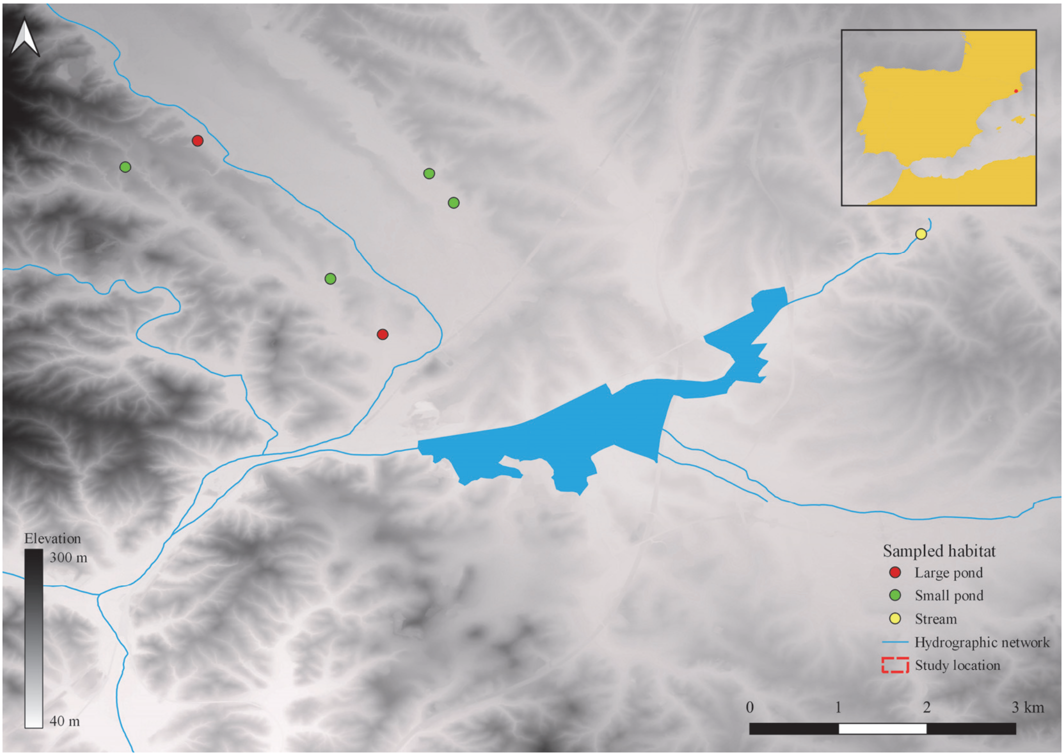

Figure 1: Study region (upper Tordera basin, northeast of Spain) and sampled habitats: green = small pond, red = large pond (> 900 m²), yellow = stream. The main hydrographic network is shown as blue lines. For a correct visualization of the figure, the reader is referred to the online, colored version of the article.

ty peaks of this species. The captured individuals were marked using different combinations of holes drilled in the marginal scutes of the carapace (PLUMMER, 1979).

Species data

For the captured turtles, we determined the sex, measured their total carapace lengths (CLs) to the nearest millimetre with a digital calliper (accuracy ± 0.01 mm), and weighed (body mass; BM) them with a digital balance (accuracy ± 0.1 g). We classified the individuals that did not show secondary sexual traits and with a CL smaller than 103 mm (or BM ~150 g) as juveniles (RAMOS *et al.*, 2009). In adult turtles, sex was assigned based on external traits, such as the colour of the irises and the head, the relative size of the tail, shape of the plastron, and claw length (ALARCOS *et al.*, 2019). The annual growth rate was calculated for total CL and BM using a formula for the percentage of growth rate per year:

$$GRY = (V_i – V_0/Ny)/V_0*100$$

Where GRY is the growth rate per year, V_0 is the initial state, V_i is the final state, and Ny is the period (in years) between the measurements V_i and V_0. This formula is

Figure 2: Examples of aquatic habitats used by *Emys orbicularis* in the study area. Left side: a slow-flowing stream associated with an open riparian gallery forest. Right side: small forest ponds with a dense canopy cover, almost completely covering the pond throughout the day. The turtle in the top circle corresponds to a forest pond individual and the lower one captured in the stream.

based on the conventional concept of growth rate (e.g., HILBERS *et al.*, 2017).

Data analysis

CL, BM, and the percentage of growth and weight gain rate per year were evaluated as response variables, and sex (male/female), age group (adult/juvenile), year of sampling, and habitat properties (small pond/large pond/stream) were evaluated as predictor variables. The response variables were included in a generalized linear mixed model (GLMM), which included fixed effects and random effects. We included the turtle codes nested within habitats as a random effect in the GLMM to account for pseudo-replication. This analysis was performed using the lme4 package (BATES *et al.*, 2015) in the R environment (R DEVELOPMENT CORE TEAM, 2021).

RESULTS

The males had lower CLs and BMs than the females (Tables 1 and 2). The CL and BM showed wide variability with habitat conditions, with smaller individuals captured in the small forest ponds and larger individuals captured in the stream (Table 2).

The analyses showed that the growth rates (CL and BM) were higher in juveniles than in adult turtles, but we did not detect significant intersexual differences (Fig. 3a and Tables 3 and 4). The growth patterns showed significant inter-annual variation (Tables 3, 4). The analyses also revealed

Table 1: Number of captured individuals (N) of *Emys orbicularis* and descriptive statistics (mean ± standard error) of the measurements obtained during the capture-recaptures (1997–2020) in the upper Tordera basin. Carapace length (CL) in mm; Body mass (BM) in g.

Group	Parameter	Value
Males	N	110
	CL	119.52 ± 1.09
	BM	254.60 ± 6.68
Females	N	313
	CL	124.27 ± 0.76
	BM	325.43 ± 6.27
Juveniles	N	328
	CL	83.45 ± 0.89
	BM	93.51 ± 2.54

that the growth rates (CL and BM) showed a positive association with the stream and a negative association with the small ponds, both significant (Fig. 3b and Tables 4 and 5). We also found high individual variability in the growth rates (CL and BM) in the turtles captured in the stream (Fig. 3b).

DISCUSSION

This study evaluated the growth patterns of *E. orbicularis* in the northeastern Iberian Peninsula, comparing individuals captured in a range of habitats. The analyses showed that the turtles that inhabit a large stream stretch, tend to grow faster and reach larger sizes, while those that occupy small forest ponds tend to be smaller and grow at slower rates. The prolonged period over which the sampling was carried out allows us to assert that the results are robust to episodic variations in growth, e.g., warmer years versus colder years (ZWEIFEL, 1989; TUCKER *et al.*, 1995), which was detectable in our samples. This emphasizes the importance of conducting long-term studies of species with long life spans (HOLLISTER-SMITH *et al.*, 2007; CURTIN *et al.*, 2009).

The studied *Emys orbicularis* showed sexual dimorphism in size, with females being larger and heavier than males, as already indicated in other subpopulations of the species (e.g., MITRUS & ZEMANEK, 2004; KAVIANI & RAHIMIBASHAR, 2015). Freshwater turtles captured in the stream and larger ponds are also larger and heavier than those captured in small forest ponds. As expected, *E. orbicularis* displays relatively rapid growth during the first years of life, and this growth stabilizes upon reaching sexual maturity. However, the growth rate was not consistent throughout the range of aquatic habitats. The analyses revealed that the individuals captured in the stream stretch (with abundant solar exposure and high water temperatures; SUNYER-SALA, 2018) had faster

Table 2: Generalized Linear Mixed Model results comparing carapace length and body mass among sexes and habitats for *Emys orbicularis* in the upper Tordera basin.

Variable	Source	Estimate	SE	p
Carapace length	Sex	–6.262	2.048	0.003
	Small pond	–10.729	1.910	$8.97e^{-8}$
	Large pond	3.312	2.888	0.253
	Stream	11.888	2.207	$2.61e^{-7}$
Body mass	Sex	–86.650	16.470	$4.41e^{-7}$
	Small pond	–118.862	16.981	$5.81e^{-11}$
	Large pond	58.400	27.930	0.038
	Stream	119.404	19.980	$1.29e^{-8}$

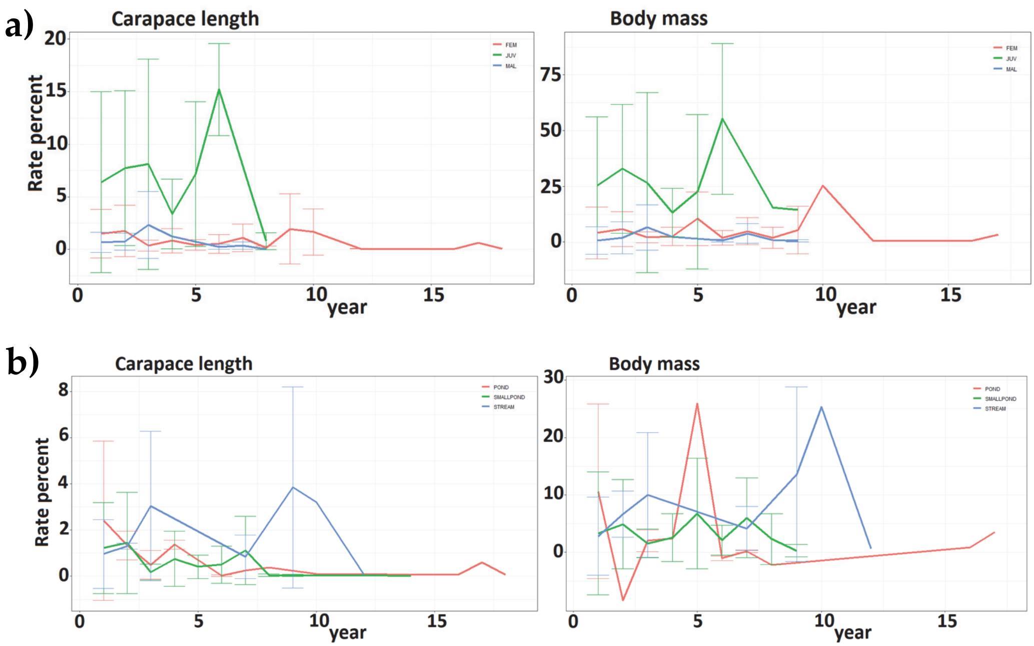

Figure 3: Annual growth rate (carapace length and body mass) for *Emys orbicularis* in the upper Tordera basin, **a)** among juveniles (green), females, (red), and males (blue); and **b)** comparing the subpopulations that inhabit small ponds (green), large ponds (red), and streams (blue). The mean values (line) and 95% confidence intervals (error bars) are shown. For a correct visualization of the figure, the reader is referred to the online, colored version of the article.

Table 3: Descriptive statistics of growth rates (CL = carapace length, BM = body mass) of *Emys orbicularis* in the upper Tordera basin, separated by age groups and sexes. SE, standard error of the mean.

	Age group	Mean ± SE
CL	Males	1.042 ± 0.224
	Females	1.264 ± 0.145
	Juveniles	6.987 ± 0.581
BM	Males	2.520 ± 0.815
	Females	4.392 ± 0.571
	Juveniles	27.223 ± 2.506

growth rates according to both the CL and BM. Overall, our results mirror those described for other species of semi-aquatic turtles when comparing groups of turtles from a range of habitats differing in their thermal quality or biological productivity, although previous studies did not evaluate patterns of growth for a range of water body sizes (BROWN *et al.*, 1994; ROWE, 1997).

In our study area, slow-flowing streams are associated with more open riparian habitats, while ponds are completely surrounded by forest (Fig. 2). Individuals from small, forested ponds may have shorter growth periods, caused by lower temperatures, as described in mountain populations of *E. orbicularis* (ZUFFI *et al.*, 2007; AYAZ *et al.*, 2008). In larger ponds, this negative effect of the canopy cover on the quality of the habitats is attenuated, as there is a central area that is exposed to more sun, at least during the central hours of the day. It is possible that these differ-

Table 4: Generalized Linear Mixed Model results comparing the growth rates (carapace length) among sexes, age groups, year of sampling, and habitats for *Emys orbicularis* in the upper Tordera basin.

Group	Estimate	SE	p
Sex	–0.269	0.374	0.472
Age group	6.555	0.834	3.54^{e-13}
Year	–0.043	0.023	0.056
Small pond	–0.803	0.355	0.026
Large pond	0.187	0.486	0.702
Stream	1.041	0.434	0.018

Table 5: Generalized Linear Mixed Model results comparing the growth rates (body mass) among sexes, age groups, year of sampling, and habitats for *Emys orbicularis* in the upper Tordera basin.

Group	Estimate	SE	p
Sex	–2.537	1.294	0.053
Age group	22.382	2.346	8.37^{e-16}
Year	–0.161	0.079	0.042
Small pond	–3.960	1.399	0.005
Large pond	1.897	2.042	0.354
Stream	4.739	1.762	0.008

ences could be mediated or enhanced by differences in diet among the subpopulations that occupy these habitats, as has been demonstrated in other aquatic turtles (BOUCHARD & BJORNDAL, 2006), but at this time we do not have sufficient data to test this hypothesis.

The individuals captured in the stream also show high inter-individual variability in growth, attributable to the marked seasonality in the conditions of these aquatic habitats (CID *et al.*, 2017). These Mediterranean streams show dramatic fluctuations in flow during the year, but with large inter-annual variation (BERNAL *et al.*, 2004; BOADA *et al.*, 2006), which in turn affects the growth rates of the turtles.

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