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Nesting activity and reproductive Success of *Emys orbicularis* in Babat Valley (Gödöllő, Hungary)

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Abstract.—**Several reproductive parameters may give valuable information to help develop conservation strategies for the European Pond Turtle (*Emys orbicularis*). We studied clutch size, double-clutching, emergence success, female body sizes and hatchling body sizes in a pond system in Hungary between 2014–2017. The mean length of the nesting season was 43 d with two distinct egg-laying periods. The body sizes of the females had a significantly positive correlation with clutch size. Females laid significantly fewer eggs during the second nesting period; however, there was no difference in clutch size in the case of single or double-clutching. The variance of the egg number was twice as high in the group, which laid eggs twice. Female body sizes (straight carapace lengths, plastron width) were positively correlated to the same body sizes of the hatchlings. Body sizes of the hatchlings were significantly smaller if they emerged from clutches laid in the second period of the nesting season or if the neonates emerged after overwintering. In addition, the larger number of hatched neonates in one nest strongly increased the emergence success, most probably because more hatchlings could dig themselves out more effectively. Based on our data, the aboveground metal square grids we used to protect nests can decrease nest predation to zero; therefore, the use of metal grids or cages are recommended in European Pond Turtle conservation programs.**

Key Words.—body size; double-clutching; emergence success; European Pond Turtle; maternal effect; nest overwintering; nest protection

Introduction

The European Pond Turtle (*Emys orbicularis*) is a widespread species in the Palearctic region and has adapted to a large variety of habitats and climatic circumstances (Lenk et al. 1999; Fritz 2003). The European Pond Turtle is mainly aquatic but uses terrestrial habitats also, especially for nesting. The main threats to the survival of the European Pond Turtle are habitat loss and degradation, fragmentation, and nest destruction caused by direct and indirect anthropogenic pressures like agriculture, urbanization and road network expansion, climate change, water pollution, the spread of alien species, and mortality of females and hatchlings during their migration to and from nesting sites (Klemens 2000; Vamberger et al. 2017). Predators may damage 75–95% of nests (Kotenko 2000; Rössler 2000; Havaš and Danko 2009), which decreases the number of hatchlings and can heavily modify the age structure of the population, causing an inverse age-pyramid. This species requires special protection to preserve its habitat and maintain undisturbed reproduction (Maciantowicz and Najbar 2004; Fritz and Chiari 2013).

Better knowledge of the quality of wetland and terrestrial habitats, such as the availability of nesting habitat, the distribution of predators, and the patterns of several life-history traits may provide information to help develop effective conservation and management strategies. The most often studied reproductive traits of European Pond Turtles are reproductive frequency, courtship, nesting behavior, nest location, incubation temperatures, clutch size-maternal body size relationships, and hatching success (Rovero and Chelazzi 1996; Zuffi and Odetti 1998; Zuffi 2004; Zuffi and Foschi 2015). The reproductive strategy of the European Pond Turtle is highly variable and depends mostly on climatic circumstances, food availability, area and number of wetlands, and female body size (Zuffi et al. 2015).

The species has been the focus of various ecological, conservation, and biological studies since the 1990s in Europe. In recent decades, the number of turtles in some areas of Hungary decreased sharply but in the absence of detailed studies, it is difficult to estimate the extent of the decrease (Farkas et al. 2013). Most studies in Hungary have dealt with empirical reviews of morphological characteristics, life cycle (Marián and Szabó 1961; Farkas et al. 1998; Farkas 2000, 2008; Farkas and Gulácsi 2009), population structure and dynamics, and seasonal activity (Kovács et al. 2004; Balázs and Györffy 2006; Kovács 2008; Lovász et al. 2012; Erdélyi et al. 2021). Other recent studies in Hungary have examined genetic diversity, basking site preference, and conservation activity (Farkas et al. 2013; Molnár et al. 2011; Erdélyi et al. 2019).

Some reproductive characteristics of the European Pond Turtle are well known. The clutch size ranges from four (Zuffi and Rovina 2006; Dely 1978; Péchy and Haraszthy 1997) to 23 (Mitrus and Zemanek 2000). Double-clutching is documented in many regions (Drobenkov 2000 in Belarus; Rössler 2000 in Austria; Díaz-Paniagua et al. 2014 in Spain) but no data are available from Hungary. Not all females produce two clutches, and not every female reproduces each year (Kotenko 2000). After approximately 3 mo of incubation in the nest chamber, hatchlings emerge from August to late October (Lebboroni and Chelazzi 1998; Rössler 2000; Novotný et al. 2004; Mitrus et al. 2012; Ayaz et al. 2017) although hatchlings may overwinter in nest chambers and emerge the following spring (Servan 1998; Kotenko 2000; Mitrus and Zemanek 2003; Najbar and Szuszkiewicz 2005; Ayaz and Çiçek 2011). Overwintering in the nest is quite widespread among turtles (Gibbons and Nelson 1978; Gibbons 2013) and the physiological ecology of overwintering on hatchling turtles are well documented (Costanzo et al. 2008). Overwintering has not been established for hatchling of European Pond Turtles in Hungary.

We intended to understand the reproductive characteristics of the European Pond Turtle population in the Babat Valley near Gödöllő, Hungary. There was a nest protection program for this population, and we aimed to determine: (1) How long is the nesting season and what are reproductive characteristics of the species in Babat Valley? (2) Does double-clutching occur in Hungary? (3) Does the timing of nesting affect the fecundity of females or the fertilization of eggs, or the hatching and emergence successes of the hatchlings? (4) Does the body size of the female have an impact on clutch size and body sizes of hatchlings? (5) Does overwintering in the nest chamber occur in Babat Valley? (6) If yes, how does the emergence success of hatchlings differ between emergence in autumn or after overwintering in the following spring? (7) How effective are above-ground metal-square grids used to protect the nests against predators?

Materials and Methods

Study area.—We carried out the survey in a pond system in Babat Valley, located on the outskirts of Gödöllő (47°36′N; 19°22′E), northeast of Budapest, Hungary. The ponds were surrounded by reeds (*Phragmites* sp.). There were mainly agricultural fields and pine and deciduous forests north of the ponds. Among the fields and forests, there were remnant patches of steppe grassland associations. At the south of the ponds, there were mostly deciduous forests, developed areas, and pioneer grasslands (Fig. 1).

Data collection.—We surveyed female turtles between the spring of 2014 and autumn of 2017 at their nesting sites. Based on the experiences of previous years, we identified two preferred nesting areas around the pond system; one small patch of grassland on the shore of pond 1–2 and one larger nesting site on the band of steppe grassland associations at the edge of an agricultural field (not regularly cultivated), above pond 5 (Fig. 1). We checked the two most preferred nesting sites almost daily, starting in the hours before

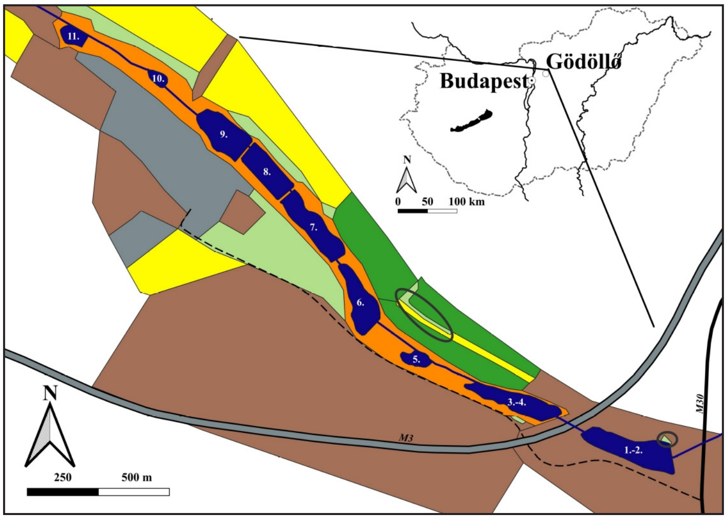

Figure 1. Location of the study area near Gödöllő (Hungary). Habitats in the study area: blue line = stream; blue area = pond; dark green = pine forest; dark brown = deciduous forest; light green = grassland; orange = reed; yellow = agricultural fields; grey = built-up areas; M3 = M3 highway; M30 = main road; dashed black line = access road, and ellipse = most preferred nesting site.

dark (usually from 1800). In the case of other ponds, we searched for nests during the day once a week and could detect only depredated nests.

Sampling events typically lasted 5 h at the preferred nesting sites, depending on the number of nesting females. Sampling consisted of two people walking 5 m apart from each other within a standard curving transect line covering the whole study area. We walked as quietly as possible to avoid disturbing arriving turtles. If we found a female searching for a nesting place, digging a hole, or laying eggs, we avoided it and continued to monitor the entire study site. Once females were finished laying eggs and had covered the nest, we caught them, recorded morphometric characteristics, and marked them with a unique mark. We made the marking on the marginal scutes of the carapace using a rasp. After measuring and marking, we immediately released the turtles at its capture location. We marked protected nests with a serial number on a plastic ticket. We also marked all depredated nests to prevent their re-assessment. We noted a nesting attempt as unsuccessful if the female did not lay eggs after she dug a nest.

We measured straight carapace and plastron lengths (SCL and PL), widths (CW and PW), carapace height (CH), and tail length (TL) of adult females with a modified caliper (± 1 mm), and their body weight (BW) with a digital scale (Model DL-3; Denver Instrument Company, Göttingen, Germany) with the accuracy of 1 g. Unfortunately, we could not measure the weight of six females due to the failure of the scale. We also do not have the tail lengths of seven females due to the lack of this size measurement at the beginning of the survey, and we did not measure one specimen that had a damaged, truncated tail. We measured the length and width of unhatched eggs, the shell sizes of dead hatchlings in the nest chamber, and the emerged live hatchlings using a manual caliper. To measure weight, we used a jeweler pocket scale (ES-Series SL-400; DigiWeight Inc., Chino Hills, California, USA) with an accuracy of 0.05 g.

Nest-protection.—After egg-laying and measuring morphometric features of female turtles at the two preferred nesting sites, we protected their nests immediately. We used aboveground metal square grids 30 × 30 cm in size with a mesh size of 30 mm, fitted with a chain at the edges (Schindler et al. 2017). Through these chain links, we fixed the mesh to the ground with five pieces of 15 cm iron pegs per side (Fig. 2). We inspected nests weekly during the summer.

A few weeks before expected emergence in 2015–2017, we attached a metal cage (5 mm mesh) above the metal grid (Fig. 2), which prevented the emerged hatchlings from leaving immediately and provided them protection from predators. After placing the protective cages, we checked for emergence daily, usually in the late morning. In this way within 1 d after emergence, we could measure hatchling body sizes, and immediately released them. After emergence, we removed the cage and grid, excavated the nest, and counted unfertilized eggs, eggs with dead embryos, and any dead hatchlings which remained in the nest cavity.

Statistical analyses.—We measured various reproductive traits of European Pond Turtles: fecundity = clutch size/female; fertilization success = number of fertilized eggs/number of all laid eggs; hatching success = hatched neonates/number of all laid eggs; emergence success = number of emerged hatchlings/number of all hatched neonates; live hatchling = hatched and alive

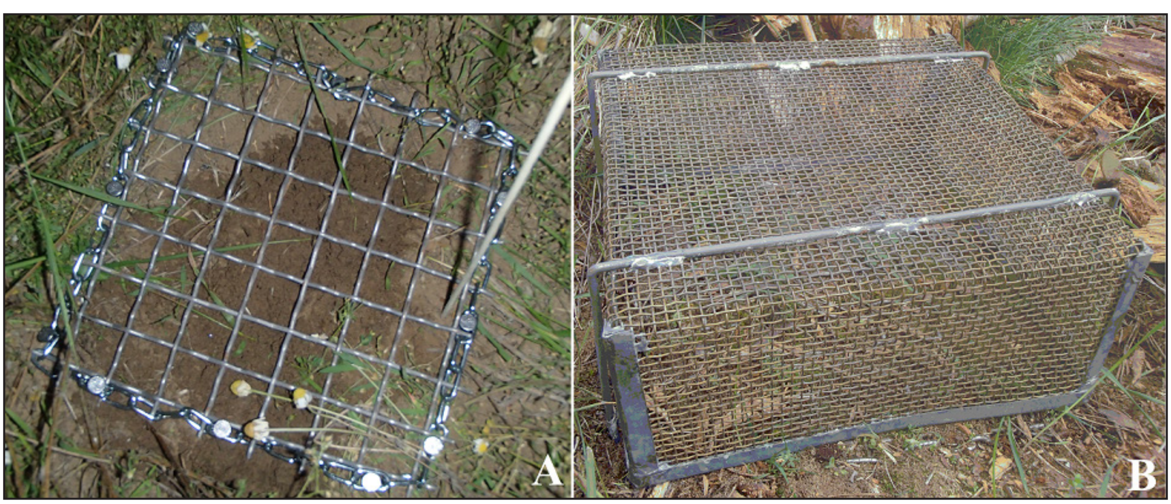

Figure 2. (A) Aboveground metal square grid fixed to the ground with iron pegs to protect the nest of European Pond Turtles (*Emys orbicularis*). Chain was fitted to the edges for stable fixing. (B) A metal cage fixed above the metal grid, which prevented the emerged hatchlings from leaving immediately (Photographed by István Kiss).

neonate, which can emerge; and dead hatchling = hatched neonate, but died in the nest. We distinguished two nesting periods during the nesting season, which were separated by a nesting pause. We carried out all statistical analysis with R Statistical program 4.0.3 (R Development Core Team 2020). We analyzed body sizes (BW, SCL, CW, PL, PW, CH, TL), hatching success, and emergence success with General Linear Models. In cases when double-clutching females were in the dataset, we used Linear Mixed Effect Models from the nlme package (Pinheiro et al. 2013) with the ID of females as the random factor (i.e., random subject). We analyzed hatching and emergence success on a logarithmic scale to meet model assumptions. We could not analyze the hatching and emergence success of 2014 separately because there were only four data points. Therefore, we drew no conclusions for that year. The models fulfilled the requirements based on the diagnostic plots (QQ plot, Cook plot, residual heteroscedasticity). We analyzed different egg numbers (unfertilized, fertilized, drowned, and total) with the Negative Binomial Model from MASS package (Venables and Ripley 2002). We tested variance difference with an F-test. We considered a value significant if $P \leq 0.05$.

Results

The mean BW of 55 females was 852.9 ± (standard deviation) 188.69 g (range, 528–1540 g), and the mean SCL of 61 females was 170.06 ± 10.61 mm (range, 135–190 mm). Other body measurements varied similarly (Appendix Table 1). We detected the earliest nesting on 28 May 2016 and 2017, 6 June in 2014, and 1 June in 2015. The continuous egg-laying of turtles ended on 2 July 2014 and 2017, 15 July 2015, and 20 July 2016. The mean length of the four nesting seasons (which lasted from the first to the last detected nesting attempt while it was continuous) in the pond system was 40 ± 11.37 d (range, 27–53 d).

We detected 156 nesting attempts between 2014–2017. We found most of the nesting attempts (78.8%) at the two preferred nesting sites at pond 1–2 and pond 5. During the 4 y, we observed 25 unsuccessful nesting attempts (17 at pond 5, six at pond 1–2, and two at other nesting sites). We recaptured five females that returned to lay their eggs after an unsuccessful nesting attempt on the previous day. We protected 50 nests and found 81 predated nests during the 4 y study. The number of protected and predated nests were the same (50) at the two preferred nesting sites.

There was a marked decrease in the number of nesting attempts during the nesting season from 11–16 June based on the merged dataset of the 4 y (Fig. 3). During this time period, we observed only two nesting attempts (both in 2017) in the two preferred nesting sites; however, across the pond system, there were five nesting attempts at the time of the pause due to the different timing of this pause. The resting pause means that the continuity of nesting attempts was interrupted, and few to no nesting attempts occurred. This nesting pause lasted 7 d in 2014 (7–13 June), 8 d in 2015 and 2017 (11–18 June), and 12 d in 2016 (11–22 June) but at the individual level, it meant that more than 20 d of resting occurred between nesting events, as we observed from double-clutching females. After the pause, the number of nesting attempts suddenly increased, and the second nesting period continued for longer than the first egg-laying period.

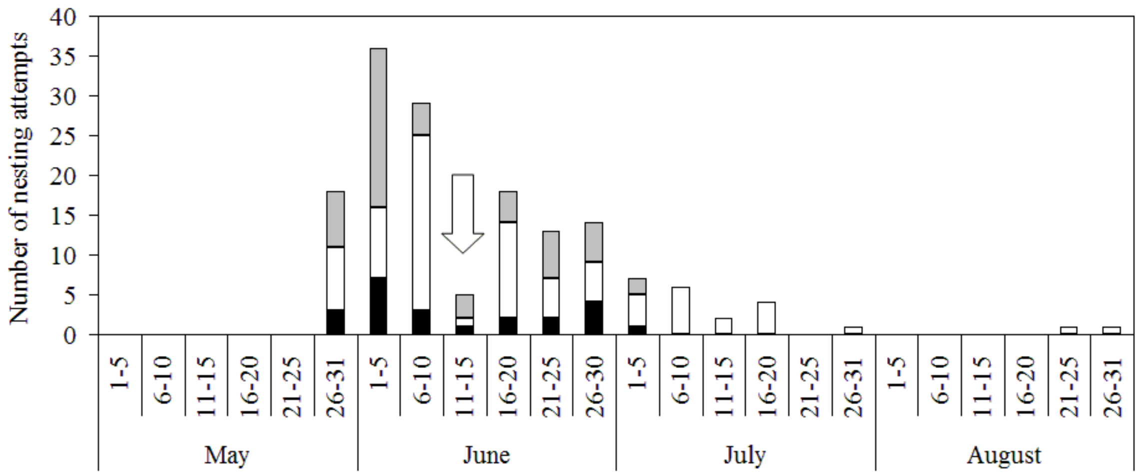

Figure 3. Temporal pattern of the merged number of unsuccessful nesting attempts (black filling), predated (white filling), and protected nests (grey filling) grouped into 5-d intervals of the European Pond Turtle (*Emys orbicularis*) in the pond system in the Babat Valley, Hungary, between 2014–2017. The arrow shows the overlap of nesting pause between the two egg-laying periods of the 4 y. The nesting pause started at a different date each year, therefore a few nesting can be observed in this interval.

We compared nesting attempts between the first and second nesting period of the nesting season on the combined data of all nesting sites (Fig. 3). The total number of nesting attempts were similar in the first (80), and second (76) periods. We documented 15 unsuccessful nesting attempts in the first nesting period and 10 in the second period. We protected 31 nests in the first nesting period, and 19 in the second at the two preferred nesting sites. The number of predated unprotected nests was higher (47) in the second nesting period than in the first (34) at the whole study area. Nest predation continued through the end of August in 2015 and 2017.

Female turtles did not arrive at the two preferred nesting sites (at pond 1–2 and pond 5) earlier than 1900, most of them arrived between 2000 and 2100. We detected four females that double-clutched in this population. We recaptured one female at pond 1–2 in 2017 and three at pond 5 in 2016 returning to lay a second clutch. In these cases, each first clutch occurred in the first nesting period, while the second occurred after the resting pause in the second nesting period. We observed that the number of days elapsed between the first and the repeated egg-laying was similar in the 4 y, the mean length was 22.5 d ± 1.3 d (range, 21–24 d).

The majority (9 of the 15) of recaptured females coming to lay eggs in subsequent years arrived within 5–10 d of the Julian date of the previous year. There was no correlation between the BW (t = 0.744, df = 15, P = 0.469), SCL (t = 0.485, df = 18, P = 0.634) of females and single and double-clutch size during the whole nesting season, but CH (t = 2.265, df = 18, P = 0.036) increased for female that arrived during the second nesting period. There was no significant difference between BW (t = -1.285, df = 20, P = 0.213) and SCL (t = -1.211, df = 24, P = 0.238) of females between the two nesting periods.

Fecundity of females.—The mean clutch size in 49 protected nests was 9.25 ± 2.65 (range, 1–13). In one protected nest, we did not find any eggs despite the female covering the egg-cavity. The body sizes of nesting females were significantly correlated with clutch size. Larger females laid more eggs (Appendix Table 2). The mean weight, length, and width of seven intact, unfertilized eggs found in the excavated nest were weight: 5.85 ± 0.42 g (range, 5.4–8.5 g); length: 32.98 ± 0.56 mm (range, 32.2–35.5 mm); and width: 19.23 ± 0.45 mm (range, 18.6–22.2 mm).

There was no significant difference in the mean clutch size found in protected nests depending on whether females laid eggs once or twice in the same year (t = -1.897, df = 44, P = 0.064), but if they laid two times, the clutch size was slightly smaller (Fig. 4). The variance of the clutch size was twice as high in the group that laid eggs twice in the same nesting season ($F_{6,38}$ = 0.330, P = 0.032). Females laid significantly fewer eggs at the second nesting period (z = -3.621, df = 127, P < 0.001; Fig. 4).

Fertilization, hatching, and emergence success.—The number of unfertilized eggs was very low in each year, and we found no significant difference between nesting periods (z = -0.449, df = 44, P = 0.653). The fertilization success was significantly greater in the second period of the nesting season in 2015 (z = 1.989, df = 12, P = 0.047) and 2016 (z = 7.937, df = 15, P < 0.001; Fig. 5), but we found no significant difference in 2017 (z = 0.134, df = 9, P = 0.894). When considering all years, fertilization success was significantly higher in the second nesting period (t = 5.982, df = 44, P < 0.001; Fig. 5). We found 19 drowned eggs in 11 of the 50 protected nests, (equivalent to 4.3% of 444 eggs). One clutch had four drowned eggs, and no other nest had more than two.

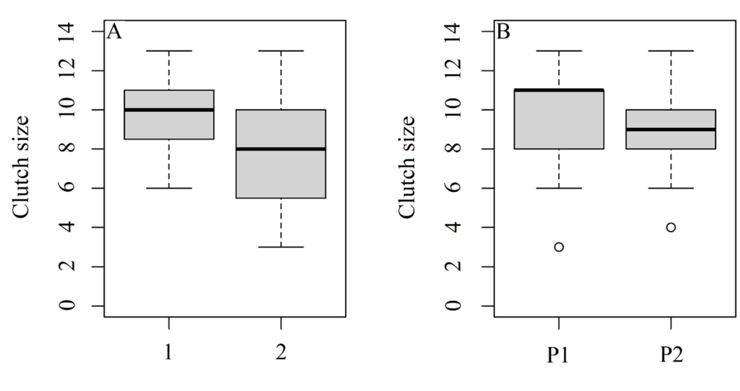

Figure 4. Clutch size in the protected nests indicating the fecundity of the European Pond Turtle (*Emys orbicularis*) females (A) laying eggs once (1) or twice (2) during the nesting season, and (B) in the first (P1) and second (P2) period of the nesting season in the pond system in the Babat Valley, Hungary, between 2014–2017. The band inside the box is the median. The bottom and the top of the box are the first and third quartiles. The ends of the whiskers are the minimum and maximum excluding outliers. Open circles are outlier (more than 3/2 times of the upper or lower quartile).

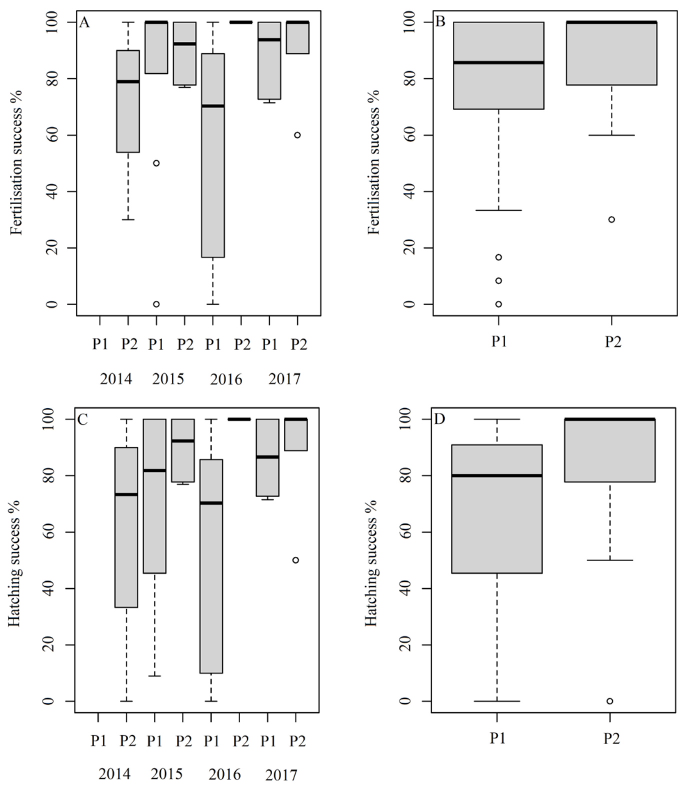

Figure 5. Fertilization success of the European Pond Turtle, *Emys orbicularis*, (A) in the first (P1) and second (P2) nesting period presented per years and (B) the merged data of 2014–2017. Hatching success of *E. orbicularis* if eggs laid (C) in the first (P1) and second (P2) periods of the nesting season presented per years and (D) with the merged data of 2014–2017 in the pond system in the Babat Valley, Hungary. See detailed description in Figure 4 of boxplot parts.

The hatching success in 2016 (z = 8.141, df = 15, P < 0.001) and with the merged data of 2014–2017 (z = 6.307, df = 44, P < 0.001) was significantly higher in clutches laid in the second nesting period (Fig. 5); however, we found no significant difference in 2015 (z = 0.915, df = 12, P = 0.360) and 2017 (z = 0.155, df = 9, P = 0.877). The hatching success of clutches laid in the second nesting period was 84.3%, while only 67.7% in the first period, independently of season of emergence.

Most hatchlings emerged from nests in autumn regardless of whether they were laid in the first or second nesting period. Eighteen of 29 hatched clutches laid in the first nesting period emerged in autumn, while 11 clutches emerged after overwintering. From the second nesting period, 10 of 17 hatched clutches emerged in autumn, while seven emerged the following spring.

The timing of emergence (autumn or after overwintering) affected the emergence success of hatchlings. The emergence success of hatched individuals in spring-emerging clutches (over-wintering nests) was much lower (64.6%) than in autumn-emerging clutches (95.2%; z = -11.24, df = 44, P < 0.001). Except for three nests, the emergence success of the hatchlings was 100% in the autumn, while it was highly variable in the case of spring emergence.

Body sizes of hatchlings and emergence success.— SCL and PW of nesting females were positively correlated with SCL and PW of their live hatchlings (Appendix Table 2). Clutch size and number of hatchlings had no effect on body size parameters of live hatchlings except CW and PW (Appendix Table 3). The periods of nesting and the season of emergence (autumn or spring) both affected the body sizes of hatchlings (Appendix Table 4; Fig. 6). Hatchling body sizes were significantly smaller if they emerged from clutches laid in the second nesting period. Hatchling size differed by season of emergence. Except for tail length, all body sizes of living emerged hatchlings were significantly smaller in spring than in autumn (Appendix Table 4).

Nests with seven or fewer live hatchlings had an emergence success of 85.67%, while nests with greater than eight hatchlings had an emergence success of 98.44%. More live hatchlings in the nest chamber significantly increased emergence success (t = 6.667, df = 44, P < 0.001, on log scale). There were significant differences in all body sizes between the 292 hatchlings that emerged from nests and the 27 that hatched but failed to emerge (Fig. 7). The body sizes of the dead hatchlings were significantly greater than the living ones calculated independently of the emerging season (Appendix Table 4).

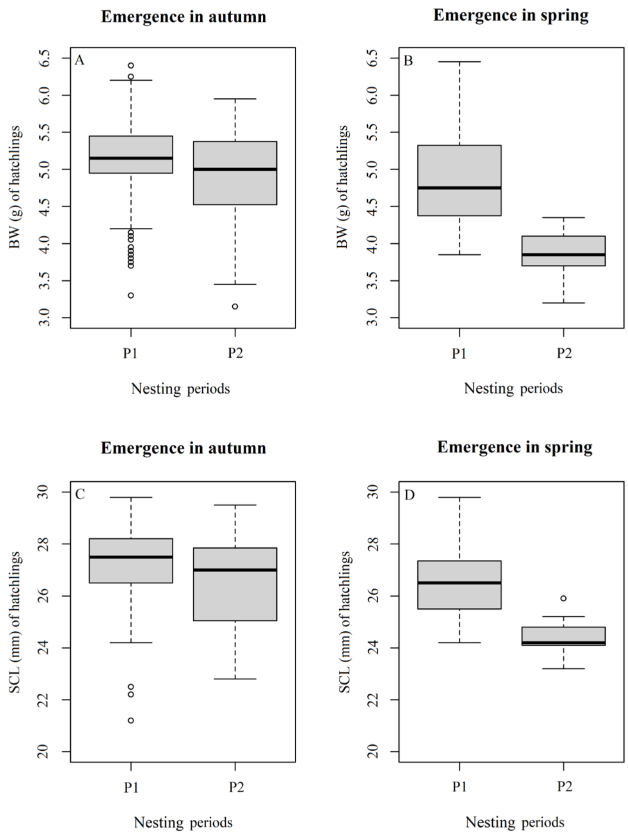

Figure 6. Patterns of the European Pond Turtle (*Emys orbicularis*) hatchlings (A) body weight (BW) emerging in autumn and (B) after overwintering in spring or straight carapace length (SCL); (C) emerging in autumn and (D) emerging after overwintering in spring depending on timing the egg-laying in the first (P1) or second (P2) period of the nesting season in the pond system of the Babat Valley, Hungary, between 2014–2017. See detailed description in Figure 4 of boxplot parts.

Nest protection efficiency.—We recorded 81 predated nests during the 4 y study. Most of the documented predation (61.7%) occurred at the two preferred nesting sites (32 at pond 5 and 18 at pond 1–2). At preferred sites, the ratio of predation was only 50% due to the nest protection. Nest protection used in Babat Valley at the two most preferred nesting sites during 2015–2017 meant 100% safety for eggs and hatchlings till emergence. We observed that predators tried to access the egg chamber from the side (eight occasions over the 4 y), but the frequently placed long spikes that fixed the iron mesh prevented the predators from reaching the eggs. Damages from unsuccessful predations occurred mainly at night but we restored them in the next days. Based on the footprints around the nests, Red Fox (*Vulpes vulpes*) were the main predator in the nesting area.

Discussion

Pattern of the nesting season.—Our data on nesting females body sizes in the case of BW and SCL is similar to what was found in both western European (Mitrus and Zemanek 2004; Zinenko 2004; Zuffi et al. 2006, 2007; Vamberger and Kos 2011) and more specifically Hungarian (Farkas et al. 1998; Kovács 2008; Lovász et al. 2012) studies. In Slovakia, Horváth et al. (2017) concluded that the mean daily temperature and the mean duration of sunshine must be 18º C and 8 h for European Pond Turtle to nest. We found that the mean daily temperature reached or exceeded this value in the Babat Valley 14 d before nesting started (https://www.eumet.hu/feleves-grafikonok/). From 2014 through 2017, nesting usually started at the end of May and ended in the middle of July in Babat Valley. Marián and Szabó (1961) report a similar nesting season in southwestern Hungary. The nesting season lasts 35–53 d in Babat Valley, which is like other European results (Schneeweiss et al. 1998; Mitrus and Zemanek 2000; Rössler 2000; Zinenko 2004; Horváth et al. 2017). Many nests were laid during the first 10 d of June during our surveys, as happened in Danube Delta (Kotenko 2000).

We documented a nesting season pause in the middle of June that lasted for 6–10 d depending on the year. Rössler (2000) found a similar nesting pause in Austria.

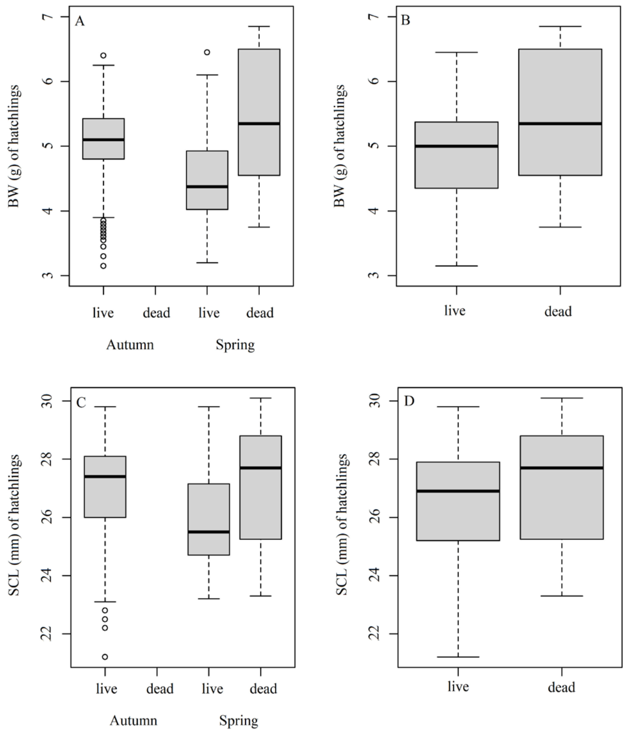

Figure 7. Body weight (BW) of live or dead hatchling European Pond Turtles (*Emys orbicularis*) (A) depending on the emerging season (Autumn, Spring) and (B) independently of emerging season and straight carapace length (SCL): (C) depending on the emerging season and (D) independently of emerging season in the pond system of the Babat Valley, Hungary, between 2014–2017. See detailed description in Figure 4 of boxplot parts.

We think it could be a sign of the female resting period between double-clutching. Previous results state that European Pond Turtles lay eggs only once in Germany (Andreas and Paul 1998; Schneeweiss et al. 1998) and Poland (Jabłoński and Jabłońska 1998; Mitrus and Zemanek 1998). We observed only four females laying eggs twice in a year. Zuffi and Foschi (2015) state that laying one clutch per year was much more frequent than multiple clutches in northern Italy, but for most populations in Italy, more than 77% of females reproduced annually and more than 50% of them laid eggs twice a year (Zuffi and Odetti 1998; Zuffi 2000, 2004). Zinenko (2004) also found two egg-laying peaks in one nesting season, which suggest double-clutching. We found that the number of days elapsed between the first and second clutches varied between 21 and 24 d. The number of days between clutches was 22–27 d in Austria (Rössler 2000), 18–29 d in Danube Delta (Kotenko 2000), and 18–27 d in Slovakia (Novotný et al. 2004). It seems that where the temperature of the summer season is balanced, there is an uninterrupted nesting season, but areas where in the middle of summer there is a drier and warmer period, some females can lay eggs in two periods, which may increase their reproductive success. Small females in the southern regions of distribution lay several but smaller clutches per season, while larger-sized northern females produce a single clutch with more eggs (Joos et al. 2017).

We found late predated nests at the end of July and August, as Marián and Szabó (1961) did in Hungary. Vamberger and Kos (2011) found newly plundered nests in September. The predation of some nests in late summer or autumn at our study area indicates that predators did not discover all nests immediately after the egg-laying, which shows that predators can predate the nests until hatching. Few newly hatched turtles, however, were observed in the ponds even before the nest protection, so the chance of successful embryonic development is possible in some nests and then probably the emergence of neonates also. Our results supported the hypothesis that females show a high degree of temporal fidelity of nesting. Most recaptured females had their nesting attempts within 5–10 d compared to the previous year. Similarly, Western Pond Turtles (*Emys marmorata*) nested within a 4 d interval in California, USA (St. John 2015).

Characteristics of reproduction success.—We can identify several reasons for the 23 unsuccessful nesting attempts at the two preferred nesting site in Babat Valley. In many cases, females may have been frightened by something that disturbed them while searching for a nesting site or digging the nest chamber. We suspect that a passing deer, mouflon, fox, or nearby people and machines could be frightening to females. In several other cases, roots were woven through the abandoned nest chambers and females could not tear them away. Because females had already used the water from the bladder to loosen the soil for digging, they left the area and came back on the next day.

The fecundity of female European Pond Turtles, characterized by clutch size, shows great variability within the distribution of the species (Rössler 1999; Zuffi et al. 1999, 2006; Zinenko 2004; Díaz-Paniagua et al. 2014; Ayaz et al. 2017). The average clutch size (9.25) in our study was similar to previously reported estimates from Hungary (Marián and Szabó 1961; Dely 1978; Péchy and Haraszthy 1997). Ayaz et al. (2017) found only a weak correlation between female body sizes and the numbers of eggs laid for seven localities in Turkey. We found that for our larger sample size of a single pond system, body sizes of nesting females were significantly correlated with the number of eggs laid and the larger females laid more eggs. We also found, however, that female turtles laid significantly fewer eggs at the second period of the nesting season.

The mean size parameters of the intact, unfertilized eggs we found in the excavated nests were very similar to other results (Marián and Szabó 1961; Mitrus 2000; Zinenko 2004; Díaz-Paniagua et al. 2014; Ayaz et al. 2017), but surprisingly egg weight was very low. We believe the lower mass value of measured eggs in our survey was due to the dehydration during the incubation period, while other researchers measured the eggs just after deposition. The low number of drowned eggs indicates that the two preferred nesting areas provide adequate environmental conditions for embryonic development. We compared the egg fertility and hatching success over the two periods of the nesting season, which is a new approach of analyzing reproduction. Overall, fertilization success was greater in the second period of the nesting season. This may be due to smaller clutch sizes. The hatching success of eggs laid in the second nesting period in 2016 and with the merged values of 2014–2017 was also significantly higher. Similar data were not available in the literature until now.

Neonates emerge from the nest usually in 3–4 mo, in August or September. Díaz-Paniagua et al. (2014) found that the emergence occurred during September and October; however, the development time of the embryo can be greatly shortened by prolonged summer heat (Marián and Szabó 1961). If hatching is delayed to the end of summer, the hatchlings may overwinter in the nest and will emerge in the following spring. This behavior is well documented in different turtle species including the European Pond Turtle (Rössler 2000; Fritz 2003; Mitrus and Zemanek 2003; Mitrus 2005; Ayaz and Cicek 2011; Lovich et al. 2014). The diversity of hatchling emergence strategies (autumn, spring, or both) can vary among locations and years. The emergence success of the hatchlings in Babat Valley was affected by the time of emergence. The emergence success of neonates in spring-emerging clutches was much lower than in autumn-emerging clutches. During harsh winters, the mortality rates of hatchlings overwintering in the nest may be very high (Andreas and Paul 1998; Najbar and Szuszkiewicz 2005). The Babat Valley is an extremely cold area of the Gödöllő-Hills region (https://www.eumet.hu/feleves-grafikonok/). The winter frost lasts for a longer period than in the surrounding areas, while the ice covering the surface of the lakes usually melts 1–2 weeks later than on nearby lakes. During our study, the harshest winter documented was in 2016 and 2017, of which January 2017 was the coldest month during the 4 y of the survey (https://www.eumet.hu/feleves-grafikonok/). Our data of mean emergence success at spring emergence, however, were 30% in 2015, 81.6% in 2016, 61.5% in 2017, so while harsh winters may decrease emergence success, it does not seem to be the only factor.

The body sizes of the hatchlings were significantly smaller if they emerged from clutches laid in the second period of the nesting season, or if the neonates emerged the next spring (after overwintering). The nearly half-year spent in the nest appeared to have a negative impact on the energy reserve of the neonates as their body sizes are smaller than the autumn emerged hatchlings. The cause of the lower emergence success of hatchlings in spring may not be only because of winter cold but also due to unsuccessful emergence attempts because the roots of plants densely invade the nest chamber during the incubation period (unpubl. data). If a small number of hatchlings try to dig themselves out of the nest, the success of emergence is reduced. In this case, we think the work of the hatchlings is less efficient and that their energy depletes faster. We found that a larger number of hatched neonates in the nest gave them a better chance to escape the egg chamber. We think in this case hatchlings can dig one after the other, so they save their energy reserves, increasing not only their own but the emergence success of the others.

The body sizes of the females were significantly positively correlated with SCL and PW of the emerged hatchlings, which means the neonates of larger females could have a better chance of surviving. Hatchlings from clutches laid in the second period of the nesting season were significantly smaller. This may be because in the case of double-clutching there was less time for females to allocate nutrients into the eggs or they had less available reserve for this purpose.

In our study, the range of body size parameters of hatchlings were higher than those found by Marián and Szabó (1961) in Hungary, likely due to our larger sample size. Other results of morphometric values of the hatchlings are not available from scientifically competent surveys in Hungary. Pupins et al. (2020) give a good review of the geographic variability of hatchling body sizes collected from the literature and grouped by country. Populations from the East-Central European countries are similar to ours, while those from the northern part of the distributional range are generally larger, and from the southern part are usually smaller (Pupins et al. 2020). The body sizes of neonates that successfully hatched but died in the nest were significantly greater than the living ones. We believe that the body sizes of living hatchlings are slightly smaller because they have used their energy reserves before emerging. Also, it could be that the body sizes of the dead hatchlings became larger than living ones because their tissues could swell due to water intake.

Nest protection effectiveness.—One of the greatest dangers in natural nesting sites is the presence of nest-robbing predators (Marián and Szabó 1961; Péchy and Haraszthy 1997). Surveys suggest that most of the nests are destroyed by predators on the same day or a day after oviposition (Zuffi and Rovina 2006; Havaš and Danko 2009; Fritz and Chiari 2013) because cues left by the nesting females are mostly detectable during the first days (Holcomb and Carr 2013). We also found that almost all unprotected nests were predated on the same night as the clutch were laid.

Almost all surveys list Red Fox (*Vulpes vulpes*), Wild Boar (*Sus scrofa*), Badger *(Meles meles*), Hedgehog (*Erinaceus concolor*), and feral Dogs *(Canis lupus familiaris)* among the possible nest predators (Mitrus and Zemaneck 1998; Mitrus 2000; Rössler 2000; Zuffi 2000; Vamberger and Kos 2011). Keeping predators away from the nesting sites is difficult. In the absence of thinning, the Red Fox population has increased in the Babat Valley. Many forms of nest protection have been developed (primarily to preserve the populations of sea turtles), and metal grids and cages have been used to protect nests of freshwater turtles, although little data are available on their effectiveness. Nest protection of freshwater turtles requires an enormous amount of human effort. Covering the nests with a protective metal grid or cage is very effective but requires the nightly presence of a researcher or volunteer during the nesting season. This can be solved only in the long term with the involvement of many citizen scientists who would be willing to devote the time necessary.

There are several solutions for the size and design of nesting grids and cages. Riley and Litzgus (2013) used belowground and aboveground cages and wooden-sided nest cages. Aboveground cages may attract multiple predators, but their effectiveness was excellent with only two nests being predated across the three design treatments. Schindler et al. (2017) compared different types of grid-based nest protection methods, and we used their Type B method. The depredation rate at this grid type was under 25%, or zero in several years over the total duration of their use. Other types of grids with smaller mesh size or which covered greater area showed lower depredation rate but may not allow the emergence of hatchlings or gave increased material costs and increased the necessary workforce. The Type B grid method provided 100% protection against predation attempts in our study while also allowing natural emergence of hatchlings.

Conclusion.—The nest protection program carried out in Babat Valley from 2014–2017 yielded two main results. The protection of 50 clutches allowed the successful development of the hatchlings under safe conditions. Another benefit of nest protection was that we managed to measure the reproductive biology parameters of the European Pond Turtle in the natural environment. Our results have shown that double-clutching occurs in Hungary, which may significantly increase the reproductive success of females. We have shown that between the two egg-laying periods, there is a resting pause which can be around 20 d on the individual level. Female body sizes had a positive correlation with the size of the live, emerged hatchlings, which can mean that offspring of larger and older females may have greater success in their early life. Some clutches overwinter in the nest. The success of hatchlings that emerged in the spring was significantly lower than that of the autumn emergence. Finally, the grid and cage method to protect turtle nests was 100% efficient, and we recommend its use for European Pond Turtle populations that are declining due to nest predation.

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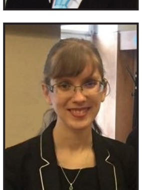

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Appendices

Appendix Table 1. Body size parameters of all female European Pond Turtles (*Emys orbicularis*) that were captured at the nesting attempts, and hatchlings in the pond system of the Babat Valley, Hungary, between 2014–2017. Abbreviations are BW: Body Weight, SCL: Straight Carapace Length, CW: Carapace Width, PL: Plastron Length, PW: Plastron Width, CH: Carapace Height, TL: Tail Length, and SD: standard deviation).

Body size		Females	Live hatchlings	Dead hatchlings
BW (g)	minimum-maximum	528–1,540	3.15–6.45	3.75–6.85
	mean ± SD	852.9 ± 188.69	4.85 ± 0.62	5.38 ± 1.01
	n	55	292	27
SCL (mm)	minimum-maximum	135–190	21.2–29.8	23.3–30.1
	mean ± SD	170.1 ± 10.60	26.5 ± 1.49	27.1 ± 2.12
	n	61	292	27
CW (mm)	minimum-maximum	110–141	18–27.1	21–27.5
	mean ± SD	129.3 ± 6.39	23.93 ± 1.38	24.52 ± 1.82
	n	61	292	27
PL (mm)	minimum-maximum	140–180	19.7–28.2	20.7–29
	mean ± SD	163.9 ± 10.13	24.26 ± 1.41	25.23 ± 2.43
	n	61	292	27
PW (mm)	minimum-maximum	88.5–112	12.6–18.5	13–18.2
	mean ± SD	99.9 ± 5.50	15.44 ± 1.07	15.74 ± 1.36
	n	61	292	27
CH (mm)	minimum-maximum	60–80	12–18.7	12.5–14.7
	mean ± SD	70.5 ± 5.04	13.95 ± 0.7	13.21 ± 0.64
	n	61	292	27
TL (mm)	minimum-maximum	45.8–83.2	11.8–25.5	18.5–25.5
	mean ± SD	68.5 ± 7.64	21.34 ± 1.39	22.65 ± 2.01
	n	53	292	27

Appendix Table 2. Effects of body size of female European Pond Turtles (*Emys orbicularis*) on the clutch size in the protected nests and hatchling body size in the pond system of the Babat Valley, Hungary, between 2014–2017. Abbreviations are BW: Body Weight, SCL: Straight Carapace Length, CW: Carapace Width, PL: Plastron Length, PW: Plastron Width, CH: Carapace Height, and TL: Tail Length. Significant values are bolded. Values marked with asterisk are marginally significant.

	Clutch size		Body size of live hatchlings	
Female body size	*t*	*P*	*t*	*P*
BW (g)	**2.30**	**0.042**	1.76	0.117
SCL (mm)	**2.66**	**0.020**	**3.00**	**0.017**
CW (mm)	**3.54**	**0.004**	0.63	0.546
PL (mm)	**3.41**	**0.005**	2.13	0.066*
PW (mm)	**2.79**	**0.015**	**3.59**	**0.007**
CH (mm)	2.07	0.058*	1.58	0.153
TL (mm)	1.50	0.163	0.54	0.606

Appendix Table 3. Regression between hatchling body size and the clutch size, hatchling number and living hatchling number of European Pond Turtles (*Emys orbicularis*) in the pond system of the Babat Valley, Hungary, between 2014–2017. Abbreviations are BW: Body Weight, SCL: Straight Carapace Length, CW: Carapace Width, PL: Plastron Length, PW: Plastron Width, CH: Carapace Height, and TL: Tail Length. Note that total number of hatchlings contains the number of dead and living hatchlings. Significant values are bolded. Values marked with asterisk are marginally significant.

	Clutch size		Total No. hatchlings		No. living hatchlings	
Body size	*t*	*P*	*t*	*P*	*t*	*P*
BW (g)	1.19	0.243	1.00	0.330	1.21	0.234
SCL (mm)	1.14	0.263	1.69	0.099	1.57	0.126
CW (mm)	1.60	0.118	2.00	0.053*	**2.15**	**0.039**
PL (mm)	0.88	0.384	1.40	0.171	1.36	0.182
PW (mm)	2.01	0.052*	**2.78**	**0.008**	**3.13**	**0.003**
CH (mm)	0.27	0.790	0.64	0.529	1.20	0.237
TL (mm)	0.27	0.790	0.42	0.675	-0.11	0.916

Appendix Table 4. Statistical results of European Pond Turtles (*Emys orbicularis*) hatchling size affected by emerging season, dead hatchlings and egg-laying periods in the pond system of the Babat Valley, Hungary, between 2014–2017. Abbreviations are BW: Body Weight, SCL: Straight Carapace Length, CW: Carapace Width, PL: Plastron Length, PW: Plastron Width, CH: Carapace Height, and, TL: Tail Length). Significant values are bolded.

					Effect of egg-laying period			
	Emerging season		Dead hatchling		Emerging in autumn		Emerging in spring	
Body size	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
BW (g)	**–5.55**	**< 0.001**	**5.43**	**< 0.001**	**–2.81**	**0.005**	**–7.79**	**< 0.001**
SCL (mm)	**–5.30**	**< 0.001**	**3.43**	**< 0.001**	**–2.69**	**0.008**	**–7.81**	**< 0.001**
CW (mm)	**–4.00**	**< 0.001**	**2.89**	**0.004**	**–6.59**	**< 0.001**	**–8.71**	**< 0.001**
PL (mm)	**–5.09**	**< 0.001**	**4.42**	**< 0.001**	**–2.69**	**0.008**	**–9.13**	**< 0.001**
PW (mm)	**–3.91**	**< 0.001**	**2.07**	**0.039**	**–3.48**	**< 0.001**	**–5.05**	**< 0.001**
CH (mm)	**–4.24**	**< 0.001**	**–2.71**	**0.007**	–0.69	0.487	**–3.86**	**< 0.001**
TL (mm)	–1.60	0.110	**3.59**	**< 0.001**	–0.05	0.957	**–2.72**	**0.008**