RESEARCH ARTICLE

Egg masses on the move: corixid oviposition on terrapin shells

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ARTICLE HISTORY

Received 4 April 2018

Accepted 14 August 2018

First published online

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ABSTRACT

In a very dry year, when aquatic habitats were scarce, we observed exceptionally massive corixid oviposition on terrapin shells in Doñana National Park, southwestern Spain. Most terrapins inhabiting a large pond devoid of aquatic vegetation exhibited a dense cover of corixid eggs, while terrapins from vegetated ponds had no egg cover. Corixid oviposition had also been observed on terrapin shells in previous periods of severe drought. Considering that terrapins frequently alternate between aquatic and terrestrial environments, we experimentally assessed the viability of corixid eggs in varying degrees of dry exposure. A significant proportion of corixid eggs did not hatch when they were occasionally dried under sun exposure, but egg mortality was lower when they were dried in the shade. The massive oviposition on terrapin shells was probably a consequence of the limited availability of adequate oviposition sites, and it might increase the odds of egg survival when terrapins migrate to other ponds.

KEYWORDS

Corixidae; freshwater turtles; dispersal; drought; Spain

Introduction

In a temporary pond network, aquatic species use different strategies to resist pond desiccation during the dry season (Wiggins, Mackay, and Smith 1980; Williams 2006). When ponds are starting to dry out, many aquatic insects disperse to other ponds that still retain water. This annual dispersal dynamics of macroinvertebrates has been described in Doñana National Park, in southwestern Spain, where a high number of temporary ponds with high interconnectivity may be flooded in wet years, while most of them do not fill in years of scarce rainfall (Díaz-Paniagua et al. 2015). More than 120 macroinvertebrate taxa have been recorded in the Doñana pond network, among which dytiscids and heteropterans are good dispersers (Florencio, Serrano, Gómez-Rodríguez, Millán, and Díaz-Paniagua 2009). During summer, when most of the ponds are dry, individuals of these species resist summer conditions in the few permanent water bodies remaining in the area. Nine species of corixids have been described in this pond network, among which *Corixa affinis* (Leach, 1817a) and *Sigara lateralis* (Leach, 1817b) are the most abundant (Florencio, Díaz-Paniagua, Gómez-Rodríguez, and Serrano 2014). The pond network supports a high diversity of other invertebrates and vertebrates, including two species of chelonians, the stripe-necked terrapin, *Mauremys leprosa* (Schweigger, 1812), and the European pond turtle, *Emys orbicularis* (Linnaeus, 1758), which are mainly associated with the larger, more permanent ponds (Keller, Díaz-Paniagua, Andreu, and Bravo 1995).

The use of terrapin shells as oviposition sites by corixids was known from Doñana ponds since the 1990's, and was recorded again in 2014. In this study, we quantified the occurrence and abundance of corixid oviposition on chelonian shells in Doñana ponds. We hypothesised that the phenomenon is associated with dry periods in which aquatic habitats are very scarce. We aimed to evaluate the possibility that terrapins disperse corixid eggs by experimentally estimating the survival probability of eggs exposed to simulations of the alternation of terrestrial and aquatic activity of these reptiles when they bask or migrate to other ponds. To our knowledge, this is the first report on dense aggregation of aquatic insect eggs on chelonian shells.

Material and methods

Study area

Doñana National Park is located between the mouth of the Guadalquivir River and the Atlantic Ocean in southwestern Spain (36°58'41"N, 6°20'40"W). In this area, most freshwater habitats are temporary, including an extensive freshwater marsh and a network of ponds located on a sandy area, in which the desiccation phase is initiated in late spring or early summer (Díaz-Paniagua et al. 2010, 2015). During summer, most ponds are dry, except for two or three permanent or semipermanent larger ponds or shallow lakes that are usually flooded year round, except in years of very severe drought. The largest of these ponds, Santa Olalla, covers an approximate area of 45 ha and is considered permanent, although it reached desiccation in summer of 1995 after a long period of severe drought (Figure 1). Besides its higher water retention capacity, Santa Olalla also differs from the other ponds in Doñana by its higher electrical conductivity and lack of aquatic vegetation (López, Toja, and Gabellone 2001). The second largest pond, Dulce, is contiguous to Santa Olalla covers an approximate area of 12 ha and is considered semipermanent, as it only dries out in very dry years (Figure 1). Unlike Santa Olalla, Dulce harbors submerged aquatic vegetation (i.e., *Ranunculus peltatus* Schrank, *Myriophyllum alterniflorum* DC, *Callitriche brutia* L., *Elatine macropoda* Guss., etc), as well as a dense stand of helophytes (mainly *Typha dominguensis* Pers.) that covers approximately 1/10 of its surface. In addition to the natural ponds, there are more than 150 semiartificial watering stations for cattle and/or wild fauna throughout the park, dug out in low parts of the basin of natural ponds that function as small permanent ponds (covering approximate areas of 30 m² in summer), and are locally known as zacallones. The basin of all ponds in the park is sandy, with no presence of rocks that could be used as substrate for corixid oviposition.

[FIGURE 1 NEAR HERE]

The climate in the area is Mediterranean, with an average annual rainfall of 550 mm, and an irregular distribution of rain from autumn to winter and spring (Díaz-Paniagua et al. 2015). Pond filling is usually associated with the month in which more than 200 mm rainfall accumulates after summer, which varies from October to March. In summer, most temporary ponds are dry. The number of ponds that persist

throughout summer varies depending on annual rainfall in the current and previous years (Gómez-Rodríguez et al. 2010). Over the last five decades, there have been periods in which the Doñana pond network was particularly deteriorated, coinciding with periods of successive dry years (1980–1983 and 1992–1995), as well as extremely low levels of summer inundation in isolated dry years (1999, 2005, 2012, 2014), when all ponds dried out in summer, except Santa Olalla and the zacallones. The dry period in the 1990's ended with the complete desiccation of Santa Olalla in 1995 (total rainfall 252 mm in the cycle 1994–1995, recorded at a meteorological station located within Doñana National Park). During the more recent dry cycle in 2013–2014 (total rainfall 347 mm), Santa Olalla was the only natural pond that retained water throughout the summer, when its inundated area decreased to less than 1/3 of its usual summer level (Díaz-Paniagua and Aragonés 2015) (Figure 1).

Field data and identification

The observation that triggered the study was made on 16 May 2014. A single adult female of stripe-necked terrapin, *Mauremys leprosa*, was observed digging a hole, probably for nesting, on the sandy ground close to the edge of Santa Olalla pond. Its carapace was covered by a thick layer of insect eggs (Figure 2). With the aim of detecting more individuals carrying similar cover of insect eggs, we captured terrapins using fyke nets in Santa Olalla and Dulce ponds on two sampling occasions. On 28 May 2014, we sampled Santa Olalla and Dulce ponds (five traps in each pond exposed during 24 hours) and captured 12 and 9 *M. leprosa* terrapins, respectively in the two ponds. On 27 June 2014, only Santa Olalla could be surveyed because Dulce was so close to desiccation that water depth was insufficient for the use of fyke nets and no terrapins were observed in the water anymore. On this occasion, we captured 31 *M. leprosa* terrapins. We counted the number of terrapins that carried insect eggs and took photographs of their shell (carapace and plastron). We estimated on the photographs the percentage of the shell area covered by eggs. Based on our experience with aquatic insect diversity in Doñana ponds, we suspected these were corixid eggs, which was later confirmed when eggs hatched in the laboratory. The development of the nymphs hatched in the laboratory was not completed, therefore we were not able to identify them to species level.

To assess the magnitude of the phenomenon, we analysed data from a capture-recapture program of terrapins in Doñana in the 1990's, when information on incrustations (algae and insect oviposition) present on the shell of terrapins was recorded systematically in five years (1991–1995). In this period, corixid oviposition cover was estimated visually. The program monitored 33 ponds throughout Doñana National Park yearly (Keller 1997). Terrapins were captured with the same trapping devices used in 2014.

We used a standardised procedure to assess the presence of corixid egg masses in Santa Olalla, Dulce, and other surrounding ponds. In the summer of 2014, we used 30-cm-long wood sticks (stick width = 4 mm) placed vertically into the pond as artificial oviposition sites. Sticks were exposed in 10-piece arrays per point for 24 hours. The number of sampling points per pond varied according to pond size from one (small ponds and zacallones) to four (Santa Olalla and Dulce), totaling 16 points. We classified our sampling points in relation to the presence or absence of aquatic vegetation. Additionally, we used a dipnet to assess the species of corixids present in the ponds sampled. We made 6–10 sweeps with the dipnet per sampling point and counted the number of individuals of the different species of corixids recorded.

Of the years with available data on terrapin shell incrustations, 1991 was a rainy year, and 1992–1995 were increasingly dry years, culminating with the complete desiccation of Santa Olalla in 1995. In 2014 (as in 1992, 1993 and 1994), Santa Olalla reached a below-average minimum inundation level while most or all other natural ponds dried out.

Experimental assessment of corixid egg viability

Because terrapins usually bask outside the water and move on land for nesting or dispersal purposes, we assessed whether corixid eggs remained viable after being exposed to dry conditions over variable time periods. In July 2014, we placed wood sticks ($N = 150$) completely submerged in Santa Olalla for 24h. All sticks were covered

with corixid eggs after this period. We transported the sticks, submerged in pond water, to our laboratory where we exposed the egg-covered sticks to different intervals of dry conditions (3, 10, 30, 60, 120, 240 and 360 minutes; $N = 10$ sticks per treatment), either in direct exposure to sun or in shade. After exposure, the sticks with eggs were kept submerged at 20°C constant water temperature for 30 days in a climatic chamber. We counted every day the number of eggs hatched. The control group consisted of 10 egg-covered sticks that were permanently kept under water. We used R software (version 3.1; R Core Team 2014) to compare the number of eggs hatched every day among treatments with the survival plugin in R commander (Fox and Carvalho 2012), based on the Kaplan-Meier function.

Results

Presence and abundance of corixid eggs on terrapin shells

Insect eggs extended over approximately 90% of the total carapace area of the first female observed in 2014 (Figure 2). Some of the eggs were hatched, and among them we spotted one individual of *Sigara lateralis* (Figure 2). Eggs were also attached to the lateral bridges of the carapace, and to the terrapin's tail and limbs. No eggs were found on the plastron, possibly because they were removed by the friction with the ground during the displacement of the animal on land.

[FIGURE 2 NEAR HERE]

In 2014, we captured only *Mauremys leprosa* in Dulce and Santa Olalla. All terrapins from Santa Olalla, but none from Dulce, carried corixid eggs (Table 1). In May, most individuals ($N = 12$) from Santa Olalla had over 30% of the shell covered with corixid eggs, while in June, most individuals ($N = 31$) only had small isolated eggs scattered on the shell, and only three terrapins had more than 10% of the shell covered.

During 1991–1995, we revised yearly data for 319 to 725 individuals of *M. leprosa* captured in the 33 surveyed ponds (in the driest year only 10 of these ponds were available). We only detected corixid oviposition on *M. leprosa* in 1992, 1993 and 1994, mostly from May to July, except for two individuals that were found in April

(Table 1). As in 2014, the infestation was mainly concentrated in Santa Olalla, while only three individuals carried corixid eggs in Dulce in 1993 (Table 1)

Emys orbicularis was not frequent in Santa Olalla, where we only captured 40 non infested individuals. They were commonly captured in Dulce ($N = 317$) where we only detected three individuals of this species carrying corixid eggs.

[TABLE 1 NEAR HERE]

Assessment of corixid oviposition in different ponds

We recorded corixid eggs on the test-sticks in four of the ten surveyed water bodies, but only in Santa Olalla a massive concentration of eggs was observed (Table 2). Corixid eggs occurred at five out of the eight points without aquatic vegetation (corresponding to two of five ponds deprived of vegetation), but only at three points out of eight with aquatic vegetation (corresponding to two out of three vegetated ponds). In Santa Olalla, we recorded three species of corixids: 42% individuals were *Sigara lateralis*, 20% *Sigara scripta* (Rambur, 1840), 20.5% *Sigara sp.* nymphs, and 17.5% *Corixa affinis* (Leach 1817a).

[TABLE 2 NEAR HERE]

Experimental assessment of viability of corixid eggs

Most of the eggs (98%) in the control group (continuously submerged) had hatched by the end of the experiment. The proportion of unhatched eggs was significantly lower than in the control in all sun and most shade treatments (Figure 3). Hatching success decreased to below 20% for sun-dried eggs from 30-min exposure onwards, and from 120-min exposure onwards for shade-dried eggs. No eggs hatched when sun exposure was 60 min or longer. No hatching was observed over 340-min exposure both for sun and shade-dried eggs. After 12 days, no more eggs hatched.

[FIGURE 3 NEAR HERE]

Discussion

We could not identify with certainty which corixid species produced the massive egg-laying on terrapin carapaces, although the highest abundance in the pond in which it was detected corresponded to *Sigara lateralis*. Corixid species are common in Doñana ponds, in which they are reported to disperse to long hydroperiod ponds when their aquatic habitats are drying out (Florencio et al. 2009). They disperse in mass when ponds are close to drying out, including high proportions of egg-bearing females (Boda and Csabai 2009).

The extensive cover of corixid eggs that we observed on terrapin shells was probably a consequence of the high abundance of corixids in their summer refuges, where females oviposited after mass dispersal from temporary ponds. However, we only recorded massive egg cover on terrapins in one pond, Santa Olalla, where the density of reproducing corixids was so high that they were likely to use any object in the pond, including terrapin shells, as oviposition substratum. Submerged sticks and fyke-nets placed into the pond were covered with eggs within a single day. Although this is the largest and most permanent pond in Doñana, it is also characterised by the absence of aquatic vegetation. Corixids commonly lay their eggs on leaves or stems of aquatic vegetation (Barahona, Millán, and Velasco 2005), therefore, the lack of optimal oviposition sites in Santa Olalla probably forced corixids to lay their eggs on any alternative substratum. Accordingly, no such egg abundance covering terrapin carapaces was observed in vegetated ponds.

Long-term data showed that, in Doñana, corixid oviposition on terrapin shells seems to be associated with exceptionally dry years. In these years, ponds dry out earlier, and the number of inundated ponds is very scarce during the summer, leading to exceptionally high concentrations of corixids, that are forced to reproduce in few crowded refugia for aquatic fauna. Some of these refugia provide adequate substrata for corixid eggs, as occurred in Dulce pond, where we observed corixid eggs attached to vegetation instead of the test-sticks or terrapin carapaces. Data for dry years in the 1990's confirmed that massive corixid egg-laying on terrapin carapaces is restricted to Santa Olalla pond. This phenomenon is likely symptomatic of the stress in the pond

network during years of severe drought, when the spatial limitation imposed by the lack of inundated ponds probably constrains the reproductive dynamics of corixids.

The absence of eggs on terrapin carapaces in other ponds indicates that this is not a preferred oviposition substratum for corixids. Yet, the repeated and massive use of terrapin shells as egg-laying substratum in Santa Olalla suggests that the presence of the reptiles likely contributes to increase the reproductive success of corixids in Doñana in exceptionally dry years, when there is an acute shortage of oviposition space in their main refugium. The main trade-off for corixid egg survival on this surrogate oviposition surface lies in the fact that terrapins spend time out of the water for various reasons. Terrapins frequently bask out of the water, implying long daily periods in which their carapaces are dry and exposed to the sun, which has been shown to be highly deleterious for corixid eggs beyond a 30-minute exposure. Basking favors thermoregulation, and can also occur in the shade, in order to dry the integument to avoid the incrustation of algae or the proliferation of parasites and bacteria (Cagle 1950, Boyer 1965), in which case higher survival rates of corixid eggs would be assured for exposures of up to one hour.

Terrapin nesting migrations, which occur in the summer, could also expose corixid eggs to deleterious dry-periods. However, nesting trips of *M. leprosa* in Doñana usually occur at dusk or during the night and at short distances from the pond margin (Díaz-Paniagua et al. 2014), so that exposure conditions would be more benign to corixid eggs. In addition, in this case only corixid oviposition on carapaces of adult terrapin females would be affected.

Terrapins migrate among ponds, mainly between Santa Olalla and Dulce (Keller 1997), which are separated by only 150 m. It is likely that terrapins harboring corixid eggs that were captured in Dulce pond had been colonised in Santa Olalla and then moved over to Dulce. Migratory movements of terrapins when ponds are close to desiccation may promote a successful dispersal of corixids when distances are short and especially if they move during the night or at dusk.

In summary, the massive deposition of corixid eggs observed on terrapin carapaces in Doñana probably is a strategy to increase oviposition substrate and reproductive success in extreme environmental conditions that limit the availability of

water to a few sub-optimal refugia. The attachment of eggs to terrapins, which may move to other water bodies, increases the possibility of successful dispersal of corixids to other ponds when the home-pond dries out, increasing their odds of survival and colonization of new ponds. However, the susceptibility of corixid eggs to drying out, even after short periods of dry-exposure (around one hour), suggests that oviposition on terrapin carapaces is not an optimal strategy of these insects to disperse their offspring to other ponds, but more likely the consequence of the low availability of water bodies with adequate substrates for oviposition.

Acknowledgements

The authors would like to thank the staff of the Monitoring Team of Natural Processes in Doñana (RBD-ICTS) for their help in the field work.

Funding

We thank the financial support obtained from the Spanish Ministry of Economy and Competitiveness to VC, through the Severo Ochoa Programme for Centres of Excellence in R&D&I (SVP-2013-067595).

Disclosure statement

No potential conflict of interest was reported by the authors.

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Table 1. Proportion (%) of individuals of stripe-necked terrapins, *Mauremys leprosa* (Schweigger, 1812), carrying corixid eggs on the shell among the total number of individuals captured (in parenthesis) in 1991–1995, and 2014 in Santa Olalla pond, Dulce pond, and other ponds surveyed in Doñana. N ponds = number of available ponds out of the maximum 33 surveyed in the rainy year of 1991. Two hyphens indicate that these ponds were not surveyed in this year. Annual rainfall = annual accumulated rainfall recorded in the study area for each hydrological cycle (from September 1 of the previous year to August 31 of the indicated year).

Years	Annual rainfall (mm)	Santa Olalla	Dulce	Other ponds	N ponds
1991	480	0 (330)	0 (174)	0 (113)	33
1992	494	58.1 (260)	4.4 (68)	0 (93)	20
1993	374	45.0 (460)	0 (111)	0 (154)	15
1994	414	10.7 (224)	0 (219)	0 (117)	11
1995	252	0 (23)	0 (252)	0 (44)	10
2014	348	100(43)	0(9)	--	2

Table 2. Doñana water bodies sampled for the presence of corixid oviposition in 2014 using wooden stick arrays, indicating the presence of corixid species, ranked after their relative abundance. Zacallón = artificially dug out watering station in the basin of a natural pond that functions as a small permanent ponds. A plus (+) sign indicates the presence of aquatic vegetation. N eggs = total approximated number of eggs among all sticks in the array. SL: *Sigara lateralis* (Leach, 1817b), SC: *Sigara scripta* (Rambur, 1840), SG: *Sigara stagnalis* (Leach, 1817b), Sn: *Sigara sp.* nymphs, CA: *Corixa affinis* (Leach, 1817a), CP: *Corixa panzeri* (Fieber, 1848), Cn: *Corixa sp.* nymphs.

id	Locations	Pond characteristics	Point		N eggs on sticks	Corixid species
			in pond	Aquatic vegetation		
1	Santa Olalla	large natural	1	-	500	SL > Sn >
2	Pond	permanent	2	-	200	SC > CA
3		pond	3	-	450	
4			4	-	300	
5	Dulce Pond	large natural	1	+	0	SL > Sn >
6		semipermanent	2	+	50	CA > Cn >
7		pond	3	+	0	SG > SC >
8			4	+	25	CP
9	Taraje 1	zacallón	1	-	25	SL > CA > SC > SG = Sn
10	Taraje 2	zacallón	1	+	30	CA > SC > Sn
11	Zacallón Santa Olalla	zacallón	1	-	0	CA > SL > SG > SC > Sn
12	Casa Santa Olalla	zacallón	1	+	0	CA
13	Baquetas	zacallón	1	-	0	Sn > CA >

						SL
14	Porquera	zacallón	1	+	0	Sn > CA > SL > SC
15	Verdes	zacallón	1	+	0	CA > SL > SG > Sn > SC
16	Pinar San Agustín	zacallón	1	-	0	CA > SC > SL > Sn

Figures :

Figure 1. (Colour online) Aerial image of the ponds of Santa Olalla and Dulce in Doñana National Park in the month of peak summer drought in August 2014. The image shows the dried out whitish pond bed and the remaining water surface (Photo: H.Garrido/EBD-CSIC).

Figure 2. (Colour online) Occurrence of massive corixid oviposition on shells of stripe-necked terrapin, *Mauremys leprosa* (Schweigger, 1812) and experimental sticks: (a) A female terrapin with the shell densely covered by corixid eggs; (b) detail of the eggs and one individual of *Sigara lateralis* (Leach, 1817b) observed on the shell of the same individual; (c) close-up of corixid eggs in different maturation stages on a terrapin carapace; (d) detail of the experimental sticks covered with corixid eggs.

Figure 3. Hatching success of corixid eggs exposed to dry conditions for different time periods. Number of eggs monitored: 1986 (continuously submerged control group), 3498 (3 min shade-dry), 5925 (3 min sun-dry), 735 (10 min shade-dry), 1290 (10 min sun-dry), 1470 (30 min shade-dry), 5280 (30 min sun-dry), 969 (60 min shade-dry), 3090 (60 min sun-dry), 1354 (120 min shade-dry), 3234 (120 min sun-dry); 740 (240 min shade-dry), 545 (240 min sun-dry), 671 (360 min shade-dry), 671 (360 min sun-dry). (*) indicates significant differences ($P < 0.05$) in relation to the control (always wet) according to survival Kaplan-Meier function comparisons.