REVISTA CHILENA DE HISTORIA NATURAL

Revista Chilena de Historia Natural 85: 281-289, 2012

RESEARCH ARTICLE

Seasonal dynamics of larvae and adults of two *Enochrus* Thomson (Coleoptera: Hydrophilidae) species in temporary and permanent water bodies of an urban park in Buenos Aires

Dinámica estacional de larvas y adultos de dos especies de *Enochrus* Thomson (Coleoptera: Hydrophilidae) en cuerpos de agua temporarios y permanentes en un parque urbano de Buenos Aires

BARBARA BYTTEBIER[1, *], SYLVIA FISCHER[1] & PATRICIA L. M. TORRES[2]

[1] Grupo de Estudio de Mosquitos, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina
[2] Laboratorio de Entomología, Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina
[*]Corresponding author: bbyttebier@ege.fcen.uba.ar

ABSTRACT

The dynamics of *Enochrus variegatus* (Steinheil) and *Enochrus vulgaris* (Steinheil) in temporary pools and permanent ponds were studied in an urban park of Buenos Aires, Argentina. Samples were collected from both types of habitats weekly throughout one year, and variables like water surface and vegetation cover were recorded. In permanent ponds, adults of both species were found throughout the study period, while in temporary pools their presence depended on the availability of water. Differences in their reproductive seasons and breeding sites were observed. *Enochrus vulgaris* was characterized by an opportunistic strategy, and its larvae were detected in both types of habitats, associated mainly with spring and summer temperatures. Conversely, *E. variegatus* larvae were recorded almost exclusively in temporary pools, during the winter and spring seasons. In permanent ponds, both species were associated with vegetation cover, which could be related to the availability of refuges from fish predators. First instar larvae showed the highest abundance and were captured more frequently, in consecutive weeks and simultaneously with third instar larvae, suggesting that the two populations studied are not synchronized in oviposition time or development of immature stages. In several occasions, second instar larvae of both species were captured in a pool that had been dry during the previous sampling date, suggesting that they had not hatched from fresh laid eggs. Our findings show that adults of these species are capable of dispersal to and from temporary pools to avoid drought. In addition, their larval stages may also be able to resist drought in the pools by burrowing into the substrate.

Key words: adaptation to drought, aquatic Coleoptera, Hydrophilidae, population dynamics, water permanence.

RESUMEN

Se estudió la dinámica de *Enochrus variegatus* (Steinheil) y *Enochrus vulgaris* (Steinheil) en ambientes acuáticos temporarios y permanentes de un parque de Buenos Aires, Argentina. Las muestras fueron colectadas semanalmente a lo largo de un año en ambos tipos de ambiente, y se registraron variables como la superficie anegada y la cobertura vegetal. En los ambientes permanentes se capturaron ejemplares adultos de ambas especies a lo largo de todo el período de estudio, mientras que en temporarios su presencia varió de acuerdo con la disponibilidad de agua. Se observaron diferencias en la época reproductiva y sitios de cría de ambas especies. *Enochrus vulgaris* mostró una estrategia más oportunista, y sus larvas fueron detectadas en los dos tipos de ambiente asociadas principalmente con temperaturas de la primavera y el verano. En cambio las larvas de *E. variegatus* fueron registradas casi exclusivamente en cuerpos de agua temporarios durante el invierno y la primavera. En ambientes permanentes, ambas especies estuvieron asociadas con una mayor cobertura vegetal, lo cual podría estar relacionado con la disponibilidad de refugios de peces predadores. Para ambas especies el primer estadio larval fue colectado en mayor abundancia y frecuencia que los restantes. Las larvas de este estadio fueron registradas en semanas consecutivas y simultáneamente con larvas del tercer estadio, indicando que la oviposición o el desarrollo de los estadios inmaduros no estaban sincronizados dentro de cada una de las dos poblaciones estudiadas. En varias ocasiones se capturaron larvas del segundo estadio de ambas especies en charcos que estuvieron secos la fecha de muestreo anterior, sugiriendo que no eclosionaron de huevos recientemente puestos. Nuestros resultados muestran que los adultos de estas especies son capaces de dispersarse desde y hacia charcos temporarios para evitar la sequía, y que sus larvas podrían resistir la sequía en los ambientes temporarios enterrándose en el sustrato.

Palabras clave: adaptación a la sequía, coleópteros acuáticos, dinámica poblacional, Hydrophilidae, permanencia de agua.

INTRODUCTION

Lentic freshwater habitats in temperate regions range from small and ephemeral pools to large and permanent ponds or lakes that could be organized along a gradient of water permanence. Organisms inhabiting these habitats differ in their ecological strategies according to the range of the water permanence gradient they occupy. The main factors that determine the presence and success of a species within a specific portion of the duration gradient are physicochemical constraints and biological interactions (Wellborn et al. 1996). The permanence of water affects the relative importance of biotic and abiotic processes in determining the presence and distribution of species in freshwater habitats (Schneider & Frost 1996).

In habitats that frequently dry out, the main physical constraint for aquatic organisms is the lack of water. However, some organisms take advantage by colonizing these habitats, exploiting both the rich resources offered by these temporary pools and the relative absence of predators (e.g., fishes). The aquatic invertebrates that colonize temporary waters have developed different strategies to survive the dry periods, which include physiological tolerance, effective capacity for migration, and/or changes in life history (Wiggins et al. 1980, Williams 2006). Although the adaptations of different species are diverse, members of the same taxonomic group show similar strategies at the same stage of life cycle (Stanley et al. 1994, Williams 2006).

Both physiological and behavioral mechanisms to survive dry periods have been documented in aquatic coleopterans. In some cases, adults disperse opportunistically or seasonally to temporary bodies of water, where oviposition and development of immature stages occur. When the pools dry out, adults return to more permanent sites, where they find refuge over the unfavorable periods (Fernando 1958, Fernando & Galbraith 1973, Wiggins et al. 1980, Wellborn et al. 1996). In other cases, instead of dispersing to sites that retain water, adults may burrow into the substrate, either superficially under dead leaves, or deeper in the ground (Williams 2006).

Among the beetles inhabiting temporary and permanent water bodies of temperate Argentina, the genus *Enochrus* Thomson (Hydrophilidae) is represented by several species (Fernández 1988, 1989, 1994, 1997, 2006, Fernández & Bachmann 1998). Two of the most frequent species in aquatic environments of Buenos Aires are *Enochrus variegatus* (Steinheil) and *Enochrus vulgaris* (Steinheil). These beetles can be found in a wide range of water bodies, such as temporary pools or permanent ponds of varying size and vegetation cover (Poi de Neiff 1983, von Ellenrieder & Fernández 2000, Fernández & López Ruf 2006, Torres et al. 2007, Fontanarrosa et al. 2009).

Although ecological studies about *Enochrus* are scarce, species of this genus are usually mentioned as part of the aquatic insect community. Several studies have reported the presence of the genus *Enochrus* in water bodies of Buenos Aires (Fischer et al. 2000, von Ellenrieder & Fernández 2000, Fontanarrosa et al. 2004, 2009, Fernández & López Ruf 2006). Regarding immature stages, most of the information is published in the context of taxonomic descriptions of the species (Archangelsky 1997). No previous studies have been performed on the seasonal dynamics and breeding sites of larval instars of *Enochrus* species, with the exception of a mention for *E. vulgaris* larvae during summer in a permanent pond (Fernández 1992). The main difficulty until now has been the impossibility to distinguish immature stages at the species level. Nevertheless, in a recent study we have described the larval morphology of *E. vulgaris* and *E. variegatus* (Byttebier & Torres 2009). This will allow the differentiation of immature stages of these species in field studies and thus represents an opportunity to investigate reproductive and ecological aspects of these species at the population level.

We aim to describe the seasonal dynamics of *E. vulgaris* and *E. variegatus* and their reproductive strategies in temporary and permanent urban water bodies of the city of Buenos Aires.

METHODS

Study area

The city of Buenos Aires is located in a temperate climate zone, with four clearly distinguishable seasons, mainly related to temperature differences. In this paper we follow the criterion of the National Meteorological Service, which classifies seasons according to the following three-month periods: December-February (summer), March-May (fall), June-August (winter), and September-November (spring). Mean temperatures are 23.6 °C during the summer, 17.8 °C during the fall, 11.5 °C during the winter, and 17.3 °C in the spring. Rainfalls occur year round, and although highest values are recorded in the summer (341 mm) and lowest values in the winter (199 mm), there is no distinguishable rainy season (National Meteorological Service 2011).

Field studies were carried out in the "Golf Club Lagos de Palermo", which covers 15 hectares, located in the north-eastern zone of the city of Buenos Aires (34º33' S, 58º26' W). The vegetation of this park is mainly grass subject to periodical cut, and isolated groups of trees. This recreational area contains five permanent, human-made ponds with surface areas of at least 500 m^2, and because of the irregular relief of the land, the formation of around 50 temporary pools with variable size and permanence is favored after rainfalls. Based on preliminary studies, we selected two permanent ponds and two temporary pools as representative habitats for the species analyzed in this study.

The permanent ponds were characterized by a constant water surface of 3000 m^2 (pond A) and 650 m^2 (pond B). Both ponds sheltered fish populations (*Cnesterodon decemmaculatus* [Jenyns]), which are potential predators of aquatic insects. Pond B lacked vegetation, while pond A was covered by floating (*Azolla filiculoides* Lam.) and submerged flora.

Both temporary pools (pool C and pool D) showed fluctuations in the water level, and dried out repeatedly through the study period. The maximum surface area and depth in each pool were less than 90 m^2 and 25 cm respectively. The substrate of both pools was covered by grass (similar to all temporary pools present in the studied area), and both pools were exposed to sunlight during most of the day.

Sampling and identification

The permanent ponds and temporary pools selected were evaluated weekly throughout a one-year period (June 2001 - May 2002). The maximum length and width (m) of each temporary pool were measured on each sampling date, and the proportion covered with water of the rectangle formed by these two variables was assessed.

Samples of aquatic insects were collected with a hand net (mesh size 300 µm, mouth opening 10.5 x 4.5 cm). The sampling effort in permanent ponds was constant (10 net sweeps covering 1 m each), whereas that in temporary pools was approximately proportional to the area covered by water on each sampling date, according to a previously adjusted scale (Fontanarrosa et al. 2004). The samples were fixed in situ in ethanol 96 % and transferred to the laboratory for identification.

In the laboratory, *Enochrus* spp. adult and larval specimens were identified to species level by using the appropriate systematic keys and original descriptions (Fernández 1989, 1994, 1997, Oliva et al. 2002, Byttebier & Torres 2009). Adult specimens were identified with a stereoscopic microscope, whereas larvae were identified with an optic microscope. For each sample, adults and larvae of each species (*E. variegatus* and *E. vulgaris*) were counted.

Data analysis

Water dynamics and seasonal distribution of adults and larvae in temporary and permanent water bodies:

For each sampling date and each temporary pool, the surface area was calculated by multiplying maximum dimensions by coverage proportion. In order to analyze flooding fluctuations, water surface data of both pools were added by sampling date and transformed to percentage values, the date with the maximum flooding was considered as 100 %. Weekly values of percent surface area were compared between seasons with a Kruskal-Wallis test. Post-hoc multiple comparisons of mean ranks for all pairs of seasons were used to identify significant differences (Siegel & Castellan 1988). Permanence of temporary pools was estimated as the sum of consecutive periods between sampling dates in which the pools contained water. After dry periods, the date of flooding of a pool was assigned to the date of the previous rainfall event. Meteorological data for the study period were provided by the National Meteorological Service.

Sampling dates were classified according to the season, and for each season the proportion of dates with adults and larvae of each species was calculated. On the other hand, the yearly number of sampling dates with adults and larvae of each species was divided by the total number of sampling dates to assess the overall proportion of detection in permanent and temporary waters separately. In the latter case, only dates when water was present were considered. The proportions obtained were compared between seasons (habitat types pooled) and between permanence categories (seasons pooled) by means of a chi square test for independent proportions (adults and larvae of each species separately). This test is comparable to computing the Pearson chi square statistic for contingency tables. Differences between pairs of seasons were examined by subdividing the contingency tables and computing the chi square value on the partial tables (Fleiss et al. 2003). Seasonal average of percentage flooding and number of collected adults and larvae of each species in ponds and pools were calculated for graphic display. For permanent ponds, which differed in vegetation cover, the proportion of dates when adults and larvae of each species were present was calculated and compared by means of the chi square test for independent proportions (Fleiss et al. 2003).

The sampling dates were also classified into three categories of temperature ranges: < 15 °C, 15-20 °C, and > 20 °C, according to the average temperature of the seven previous days. These temperature ranges were defined to be representative of winter, spring-fall, and summer seasons respectively. The number of dates with presence of adults and larvae of each species was divided by the total number of dates for each temperature range category to calculate proportions. These proportions were compared by means of the chi square test for independent proportions, and differences between pairs of ranges were examined by subdividing the contingency tables and computing the chi square value on the partial tables (Fleiss et al. 2003). Average abundances of adults and larvae of each species by temperature range were used for graphic analysis.

Development time estimation

Data of development time and survival were obtained in laboratory conditions in the context of the taxonomic description of the larval stages (detailed description of methods in Byttebier & Torres 2009). Specimens of *E. variegatus* were raised from November 2006 to February 2007 (environmental temperature of 23-27 °C), and *E. vulgaris* from April 2007 to June 2007 (environmental temperature of 19-22 °C). After oviposition, egg cases and afterwards larvae were checked and fed, and the molts or deaths recorded daily. The average and range of duration of each larval instar was estimated, being the day of oviposition of egg cases considered as day zero. The mortality rate of each instar was calculated for each species as the number of individuals that completed the instar divided by the number of individuals that reached the stage.

Larval dynamics in temporary pools

The presence and abundance of different larval instars of each species was analyzed in both pools. The time elapsed since flooding and the development time observed for each species in the laboratory were taken into account to estimate the expected larval instar for each sampling date. Dates when expected larval instars did not correspond to those observed in the field were analyzed and described in detail. For these situations, average temperatures of the periods since flooding were calculated, and compared to those recorded in the laboratory during the development time estimations.

RESULTS

Water dynamics and seasonal distribution of adults and larvae in temporary and permanent water bodies

The water level in the permanent ponds remained constant. In contrast, the surface area of the temporary pools showed pronounced fluctuations over the study period. Significant differences of water surface were detected between seasons (H_3 = 23.08; N = 51; P < 0.001). The lowest values were observed during summer (Fig. 1) and were significantly lower than those observed during winter (P < 0.001) and spring (P < 0.001), when maximum flooding occurred. In fall, the water surface attained intermediate values and showed no significant differences with the other periods. With regard to permanence, in general, flooding times were slightly longer in pool C than in pool D, although it varied seasonally in both cases. In pool C, the longest periods with water were 16 weeks in winter, nine weeks in spring, one week in summer and one to six weeks in fall (Fig. 2A). In pool D, water permanence was five and six weeks in winter, five and three weeks in spring, one week in summer and one to four weeks in fall (Fig. 2B).

Adults of *E. vulgaris* were collected in both types of habitats throughout most of the year, except during the driest period (summer), when they were recorded only in the permanent water bodies. Immature stages of this species were collected in both habitat types in spring and fall, only in permanent pools in summer, and no individuals were recorded in winter (Fig. 1A). Neither differences between seasons nor differences between types of habitats were detected in the proportions of presence of adults or larvae of this species (Table 1). Adults were detected in both permanent ponds, although mainly in pond A (which harbored both floating and submerged flora) (X^2_1 = 3.9; N = 102; P < 0.05), and larvae exclusively in this pond (X^2_1 = 6.38; N = 102; P < 0.05). With regard to temperature, adults of *E. vulgaris* were collected at the whole temperature

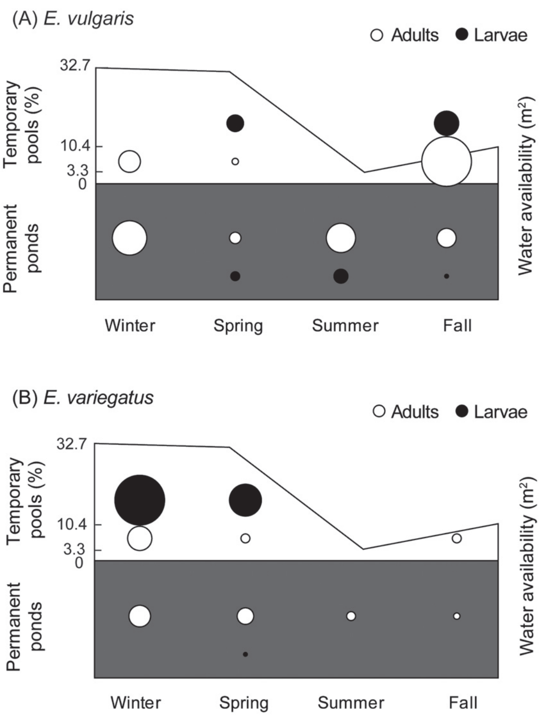

Fig. 1: Water availability (seasonal average flooded area [m^2] in temporary pools) and relative abundance (average number of individuals per sampling date) by season and type of habitat, of adults and larvae of *Enochrus*. The size of the circles is indicative of the relative abundance of individuals. (A) *E. vulgaris*; (B) *E. variegatus.*

Disponibilidad de agua (área media inundada estacional [m^2] de charcos temporarios) y abundancia relativa (número medio de individuos por fecha de muestreo) de adultos y larvas de *Enochrus* por estación y tipo de ambiente. El tamaño de los círculos es representativo de la abundancia relativa de los individuos. (A) *E. vulgaris*; (B) *E. variegatus.*

range recorded during the study period in Buenos Aires and showed no defined pattern in relationship to temperature. Larvae were collected at temperatures above 12.9 °C, and higher proportions of dates and abundance were recorded at increasing temperatures (Fig. 3A). No statistical differences in proportions of dates with presence of adults or larvae were detected between temperature ranges. Relative abundances of adults and larvae showed a pattern similar to the described proportions (Fig. 3A).

Adults of *E. variegatus* were collected both in temporary and permanent habitats during most of the year, with the exception of the driest period, when they were recorded only in the permanent ponds (Fig. 1B). No statistical differences in the proportions of presence were detected between sites of different permanence, whereas significant differences were detected between seasons (Table 1). The proportions of dates on which this species was present were higher in the winter-spring period than in the summer-fall period ($X^2_1 = 9.08$; $P < 0.005$). Immature stages were observed almost exclusively in temporary habitats (with the exception of one larva during the spring season), and the difference of detection in

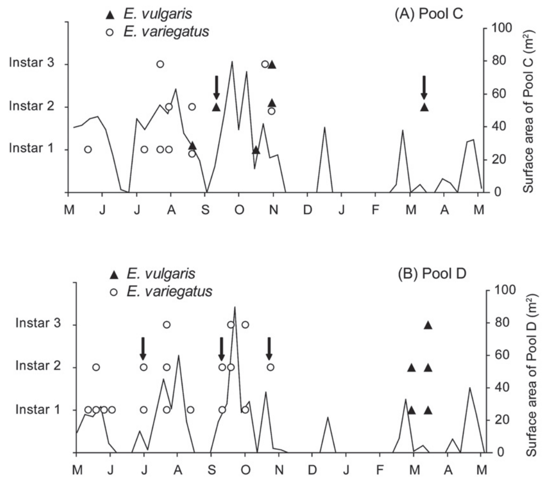

Fig. 2: Presence of three larval instars of *E. vulgaris* and *E. variegatus* in two temporary pools: (A) Pool C, (B) Pool D. Arrows indicate dates when second instar larvae were captured after the pool had dried out during the previous sampling.

Presencia de los tres estadios larvales de *E. vulgaris* y *E. variegatus* en dos charcos temporarios: (A) Charco C, (B) Charco D. Las flechas indican fechas de captura de larvas del segundo estadio después de que el charco estuviera seco en la fecha de muestreo anterior.

TABLE 1

Comparison of proportions of dates when the presence of *Enochrus* was recorded according to habitat permanence and season.

Comparación de las proporciones de fechas con presencia de *Enochrus* de acuerdo a la permanencia del hábitat y la estación.

	Species	*Enochrus vulgaris*		*Enochrus variegatus*	
	Stage	adults	larvae	adults	larvae
Habitat permanence	Permanent (proportion)	0.45	0.12	0.27	0.02
	Temporary (proportion)	0.31	0.17	0.31	0.43
	X^2 of differences	1.62	0.5	0.16	22.92
	P (df = 1)	ns	ns	ns	< 0.001
Season	Winter (proportion)	0.77	0.00	0.77	0.68
	Spring (proportion)	0.23	0.38	0.46	0.54
	Summer (proportion)	0.55	0.27	0.09	0.00
	Fall (proportion)	0.50	0.21	0.29	0.00
	X^2 of differences	7.61	5.98	12.58	20.62
	P (df = 3)	ns	ns	< 0.01	< 0.001

ns: non-significant differences

both types of habitat was significant (Table 1). Larvae were collected only during the winter and spring seasons (Fig. 1B), when proportions showed significantly higher values than during the summer-fall period (X^2_1 = 20.43; P < 0.001). Adults were collected more frequently in Pond A, although statistical results were only marginally significant (X^2_1 = 3.46; N = 102; P = 0.06). The single larva of this species collected in permanent water was also found in this pond. Adults were observed at the whole temperature range recorded during the study period (Fig. 3B). Differences in proportions of dates with presence were significant among temperature ranges (X^2_2 = 9.38; N = 51; P < 0.01), with higher values at temperatures below 15 ºC (X^2_1 = 9.20; P < 0.005). Larvae of *E. variegatus* were captured only at temperatures below 20 ºC (Fig. 3B). The proportion of dates with detection of larvae differed between temperature ranges (X^2_2 = 10.92; N = 51; P < 0.005), with significantly higher proportions of dates with presence of larvae below 20º C than above this temperature (X^2_1= 9.71; P < 0.005). Relative abundances of both adults and larvae showed the same trend as the described proportions (Fig. 3B).

Development time estimation

The development times observed for *E. vulgaris* were slightly slower than those for *E. variegatus*. The fastest instars for both species were the second larval and the pupal stage (mean ± DE = 4.2 ± 1.48 and 3.27 ± 1.1). The third instar larva was the slowest in average (10.83 ± 1.82) (Fig. 4).

E. vulgaris hatched from the egg case on day 6 and reached the second and third larval instar on days 13 and 16 respectively. Specimens moulted to pupa from day 26 on (Fig. 4A). Mortality for the first larval instar

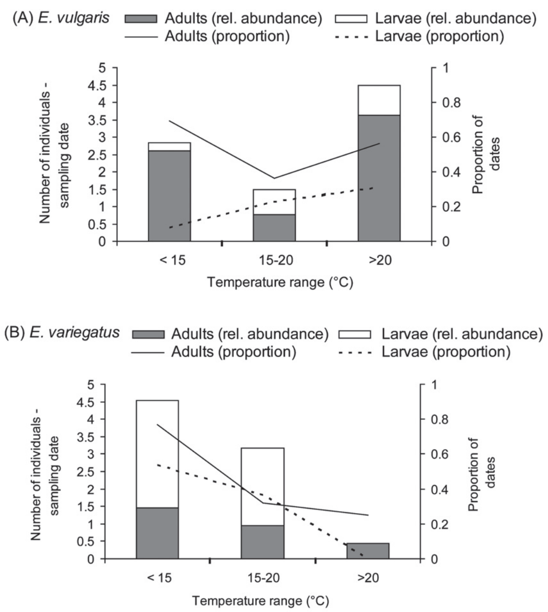

Fig. 3: Relative abundance and proportion of dates with presence of adults and larvae of *Enochrus* at different temperature ranges, representative of winter, spring-fall, and summer seasons: (A) *E. vulgaris*, (B) *E. variegates.*

Abundancia relativa y proporción de fechas con presencia de adultos y larvas de *Enochrus* a diferente rangos de temperatura representativos del invierno, primavera-otoño y verano: (A) *E. vulgaris*, (B) *E. variegatus.*

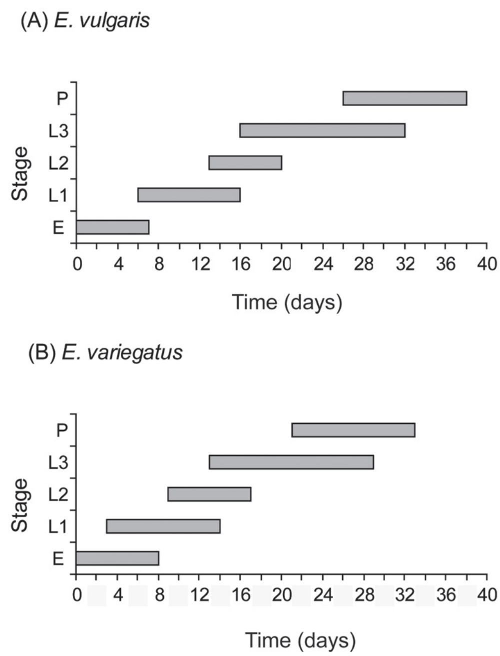

Fig. 4: Development times of *Enochrus* in laboratory conditions. E: egg case; L1: first-instar larva; L2: second-instar larva; L3: third-instar larva; P: pupae. (A) *E. vulgaris*, (B) *E. variegatus.*

Tiempos de desarrollo de *Enochrus* en condiciones de laboratorio. E: ooteca; L1: primer estadio larval; L2: segundo estadio larval; L3: tercer estadio larval; P: pupa. (A) *E. vulgaris*, (B) *E. variegatus.*

was 0.65, while no mortality was recorded during the second and third larval instars, or the pupal stage. *E. variegatus* emerged from the egg case on day 3, reaching the second and third instar on days 9 and 13 respectively. The pupal stage started on day 21 (Fig. 4B). The mortality rates for the first and third larval instar were 0.84 and 0.22 respectively, while no mortality was recorded during the second larval instar and the pupal stage.

Larval dynamics in temporary pools

The first instar larvae of both species showed the highest abundance and were captured more frequently, while third instar larvae recorded the minimum frequency and abundance. First instar larvae were observed in the first week after flooding, and also several weeks after. They were also observed in consecutive weeks and simultaneously with third instar larvae. The presence of the two first larval stages of *E. variegatus* and *E. vulgaris* was observed on dates immediately before the pools dried out completely in several opportunities.

In two opportunities (October and April), the instar of *E. vulgaris* larvae observed in pool C did not match the expected one according to the flooding time and the development time recorded in the laboratory. On these dates, second instar larvae were captured after the pool had dried out on the previous date. In October, the average temperature was 17.3 °C and the time elapsed since the previous rainfall event was two days, whereas in April, these values were 18.0 °C and six days respectively (Fig. 2A).

Similar observations were made for *E. variegatus* in pool D in three different opportunities. Second instar larvae were collected on dates immediately after flooding in July, October and November. In July, the average temperature was 12.6 °C and the time elapsed since the previous rainfall event was seven days, whereas in October the values were 17.3 °C and two days respectively and in November 19.1 °C and eight days respectively (Fig. 2B).

DISCUSSION

Larvae and adults of both species were observed in temporary pools and permanent ponds during the study period, with differences between seasons and type of water body in which they were recorded.

Results show that the reproductive seasons of *E. variegatus* and *E. vulgaris* differed through the study period, with a short overlapping period in spring. This differentiation is consistent with the association of each species to a particular temperature range. *Enochrus variegatus* reproduced at lower temperatures (especially during the winter season), while *E. vulgaris* was associated with higher temperatures (especially during the summer season). No previous data are available regarding the breeding season of these species of *Enochrus* to assess the inter-annual constancy of the pattern observed.

The presence of immature stages and adults of *E. variegatus* and *E. vulgaris* both in temporary and permanent water bodies is consistent with other reports for the region (von Ellenrieder & Fernández 2000, Fontanarrosa et al. 2004), and indicates good dispersal capacity of both species. This migration behavior is a common adaptation in insects that colonize temporary water bodies, and is also widespread among coleopterans (Wiggins et al. 1980, Williams 2006).

Among permanent habitats, those containing vegetation seem to represent more favorable environments for these insects, and the association of *E. vulgaris* and *E. variegatus* to aquatic vegetation has been reported previously in permanent ponds and marshes in central-eastern Argentina (Poi de Neiff 1983). The association of *Enochrus* with vegetation could be related to the availability of substrate for adults to attach their egg cases, as well as suitable places for larvae to rest and feed. On the other hand, vegetation may offer refuges to hide from predators, taking into account the presence of fishes in both ponds studied. Experimental studies have shown lower colonization of *Enochrus* species in ponds that contained caged fishes, as compared to fishless ones (Binckley & Resetarits 2005). Nevertheless, it is not possible to infer from this work whether adults avoid colonizing sites without vegetation, or whether they colonize them and low abundances result from predation pressure. Our results differ from those of another study in Buenos Aires, which reported higher abundances of larvae and adults of *Enochrus* in ponds without vegetation as compared to vegetated ones (Fontanarrosa et al. 2004), but the presence of fishes was not mentioned in this work.

The predominant presence of larvae in temporary pools indicates that they are favorable habitats for both species despite the unpredictable permanence of water. Our results suggest that *E. variegatus* prefers temporary waters for reproduction. In contrast, the presence of *E. vulgaris* larvae was only slightly higher in temporary pools than in ponds. This might indicate a more opportunistic strategy of this species regarding the selection of breeding sites, especially taking into account that the reproductive season of *E. vulgaris* was coincident with the drought period during the study period. Different species of *Enochrus* have been reported to breed at different points of the permanence gradient, ranging from temporary pools to permanent ponds with fishes (Poi de Neiff & Neiff 1984, Fairchild et al. 2003, Fontanarrosa et al. 2004). Further research is needed to establish whether the strategy of exploiting temporary habitats differs between the species studied or whether it varies according to the environmental conditions (e.g., drought during the reproductive period).

The presence of first instar larvae in temporary pools over several consecutive weeks, and their coexistence with third instar larvae indicate that populations are not synchronized in oviposition time and development of immature stages. These results and the detection of first instar larvae soon after the filling of the pools are consistent with an opportunistic strategy of both populations, exploiting temporary habitats for reproduction during the whole wet period (Williams 2006). On the other hand, the relatively low abundances of the second and third larval instars suggest high mortality rates during immature development, with only a reduced proportion of individuals reaching maturity. Nevertheless, it is not possible to assign the low survival in the pools to the effects of drought, since first instar mortality of different *Enochrus* species has shown to be high in laboratory observations as well (this study, Hosseinie 1995).

The observation of second instar larvae few days after the filling of the pools is an unexpected result, especially since laboratory data showed a longer development time (nine days for *E. variegatus* and 13 days for *E. vulgaris* to reach the second larval instar) even at temperatures higher than those observed in the field. These results suggest the possibility that those larvae survived the drought and did not hatch from egg-cases laid after flooding, although we did not search for buried larvae to confirm this hypothesis. Nevertheless, a previous study of benthonic invertebrates from the floodplain of the Paraná River (Montalto 2008) reported the presence of larvae of the genus *Enochrus* in soil samples during the drought phase of the wetland.

To our knowledge, this is the first study in temperate Argentina, where the abundances of larvae and adults are compared between temporary and permanent aquatic habitats. The results suggest that the *Enochrus* species studied present two strategies to cope with habitat desiccation, which allow them to tolerate and/or avoid dry periods in the study region.

Future studies should assess the relative importance of tolerance/resistance (burrowing into the soil when the habitat dries out) and avoidance (migration to permanent habitats) of *E. vulgaris* and *E. variegatus* as strategies to deal with dry periods.

ACKNOWLEDGEMENTS: We are grateful to Dr. Mariano Michat for his help with the field work. We want to thank the National Meteorological Service of Argentina (Servicio Meteorológico Nacional) for providing the meteorological data. This study was partly supported by grants UBACyT X617, and PICT-2008-2220.

LITERATURE CITED

ARCHANGELSKY M (1997) Studies on the biology, ecology, and systematics of the immature stages of New World Hydrophiloidea (Coleoptera: Staphyliniformia). Ohio Biology Survey Bulletin New Series (USA) 12: 1-207.

BINCKLEY CA & WJ RESETARITS JR (2005) Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. Biology Letters 1: 370-374.

BYTTEBIER B & PLM TORRES (2009) Description of the preimaginal stages of *Enochrus* (*Hugoscottia*) *variegatus* (Steinheil, 1869) and *E.* (*Methydrus*) *vulgaris* (Steinheil, 1869) (Coleoptera: Hydrophilidae), with emphasis on larval morphometry and chaetotaxy. Zootaxa 2139: 1-22.

FAIRCHILD GW, AM FAULDS & JF MATTA (2000) Beetle assemblages in ponds: Effects of habitat and site age. Freshwater Biology 44: 523-534.

FAIRCHILD GW, J CRUZ & AM FAULDS (2003) Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. Journal of the North American Benthological Society 22: 224-240.

FERNÁNDEZ LA (1988) Contribución al conocimiento del género *Enochrus* Thomson. I. (Coleoptera: Hydrophilidae). Physis (Argentina) 46: 85-89.

FERNÁNDEZ LA (1989) Las especies de *Enochrus* descriptas por Bruch. Redescripciones basadas sobre material típico. Revista de la Sociedad Entomológica Argentina 46: 121-128.

FERNÁNDEZ LA (1992) Descripción de la ooteca y estadios larvales de *Enochrus* (*Hugoscottia*) *scutellaris* (Bruch) y *Enochrus* (*Methydrus*) *vulgaris* (Steinheil) (Coleoptera, Hydrophilidae). Revista de la Sociedad Entomológica Argentina 50: 343-352.

FERNÁNDEZ LA (1994) Contribución al conocimiento del género *Enochrus* Thomson (Coleoptera: Hydrophilidae). II. El subgénero *Hugoscottia* en la Argentina. Physis (Argentina) 49: 37-45.

FERNÁNDEZ LA (1997) Nuevos aportes para el conocimiento del género *Enochrus* Thomson (Coleoptera: Hydrophilidae). Physis (Argentina) 53: 21-29.

FERNÁNDEZ LA (2006) Two new species of *Enochrus* Thomson (Coleoptera, Hydrophilidae) from the Neotropical Region. Transactions of the American Entomological Society 132: 279-284.

FERNÁNDEZ LA & ML LÓPEZ RUF (2006) Aquatic Coleoptera and Heteroptera inhabiting waterbodies from Berisso, Buenos Aires province, Argentina. Revista de Biología Tropical 54: 139-148.

FERNÁNDEZ LA & AO BACHMANN (1998) Hydrophiloidea. In: Morrone JJ & S Coscarón (eds) Biodiversidad de artrópodos argentinos. Una perspectiva biotaxonómica: 218-226. Ediciones Sur, La Plata, Argentina.

FERNANDO CH (1958) The colonization of small freshwater habitats by aquatic insects. 1. General discussion, methods and colonization in the aquatic Coleoptera. Ceylon Journal of Science (Sri Lanka) 1: 117-154.

FERNANDO CH & D GALBRAITH (1973) Seasonality and dynamics of aquatic insects colonizing small habitats. Verhandlungen des Internationalen Verein Limnologie (Germany) 18: 1564-1575.

FISCHER S, C MARINONE, MS FONTANARROSA, M NIEVES & N SCHWEIGMANN (2000) Urban rain pools: Seasonal dynamics and entomofauna in a park of Buenos Aires. Hydrobiologia 441: 45-53.

FLEISS JL, B LEWIN & MC PAIK (eds) (2003) Statistical methods for rates and proportions. Third edition. John Wiley & Sons, New Jersey, USA.

FONTANARROSA MS, MB COLLANTES & AO BACHMANN (2009) Seasonal patterns of the insect community structure in urban rain pools of temperate Argentina. Journal of Insect Science 9: 1-18.

FONTANARROSA MS, PLM TORRES & MC MICHAT (2004) Comunidades de insectos acuáticos de charcos temporarios y lagunas en la ciudad de Buenos Aires (Argentina). Revista de la Sociedad Entomológica Argentina 63: 55-65.

HOSSEINIE SO (1995) Life history, behavior and morphology of the immature stages of *Enochrus quadripunctatus* Herbst in the laboratory (Coleoptera: Hydrophilidae). 1 - Life history and behavior. Journal of Sciences Islamic Republic of Iran (Iran) 6: 8-13.

MONTALTO L (2008) Dinámica espacio-temporal de asociaciones de invertebrados en un humedal marginal fluvial de la llanura aluvial del Río Paraná medio. Doctoral Thesis, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Buenos Aires, Argentina.

OLIVA A, LA FERNÁNDEZ & AO BACHMANN (2002) Sinopsis de los Hydrophiloidea acuáticos de la Argentina (Insecta, Coleoptera). Monografías del Museo Argentino de Ciencias Naturales (Argentina) 2: 1-67.

POI de NEIFF A (1983) Observaciones comparativas de la mesofauna asociada a *Pistia stratiotes* L. (Araceae) en algunos ambientes acuáticos permanentes y temporarios (Chaco, Argentina). Physis B (Argentina) 41: 95-102.

POI de NEIFF A & JJ NEIFF (1984) Dinámica de la vegetación acuática flotante y su fauna en charcos temporarios del Sudeste del Chaco (Argentina). Physis B (Argentina) 42: 53-67.

SCHNEIDER DW & TM FROST (1996) Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society 15: 61-86.

SIEGEL S. & NJ CASTELLAN JR (1988) Nonparametric statistics for the behavioral sciences. Second edition, McGraw-Hill, New York.

SMN (2011) Servicio Meteorológico Nacional, Secretaría de Planeamiento, Ministerio de Defensa de la Nación, Argentina. URL: http://www.smn.gov.ar (accessed august 15, 2011).

STANLEY EH, DL BUSCHMAN, AJ BOULTON, NB GRIMM & SG FISHER (1994) Invertebrate resistance and resilience to intermittency in a desert stream. The American Midland Naturalist (USA) 131: 288-300.

TORRES PLM, S MAZZUCCONI & MC MICHAT (2007) Los coleópteros y heterópteros acuáticos del Parque Nacional el Palmar (Provincia de Entre Ríos, Argentina): Lista faunística, diversidad y distribución. Revista de la Sociedad Entomológica Argentina 66: 127-153.

VON ELLENRIEDER N & LA FERNÁNDEZ (2000) Aquatic Coleoptera in the subtropical-pampasic ecotone (Argentina, Buenos Aires): Species composition and temporal changes. The Coleopterists Bulletin 54: 23-35.

WELLBORN GA, DK SKELLY & EE WERNER (1996) Mechanisms creating community structure across a freshwater habitat gradient. The Annual Review of Ecology, Evolution, and Systematics 27: 337-363.

WIGGINS GB, RJ MACKAY & IM SMITH (1980) Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie – Supplement (Germany) 58: 97-206.

WILLIAMS DD (2006) The biology of temporary waters. Oxford University Press, University of Toronto at Scarborough, Canada.

Editorial responsibility: Sergio Roig-Juñent
Received September 5, 2011; accepted May 31, 2012