

Reproductive behaviour of a North African endemic damselfly, *Platycnemis subdilatata* (Odonata: Platycnemididae) and probable senescence effects

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Although the endemic damselfly, *Platycnemis subdilatata* Selys, 1849, is widespread in the Maghreb, many aspects of its reproductive behaviour, biology and ecology are still unstudied. One particular feature of this species is that its coloration pattern continues to change during maturation and afterwards, which makes it a good model for assessing age effects on behavioural and biological components. This study aims first to investigate the reproductive behaviour and choice of oviposition site, and second to assess clutch size and egg deposition rate as a function of age in a natural population located in North-East Algeria during the reproductive season of 2012. Males seized females next to reproductive sites and in foraging sites. Non-receptive females refused to mate with males by raising their abdomen up while perched or by curving the abdomen up while flying; the angle of abdomen elevation when perched was correlated to male persistence (the number of times that a male tried to grasp the female prothorax while flying over her). Copulation lasted about 14 min, the subsequent oviposition 54 min. Field experiments on oviposition site selection showed that the females prefer to lay eggs in *Typha angustifolia* leaves. Clutch size and egg deposition rate pattern through age showed an increase in early mature life followed by a decrease later on.

Keywords: damselfly; reproduction; refusal behaviour; oviposition; ageing; clutch size

Introduction

The reproductive behaviour of many species of odonates from different regions worldwide has not yet been studied. This is the case of African species in general (Martens, 2003), and Maghrebian ones in particular. Part of the Maghreb belongs to the Mediterranean Basin which harbours high faunal and floral richness and endemism, and consequently is considered as a hotspot of biodiversity (Medail & Quezel, 1997; Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). *Platycnemis subdilatata* is the only platycnemidid on the African side of the Mediterranean Basin, having resident populations only in Tunisia, Algeria, and Morocco. Although the species is listed as Least Concern in the IUCN red list, its habitat is under high anthropogenic pressure and this could have future impacts on populations (Samraoui, 2010; Guettaf, Maoui, & Ihdene, 2014). It inhabits parts of rivers and streams where water flow is relatively slow, and is on the

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wing from May to October (Dijkstra & Lewington, 2007). Apart from the recent description of the life history of the species (Khelifa, 2015), this damselfly has not been subject of any detailed study. In order to get basic information on some facets of reproductive behaviour, biology and ecology of this species, a field study was conducted in a population located in North-East Algeria.

In odonates, a typical reproductive episode includes species recognition, pair formation, copulation, and oviposition (Corbet, 1999). The description of the reproductive behaviour of any species ideally should answer the questions of when, where, and how each of the four components takes place, and also how much time species spend while performing each component. In zygopterans, oviposition is usually long-lasting because the female is endophytic (eggs are inserted in plant tissues, one egg at a time) and usually choosy in terms of oviposition sites and substrates (Fincke, 1985; Martens, 1992; Waage, 1978). The assessment of this behaviour is crucial because its duration is correlated to clutch size (Martens, 1992), which represents the initial population size after hatching. In addition, the location where egg laying is performed gives a good indication of habitat requirements of both adults and larvae (Corbet, 1999).

Extensive data on fecundity pattern over individual age have been challenging to collect in odonates (Banks & Thompson, 1987; Khelifa, Zebsa, Kahalerras, & Mahdjoub, 2012), mainly because individuals have to be captured, marked, and surveyed during their entire lifespan. Age is known to be a key factor that influences fecundity in many living organisms including odonates (Sherratt & Wilkinson, 2009). Some evolutionary theories of senescence predict that fecundity decreases after reproductive maturity (Hamilton, 1966; Williams, 1957). However, field and experimental studies have refuted this hypothesis and suggested rather an increased fecundity in early mature life and a decrease later (Carey, Liedo, Müller, Wang, & Vaupel, 1998; Gustafsson & Pärt, 1990; Nussey, Kruuk, Donald, Fowlie, & Clutton-Brock, 2006; Reed et al., 2008; Sharp & Clutton-Brock, 2011). In this study, due to the fact that the visible phenotype of *P. subdilatata* females changes with age even after maturity, the species becomes an excellent model to investigate the effects of age on some biological and behavioural features.

This study aims first to describe the reproductive behaviour and choice of oviposition site. Second, we investigate the pattern of fecundity and the egg deposition rate over age in a natural population.

Material and methods

Study site

The study was conducted in a shallow stream (36°27'24"N, 7°30'31"E), located 6 km east from Guelma city, North-East Algeria. The stream flows into the Seybouse River where *P. subdilatata* is widely distributed (Khelifa et al., 2016). A large part of the stream bed is shaded by trees of *Salix pedicellata*, *Populus alba* and *Eucalyptus globulus*. Vegetation of the stream banks consisted mainly of *Typha angustifolia*, *Helosciadium nodiflorum*, and *Nasturtium officinale*. Many plants along the banks were floating on the water surface (horizontal instead of vertical), probably due to flooding. Outside the stream banks, there was a meadow with stands of *Daucus c. carota*, *Carduus tenuiflorus*, *Anacyclus clavatus*, *Bellis annua*, *Calendula arvensis*, and *Dittrichia viscosa*. The studied species coexisted with *Calopteryx haemorrhoidalis* (Vander Linden), *Gomphus lucasii* (Selys) and *Orthetrum coerulescens anceps* (Schneider).

Reproductive behaviour survey

As part of a study investigating demographic parameters of the species (Khelifa, unpublished data), adults were daily marked with permanent markers on one of the hind wings with numeric

codes. Daily visits to the study site were conducted from 3 May to 16 June 2012. From 09:00 to 10:30 h (solar time: -27 min), mature marked adults were surveyed in three plots (10×5 m) parallel to the water (foraging sites) to survey potential pair formation in terrestrial habitat. From 10:30 to 16:00 h (the period of reproductive activity), the entire reproductive episodes of marked individuals were surveyed. The duration of copulation and post-copulation resting were recorded to the nearest second and that of oviposition to the nearest minute. In many damselfly species, particularly in *Platycnemis* species, a common female refusal behaviour is to raise the abdomen up to avoid having males grasp her prothorax and copulate with her (Buchholtz, 1956; Corbet, 1999; Gorb, 1992). To understand the variability in the extent at which the abdomen was raised, we calculated visually the angle made with a theoretical horizontal line of abdomen raising (e.g. 45° , 60° , 90° . . .) and we tested the implication of male persistence by calculating the number of times that a male tried to grasp the female prothorax while flying over her.

In order to test for potential preferences among different oviposition substrates (leaves of *Typha angustifolia*, stems of *Apium nodiflorum*, submerged tree rootlets and twigs), their abundance within a plot of 2×2 m was manipulated and the number of minutes spent in each substrate was counted. First, on 25 and 26 May we removed all substrates and provided equal abundance of the four dominant substrates (25% for each one). Second, knowing the extensive use of leaves of *T. angustifolia* as oviposition sites (see Results) we reduced the abundance of the latter on 27 and 28 May to 10% and increased the three other substrates to 30% in order to check whether the species prefers *T. angustifolia* with respect to others.

Age effects on fecundity and egg deposition rate

Age estimation

Females show remarkable changes in coloration of the body. Using capture-mark-recapture on a sample of teneral females (40 individuals), the change of the coloration pattern over age was surveyed to determine the key characters that are useful for age estimation. The analysis was made on the basis of pictures taken on each recapture occasion. Three age classes was identified using combinations of coloration patterns of abdomen, thorax, head and legs ($N = 12, 14, 9, 6$ for age class A, B, C and D, respectively). The coloration of the thorax, legs and head varies in the same way over age. From teneral to early maturity (0–6 days), coloration of female's head, thorax, and legs changes from yellowish to orange. From 7 to 10 days (age class A), the abdomen is completely yellowish (Figure 1a). Age class B (11 to 14 days) is an intermediate state between A and C and is characterized by two thin parallel submedian abdominal black lines. From 11 to 18 days (age class C), the two parallel abdominal black lines look like one thick line interrupted in the middle with a longitudinal pale line (Figure 1b). After the age of 18 days (age class D), the yellowish part of the abdomen, thorax and head becomes light brownish (Figure 1c). Besides age specific polymorphism there is no variation in female coloration, at least in the current study population.

Fecundity and egg deposition rate estimation

A sample of females from each age class was captured with a hand net during copulation (before starting egg laying) from another nearby population and instantly killed with 70% ethanol. The number of eggs carried by each female was later counted after dissection in the laboratory. The egg deposition rate, considered here as the number of eggs inserted per minute, was estimated following a precise protocol. The same type of oviposition substrate (*Typha angustifolia*) was utilized throughout the experiment because the egg deposition rate is known to be

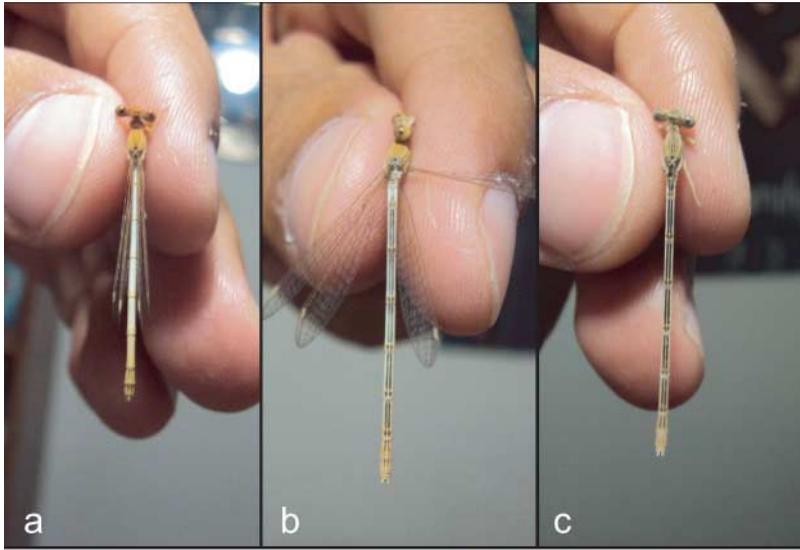


Figure 1. Chronological changes in the body coloration of mature females of *Platynemesis subdilataata*. (a) age class A (7–10 days); (b) age class C (15–18 days); (c) age class D (19 days onwards).

influenced by the type of substrate (Grunert, 1995; Lambret, Besnard, & Matushkina, 2015; Martens, 1992). These oviposition substrates were prepared beforehand by taking erected leaves of *T. angustifolia*, which do not contain eggs because they are used by the species for oviposition only when they float on the water, and immersing them in the water for 24 h in the laboratory. After, they were placed on the water surface within the area where egg deposition often takes place. In addition, we carefully chose periods of the day when temperature was 26°C ($\pm 0.3^\circ\text{C}$) to avoid thermal effects on egg deposition rate. Data on egg deposition rate were collected from different females. The leaves used for oviposition were taken to the laboratory to be dissected, and the number of eggs was counted using a dissecting microscope after one to two days.

Statistical analyses

Statistical analyses were conducted using software R 3.1.2 (R Development Core Team, 2014). Knowing that the angle at which females raise their abdomen is limited between 0 and 180° (total reversal of the female), we analysed the relationship between the angle of abdomen raising (response variable) and male persistence (explanatory variable) using mixed effects beta regression models with the R package hglm (Rönnegård, Shen, & Alam, 2010). Chi-square tests were used to check whether females discriminate between different oviposition substrates, first with equal frequencies (0.25 for each substrate) and second with biased frequencies (*T. angustifolia* = 0.1, *A. nodifolium* = 0.3, tree rootlets = 0.3, and twigs = 0.3). Given that there was no pseudoreplication among age classes, the homogeneity of clutch size and egg deposition rate among age classes was analysed with Kruskal–Wallis tests. Nemenyi post-hoc tests were computed with the R package PMCMR (Pohlert, 2015) for pairwise comparison of the two latter variables among age classes. Values presented afterwards are means and 95% confidence intervals, unless indicated. Minimum and maximum are presented between brackets.

Results

Reproductive behaviour

Males did not defend a reproductive area against rivals. Several males were observed perching on the same support next to oviposition sites, which is typical of a non-territorial species. Pair formation was conducted in two ways. First, mature males waited next to oviposition sites (in bank vegetation) and seized females when they came to the water ($N = 34$). All females that came to the water copulated successfully. Second, mature males patrolled foraging sites and grasped females while foraging ($N = 17$). In 51 observed attempts of males trying to seize females in foraging sites, only 17 (33.33%) led to successful tandem formation with no evident abdomen raising.

Females refused copulation both at perching sites and during flight in different ways. When perched, they raised their abdomen up, spread out their wings and moved the posterior legs towards the male who tried to grasp her. The angle at which the abdomen was raised varied between 45° to 180° and it was positively correlated to male persistence (Table 1; Figure 2).

Table 1. Summary results of the mixed effects beta regression model for the effects of male persistence on female refusal behaviour. Male persistence refers to the number of time that a single male tries to grasp the female by her neck within the same flight. The response variable is the angle of abdomen raising of the harassed female. The results clearly show that the higher the male persistence the larger the angle at which the female raises her abdomen.

	Estimate	Standard error	t-value	<i>p</i>
(Intercept)	-1.29980	0.14753	-8.811	< 0.0001
Persistence	0.86952	0.03518	24.719	< 0.0001

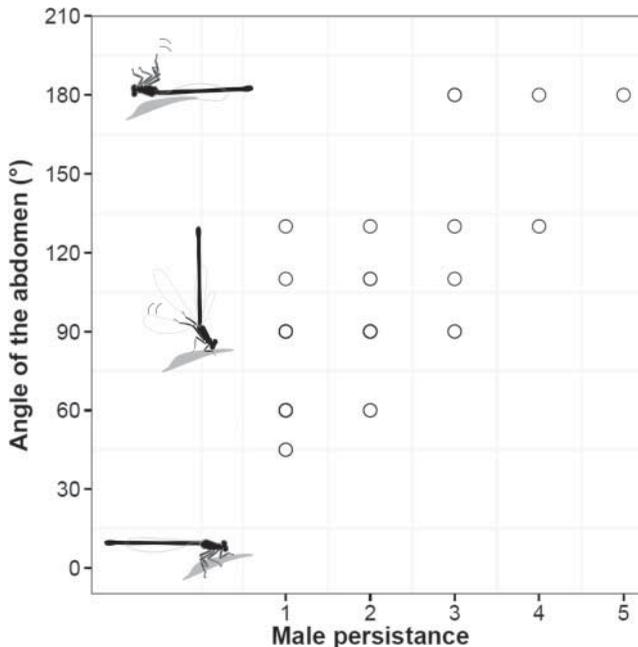


Figure 2. Relationship between male persistence and the angle of abdomen raising during female refusal. The three logos in the figure are for illustrative purpose and indicate an angle of 0° (bottom), 90° (middle), and 180° (upper). Under highly persistent males, the female completely reverse her body to avoid being grasped by the male.

When flying, females refused copulation by both raising and curving up her three to four distal abdominal segments. In 13 cases, the female flew in a stationary position facing the male, raising and curving the last three to four abdominal segments and spreading out her legs. As the flying male moved in one way or another, the female flew face to face (symmetrically). Less frequently observed in foraging sites ($N = 5$) and commonly recorded after oviposition ($N = 49$), the female flew away from the harassing male with a raised and curved abdomen without facing him (see Supplemental video).

After tandem formation, the copulatory wheel was formed next to the water, that is, reproductive pairs that were formed in terrestrial habitat moved next to the water to copulate. Mean copulation duration was $13 \text{ min } 57.6 \text{ s} \pm 1 \text{ min } 27.6 \text{ s}$ (7 min 3 s–16 min 17 s, $N = 34$). After copulation, reproductive pairs rested a mean period of $59.88 \pm 6.13 \text{ s}$ (33–107 s, $N = 34$) before laying eggs. Tandem oviposition was performed usually on horizontal substrates with the male staying upright on the female prothorax. The whole oviposition (from the beginning of first landing with ovipositor contact until the end of the last one) lasted a mean duration of $53 \text{ min } 45.6 \text{ s} \pm 49.5 \text{ s}$ (43–74 min, $N = 34$).

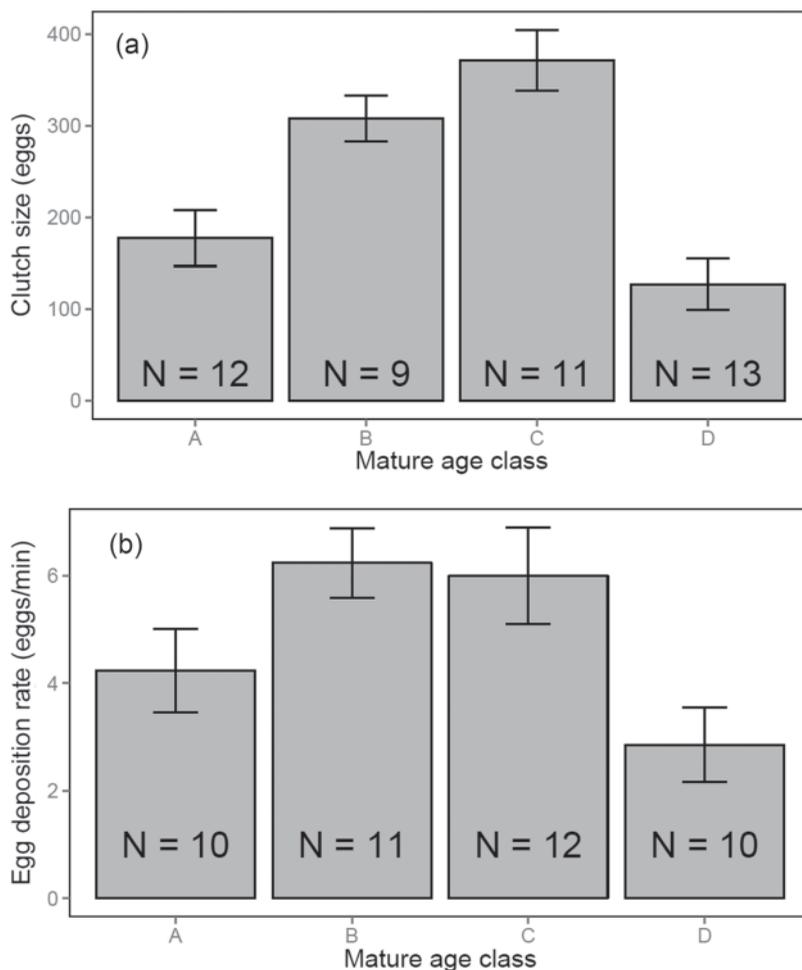


Figure 3. (a) Clutch size and (b) egg deposition rate of four mature age classes of *Platycnemis subdilatata* females. Clutch size of age class A, B, C and D is 177.50 ± 30.76 eggs, 307.90 ± 24.79 eggs, 371.58 ± 33.00 eggs and 126.90 ± 28.08 eggs, respectively. Egg deposition rate of age class A, B, C and D is $4.23 \pm 0.77 \text{ eggs min}^{-1}$, $6.23 \pm 0.64 \text{ eggs min}^{-1}$, $5.99 \pm 0.89 \text{ eggs min}^{-1}$ and $2.85 \pm 0.68 \text{ eggs min}^{-1}$, respectively. Error bars are 95% confidence intervals.

Table 2. Pairwise comparison of clutch size and estimated egg deposition rate of the four mature age classes of *P. subdilatata*.

	Age class	A	B	C
Clutch size (eggs)	B	0.04		
	C	0.0002	0.42	
	D	0.67	0.001	< 0.0001
Egg deposition rate (eggs min ⁻¹)	B	0.02		
	C	0.05	0.97	
	D	0.33	< 0.0001	0.0001

Note: The values which are in bold represents *p*-values.

The substrates used for oviposition consisted of floating leaves of *Typha angustifolia* and stems of *Apium nodiflorum*, submerged tree rootlets and twigs. No underwater oviposition was recorded. Based on 34 complete oviposition episodes, females spent more time on leaves of *T. angustifolia* (88.27%) than on all other substrates combined, and in 19 cases (44.18%) they spent their entire oviposition duration on the same *T. angustifolia* leaf. *Apium nodiflorum*, submerged tree rootlets, and twigs were used for 5.80%, 3.61% and 2.91% of the total oviposition duration. After the abundance of the substrate has been manipulated, *T. angustifolia* was preferred both when it was equally abundant ($\chi^2 = 873.74$, $df = 3$, $p < 0.0001$) and less abundant than the other substrates ($\chi^2 = 1381.57$, $df = 3$, $p < 0.0001$).

Age effects on fecundity and egg deposition rate

Clutch size had a mean of 253.25 ± 33.30 eggs ($N = 43$) and showed significant differences among age classes (Kruskal–Wallis: $\chi^2 = 34.65$, $df = 3$, $p < 0.0001$) (Figure 3a). Clutch size increased gradually from age class A to C by a factor of 2.03, but decreased abruptly from age class C to D by a factor of 2.85 (Figure 3a). Table 2 shows all possible pairwise comparisons of clutch sizes among mature age classes. Differences were significant between age classes A–B, A–C, B–D and C–D, but not between A–D and B–C.

With a mean of 4.66 ± 0.54 eggs min⁻¹ ($N = 45$), the egg deposition rate showed significant difference among age classes ($\chi^2 = 28.044$, $df = 3$, $p < 0.0001$) (Figure 3b). It peaked in age class B, increasing by a factor of 1.47, and rapidly decreased from class C to D by a factor of 2.18 (Figure 3b). It differed significantly in age classes A–B, B–D, and C–D (Table 2).

Discussion

As in the congeneric *P. pennipes* (Martens, 1996), *P. subdilatata* did not show territoriality at reproductive sites. Besides the scramble competitive mating strategy in which mature males wait for females next to the water, *P. subdilatata* males displayed an alternative mate-finding tactic which consisted of wandering males grasping females while foraging in terrestrial habitats. Such reproductive behaviour was also recorded in its closest relative *P. pennipes* (Martens, 1996). The low success in wheel formation at foraging sites might indicate that this strategy is mildly successful and that the more successful one is waiting for females at the water edge, but this needs further investigations. Studies have shown that the adoption of an alternative reproductive tactic depends on population size, age and energy reserves (Corbet, 1999; Forsyth & Montgomerie, 1987; Plaistow, 1997; Plaistow & Siva-Jothy, 1996).

Copulation duration of *P. subdilatata* (13 min 58.2 s \pm 3 min 13.2 s) was considerably shorter than that of its three European relatives, namely *P. pennipes* (45 \pm 33 min (mean \pm

SD)) (Martens, 1992), *P. acutipennis* (non-virgin females: 65.99 ± 4.89 min (mean \pm SD)) and *P. latipes* (non-virgin females: 71.37 ± 6.16 min (mean \pm SD)) (Cordoba-Aguilar & Cordero-Rivera, 2008). In addition, oviposition duration was shorter than that of *P. pennipes* (85 ± 24 min (mean \pm SD)) (Martens, 1992). Uhía and Cordero Rivera (2005) showed that copulations with virgin females last a shorter time than with non-virgin females. Further studies are needed to determine whether the short copulations of *P. subdilatata* are related to female virginity. The differences in copulation and oviposition duration between *P. subdilatata* and the other congeneric species might also be related to ambient temperature. The African species clearly live in a warmer climate than the European species. Several studies have shown that the temperature is negatively correlated to copulation duration in odonates (e.g. Michiels, 1992) and other insects (e.g. Katsuki & Miyatake, 2009), and that the egg deposition rate is faster at higher temperatures (Fincke, 1985), shortening the oviposition duration.

The female refusal behaviour was signified to males by raising the abdomen when perched and curving it up when flying. The first case was similar to that observed in *P. pennipes* (Buchholtz, 1956; Gorb, 1992; Papazian, 1998). The more persistent the male was, the higher the female abdomen was raised. In some cases of male over-persistence the female's body turned over completely. Females did not only raise their abdomen but also moved the posterior legs, probably to avoid physical contact and to keep the male far from them. This behavioural display was quite effective because most males were unable to grasp the female prothorax. Moreover, refusal behaviour during female flight was done by either facing the male or flying away. One hypothesis to explain why a female chooses one way or the other is that her ecological and biological priorities change. During foraging, the priority of a female is to choose a suitable habitat to acquire food and produce eggs. If the female was foraging in a good site and a male tried to copulate with her, the female should better face the male and continue her foraging at the same place. However, after oviposition the female priority is to get away from the water, so if she finished oviposition and a male harassed her in flight, she would better leave the reproductive site without facing him (Khelifa, 2015). A second hypothesis is that females face harassing males when the latter get so close that it can contact her. Further observations using video recording and analyzing refusal behaviour in slow motions are needed to understand what influences the choice of a specific refusal behaviour.

The use of various types of substrates to lay eggs was also observed in *P. pennipes* (Martens, 1992). We revealed experimentally that *P. subdilatata* shows a marked preference for live *T. angustifolia* leaves by manipulating the proportion of plant types available in oviposition sites. Fitness benefits of oviposition site selection need more research that assesses larval survival in different plant tissues. However, we may hypothesize that although the water level varies, floating leaves of *T. angustifolia* remain on the water surface and thus insure the survival of eggs and prevent desiccation (Fincke, 1986). It is important to mention that *Platycnemis* species aggregate during oviposition (Martens, 1992, 1996, 2002) and therefore habitat preferences is difficult to assess due to the social cues.

The pattern of clutch size over age does not follow the prediction made by evolutionary theories of senescence which suggest reduced fecundity from reproductive maturity (Hamilton, 1966; Williams, 1957). Instead, it rather goes in line with an upward-convex pattern, i.e. an increase of fecundity after maturation and a decrease at the end of life. We assume that the first increase in clutch size from age class A to age class C was the result of an increase in body weight (e.g. Matsubara, Tojo, & Suzuki, 2005), as was observed in female crickets of *Gryllus bimaculatus* (Lorenz & Anand, 2004). The decline in age class D was rapid, as the one recorded in unguilates (Nussey et al., 2006) and it was probably due to senescence. In fact, senescence of egg production could be influenced by both physiological and behavioural mechanisms (Bouwhuis, Sheldon, Verhulst, & Charmantier, 2009; Sharp & Clutton-Brock, 2010). First, physiological processes involved in converting proteins and fat to eggs may become slower in late female life.

Second, low egg production could also be related to low foraging success (Richardson & Baker, 1997), that is, as females become older, their ability to fly and thus to catch prey becomes lower (Corbet, 1999). Further studies should take into account the role of inter-clutch interval (Banks and Thompson, 1987) to confirm our hypothesis. In the current study, we did not have proof of physiological degradation due to ageing, but we detected behavioural decline through the egg deposition rate which was considerably slower in the last age class than the previous ones. This supports, to some extent, the assumption that besides the potential deterioration of physiological processes related to egg production, behavioural activities were also affected by senescence.

This study revealed that two different male mating strategies occur specifically in *P. subdilatata*: waiting for females next to the water apparently being the more successful one and searching for females in foraging sites resulting in a relatively low frequency of successful mating. Besides, we provide evidence for two signs of biological senescence, the first affecting the number of eggs produced, the second influencing the rate at which eggs are laid. Finally, compared to *P. pennipes* in which the coloration of the abdomen is a result of moisture during emergence (Martens, 1996), the remarkable changes of the coloration of abdomen in *P. subdilatata* females is rather related to age. Although the use of four age classes is useful in determining the age effects on biological and demographic parameters, the next challenge in future studies will be to estimate age in a continuous rather than a categorical way by combining coloration of morphological characters.

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Supplemental data

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/13887890.2016.1196619>

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