

Phenotypic Plasticity and Parental Effect on Rearing of Two Diverse Habitat Environment for Laboratory Reared *Sympetrum Meridionale*

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**PHENOTYPIC PLASTICITY AND PARENTAL EFFECT ON REARING OF TWO
DIVERSE HABITAT ENVIRONMENT FOR LABORATORY REARED
*SYMPETRUM MERIDIONALE***

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ABSTARCT

Laboratory observations on rearing experiment of Odonata serve to answer many evolutionary and ecological questions. In order to evidences the role of species parental habitat provenience in the development behaviour of their offspring, we surveyed several life history traits of two rearing populations of *Sympetrum meridionale* (Anisoptera: Sympetrinae), coming from two different habitats across north-eastern Algeria. The first one is a RAMSAR wetland called 'Mekhada' (a perennial water body), and the second one is a temporary pond located at "Maouna" Mountain (1400 m altitude). Overall, the development patterns of the two populations of dragonflies vary with the type of habitat the parental generation of the species occupy (Factorial ANCOVA: all $p < 0.05$). Firstly, egg mortality was very low in dragonfly population inhabiting the RAMSAR wetland compared of those belonging to Maouna Mountain. Secondly new-borne larvae stemming from females inhabiting the Mekhada wetland develop more slowly than did those coming from the "Maouna" Mountain pond. Finally, larvae of *Sympetrum meridionale* stemming from females inhabiting the temporary wetland were heavier than those inhabiting the perennial wetland. Such studies will ads considerably to our understanding of the mechanisms that are responsible for possible effects of environmental changes on life history traits of dragonflies across the southern part of their distribution range.

Keywords: Environmental heterogeneity, factorial ANOVA, parental effects, reproductive performance, *Sympetrum meridionale*.

INTRODUCTION

Development behaviour of a species is generally governed by two major constraints, (i) the habitat conditions the individuals occupy, and (ii) the traits that inherited from their ancestors (Waringer and Humpesch, 1984; Richardson, 2001; Hughes et al., 2008). How individuals and populations maximize their local performance given environmental heterogeneity in time and space is, therefore, of great interest in ecology and

evolution (Edelaar et al., 2017). Many invertebrate taxa including insects are good models permits prediction of the impacts that environmental variation will have on the development behaviour of organisms (Minot et al., 2019). Among them, odonates are one of the well suited taxa for studying traits variability among environmental gradients since they have a fascinating life cycle, a huge diversity in reproductive strategies, and easy to rear (Johansson & Suhling, 2004). The life history characteristics (life time, clutch size, hatching and larval duration,

locomotory activity and body mass) of a species are driven by environmental gradients, they are there by widely used in studies of behavioural and life-history ecology of organisms (Lailvaux & Husak, 2014). Also, phenotypic traits are components of the species evolutionary lineage and can be used as a proxy for organismal fitness (Blanckenhorn, 2000). For example, rapid growth is expected to occur in organisms that inhabiting temporary waters (Williams, 1996; Suhling et al., 2015; Johansso et al., 2004).

Rapid development is likely to be the key trait that enables them to be successful in such unpredictable habitats that dry up within a short lapse of time (Suhling et al., 2005). Furthermore, a significant association between the size of eggs, nymphs and adults with latitudinal and warming gradients is commonly assumed in most lifetime studies, and often associated with male and female fertility in dragonfly species (Stoks & De Block, 2011; Be Block and Stoks, 2003; Minot et al., 2019). Studies on North African populations of odonates are very interesting; Garcia and Arroyo (2001) expected that different environmental factors influencing life histories may reach their extreme values at the southern edge of the species breeding range. Having analysed the reproductive ecology of a North African zygoptereans (*Calopteryx haemorrhoidalis*) Benchalel et al., (2020) found that the breeding strategy of the majority of local species differ in many aspects from those occurring in Europe, especially the reduction in copulation and spawning time. It seemed probable that similar special features would be revealed in other Algerian odonates, as these populations undergoing similar environmental constraint.

Observations on laboratory rearing experiment of odonates serve to answer many evolutionary and ecological questions (van Gossum et al., 2003). Such studies will add considerably to our understanding of the mechanisms

responsible for possible effects of environmental changes on life history traits of dragonflies across the southern part of their distribution range. In pursuance of this goal, we performed a rearing experiment for a threatened anisopteran species (*S. meridionale*) obtained from two populations inhabiting two different meso-habitats of north-eastern Algeria. The first one is a RAMSAR wetland called ‘‘Mekhada’’ experiencing a humid climate and situated near to the Mediterranean Sea (with 10 m altitude), and the second one is a temporary pond located at ‘‘Mouna’’ Mountain (1400 m altitude) characterised by a sub-humid climate. Then, several life history traits have been surveyed from eggs hatching until the end of the experiment in order to evidences the role of the species parental habitat provenience in the development behaviour of their offspring. According to previous studies (above), we predict that offspring stemming from females inhabiting the two different habitats will not develop similarly, and parental origin will affect differently the breeding behaviour of the two populations. Such variability can be useful indicators of species-level responses to ecological constraints in an Algerian population of *S. meridionale*, a country that already experiencing a severe drought stress and have also been subjected to uncontrolled urbanization and high deforestation rate (Brahmia et al., 2021).

METHODS

Study Species

S. meridionale is a widespread and abundant dragonfly of the Mediterranean regions (Jacquier and Deliry 2005; Hoess 2005). Occurring throughout the southern part of Europe, the north of the Maghreb and extends eastward to China (Jourde, 2009). It lives near stagnant and shallow waters with abundant emergent vegetation (Grand and Boudot, 2006).The

flight period is from mid-June to late September mostly, and from mid-May to early November occasionally (Bailleux et al. 2017). A strong flier that is often found away from water, it perches on the ground or amongst tall vegetation (Smallshire & Swash, 2014). For reproduction *S. meridionale* needs shallow water bodies with low water-level for oviposition and flooding during the subsequent months until emergence in the following year (Roland and Stübing, 2014). Oviposition in *Sympetrum* spp. typically performed by pairs in flight in tandem position and sometimes by females alone (Ishizawa, 2012).

Egg Collection

Eggs of *S. meridionale* were obtained by catching using aerial insect nets copulating or ovipositing females (Schiel and Buchwald, 2014). Their eggs were obtained from females, by the method of Boehms (1971) by dipping the female's abdomen into a tube with water. Copulating females of the dragonfly *S. meridionale* were collected at irregular intervals between November 21 and December 6, 2018 from two different meso-habitats of north-eastern Algeria. The first one is a RAMSAR wetland called "Mekhada" (36°47'19" N; 8°45'41" E) experiencing a humid climate and situated near to the Mediterranean Sea (with 7 m altitude). The second one is a temporary pond located at "Mouna" mountain (1400 m altitude) (36°22'05" N; 7°24'47") characterised by a sub-humid climate, and at 1100 m altitude

Experimental Setup

Tubes with eggs were transferred immediately from the field to the laboratory. Each female eggs were submerged in spring water in small container (9 × 15 × 22 cm³) at 20 ± 1 °C, with a 14:10 h light to dark photoperiod and continuous aeration. Water changes were not made. Spring water, however,

was occasionally added to maintain a minimum depth of 3 cm in each container (Locklin et al., 2012). The eggs were examined twice a week, then daily once hatching started.

The hatching process was observed for twelve containers (7 for Mekhada wetland and 5 for "Mouna" Mountain), after hatching the freshly emerged larvae were left together, to enhance survival (De block & Stoks, 2003). Ten days after hatching, larvae were removed using a transfer pipette and placed individually in 200 ml cups filled with spring water and reared under standard conditions of light (14:10:L:D), temperature (20° C). Larvae were daily fed ad libitum with *Artemianaupliiv* five days a week. Water in cups was changed completely every 4–6 days, or more frequently if needed.

We survived up to 60 Nymph containers, for each group we calculated several life history traits from eggs hatching until the end of the experiment. The hatching success was the number of eggs hatched per total number of eggs reared, mortality rate was the number of larvae survive to the last larval instar per total number of eggs hatched, and finally, life duration was the number of days individuals survive until the death of the last larvae.



Figure 1: Exuvia first stadia.

We separated randomly 10 nymphs from each group at each stage to determine (i) the stadium of individual based on

counting each shed exuvia (Fig.1) (Tennessen, 2017), and (ii) body mass using RADWAG Weighing Scales 0.1mg precision.

Data Analysis

In order to analyse the influence of the habitat provenience on the Southern darter's phenotypic traits, we conducted factorial ANCOVA with habitat origin as independent factors, larval stadia as covariate, and number of death as dependent variables. We test the effect of habitat origin and larval stadia on the larval stadia duration using Factorial ANOVA. Factorial ANOVA and pairwise comparisons with habitat origin and larval stadia as independent factors, and larval body mass as dependent variables. Number of death, larval stadia duration, and larval body mass were normally distributed. All statistical analyses were performed in PASW Statistics 18 software (SPSS Inc. Released, 2009), and results were considered significant at $p < 0.05$.

RESULTS

Life Span

During a single reproductive event, we followed some life history traits of 34000 eggs of *S. meridionale* from different proveniences (Table 1). Overall, the two populations did not behave similarly at the course of the experiment period. Firstly, eggs obtained from females inhabiting the Mekhada wetland experiencing a high hatching success (77.77%) than obtained from females inhabiting Maouna Mountain (temporary pound)(37.68%). Then, numbers of emerged larvae survive to the last larval instar (fifth stadium) appeared to be very low (25.33%) in Maouna's population compared to the second meso-habitat (50.95%). And finally, there was an interaction between habitat types and duration of larval life (Independent samples T test: $t = -7.96$; $df = 12$; $p < 0.05$) (Figure

1), when new born larvae obtained from females inhabiting the Mekhada wetland span more days (68 days) (Table 1) (Fig.2) surviving than did individuals stemming from females inhabiting Maouna Mountain.

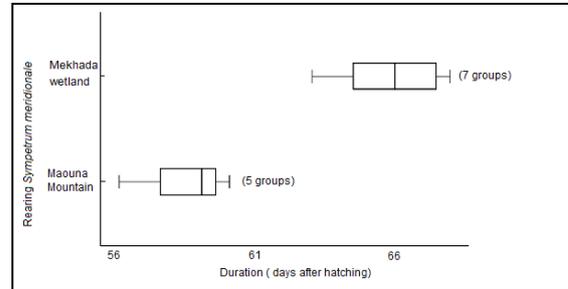


Figure 2: Average larval life duration of *S. meridionale* that emerged in the laboratory (up to 60 larvae per group).

Mortality Patterns

We found that larval stadia, habitat origin, and their interaction significantly affected mortality rates (Factorial ANCOVA: all $p < 0.05$, Table 2). Individuals stemming from females inhabiting Mouna Mountain experienced higher mortality rates than did individuals of the Mekhada wetland population (Fig. 3). For both populations, generally there is a decreasing trend in the number of deceased of *S. meridionale* throughout the experiment (Fig. 3).

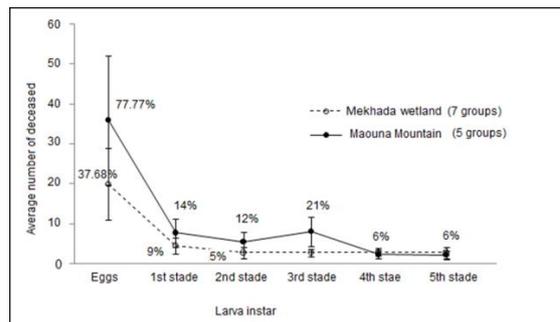


Figure 3: Average numbers of deceased of *S. meridionale* that emerged in the laboratory (up to 60 larvae per group).

Larval Development and Body Mass Variation

After eggs hatching until the end of the experiment, our laboratory conditions

enabled us to attained five larval stadiums for both populations. The factorial ANOVA indicate that the overall model is statistically significant (Table 3). The variable larval stadium and their interaction with habitat origin are also statistically significant (Table 3). However, the variable habitat origin is not statistically significant (Table 3). These results demonstrate that the significant influence of habitat origin on the duration of each larval stadium is depending on the larvae age. The pair-wise comparisons showed that similarity was noted exclusively in hatching duration ($t=-0.13$; $p=0.98$) (Fig.4), i.e., there is no variability in the time of hatching of eggs among populations.

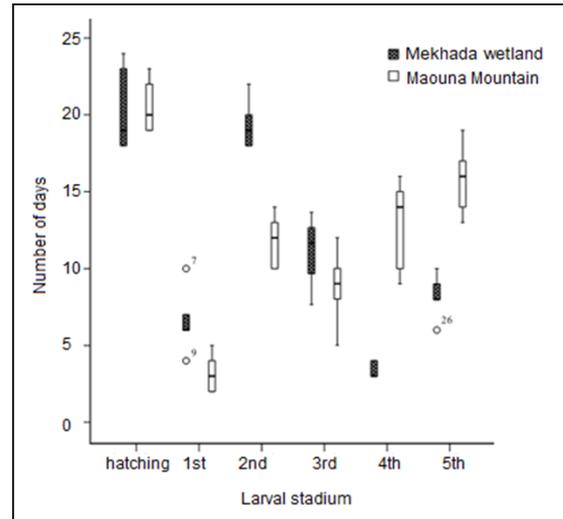


Figure 4: Duration of each larval stadium rearing Southern Darter from different habitats provenience: mean values and standard deviations are shown.

Table 1: Overview of initial number of eggs, hatching success, survival, and larval life duration of *S. meridionale*

	Mekhada wetland		Maouna Mountain	
	Number	Value	Number	Value
Number of eggs	1800		1600	
Number of egg hatched	1400	77.77%	603	37.68 %
survival rate during rearing period (Five stadia)	214 (n 420)	50.95%	76(n 300)	25.33%
Life span [days]	Minimal	63	56	
	Maximal	68	60	

Table 2: Results of a factorial ANCOVA for *S. meridionale* with habitat origin as independent factors, larval stadia as covariate, and number of death as dependent variables.

Source	df	Mean Square	F	Sig.
Corrected Model	12	472.18	28.15	.00
Intercept	1	31.32	1.86	.17
Larval stadia	5	501.91	29.92	.00
Habitat origin	1	260.35	15.52	.00
Habitat origin * Larval_stadium	5	94.94	5.66	.00

R Squared = .878 (Adjusted R Squared = .847)

While interaction term between habitat origin and larval stadium duration arise from the first larval stadia. New-borne larvae stemming from females inhabiting the Mekhada wetland span

higher duration on the first ($t=2.98$; $p=0.02$), the second ($t= 9.93$; $p=0.007$), and the third ($t=2.01$; $p=0.03$) larval stadium and lower duration on the fourth ($t=-6.64$; $p=0.007$) and the fifth ($t=-6.04$;

p=0.06) larval stadium than did individuals of Maouna Mountain habitat origin (Fig.4).

We measured larval body mass of 480 individuals (280 for the Mekhada wetland and 200 individual for Mouna Mountain). The factorial ANOVA indicated that larval stadium and their interaction with habitat origin had a significant effect on larval body mass variation (Table 4) (Fig. 5). The pair-wise comparisons showed that larval body mass among the insect populations was similar at the first larval stadium ($t = -1.4$, $p = 0.15$) and varied significantly when the life cycle progressed (2 nd stadia: $t = -4.15$; $p < 0.05$, 3

rd stadia: $t = 15.47$; $p < 0.05$, and 4 th stadia: $t = -6.49$, $p < 0.05$).

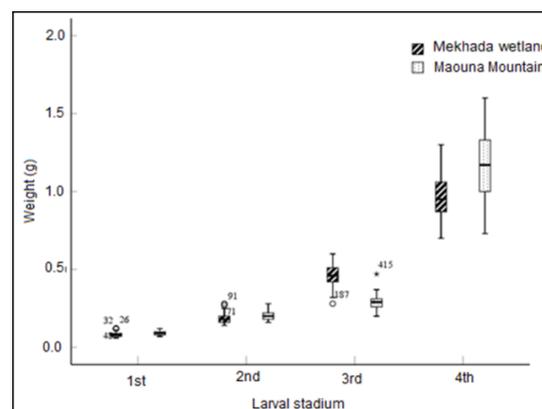


Figure 5: Larval body mass variation of rearing *Sympetrum meridionale*.

Table 3: Results of a factorial ANOVA for *S. meridionale* with habitat origin and larval stadia as independent factors, and larval stadia duration as dependent variables.

Source	df	Mean Square	F	Sig.
Corrected Model	11	189.35	41.69	.00
Intercept	1	8449.06	1860.34	.00
Larval stadium	5	308.66	67.96	.00
Habitat origin	1	13.06	2.87	.09
Larval stadium * Habitat origin	5	105.30	23.18	.00

R Squared = .90 (Adjusted R Squared = .88)

Table 4: Results of a factorial ANOVA for *S. meridionale* with habitat origin and larval stadia as independent factor, and larval body mass as dependent variables.

Source	Df	Mean Square	F	Sig.
Corrected Model	7	9.97	1105.99	.00
Intercept	1	86.76	9621.68	.00
Habitat origin	1	0.02	2.43	.11
Larval stadium	3	22.75	2522.94	.00
Larval stadium * Habitat origin	3	0.75	84.11	.00

(R Squared = .943 (Adjusted R Squared = .942)

DISCUSSION

We established a laboratory rearing experiment for *S. meridionale* obtained from two populations inhabiting two different meso-habitats of north-eastern Algeria. Both rearing insect populations experienced the same laboratory conditions, so that's why variability in the

development and life history traits observed in this study was mainly related to the heritable trait variation between the two populations. This contribution of genetics on the phenotypic pattern of individuals is amply demonstrated by scientific researchers (Schenk et al., 2004; Hassall et al., 2008), and many laboratory, semi-natural, and natural studies have

confirmed the large role of genetic diversity in increasing individual fitness (Jeffrey et al., 2010). The environments of the two populations differ in important aspect such as climate, resources availability, pathogens or the occurrence of other competing species, leading to local adaptations, and then different development tactics might evolve in the two Southern Darter populations, such phenomenon is known as phenotypic plasticity (Schradin, 2012). This phenomenon is non-reversible (Piersma & Drent, 2003), thus basically, the new acquired characters pass across generations, and offspring inherited traits from their ancestors. In other words, the phenotype of an offspring depends on their paternal and maternal phenotype, (genetic or non-genetic inheritance) (Kirkpatrick & Lande, 1989; Mousseau and Fox, 1998; Luquet & Tariel, 2016). Therefore, our laboratory observation on the development behaviour of rearing Southern darter populations might reveals strong insights in documenting the presence of genetic diversity effects on population viability and the evolutionary potential of a species to respond to environmental change. Such variability offered us an ideal opportunity to test phenotypic variations along gradients which can be useful indicators of species-level responses to ecological constraints in a country that already experiencing a severe drought stress and have also been subjected to uncontrolled urbanization and high deforestation rate (Brahmia et al., 2021).

Overall, and as expected the development patterns of the two populations of dragonflies vary with the type of habitat the parental generation of the species occupy. Moreover, we found that this variability is depending on the larval ages of individuals. This is to a large extent due to the fact that physiological and behavioural characteristics of individuals may vary as a consequence of many factors such as animal age (Childs et al., 2016).

We found that egg mortality was very low in dragonfly population inhabiting the RAMSAR wetland compared of those belonging to Maouna Mountain. This observation evidences that fecundity is very high in the RAMSAR wetland odonates, since that fecundity is commonly known to be very high while egg mortality is estimated to be very low (Corbet, 1999). In the laboratory, , and both populations were exposed to similar conditions over the whole experiment. Thus, the differences in infertility and unhatchability among populations are the two possible causes. Hatching success is an accurate indicator and constitutes a potential angle for understanding fitness and life history of odonates (Howard, 1979; Bennett and Mill, 1995; Anholt, 2008). Environmental differences among habitats may amplify differences in fitness between individuals (Kelly et al., 2013) since females with different conditions have different resources to allocate to their offspring (maternal effects) (Hottenbacher and Koch, 2006). Until recently, the Mekhada wetland was a perennial wetland that have the conservation RAMSAR status since 1999 and supports a surprising diversity of vegetation (some 200 species), birds, and considered as suitable breeding habitat of wide range of insects such as Odonates (Halassi et al., 2016). On the other side, the Maouna Mountain pond was a temporary wetland that experienced highly unpredictable conditions, thus organisms as libellulid dragonflies that breed in such habitats circumstance (unsuitable habitats) expected to have lower fitness (Kelly et al., 2013).

The second point of divergence between the two populations was the duration of development. New-borne larvae stemming from females inhabiting the Mekhada wetland develop more slowly than did those coming from the Maouna Mountain pond. In line with previous studies on dragonflies, Hodgkin and Watson (1958) in tropical and subtropical arid regions, Kumar (1976) in India, and

Suhling et al., (2004) in African arid region have revealed that species which breed in such temporary waters exhibit rapid larval growth. This reduction of development time is likely to be the key trait that enables Odonates to be successful in such unpredictable habitats (Suhling et al., 2005).

Finally, we found that body mass differed significantly between the two populations; larvae of *S.meridionales* temming from females inhabiting Mouna Mountain pond (temporary pond) were heavier than those inhabiting the Mekhada wetland (a perennial wetland). An accurate indicator of growth rate, body mass was a phenotypic trait that is widely used in studies on the performance of female fertility and male mating success (Minot et al., 2019). It was influenced by feeding effectiveness and prey consumption ability i.e., the amount of food intake per period of time (Arendt, 1997). High foraging activity increasing encounter with prey, and results in a higher food intake (Wissinger et al., 1999) leading thereby to a higher growth (body mass) and development rate. This fact have been previously identified to be particularly important to species in temporary waters (Johansson and Suhling, 2004; Suhling et al., 2005), which is in concordance with our finding. The purpose of our laboratory rearing experiment was not to study the exact mechanism influencing the hatching success, life duration, mortality, and growth rate differences, as much as it was an attempt to evidences the role of the species parental habitat provenience (temporary vs. perennial water bodies) in the development behaviour of their offspring.

Despite this experiment was very short and only performed on very early instar larvae. It is, however, believed that these results can be used to predict species-level responses to ecological constraints in *S.meridionale* populations across the southern part of their breeding range. Garcia and Arroyo (2001) expected that

different environmental factors influencing life histories may reach their extreme values at the southern edge of the species breeding range, thus studies on North African populations of this dragonfly are very interesting.

Our results allow preliminary insights into the interrelation between development behaviour and habitat origin of *S.meridionale* populations across their southern breeding range (North Africa). Two major points of divergence have been observed between the two populations: firstly, the perennial water specialists have lower fitness than the corresponding temporary water specialists, that secondly they exhibit higher growth rate (body mass) and faster development time compared to permanent water species. Although the different behaviours of the two groups of species that we examined were determined by differences in the inherited traits from their ancestors, variation of the life cycle within species may be related toother several factors (Waringer & Humpesch, 1984). Comparative studies to this subject may have to include more odonates species belonging to several habitats category and more life history traits during more breeding seasons are needed to decipher mechanisms that are responsible for carry-over effects between the habitat provenience and the development behaviour patterns.

AUTHORS CONTRIBUTION

Conceptualization, Elafri Ali and Halassi Imen; methodology, Elafri Ali; data collection Hichem Amari; data validation, Sofiane BOUDALIA, Elafri Ali and Houhamdi Moussa; data processing Elafri Ali; writing—original draft preparation, Elafri Ali and Halassi Ismahen; writing—review and editing all authors.

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CONFLICT OF INTEREST

The authors have not any competing financial, professional, or personal interests from other parties"/ "The authors declare no conflict of interest"/ "The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results".

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