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Phenology of Early-Season and Mid-Season Grasshoppers Shows Contrasted Responses Toward Climatic Variations in an Arid Area

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Abstract: The response of grasshoppers to climatic changes is rarely documented in arid areas. Here we address this subject in terms of phenology, i.e. the peaks of larva and adult abundance, according to species through bimonthly samplings in 2012 and 2013. The study was conducted in the Belezma National Park (northern Algeria) at Djerma (1021 m). The arid character is assessed by annual rainfalls around 330 mm. 2365 grasshoppers from 15 species were collected. Two assemblages were found, separated by the date of adult peaks, a spring one composed of 6 species (Pamphagidae and Pyrgomorphidae) and a summer one composed of 9 species (mainly Acrididae, Oedipodinae). Temperatures recorded *in situ* in 2102 were regularly higher than in 2013, almost from mid-May, whereas there was a humidity in spring 2012, and in summer 2013. In response to temperature and rainfall variations between these two years, the species of spring assemblage are in advance in 2012, and the contrary for those of summer assemblage. The phenology advance of spring assemblage species corresponds to a greater accumulation of degree-days during spring 2012.

As regard summer assemblage, the 17 days-delay of nymphs observed in 2012 is reduced by 9 days in adults, in relation with the highest temperatures of summer 2012. Here it is hypothesized the major role of winter humidity that may have slowed down the hatching time of eggs and/or development of the first instars of summer assemblage species, surpassing the effect of temperatures. This winter humidity does not seem to affect the species of spring assemblage, mainly sensitive to warming.

Keywords: Grasshoppers, Adult phenology, Plasticity, Arid climate, Algeria

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Introduction

According to many studies on the effect of climate changes on insect populations (Guo *et al*., 2010), it has been shown that increasing temperatures result in (i) displacement of populations northward in Northern hemisphere, or higher places in altitude, (ii) changes in community structures (Parmesan and Yohe, 2003; DeVictor *et al*., 2012) and (iii) advanced lag of phenology (Begon, 1983; Buckley *et al*., 2015). This influence of temperature on the life cycle is not linear as there is a shortening of life cycle until a critical body temperature over which there is a relaxing effect (Logan *et al*., 2006). In arid or semi-arid areas, humidity is another constraint that affects the life cycle of insects. As a proximal effect, the experiments of Guo *et al*. (2009) in Inner Mongolia showed contrasting responses of periodic irrigation and periodic heating on grasshopper hatching and development. Although warming by itself allowed an advanced hatching and faster nymph development, periodic irrigation could offset the temperature influence in a species-dependent manner. Moreover, previous works conducted in Algeria concluded that several species of grasshoppers begin their larval development earlier when faced an early drought at the end of spring in order to complete their adult life when grass resources are still available (Guendouz-Benrima *et al*., 2011). It has also been shown that the constraint of summer drought, linked to Mediterranean climate, is an unfavorable factor for univoltine insects that present a peak of adults in summer. Several strategies were recorded to cope with this Mediterranean feature: a shift toward spring or autumn in the case of a single generation, or two generations occurring in spring and autumn (Moussi *et al*., 2011; Petit, 2014). As a result, there is a peak of adults occurring before or after the shortage of plant resources due to summer drought. In summary, there is a double effect of increasing temperature and drought/humidity modulating the response of grasshoppers.

In this study we attempted to find links between the onset of late nymphs and adult stages and climatic variations. The goal was to understand the capacity of grasshopper species to cope with climatic changes and predict the changes in the community structure. This last point has consequences on the functioning of food web as these insects are the main food of numerous birds, lizards and other vertebrates.

Materials and Methods

Study stations

The study was undertaken in a project of inventory and bio-ecology of the grasshopper fauna of the Belezma National Park at the western end of the Aures Mountains (eastern part of northern Algeria). This Park covers an area of 26250 hectares (Beloula, 2008). In a previous study (Betina *et al*., 2017), a high species diversity was observed in Djerma site, around 1020 m a.s.l. (coordinates 35°40'31.87" N and 6°16'32.94" E). This site belongs to the municipality of El-Madher and is located 20 km north-east of Batna. It extends over an area of 9966 hectares and is devoted to rural activity. The steppe vegetation mainly composed of Alfa tufts (*Stipa tenacissima*) which occupies hundreds of hectares, dotted with *Pinus halepensis* trees and *Juniperus oxycedrus* shrubs. The climatic context of the station, given from the 1982-2012 data, is upper arid stage (mean annual rainfalls around 330 mm) with a fresh winter (mean of the coldest month is 0.3 C). The climate is Mediterranean as the hottest months are the driest (Le Houerou *et al*., 1977) and the drought extends generally from the second fortnight of May to mid-October.

During the study period (March 2012 to December 2013), three temperature measures were recorded at 5 cm above the ground level, between 9:30 to 17:00, i.e. when grasshoppers show an activity, to calculate a daily temperature mean (DTM), at a rate of 2 to 3 times per month. These DTM values were then smoothed over a window of five weeks to obtain the temperature profile of each year. As a proxy, monthly rainfalls were taken from Batna climatic station (1058 m), available at www.infloclimat.fr/website, and we can hypothesize that parallel variations occurred in Batna and Djerma station.

Grasshopper sampling

Two to three field samplings of grasshoppers per months were conducted from March 2012 to December 2013, between 10:00 and 16:30 during winter and autumn and between 09:30 and 17:00 during spring and summer. In total, we made 43 field tests. As described by Sobhi *et al*. (2013) and Mahloul *et al*. (2016) the samplings were conducted on areas of 100 to 150 m^2, and care was taken for choosing very distant places of samplings in the successive weeks. The abondance values obtained for each species were then adjusted to 100 m^2 to obtain comparable densities. We caught the winged individuals using a sweep net whereas wingless ones (including nymphs of stages 3, 4, and 5) were collected by hand. Approximately 35% of recorded insects were captured and carefully placed in plastic boxes with the mention of date, location and sex. The rest were identified in the field and released immediately to prevent an impoverishment of the fauna.

The insects were identified using the works of Chopard (1943), Massa *et al*. (1993), Ihsan (1988), and Massa (2013). The nomenclature was updated using OSF2 website http://orthoptera.speciesfile.org and MNHN Paris website http://acrinwafrica.mnhn.fr. In the case of Pamphagidae, male genitalia were dissected for their specific identification (Benkenana *et al*., 2012).

Data analyses

To determine the Growing Degree Days, i.e. the accumulated daily heat required to reach adult stage, it was necessary to estimate the two limit temperatures allowing growth. The lower developmental temperature (LDT) was deduced from the DTM measured in the field on the appearance date of third instar. As night temperatures and further the minimum daily temperatures were not recorded, the DTM considered here was only an approximation of the single sine method developed by Allen (1976). The upper developmental temperature (UDT) was assumed at 40 C according to measure performed on other grasshopper species (Huckley and Nufio, 2014). The phenology of species is usually expressed by a development index based on the proportion of individuals of each developmental stage (Przybyszewski and Capinera, 1990; Bucley *et al*., 2015). As it was not possible to capture the early nymphal stages in region of Alpha tuft density, we only recorded the abundances of pooled late instars and of adults. Then for each species, the temporal barycenter (=centroid) i.e. the period of maximum abundance of each species, was calculated, following Guendouz-Benrima *et al*. (2011) method. The temporal barycenter (=centroid) of the adults was calculated by the formula:

$$B=\Sigma(Ni*abundance_{i})/\Sigma(abundance_{i})$$

The dates were expressed in the decimal format, more easily understandable than the Julian one. For example, March the 20th becomes 3.67; Ni is the decimal date and abundance; $_{I}$ i.e. the abundance at this date. The significance between the differences in barycenters of two years was calculated from a cross-correlation test.

To describe the annual composition of grasshopper communities, a cluster analysis was performed using the 43 dates of sampling and the abundances of 15 species x 2 (adults and nymphs) grasshopper species. The Euclidean distance was considered as a measure of distance. To assess the significance of the barycenter differences between the early and late developing species, Wilcoxon tests were performed. All the statistical analyzes were conducted using again Past 2.17 (Hammer *et al*., 2001)

Results

Comparison between meteorological data of the stations

During the two years of sampling (43 days of measures), there were marked variations in rainfall and temperature regimes. The temperatures were higher in 2012 than in 2013, especially during mid-May (Fig. 1A). In winter from February to March, the humidity was higher in 2012 than in 2013 while from June to the end of the year there was a greater amount of precipitations in 2013 than in 2012 (Fig. 1B).

Annual cycle of grasshoppers

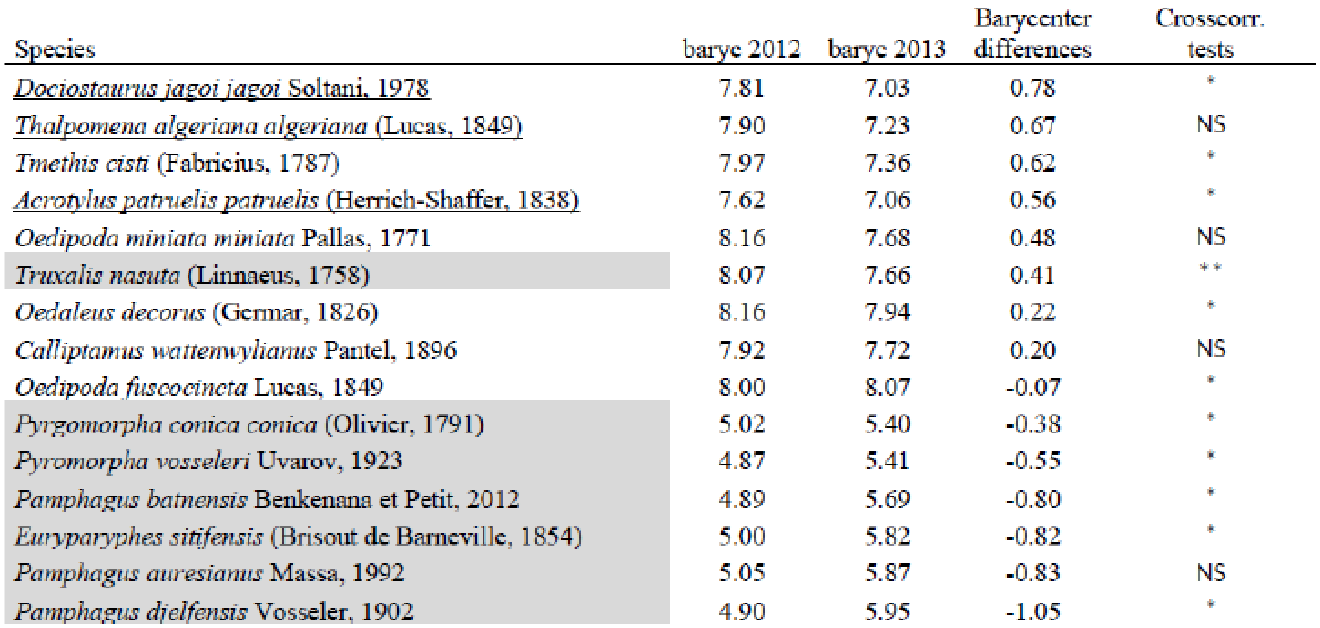
2365 grasshoppers belonging to 15 species (appendix 1) were recorded. The three families encountered were the Acrididae (8 species, among which five belong to Oedipodinae), the Pamphagidae (five species) and the Pyrgomorphidae (two species). The consideration of abundance variations of both nymphs and adults shows that most species were univoltine but three species i.e. *Dociostaurus jagoi jagoi*, *Acrotylus patruelis patruelis* and *Thalpomena algeriana algeriana* presented two generations per year.

Variation in plasticity of grasshopper phenology

The lags between the barycenters observed in 2012 and 2013 were calculated for each grasshopper (Table 1), separately for late nymphs and adults. It should be noted that the population sizes for the second generation were generally much lower than for the first one, preventing us to calculate accurate barycenters for the second generation. As a result, only the first generation was used in the calculation of barycenters.

The lags between adult peaks vary from 0.78 month in *Dociostaurus jagoi jagoi*, i.e. a delay of 22 days (in 2012 relatively to 2013) and -1.05 months in *Pamphagus djelfensis*, i.e. an advance of about 30 days. Taken together, it seems that the species peaking in April or May are in advance in 2012 and that those peaking in July and August are late in 2012. This first approach motivated a cluster analysis based on the total dataset (43 samplings and 30 abundance lines). The cluster obtained in Fig. 2 confirms two assemblages for the adults, distinct by their abundance profile. As regard the nymphs, well separated groups were also observed for univoltine spring and summer species. To establish the significance of these results, all the combinations of categories (nymphs, adults, spring assemblage, summer assemblage) were compared using Wilcoxon tests. The results presented in Fig. 3 show that

Table 1: Plasticity of adult grasshoppers in Djerma station. The species of spring assemblage are on grey background. The bivoltine species are underlined.



Species	baryc 2012	baryc 2013	Barycenter differences	Crosscorr. tests
Dociostaurus jagoi jagoi Soltani, 1978	7.81	7.03	0.78	*
Thalpomena algeriana algeriana (Lucas, 1849)	7.90	7.23	0.67	NS
Tmethis cisti (Fabricius, 1787)	7.97	7.36	0.62	*
Acrotylus patruelis patruelis (Herrich-Shaffer, 1838)	7.62	7.06	0.56	*
Oedipoda miniata miniata Pallas, 1771	8.16	7.68	0.48	NS
Truxalis nasuta (Linnaeus, 1758)	8.07	7.66	0.41	**
Oedaleus decorus (Germar, 1826)	8.16	7.94	0.22	*
Calliptamus wattenwylianus Pantel, 1896	7.92	7.72	0.20	NS
Oedipoda fuscocincta Lucas, 1849	8.00	8.07	-0.07	*
Pyrgomorpha conica conica (Olivier, 1791)	5.02	5.40	-0.38	*
Pyromorpha vosseleri Uvarov, 1923	4.87	5.41	-0.55	*
Pamphagus batnensis Benkenana et Petit, 2012	4.89	5.69	-0.80	*
Euryparyphes sitifensis (Brisout de Barneville, 1854)	5.00	5.82	-0.82	*
Pamphagus auresianus Massa, 1992	5.05	5.87	-0.83	NS
Pamphagus djelfensis Vosseler, 1902	4.90	5.95	-1.05	*

NS = non significant, * = p<0.05, ** = p<0.01

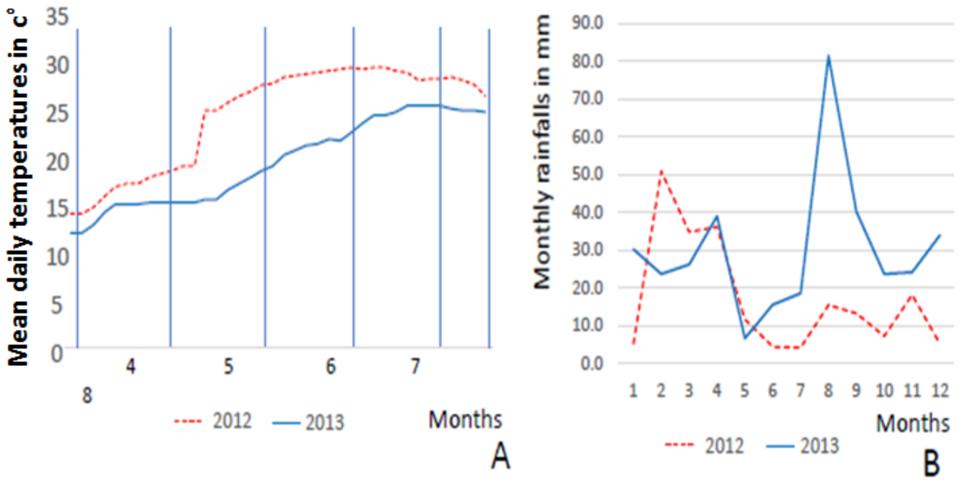


Fig. 1: Monthly variations of climatic parameters in Djerma. A: mean daily temperatures; B = rainfalls (data from Batna).

Appendix 1

Family	Subfamily	Species
Acrididae	Acridinae	*Truxalis nasuta* (Linnaeus, 1758)
	Calliptamininae	*Calliptamus wattenwylianus* (Pantel, 1896)
	Gomphocerinae	*Dociostaurus jagoi jagoi* (Soltani, 1978)
	Oedipodinae	*Acrotylus patruelis patruelis* (Herrich-Shaffer, 1838)
		Oedaleus decorus (Germar, 1826)
		Oedipoda fuscocincta (Lucas, 1849)
		Oedipoda miniata miniata (Pallas, 1771)
		Thalpomena algeriana algeriana (Lucas, 1849)
Pamphagidae	Pamphaginae	*Euryparyphes sitifensis* *(*Brisout de Barneville, 1854)
		Pamphagus auresianus (Massa, 1992)
		Pamphagus batnensis (Benkenana and Petit, 2012)
		Pamphagus djelfensis (Vosseler, 1902)
	Thrinchinae	*Tmethis cisti* (Fabricius, 1787)
Pyrgomorphidae	Pyrgomorphinae	*Pyrgomorpha conica conica* (Olivier, 1791)
		Pyromorpha vosseleri (Uvarov, 1923)

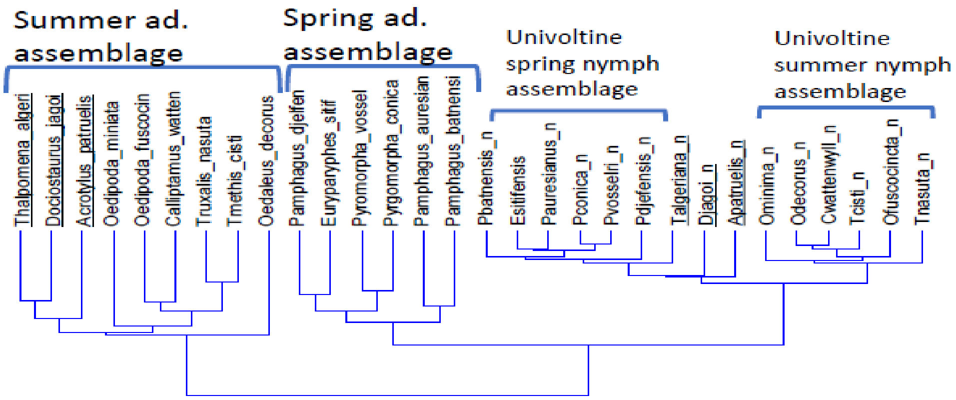


Fig. 2: Clustering of grasshoppers using Euclidean distance. Abbreviation: n = nymph.

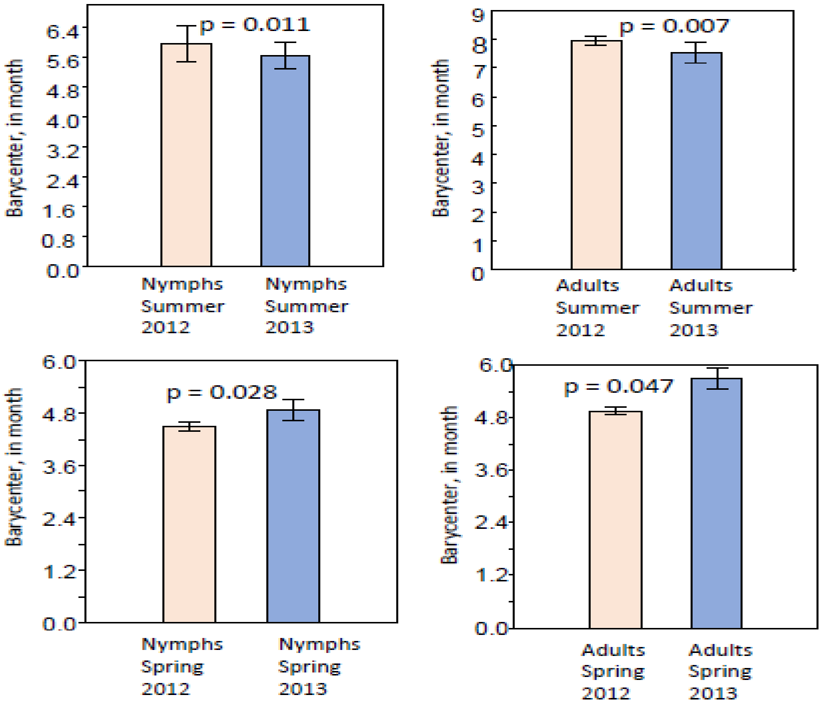
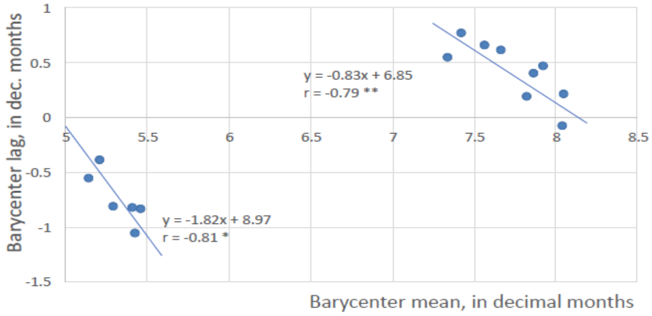


Fig. 3: Temporal barycenters for nymphs and adults for spring and summer assemblages. The significance of differences is given by Wilcoxon tests.

both nymphs and adults of spring assemblage were significantly in advance in 2012, and contrary for nymph and adults of summer assemblage. For each assemblage, there is a decreasing regression line between the mean barycenter (over the two years) and the barycenter lag in adults (Fig. 4). The delay of adult peak enhanced in spring assemblage species but diminished in the summer ones. To understand the influence of temperatures on the life cycle, degree days variations were calculated for each assemblage. Mean values of 12.3 C and 17.9 C were taken as LDT for species peaking in spring and summer, respectively. The UDT of 40 C was never reached during these years. The degree-day curves (Fig. 5) confirm a greater amount of heat in 2012 than in 2013 for the species of both assemblages. As regard spring one, the peak of adults around mid-May corresponded to a moderate difference of 90 degree-days between the two years. Concerning the summer assemblage, the peak of adults happened in the end of June, associated with a difference of around 120 degree-days.



* = p ≤ 0.05; ** = p ≤ 0.01

Fig. 4: Difference of date in adult peaks between 2012 and 2013 according to temporal barycenters (means between the two years).

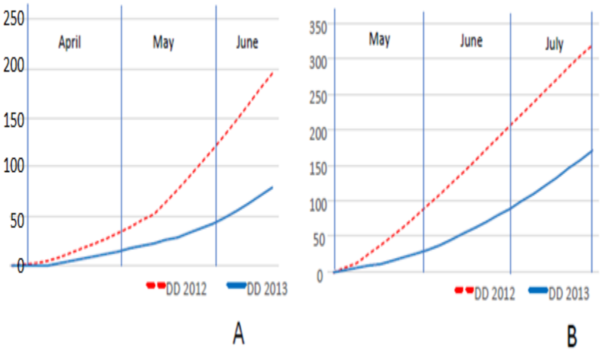


Fig. 5: Degree-days variations according to the date. A: Spring assemblage; B: Summer assemblage.

To resume the trends observed during this study, a schedule of population peaks was drawn in Fig. 6. It appears that for the spring assemblage, the advance of 9 days in 2012 observed for late nymphs was amplified to 12 days in adults. In contrast, the delay of 17 days in 2012 for late nymphs was reduced to 9 days for adults.

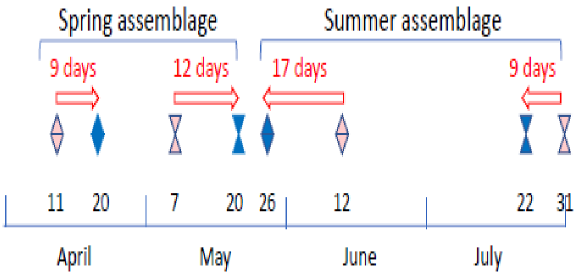


Fig. 6: Synthetic schedule of nymph and adult peaks. Symbols: Lozenge = nymphs; sandglass = adults; wide = 2012, empty = 2013.

Discussion

During two years of samplings contrasted climatic conditions were observed. In the study station of Djerma there extsts temporal variations in the peak of population abundance between the two years for the univoltine species and the first generations of bivoltine ones, as well for the late nymphs and adults. According to species, there is variations in the direction and absolute value of the shift in temporal barycenter. Considering the direction of the shift, there are opposite responses according to the temporal assemblages of the grasshoppers. Moreover, the barycenter lag of adults between the two years increases with the date of peak for species of spring assemblage, and the contrary for the ones of summer assemblage. As the temperatures in 2012 were regularly higher than in 2013, it is clear that temperature itself was not the only explanatory variable.

Regarding spring assemblage, the earlier peak for both nymphs and adults in 2012 is associated to the higher accumulated degree-days observed in 2012. Although our method of describing phenology differs from that of

Kemp and Onsager (1986) for example, our results are concordant with their work. Interestingly, the phenology advance is greater for the species peaking later. Likewise, there is an increase in the advance of adults against nymphs in 2012 over 2103. These two observations fit well with an increase of DD differences during the season between the two study years. The humidity in February and March was higher in 2012 than in 2013, whereas it did not differ in April and May between the two years.

Regarding the summer assemblage, their population peak earlier in 2013 than in 2012 as for adults and nymphs. This result is counterintuitive if temperature variations are only considered. However, the lag between adults in late July is lower than between nymphs in early June. It is reasonable to admit that the shortening of time to reach adulthood from late nymphs is due to higher degree-days in 2012. This view is supported by the variation in the peak date according to adult species.

As described earlier, it is logical that late developing adults take advantage of greater degree-days in 2012 than in 2013 with the season, ensuring a delay reduced to almost zero for the latest adult species (e.g. *Oedipoda fuscocincta*). This accelerated development of late nymphs in relation to increased warming is again in accordance with studies of Guo *et al.* (2010). The issue is then to understand the late onset of nymphs of stages 3, 4 and 5 in 2012. As seen before, the rains were more abundant in February and March 2012, and in June and July 2013. Several hypotheses could explain the connection between humidity and late onset of early nymph stages. The first one is nutritional, as more humidity in June 2013 obviously enhanced the sources of food, preventing a rapid dryness of herbs. This trophic availability would have favored the food intake, and hence the development (Uvarov, 1966). This view can be criticized by the fact that the recruitment of third instars depends on the previous stages at a period (May) where humidity was relatively equal between the two years. As a result, early summer humidity in 2013 could have affected rather abundances and survival of grasshoppers (Kemp and Cigliano, 1994) than their cycle. The second one is related to the higher humidity recorded in winter 2012, which could have influenced hatching of summer assemblage species, but not of spring ones. In their field experimental work, Guo *et al*. (2009) demonstrated that an increase in soil water content by irrigation induced a delay in the hatching of the mid-season *Oedaleus asiaticus* (Acrididae, Oedipodinae) but not for the early-season *Dasyhippus barbipes* (Acrididae, Gomphocerinae). Even when *Oedaleus asiaticus* was submitted to both increased warming and precipitations, the onset of its first nymphs was delayed. It seems that the situation here is similar. We hypothesize that the spring assemblage phenology was only influenced by temperatures, whereas the first instars of summer assemblage species was late in 2012 due to soil humidity. It can be questioned whether winter humidity had still an effect for mid-season grasshoppers. Alpha tufts have a protective effect against soil evaporation, but experiments are needed to give satisfactory responses.

Conclusion

In conclusion, there are two contrasting assemblages of grasshopper species as regard their phenology and response to climatic variations. The species developing in spring do not seem to be affected by winter precipitation but can accelerate their development as result of warmer conditions.

The mid-season species could be more sensitive to winter rainfalls that would affect hatching date, and further a delay to reach adulthood, not necessarily offset by late spring warming. To understand the physiology of hatching date, considering the studies of Guo *et al*. (2009) it would be useful to study the percentage of diapausing eggs for the species of each assemblage. Otherwise, the habitats of both kinds of species are also different, as early-season assemblage contains mesophytous species requiring moisture and frequently found on the vegetation, while mid-season one is composed of more xerophilous species, mainly geophilous (Uvarov, 1977). It should be interesting to describe precisely the dependence of these two categories of species on vegetation and decipher eventual links between phenology and habitat. Further investigations are needed to provide new data on the fine ecology of North-African grasshoppers.

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