

REPRODUCTIVE PHENOLOGY OF THE SPIDER *Micrommata ligurina* (C.L. KOCH, 1845) (ARANEAE; SPARASSIDAE) ACROSS AN ELEVATIONAL GRADIENT IN NORTHEAST ALGERIA

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Abstract

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Decreased ambient temperature and shorter reproductive seasons are the two main obstacles that ectotherms face at higher elevations. Studies have shown that some life history traits such as phenological windows of activity, duration, and fitness components vary as elevation increases. However, studies on the elevational gradient at the southern range limit of species are lacking. In this study, we aim at assessing some aspects of the life history of a spider species, the sprassid *Micrommata ligurina* (C.L. Koch, 1845), across an elevational gradient from 30 to 1030 m in Northeast Algeria. There was strong evidence of an elevational shift in the phenology of reproduction with a delay rate of 2.2 days per 100 m of elevation, and the three quantiles of the phenology (10, 50, and 90%) shifted with the same magnitude across elevation. In all sites from low to high elevation, the species showed a decrease in number of individuals. The mean number of eggs was 200 ± 35 eggs, and the mean number of hatching eggs was 110.9 ± 23.5 eggs. The clutch size at high elevation sites was higher than that of low-elevation sites, but in contrast, the hatching success was higher at lower elevation sites. Overall, the species exhibited clear elevational clines in life history traits and abundance, suggesting a high potential of plasticity. This work constitutes the first study carried out on spider species ecology in the region.

Key words: *Micrommata ligurina*, life history, hatching success, elevation gradients, North Africa.

Introduction

The effects of the spatial gradients on species life history are well-documented, and understanding these patterns remains a central theme in biogeography and ecology (Hodkinson, 2005; Willig, Bloch, 2006; Jenkins, Ricklefs, 2011). The effects of major spatial gradients such as elevation on species are well-documented (reviewed by Hodkinson, 2005). Studies in insects and plants have supported that as elevation increases, traits such as phenological windows of activity, duration, and fitness components vary (Rahbek, 1995; Arroyo et al., 1981; Illán et al., 2012; Khelifa, 2017; Amari et al., 2019; Ahmad et al., 2021).

As expected from theory, environmental conditions (e.g. temperature, precipitation, atmospheric pressure, and land area) change rapidly with elevation, and species typically respond accordingly (McCain, 2007; Körner, 2007; Lieth, 2013). Studies have revealed that different patterns of phenology, abundance, and richness often reveal a decrease or a mid-elevation peak in response to elevation for both animals and plants but the elevational clines vary among taxa and geographic areas (Rahbek, 2005; Brehm et al., 2007; Sundqvist et al., 2013). Specifically, in insects and others arthropods, an effort has been made to try to clarify this variation in life-history characteristics (Laiolo, Obeso, 2017). For instance, at high elevations, populations have a prolonged generation time and faster growth with fewer but larger

eggs compared to the population in lowland (Hodkinson, 2005; Chown, Klok, 2003; Wilhelm, Schindler, 2000). What remains relatively unexplored are the elevational clines in species interactions and traits of specialist taxa that rely on a specific resource.

Spiders are ectothermic terrestrial arthropods, mostly opportunistic predators, and are among the most common animals in terrestrial environments with 50,077 species worldwide (World Spider Catalog, 2022). They inhabit areas ranging from lower to higher altitudes with a wide variety of lifestyles and behaviours (Foelix, 2011). Plant vegetation represents a heterogeneous and complex environment and benefits spiders by providing shelter and substrates for web building, attracting prey, and offering suitable micro-habitat for reproduction, whereas spiders can benefit plants by providing nutritional resources by consuming or deterring herbivores insects (Schmalhofer, 2001; Whitney, 2004). In fact, a spider's habitat occupancy at the large or small scale is not a random decision. For example, the macro-level includes habitats attributes such as forest types; the micro-level includes the process of selection and use of specific plants; finally, the nano-level includes the selection of some parts within an individual plant (reviewed in Dinesh, 2017).

There is a considerable lack of studies on spiders in Algeria, and most of them focus on taxonomy and inventories (Bosmans, Beladjal, 1991; Bosmans, Abrous, 1992; Bosmans, Chergui, 1993; Alioua et al., 2016). Thus, the current study which includes aspects of the biology, ecology, and life history plasticity across geographic gradients fills a huge knowledge gap about this taxon. Here we assess some aspects of life history of a species of spider *Micrommata ligurina* (C.L. Koch, 1845) across an elevational gradient in Northeast Algeria. This species, which has not been studied before in North Africa, is a huntsman spider that occurs across a large area from the Mediterranean basin to central Asia (Platnick, 2011). It lives on herbaceous vegetation (Lissner, 2011) where the female lays eggs in small sacs in the closed envelope of plant leaves (personal observation). In Northeast Algeria, *M. ligurina* uses mainly *Drimia maritima* (Stearn, 1978) during the reproductive season in the spring. In fact, the inside base of the plant is shaped like a bowl that accumulates water where a variety of insects are trapped and used as food for the spider (Zebba R. personal observation). We combined field and laboratory studies to explore the temporal pattern of the breeding of the species, abundance, clutch size, and hatching success across an elevational gradient.

Material and methods

Sampling area

Our study was conducted in Northeast Algeria and specifically in seven sites (Fig. 1) with elevations ranging from 50 to 1,030 m (Table 1). Preliminary visits to the sites were carried out to confirm the existence of the spider across the elevational range. The coastal area (Annaba province) where the low-elevation sites (sites 1–3) occur has a warmer annual temperature (average = 18.3 °C) ranging from 8 to 30 °C (rarely below 5 or above 34 °C), and receives higher precipitation (703 mm) compared with the mainland area (Guelma province) where the medium- and higher elevation sites (sites 4–7) are located. The latter have temperatures (average 17.2 °C) ranging from 4 to 35 °C that rarely fall below 0 or exceed 39 °C with an annual precipitation of 557 mm.

Sampling procedures

The species *Micrommata ligurina* is a widespread spider and has a large niche breadth in Northeast Algeria. The body size of *M. ligurina* female is up to 12 and 9 mm for male. The abdomen of female is bright green, and distinguished from *M. virescens* (Clerck, 1757) by the darkened of the last segments of legs, especially of the 4th posterior pair. Male of *M. ligurina* is distinguished from *M. virescens* by the colour of the middle band of the abdomen, blackish, and the absence of yellow bands. Prior to the study, we conducted visits for each three days in late February 2020 in order to record a good approximation of the start of the reproductive season. We first identified patches of *Drimia maritima* where the spider is known to occupy. Then, for each site, three plots (5×5 m²) were selected and labelled with relatively similar density of vegetation across all sites. In each plot, we surveyed 20 individuals of *D. maritima* (Fig. 1). After the reproductive season started, we carried out a weekly count of reproductive pairs between 17 March and 02 May 2020 to determine the temporal pattern of abundance and reproductive phenology of the species. The end of the reproductive period was confirmed when no pairs found anymore after seven subsequent visits at each site. Ten clutches of eggs (egg sacs) were collected randomly outside of the study plots at each site in the second week of the reproductive season.

In the laboratory, each clutch with a piece of the host vegetation was placed in a vial (10×10×10 = 10cm³) under natural light conditions. The number of eggs was counted to determine the clutch size. Eggs were checked for hatching daily. Spiderlings were isolated from the original vial and placed in another one. They were counted and then returned to the original site. Egg hatching was considered to have finished when no spiderling was found after 5 consecutive days of checking.

Statistical analysis

Statistical analyses were carried out with R 4.0.2 (by R Development Core Team, 2021). Multiple linear regressions were conducted to analyse the elevational pattern of three quantiles of the phenology of the reproductive season (hereafter phenophases). Based on the frequency distribution of Julian dates generated based on all recorded individuals throughout the season (quantile 0 is the first record and quantile 100 is the last record), we calculated three quantiles which correspond to quantiles 0.1, 0.5, and 0.9. For instance, quantile 0.1 indicates the Julian date where 10% of observed individuals were recorded. The model included Julian date (day of the year) as a response variable, and elevation (continuous variable) and quantile (grouping variable with three levels: 10, 50, and 90%) as explanatory variables with interaction. The length of the phenology period of the species was analysed with linear mixed-effects models including elevation as fixed effect, and plots as random intercept. A generalised linear mixed effect model with Poisson error distribution was applied to assess the temporal pattern of abundance (density of pairs in each plot) across elevation with Julian date (including the quadratic effect) and elevation as fixed effect including one-way interaction, observation id (to account for over-dispersion), and plots as random effect. All models were fitted using the R package lme4 (Bates et al., 2015), and R package car for p values. We assessed the effect of elevation on clutch size and hatching success using Negative binomial GLM in R package MASS. Clutch size and

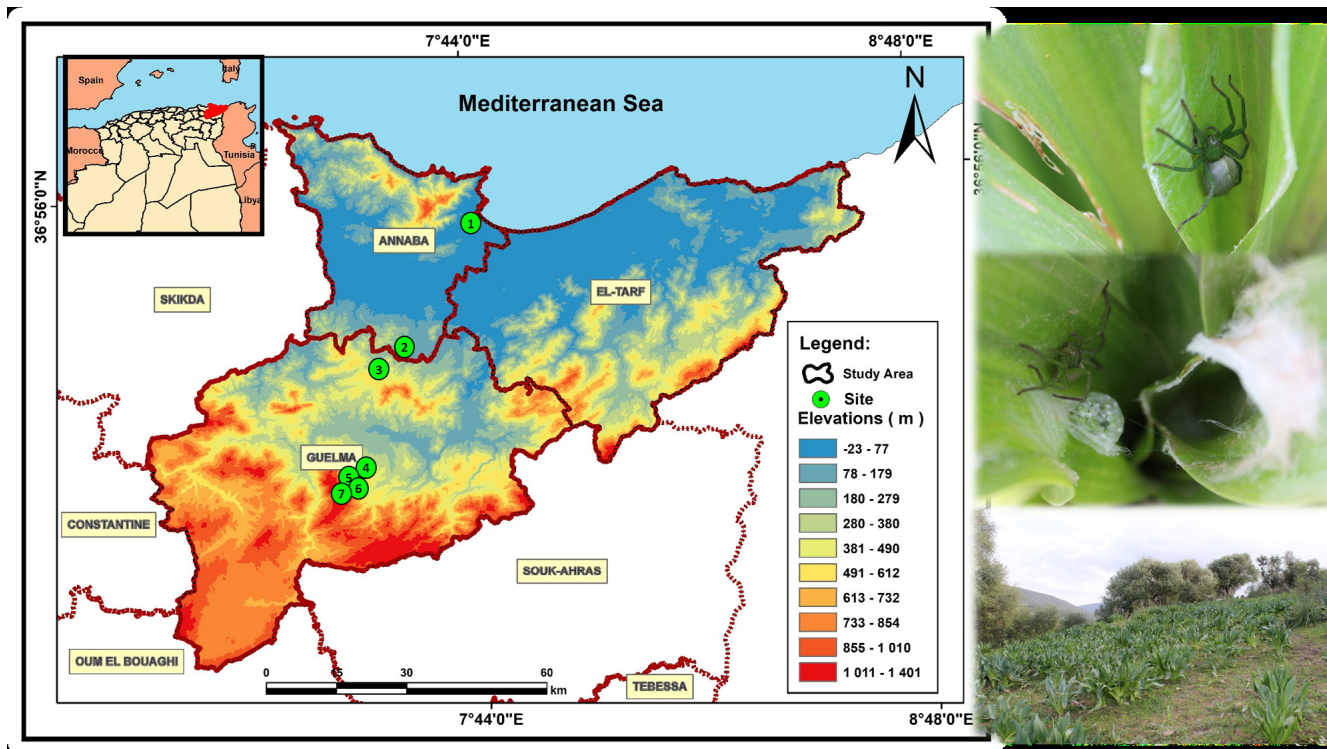


Fig. 1. Topographic map showing the study sites in Northeast Algeria. The numbers refer to the sites. The elevational gradient in this area ranges from 0 to 1401 m (from blue to red).

Table 1. Study sites with geographic coordinates and elevation in Northeast Algeria.

Site code	Province	Latitude	Longitude	Elevation (m)
1	Annaba	36°52'9.56"N	7°44'53.65"E	50
2	Annaba	36°37'40.05"N	7°34'20.03"E	150
3	Gulema	36°35'52.23"N	7°30'34.75"E	310
4	Gulema	36°24'28.08"N	7°25'49.45"E	490
5	Gulema	36°23'4.70"N	7°25'44.87"E	720
6	Gulema	36°22'2.42"N	7°25'24.48"E	900
7	Gulema	36°21'40.83"N	7°24'45.34"E	1030

hatching success as response variables and elevation as explanatory variable. Values presented hereafter are mean $\pm$ SD.

Results

Phenology pattern of breeding across elevation

The reproductive season spanned mid-March through the first week of May. There was a significant seasonal delay of the reproductive season across elevation for the three phenological phases ($t = 4.618$, $P = 0.003$) (Fig. 2, Table 2), revealing that populations at higher elevations start to lay later than populations at lower elevations. We estimated a delay rate of 2.2 days per 100 m. There was no significant difference between the elevational pattern of the three phenophases, revealed by the nonsignificant interaction between quantile and elevation. This means that the

three phases of the phenology shifted with the same magnitude across elevation, maintaining a similar length of the 80% of the reproductive season (number of days between the early and late phase of the phenology) (Table 2). When including the entire season from the first to the last day of the reproductive season, the estimated length period of the reproductive season was 36, 29, and 22 days for the low elevations (50–310 m), intermediate (490 m), and high (720–1030 m), respectively. The duration of the reproductive season changes across elevation, revealed by the significant negative relationship between elevation and the length period of the reproductive season (Table 3).

Temporal pattern of abundance across elevation

The temporal distribution of abundance showed different timing of peaks across elevation. The number of pairs peaked between the

Table 2. Summary results of the linear regression assessing the elevational pattern of the phenology of reproductive season of *Micrommata ligurina* in Northeast Algeria. The quantile 10% is used as the baseline level (intercept) for contrast calculation.

Model parameter	Estimate	SE	t-value	p-value
(Intercept)	7.874e+01	2.932e+00	26.857	<0.0001 ***
Altitude	2.160e-02	4.677e-03	4.618	0.0003 ***
Quantile 50%	9.834e+00	4.146e+00	2.372	0.0315 *
Quantile 90%	1.986e+01	4.146e+00	4.791	0.0002 ***
Altitude:quantile 50%	4.154e-03	6.614e-03	0.628	0.5393
Altitude:quantile 90%	2.597e-04	6.614e-03	0.039	0.9692

Table 3. Summary statistics of the linear mixed-effects model assessing elevational pattern of the length of the reproductive phenology of *Micrommata ligurina* in Northeastern Algeria.

Model parameters	Estimate	Std. Error	df	t-value	P-value
Length period					
(Intercept)	3.822e+01	4.708e-01	4.788e+02	81.18	<0.0001***
Elevation	-1.768e-02	7.511e-04	4.788e+02	-23.54	<0.0001***

Table 4. Summary statistics of the generalized mixed-effects model assessing the temporal pattern of abundance across elevation during the reproductive season of *Micrommata ligurina* in Northeastern Algeria.

Model parameters	Estimate	Std. Error	z value	P value
(Intercept)	-3.702e+01	2.509e+00	-14.756	<0.0001***
Elevation	2.605e-02	5.294e-03	4.920	0.008***
Julian date	8.702e-01	5.381e-02	16.172	<0.000***
Julian date ²	-4.732e-03	2.871e-04	-16.479	<0.000***
Elevation × Julian_date	-6.447e-04	1.045e-04	-6.172	0.0003***
Elevation × Julian date ²	3.733e-06	5.156e-07	7.240	<0.000***

end of March and mid-April in low elevations (50–310 m), and in the third week of April in intermediate elevations (490 m), and in the fourth week of April at high elevation (720–1030 m) (Fig. 3).

The change of abundance of pairs during the reproductive season is shown in Figure 4. By regressing the abundance by the elevation and Julian date (including the quadratic effect), we found a negative effect of elevation ($P < 0.000$), showing that the number of reproductive pairs decreased with elevation ($P < 0.000$) (Table 4). The significant elevation-by-Julian date and elevation-by-Julian date² interactions revealed that the seasonal pattern of pair abundance was dependent on elevation (Table 4). The seasonal pattern of abundance showed a quadratic trend with an increase in the early season up until a peak, then a decrease in the late season ($P < 0.000$) (Table 4). The interaction between altitude and Julian date (including the quadratic term) indicates that the seasonal pattern of abundance varied across altitude ($P < 0.001$).

Clutch size and hatching success across elevation

A total of 105 clutches (21,054 eggs) were collected across all sites. Overall, the mean number of eggs was 200 ± 35 eggs, and

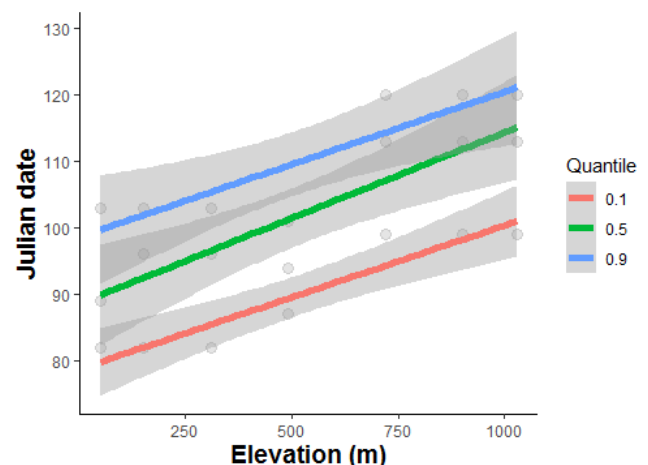


Fig. 2. Elevational pattern of the breeding phenology of *Micrommata ligurina* in Northeast Algeria. The lines are linear regressions. Light (circle), intermediate (triangle), and dark (square) colours refer to the quantile 10, 50, and 90%, respectively.

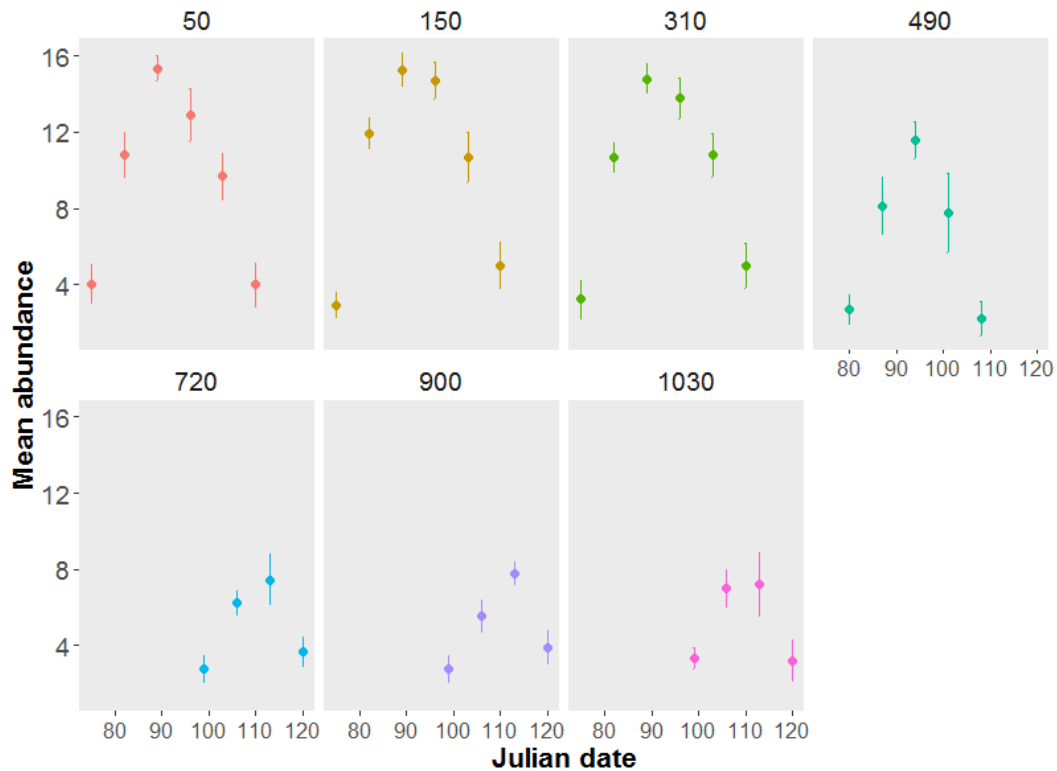


Fig. 3. Temporal distribution of abundance of pairs of *Micrommata ligurina* at each altitude. Counts were weekly during the study period.

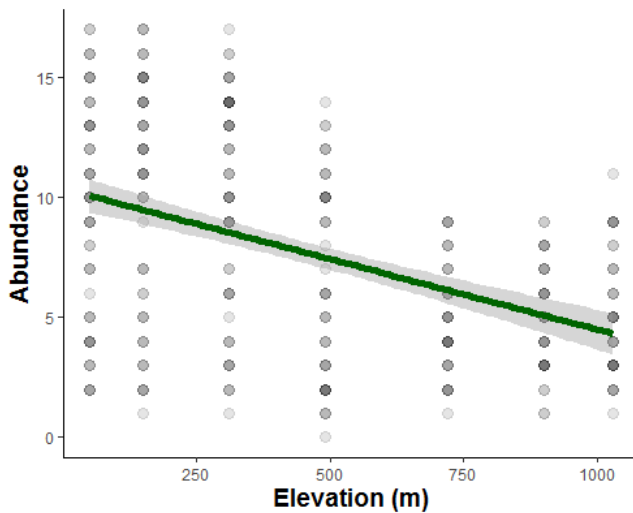


Fig. 4. Elevational pattern of the abundance of pairs of *Micrommata ligurina* in Northeast Algeria. The line is a Poisson regression and the envelope is the standard error.

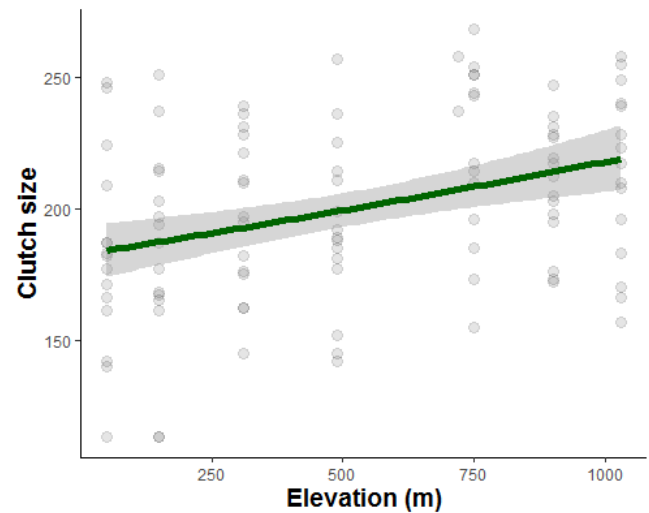


Fig. 5. Pattern of clutch size across elevation of *Micrommata ligurina* in Northeast Algeria. The envelope is the standard error.

the mean number of hatching eggs was 110 ± 23 eggs. The clutch size increased across elevation, revealed by the significant positive relationship between elevation and the number of eggs (Table 5, Fig. 5). We did not find a significant relationship between the number of hatched eggs and elevation (Table 5).

Discussion

Based on our survey of natural populations of *Micrommata ligurina* during the reproductive season, we provide strong support for an elevational shift in the phenology of reproduction, and

Table 5. Summary statistics of negative binomial GLM assessing the change of clutch size and hatching success across elevation during the reproductive season of *Micrommata ligurina* in Northeastern Algeria.

Model parameters	Estimate	Std. Error	z value	P value
Clutch size				
(Intercept)	5.206	0.029	174.042	<0.0001***
Altitude	1.774e-04	4.715e-05	3.762	<0.0001***
Hatching success				
(Intercept)	4.685	0.0376	124.354	< 0.0001 ***
Altitude	4.603e-05	5.960e-05	0.772	0.44

cline in abundance, length of the reproductive phenology, and clutch size across elevation. Our study reveals new data on some important aspects of the life history and distribution of the species in Northeast Algeria.

In general, the warmer the habitat, the earlier the phenology (Cleland et al., 2007; Kharouba et al., 2014). Based on the sampling of reproductive pairs, we detected a strong shift of the phenological distribution of the reproductive season across elevation, revealing that populations at higher elevations start laying eggs later than populations at lower elevations. Similar patterns are found in ground spiders (Chatzaki et al., 2005) and in another of arachnids, Opiliones in Greece (Chatzaki et al., 2009). Temperature is an important determinant of spider phenology that influences embryonic development as well as adult activity (Belozarov, 2012). In the studied region, a study on a damselfly showed a similar delay of the reproductive season with elevation (Amari et al., 2019).

Our results showed an elevational cline in the length of the reproductive season, which was shorter at high-elevation sites. In general, and at higher altitude, organisms use different mechanisms such as diapause, fast development, and restriction of activity to face the decreased ambient temperature and short breeding seasons (Stamou, 1998; Zettel, 2000; Laiolo et al., 2013). A recent comparative global study on harvestmen showed that the length of the breeding season is primarily significantly influenced by the number of warm months and secondarily by precipitation (Machado et al., 2016). In seasonal environments, the breeding season in many ectotherms is restricted to a few months of the year, and organisms are confronted with two periods of stress, winter with low temperatures and long summer season with high drought. A study on a harvestman *Discocyrtus prosopius* inhabiting a freshwater wetland in Argentina showed that the length of the breeding season is primarily influenced by the number of months with a mean temperature above 5 °C (Iglesias, Pereyra, 2020). It seems that *Micrommata ligurina* prefers to reproduce within a specific range of intermediate temperatures during the spring. Since the optimal conditions for the species start earlier and last longer at low elevations, the phenology of the reproductive season is expected to shift in timing and length across the elevational gradient (Hodkinson, 2005; Amari et al., 2019).

Our results on abundance at breeding season show that the number of pairs [see above] decreases across an elevation gradient. This geographic pattern of abundance is most likely related to the temperature. In a study conducted along three elevational gradients in the Brazilian Forest, the authors showed that the abundance of harvestmen was positively correlated with temperature and humidity (Almeida-Neto et al., 2006). In the past,

despite several studies reporting a decrease in abundance across elevational gradients in arthropods, mainly spider and insects (Janzen, 1973; Wolda, 1987; McCoy, 1990; Almeida-Neto et al., 2006), others studies, e.g. on harvestmen in Norway found that species reach a maximum number of individuals at higher elevation sites (Hågvær et al., 1978), and a similar pattern is seen in Greece in some Opiliones species (Chatzaki et al., 2009). In fact, abundance variations across elevation could be also driven by a range of other abiotic and biotic factors that may also influence the dynamics and structuring of spider assemblages as well as the ability of the species to disperse and establish populations (Bonte et al., 2004). For instance, abiotic factors such as habitat structure at smaller or broader spatial scale (Muff et al., 2009; Rypstra et al., 1999; Whitehouse et al., 2009) and biotic factors such as food availability (Halaj et al., 2000; Batzer, Boix, 2016). Therefore, *M. ligurina* in Algeria should be able to reach the higher elevation areas.

Our results revealed that there is a positive relationship between the number of eggs and elevation. Previous studies showed that arthropods at high elevation are characterised by short larval stage, small adult size, low fecundity, and fewer but larger eggs (Honěk, 1993; Wilhelm, Schindler, 2000; Zettel, 2000; Laiolo et al., 2013). In spiders, many studies have found that wolf spider body size and fecundity decrease with rising elevation, a proxy for shortening growing season length (Høye, Hammel, 2010; Bowden et al., 2013). Interestingly, our findings are markedly different from those reported in other spider species. Although we have not measured the size of adults across elevation, it is reasonable to predict that the size of ectotherms increases in colder conditions because individuals spend longer time growing (Angilletta et al., 2004; Valenzuela-Sánchez et al., 2015). Many studies have shown that several others factors affect spider body size such as predators being selective in their choice of prey, habitat complexity, and nutritional quality (Stańska, Stański, 2017; Stańska et al., 2018). Further investigations on the complexity of mechanisms that are responsible for this difference in body size are needed. Since fecundity is typically positively associated with body size in invertebrates (Blanckenhorn, 2000), including spiders (Fritz, Morse, 1985; Reed, Nicholas, 2008), it is likely that the larger clutch size at higher elevation is due to differences in body size. However, explaining the mechanism behind this pattern will require laboratory experiments to disentangle maternal effects (investment in egg number vs. egg size) (Roff, 1993) and paternal effects (fertilization success) (Pitnick et al., 2008) and unravel the intriguing geographic pattern of life history of *M. ligurina*, which is different from what theory predicts (species invest in egg size rather than egg number in stressful environ-

ments such as in high elevation) (Blanckenhorn, 1997; Wilhelm, Schindler, 2000; Kaplan, Phillips, 2006; Liao et al., 2014).

Conclusion

In conclusion, *M. ligurina* showed a large niche breadth in Northeast Algeria, occupying a wide range of elevations where the environmental conditions vary considerably. The species exhibited elevational clines in life history traits and abundance suggesting a high potential of plasticity. Some traits varied geographically in ways that are different from what theory predicts. The species is therefore suitable for studies in ecology and evolution, particularly on local adaptation, dispersal, and range dynamics, and especially in Northeast Algeria where climate is projected to become warmer and drier, and expected to impact arthropod communities (Khelifa et al., 2021). We hope that this pioneer study will engage scientists in North Africa in using this interesting biological system in future studies. Further studies should explore plasticity of important fitness components such as fecundity and life span and the role of biotic factors such as intraspecific competition in combination with quantitative climate change projections for Northeast Algeria across a large environmental gradient to predict the effect of global heating on *M. ligurina* and its distribution.

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