

# Differential elevational cline in the phenology and demography of two temporally isolated populations of a damselfly: Not two but one taxon?

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**Abstract.** 1. Temporal isolation by cohort splitting is a life-history mechanism that has been reported in many temperate insects, including those inhabiting freshwater habitats. Although the cohorts seem to maintain separate temporal niches in a specific location, the temporal isolation may be disrupted across a geographic gradient due to constraints imposed by seasonality.

2. This prediction was tested on two temporally isolated populations of the obligatory univoltine *Lestes virens* (Odonata, Lestidae) in north-east Algeria. Although the two cohorts emerge at the same time in spring, one cohort reproduces in summer, while the second cohort estivates in summer and reproduces in autumn. A survey assessing the phenology and abundance was conducted on eight ponds across an elevational gradient (5–1012 m asl) using capture–mark–recapture and adult density sampling.

3. In all sites from low to high elevation, the species showed cohort splitting. The phenology of reproduction of both cohorts showed a delay with elevation, but the cline was 2.2 days for the summer cohort and 0.7 days for the autumn cohort per 100 m of elevation. Moreover, the density of adults in the autumn cohort was higher than that of summer cohort across the entire elevational range, and the difference increased with elevation.

4. These findings regarding the differential elevational cline in the phenology show that the temporal isolation of the two cohorts becomes narrower at high elevation, suggesting potential inter-cohort temporal overlap at higher elevations.

5. The claim that the two cohorts of *L. virens* are true temporally isolated species needs further investigation.

**Key words.** Algeria, damselfly, Lestidae, life history, North Africa, odonate.

## Introduction

Phenology, the timing of recurrent biological events, is a plastic life-history trait that shows intraspecific variation in many taxa (Lieth, 2013). Local environmental conditions and temperature,

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in particular, influence the phenology of populations (Visser & Both, 2005; Körner & Basler, 2010). The general pattern is that the warmer the habitat, the earlier the phenology (Cleland *et al.*, 2007; Kharouba *et al.*, 2014). Given that temperature and other environmental factors change across geographic gradients such as elevation, phenology often shows elevational shifts (Butler, 1984; Hodkinson, 2005).

Variation in life history can be a driver of evolution and ultimately speciation through reproductive isolation of populations adapted to different environmental conditions (Mayr, 1970; Coyne & Orr, 2004; Rundle & Nosil, 2005). Although temporal isolation is among the least investigated evolutionary forces of speciation (Coyne & Orr, 2004), various instances have been reported in insects (Marshall & Cooley, 2000; Santos *et al.*, 2007; Yamamoto & Sota, 2009; Sota *et al.*, 2014; Boumans *et al.*, 2017). In freshwater insects, there is not much evidence that diversification by temporal isolation is a common mechanism for speciation (Dijkstra *et al.*, 2014). Genetic difference may arise between cohorts hinting at temporal diversification, but the level of differentiation that has been reported was high in some cases and low in others. In the mayfly *Baetis rhodani*, three clades that live in sympatry have different phenologies and show high genetic differentiation (Lucentini *et al.*, 2011). Here we analyse the phenology of the adults of *Lestes virens*, a damselfly species that has been reported to show cohort splitting in reproductive phenology. The two cohorts emerge at the same time, but one cohort reproduces in summer and the other reproduces in autumn. The two cohorts were first reported as separate species, *L. virens virens* and *Lestes numidicus* (Samraoui *et al.*, 2003), but it is still a matter of debate whether these are truly isolated species, because of the small genetic differentiation (Dijkstra *et al.*, 2014) and potential gene flow between the cohorts. There is a lack of knowledge about the elevational variation of the phenology of emergence and reproduction. Information on the intraspecific plasticity of the phenology in these cohorts may shed light on the adaptive temporal segregation and the evolution of the phenology of these species.

Odonates have a complex life cycle where the adult is terrestrial but the larva is aquatic (Stoks & Córdoba-Aguilar, 2012). The phenology of odonates (dragonflies and damselflies), and especially its plasticity to climate change, has been studied (Hassall *et al.*, 2007; Dingemans & Kalkman, 2008; Hassall, 2015). Geographic gradients of odonate phenology, however, have not been investigated thoroughly (Richter *et al.*, 2008; Simaika & Samways, 2015). Some odonates are obligatorily univoltine, that is, they produce one generation per year at any location in their distribution range (Corbet *et al.*, 2006). Such cases are known for species of Lestidae in the temperate region. In fact, the eggs of these species enter diapause, and after hatching, they complete larval development and emerge in the same year. Therefore, *Lestes* species encounter time constraints in cold habitats compared with warm habitats due to the shorter warm season (Johansson & Rowe, 1999; Johansson *et al.*, 2001). Hence, populations in different parts of the geographic range have adapted mechanisms to accomplish univoltinism by manipulating development and emergence (Śniegula *et al.*, 2012). Such adaptive mechanisms to local environmental conditions have not been investigated in the *L. virens* in north-east Algeria

where the species shows cohort splitting. One would expect geographic variation across elevation in the phenology, maturation period and reproductive season because of the ecological limitations dictated by seasonality (De Block *et al.*, 2008). Furthermore, it is predictable that the maintenance of reproductive isolation becomes less likely in environments where the warm season is too short, such as at higher elevation. Here we investigate whether seasonal limitation disrupts the cohort splitting of *L. virens* across elevation.

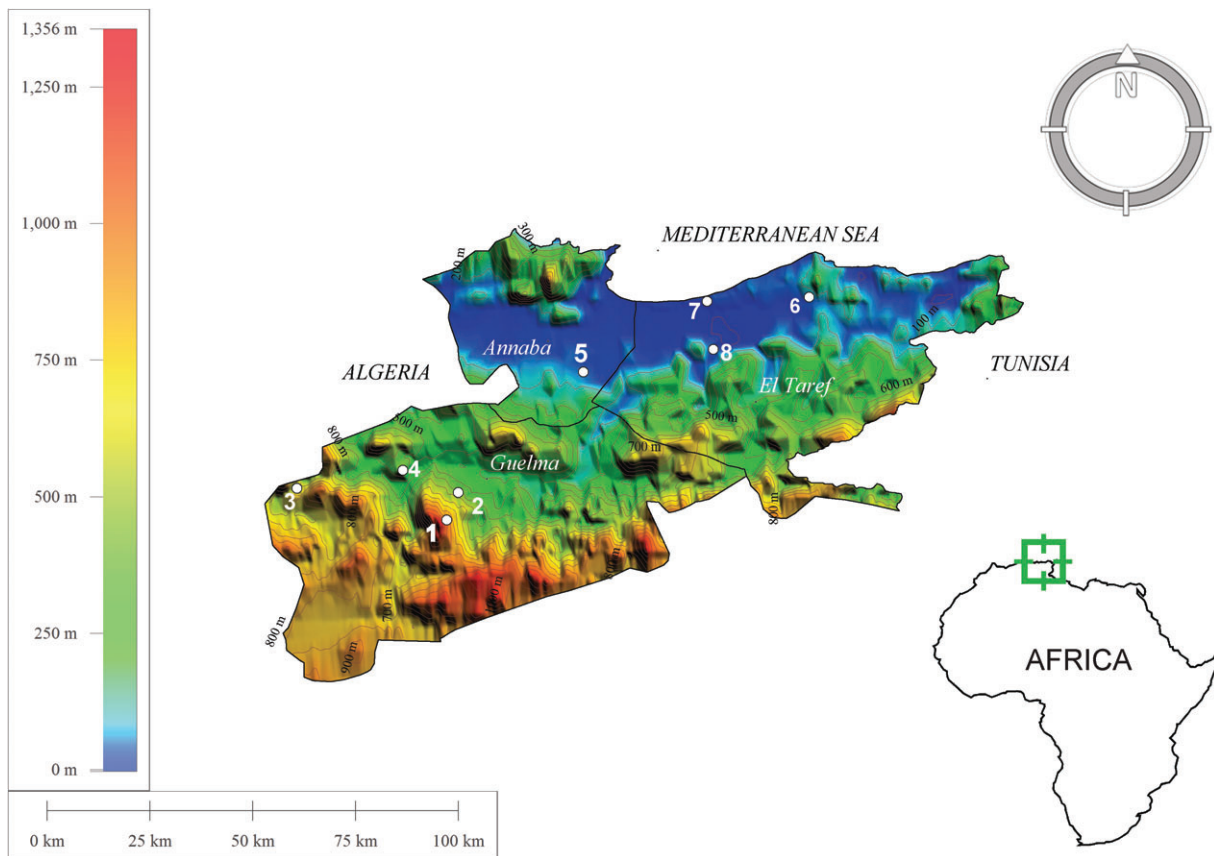
Population size is an important component of the population dynamics. This demographic parameter is determined by the birth and mortality rates and thereby reflects the fitness of the population in a given habitat (Pielou, 1969). The monitoring of population size is crucial for wildlife management and conservation. Capture–mark–recapture (CMR) survey is an effective tool to estimate population size and other demographic parameters (Cormack, 1964; Jolly, 1965; Seber, 1965), and it has been widely used in natural populations of many taxa (Pradel, 1996). The technique consists of marking a sample of individuals from a wild population and then regularly recapturing them across their lifetime. The frequency of recaptures enables the estimation of population size, apparent survival and recapture probabilities (Seber, 1965; Pollock *et al.*, 1990). The abundance is determined by abiotic and biotic factors that can change across geographic gradients, which results in spatial patterns of species abundance (Hengeveld & Haeck, 1982; Brown, 1984). For species with seasonal regulation strategies, such as cohort splitting (Hughes *et al.*, 1999; Schultheis *et al.*, 2002), it is important to determine whether one strategy is dominant over the other. More importantly, it is crucial to examine if there are geographic patterns across geographic gradients such as strategy switch in order to understand the evolution of life histories (Stearns, 1992). Here, we assess the elevational pattern of abundance at reproduction in the two seasonal cohorts of *L. virens* to determine the geographic extent of coexistence of the two life-history strategies and the potential geographical cline in their demography (dominance of one strategy over the other).

In this study, we investigate the emergence and reproductive phenology of the obligatorily univoltine *L. virens* in eight different populations across an elevational gradient in north-east Algeria to characterise the elevational cline of each seasonal cohort and to reveal a potential temporal overlap in their reproductive season. We also investigate the elevational pattern of abundance at reproduction by combining the CMR technique with systematic estimations across the reproductive season.

## Materials and methods

### Study sites

The study took place in eight sites in north-east Algeria (Fig. 1) with elevations ranging from 5 to 1012 m (Table S1). The region has a typically Mediterranean climate with a long dry summer and a mild winter. The average annual temperature across three provinces is 17.9 °C and the average annual precipitation is 654.3 mm. The two coastal provinces, Annaba and El Taref, where the low-elevation sites (sites 5–8) are located, have a warmer annual temperature (18.3 °C) and higher precipitation



**Fig. 1.** Topographic map showing the study sites in north-east Algeria. The numbers refer to the sites' codes, given in Table S1. The elevational gradient in this area ranges from 0 to 1356 m (from blue to red). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

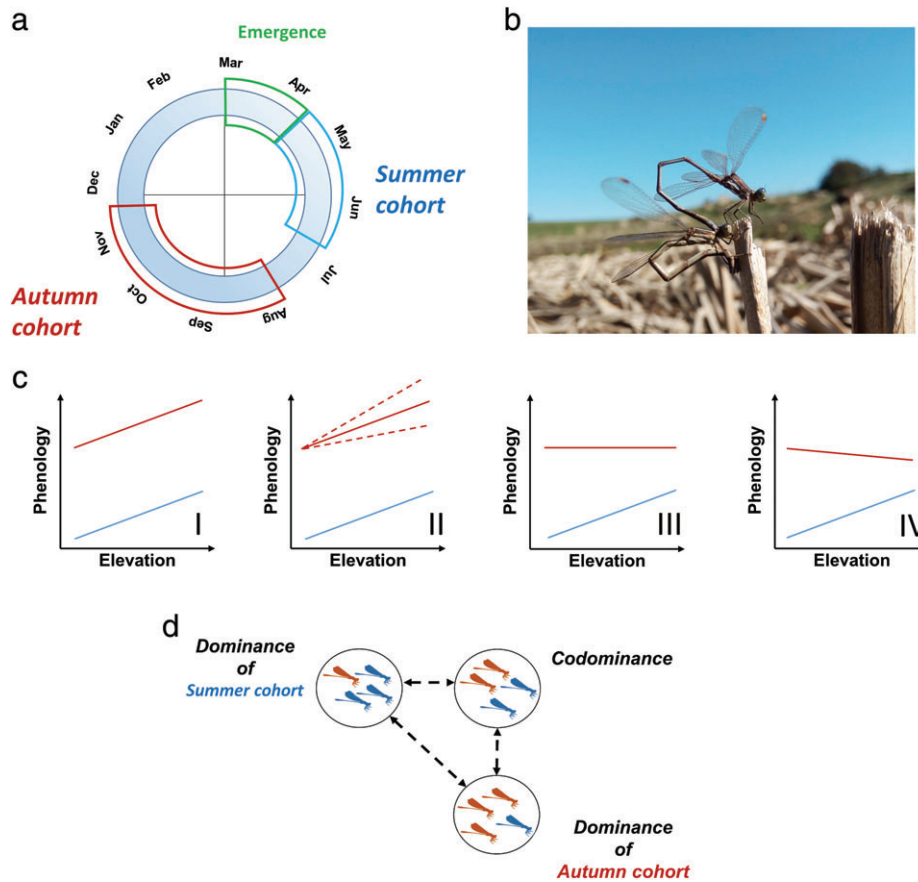
(703 mm) compared with Guelma (17.2 °C and 557 mm) where the higher-elevation sites (sites 1–4) are found. This region is a hotspot for odonatological diversity with high endemism (Riservato *et al.*, 2009; Khelifa *et al.*, 2016).

#### Theoretical background

In this manuscript, we do not consider the two cohorts as separate species, as suggested by Samraoui *et al.* (2003). The logic behind this consideration is that there is low genetic variation between the two cohorts, no apparent phenotypic difference, and a potential gene flow between cohorts of different elevations. We refer to the two sympatric populations as the summer cohort and the autumn cohort. To propose some hypotheses regarding the elevational pattern of the phenology of the two cohorts, it is important to describe the seasonal pattern of emergence and reproduction of each cohort (Fig. 2a). First, the emergence of both cohorts takes place at the same time during the spring. After emergence, the summer cohort matures relatively quickly (1 month) and starts to reproduce in late spring or early summer. The autumn cohort, on the other hand, postpones its maturation and starts reproducing in late summer/early autumn (Fig. 2b). In principle, there is a temporal gap of 1 or 3 months between the two cohorts depending on the elevation (see Results).

The potential effects of elevation on the phenology of the two cohorts of *L. virens* is variable. In fact, the reproductive phenology of the summer cohort is mainly dependent on the development of larvae and thus on the climatic conditions encountered during this life stage (Aguero-Pelegrin *et al.*, 1999). However, the reproductive phenology of the autumn cohort might be dependent not only on larval development but also on the maturation and other environmental cues such as rainfall, photoperiod or temperature, affecting the adult stage. Here we present four potential scenarios of the effect of elevation on the reproductive phenology of the two cohorts (Fig. 2c). Scenarios I and II assume that there is no (or little) time constraint at high elevation, particularly for the autumn cohort:

- Scenario I – parallel elevational delay: both cohorts shift their phenology to the same magnitude with elevation, because the larval development and maturation period lasts longer at higher elevation due to lower temperature.
- Scenario II – differential elevational delay: the magnitude of the phenological shift with elevation is higher or lower in the autumn cohort than in the summer cohort probably because the two cohorts use different cues to time the start of the reproductive season.



**Fig. 2.** Theoretical predictions of the elevational cline in the phenology of the summer cohort and autumn cohort of *Lestes virens*. (a) Phenology of emergence and reproduction of the two cohorts. (b) Oviposition of a reproductive pair of the autumn cohort in the natural habitat. (c) Elevational cline in the phenology: (I) both cohorts shift their phenology similarly with elevation (parallel shift); (II) there is an interaction between cohort and elevation, i.e. one cohort (autumn cohort) shifts less or more than the other (summer cohort); (III) one cohort (summer cohort) shifts its phenology but the other (autumn cohort) does not shift at all; (IV) there is a contrasting elevational shift, i.e. one cohort (summer cohort) shows a delay across elevation but the other (autumn cohort) shows an advancement. (d) Potential elevational cline in the dominance state of the two sympatric cohorts. It is possible that under certain environmental conditions, one cohort can be dominant in terms of abundance (summer cohort and autumn cohort) or the two cohorts can be co-dominant (relatively equal abundance). Across elevation, it is possible we might find a transition in the dominance state such that, for instance, co-dominance can shift to dominance or the direction of dominance can switch from low to high elevation. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

In Scenarios III and IV, the elevational cline (magnitude of phenological shift) of the autumn cohort is either absent or reversed due to time constraints. As with many temperate odonates (Corbet *et al.*, 2006), the length of the phenology of reproduction is generally restricted by winter. Thus, at higher elevation, individuals should have physiological or ecological mechanisms that allow them to start reproduction earlier, responding to photoperiodic rather than thermal cues. In other words, although temperature changes dramatically across elevation, day length does not. Thus, unlike temperature, photoperiod is a more reliable cue in a context of seasonal constraints:

- Scenario III – absence of elevational shift in the autumn cohort: low and high elevation populations start reproduction at the same time.

- Scenario IV – opposite phenological shift: in contrast to the summer cohort, the phenology of the autumn cohort shifts towards earlier dates with elevation.

Regarding the co-occurrence of cohorts across the elevational range and the population of each cohort, we assume that, in a given population, it is likely that one cohort outnumbers the other cohort (dominance) or that they have a relatively similar abundance (codominance). Across an elevational gradient, it is likely that the state of dominance either stays the same or switches (Fig. 2d).

#### Teneral and adult sampling

A 30-m transect was conducted at each site at least twice a month from March to December 2016. Sampling was carried



out in good weather only (no rain or heavy winds). We recorded the number of teneral (very soft and pale-coloured body), immature, single males, single females and reproductive pairs. Due to the low number of single females, they were removed for further analysis. With the abundance data, we were able to draw a phenological distribution for emergence and reproduction and calculate three quantiles, 10%, 50% and 90%, to describe the early, middle, and late phases, respectively. Phenological phase (phenophase) here can be defined as a period that describes the stage of the flight season of the insect. For instance, early phase is calculated as the date at which 10% (quantile 10%) of the phenological distribution is reached, and it describes the start of the season. The calculation of phenophases allows us to investigate whether the different phenophases shift differently across elevation.

We measured a sample of individuals in the autumn cohort at low- (Lac Mecada) and high-elevation (Messmasa) sites during the reproductive season of 2017 to assess whether there were geographic differences in body size across elevation, hinting at costs of seasonal constraints (Śniegula *et al.*, 2012). Shorter development time induces a faster development rate, which results in a smaller body size (Johansson & Rowe, 1999). Body length and posterior wing length were measured with an electronic caliper to the nearest 0.01 mm.

#### Estimation of population size

Capture–mark–recapture was carried out during the reproductive season of the two cohorts of 2015 at Messmasa (site 1). The sampling took place from 21 June to 9 August for the summer cohort and from 18 September to 24 October for the autumn cohort. To avoid bias in abundance estimation, we used data for 17 sampling occasions that took place within 35 and 36 days for the summer and autumn cohorts, respectively. The recapture was continued until marked individuals were no longer observed. The same methodology was carried out for the two cohorts. Starting in the morning (09.00 hours; solar time = –27 min), one observer spent 4 h at the site during which mature individuals were captured with a hand net and marked with a permanent marker on the left hindwing. Recaptures were also carried out on every sampling occasion. As the mark was conspicuous, individuals were not captured again after the first release. An encounter history was generated for each individual, recorded as either a ‘1’ or a ‘0’, with a ‘1’ signifying that the damselfly was detected, and ‘0’ that it was not. For example, an encounter history of ‘101’ for three sampling occasion means that the damselfly was marked and released on the first occasion, not observed on the second occasion, but detected again on the third occasion.

We evaluated the validity of the estimates derived from the CMR model by checking two fundamental assumptions (Lebreton *et al.*, 1992). We assessed whether there was any structural problem in the CMR data and whether the behaviour or the recapture of the damselflies was independent of their initial capture. The tests for the goodness-of-fit were performed with the function *release.gof* in the *RMARK* package (Laake, 2013) which computes Test2, Test3, and the Total (sum of Test2 and Test3) (Burnham, 1987). Test2 assesses whether marked

damselflies have an equal probability of capture by testing whether the recapture probability of the damselfly depends on when that individual insect was first captured. Test3 tests whether apparent survival probability is heterogeneous among individuals. The significance of any these tests shows a violation of the model assumptions. We investigated the occurrence of overdispersion by calculating  $\hat{c}$ , which is the total  $\chi^2$  divided by the degrees of freedom. When the  $\hat{c} > 1$ , there is overdispersion that should be taken into account by adjusting the models to the  $\hat{c}$  value, but when  $\hat{c} < 1$ , there is underdispersion which is not considered with adjustments (Cooch & White, 2006). In our data,  $\hat{c}$ -values were 0.83 and 0.81 for the summer and autumn cohorts, respectively, and thus our models, which show a slight underdispersion, were not adjusted to these values.

We used the Jolly–Seber model (POPAN formulation) (Schwarz & Arnason, 1996) to estimate overall population size and abundance during each sampling occasion. The POPAN formulation models four parameters, namely apparent survival probability ( $\Psi$ ), recapture probability ( $p$ ), the probability of entry into the population per occasion (*pent*) and superpopulation size ( $N$ ). The superpopulation is the cumulative abundance estimated for each sampling occasion. The estimates for all four parameters were estimated with maximum likelihood using the *R* package *RMARK*. We tested the effect of time (days) and sex on recapture, survival, and population entry probabilities. The superpopulation size was tested only for the effect of sex. We fitted different models for each parameter, increasing the complexity of the model gradually from a constant model to a time- and sex-dependent model, then we ranked all models based on the corrected Akaike information criterion (AICc) (Burnham & Anderson, 2004). To generate abundance estimates, we used a model averaging approach.

#### Density of individuals as a surrogate for abundance

For each sampling occasion during the CMR survey, the density of individuals within the 30-m transect was estimated hourly at three different times of the day (11.00, 12.00 and 13.00 hours) when the abundance and reproductive activity are usually at their peak (Stoks *et al.*, 1997; Corbet, 1999). The average density of individuals per sampling occasion was calculated and correlated with the estimated abundance that exists at the study site during the same sampling occasion derived from the POPAN model (see Results). The strong positive relationship in both the summer and autumn cohorts, derived from linear regressions in *R* 3.3.2 ( $P < 0.0001$ ; Fig. S1; Table S2), shows that the density of individuals within 30 m could be used as a surrogate for abundance.

#### Statistical analysis

Statistical analyses were carried out with *R* 3.3.2 (R Development Core Team, 2017). Linear regressions were conducted to analyse the elevational pattern of the three phenophases of the emergence and reproductive season. Instead of using a separate model for each phenophase, we used a global model that analyses all phenophases at once. The model contains phenophase as a

response variable, and elevation (continuous variable) and quantile (grouping variable with three levels: 10%, 50% and 90%) as explanatory variables. The use of the grouping variable quantile allows us to test for interaction with elevation, which unravels potential change in the duration of the emergence or reproductive season across elevation. To assess potential differences between the body sizes of low- and high-elevation populations, we computed two linear models – one for body length and one for wing length (response variables) – testing for the effect of sex, site (low and high elevation) and their interaction. To investigate the spatial pattern of the density of mature adults across elevation, we carried out a linear regression for both single males and reproductive pairs grouped as a factor (with two levels: male and pair).

## Results

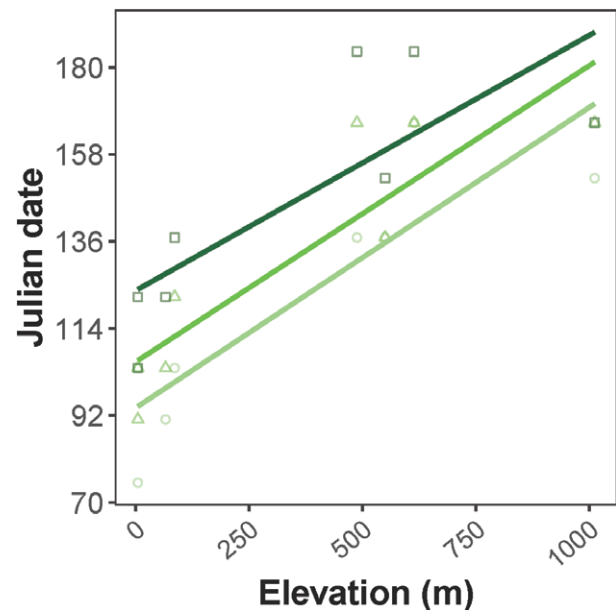
### Phenology of emergence across elevation

Due to the lack of morphological traits to differentiate the two cohorts, the phenology of emergence of both cohorts was pooled together. There was a significant seasonal delay of emergence across elevation for the three phenological phases (Fig. 3, Table 1a), revealing that populations at higher elevations emerged later than populations at lower elevations. The delay rate was 3.3 days per 100 m. The duration of emergence season did not change across elevation, revealed by the non-significant elevation  $\times$  quantile interaction ( $P = 0.89$ ). This non-significant interaction means that the three phases of the phenology shifted in parallel (with the same magnitude) across elevation.

### Phenology of reproduction across elevation

In both cohorts, we found a significant seasonal delay across elevation for the three phenological phases (Fig. 4), i.e. the higher the elevation, the later the phenological phase (Table 1b). However, there was a significant interaction between elevation and cohort ( $P < 0.0001$ ), showing that the elevational cline in the reproductive phenology was steeper in the summer cohort than in the autumn cohort (Table 1b). The phenology shifted 2.2 and 0.7 days per 100 m of elevation for the summer and autumn cohorts, respectively. The non-significant interaction between quantile and elevation ( $P = 0.74$ ) shows that the duration of the season did not change significantly across elevation. Our model predicts that the temporal isolation of the two cohorts, estimated as the distance between quantile 90% of the summer cohort and quantile 10% of the autumn cohort, was 60.1 days at sea level (0 m of elevation) and 27.9 days at 1000 m of elevation. At the highest elevation site (site 1), an old summer cohort male marked in the summer was observed at the start of the reproductive season of the autumn cohort far from reproductive sites; however, no reproductive pair between the two cohorts was observed.

To investigate the potential costs of seasonal constraint on body size, we compared body and wing length in the autumn cohort between low- (site 8) and high-elevation sites (site 1) (Fig. 5). We measured 52 (27 males and 25 females) and 51

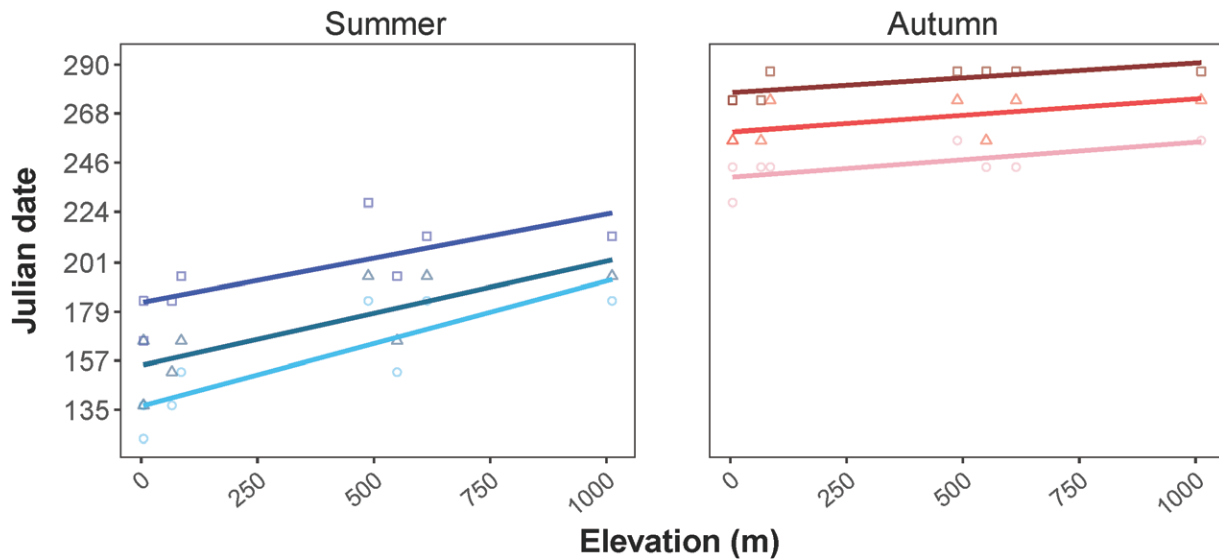


**Fig. 3.** Elevational pattern of the emergence of *Lestes virens* in north-east Algeria. The lines are linear regressions. Light (circle), intermediate (triangle) and dark (square) colours refer to the quantile 10%, 50% and 90%, respectively. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].

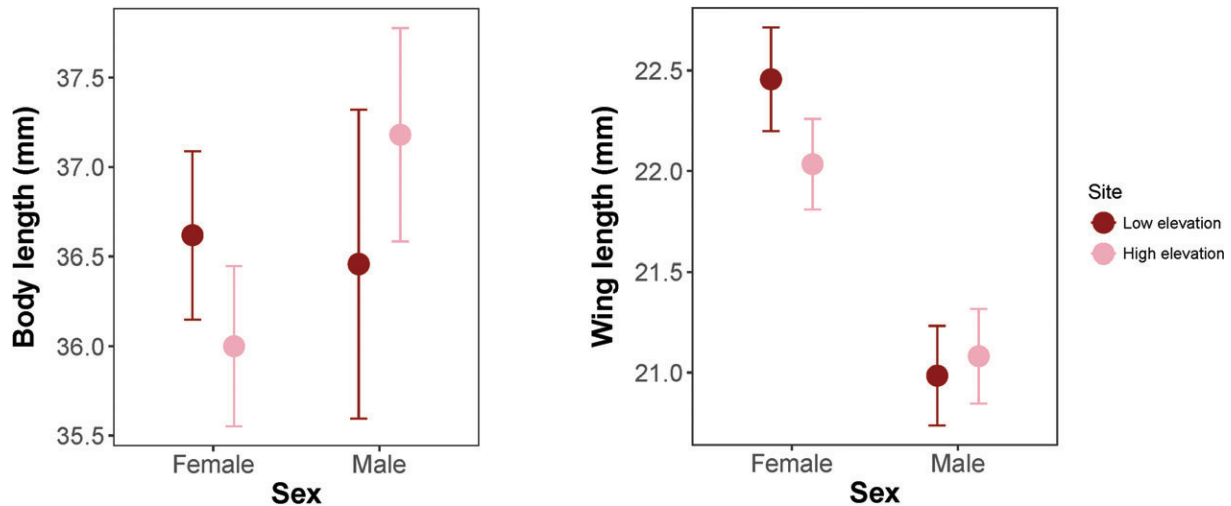
**Table 1.** Summary results of the linear regression assessing the elevational pattern of the phenology of emergence and reproductive season of the summer and autumn cohorts of *Lestes virens* in north-east Algeria. The quantile 10% is used as the baseline level (intercept) for contrast calculation.

	Estimate	SE	t-value	P
<b>General</b>				
Intercept	93.919	8.756	10.726	< 0.0001
Elevation	0.076	0.018	4.287	0.0004
Quantile 50%	11.615	12.383	0.938	0.361
Quantile 90%	29.652	12.383	2.395	0.028
Elevation: quantile 50%	-0.001	0.025	-0.041	0.968
Elevation: quantile 90%	-0.011	0.025	-0.455	0.655
<b>Mature adults</b>				
Intercept	137.728	4.525	30.438	< 0.0001
Elevation	0.052	0.009	5.733	< 0.0001
Cohort (autumn)	100.600	4.525	22.232	< 0.0001
Quantile 50%	19.340	5.542	3.490	0.001
Quantile 90%	42.253	5.542	7.624	< 0.0001
Elevation: cohort (autumn)	-0.033	0.009	-3.599	0.001
Elevation: quantile 50%	-0.005	0.011	-0.464	0.645
Elevation: quantile 90%	-0.009	0.011	-0.837	0.408

(26 males and 25 females) autumn cohort adults at low- and high-elevation sites, respectively (Table S3). The variation in body length was poorly explained by sex and site (and their interaction), as revealed by the low  $R^2$  of 0.06 (Table 2a). However, wing length was relatively well explained by sex, site and sex  $\times$  site interaction ( $R^2 = 0.50$ ). We found female-biased sexual dimorphism in wing length ( $P < 0.0001$ ) and a significant



**Fig. 4.** Phenological distribution across elevation of mature males and reproductive pairs of summer and autumn cohorts in north-east Algeria. The lines are linear regressions. Light, intermediate and dark colours refer to the quantile 10%, 50% and 90% of the phenology, respectively. [Colour figure can be viewed at [wileyonlinelibrary.com](#)].



**Fig. 5.** Body and wing length of the autumn cohort of *Lestes virens* at low (Lac Mecada) and high elevations (Messmasa). Error bars are 95% confidence intervals. [Colour figure can be viewed at [wileyonlinelibrary.com](#)].

site ( $P = 0.01$ ) and site-by-sex effects ( $P = 0.03$ ) (Table 2b), showing that females at high elevation site had shorter wings than females at low elevation site.

#### Abundance across elevation

The two cohorts of *L. virens* were sympatric in all studied populations from sea level to 1012 m. The seasonal distribution of density of adult males and reproductive pairs during the reproductive season is shown in Fig. S2. By regressing the abundance by the elevation, cohort and group (single male or pair), we found a positive effect of elevation, showing that the number of reproductive pairs increased with elevation ( $P = 0.004$ ) (Fig. 6),

but the significant elevation  $\times$  group interaction revealed that the density of single males did not change geographically ( $P = 0.04$ ) (Table 3). In addition, the significant cohort effect ( $P = 0.006$ ) shows that the density of autumn cohort adults was larger than that of summer cohort adults, and the significant interaction of cohort  $\times$  group ( $P = 0.04$ ) indicates that the difference in densities of individuals is significant only for reproductive pairs, and not for single males.

To test whether the interspecific difference in adult density was due to an actual difference in population size, we carried out CMR during the reproductive season of the two cohorts in the same site and year. The CMR yielded a total of 448 marked adults (229 males and 219 females) for the summer cohort and 994 marked adults (497 males and 497 females)

**Table 2.** Summary results of the linear regression assessing the differences in body length and wing length of the autumn cohort between low- and high-elevation sites and between sexes. Female and low-elevation site are used as the baseline level for contrast calculation.

	Estimate	Std. Error	t value	P
<b>Body length</b>				
Intercept	36.5754	0.3112	117.546	< 0.0001
Sex (male)	-0.1746	0.4484	-0.389	0.698
Site (high)	-0.7191	0.4441	-1.619	0.108
Sex (male): site (high)	1.3460	0.6370	2.113	0.037
<b>Wing length</b>				
Intercept	22.4563	0.1208	185.877	< 0.0001
Sex (male)	-1.4719	0.1742	-8.448	< 0.0001
Site (high)	-0.4225	0.1725	-2.449	0.0161
Sex (male): site (high)	0.5193	0.2475	2.098	0.0385

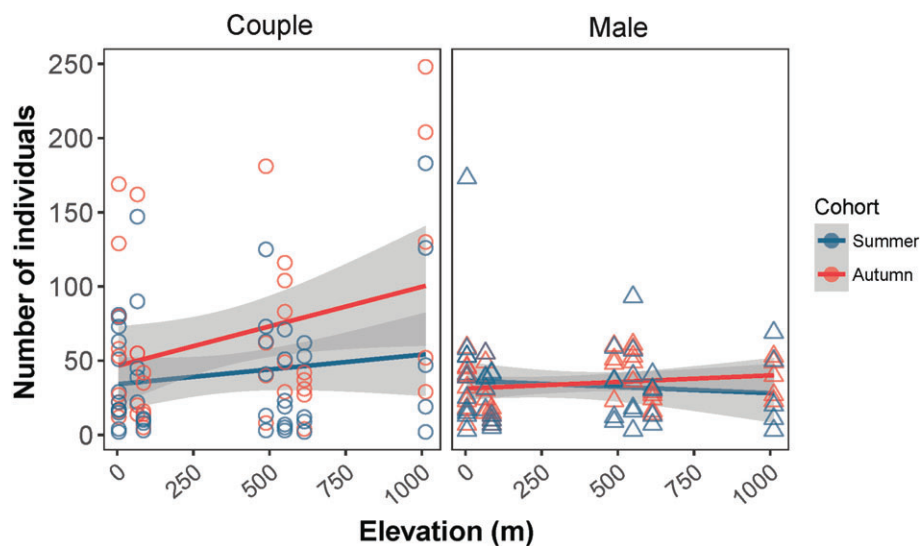
for the autumn cohort. Our data met the assumptions for CMR analysis (Table S4). We fitted different POPAN models to explain the CMR data, then we performed model selection based on the AICc (Table S5). For the summer cohort, the best model [ $\Psi(\sim 1)p(\sim \text{time})\text{pent}(\sim \text{time} + \text{sex})N(\sim \text{sex})$ ] included a constant survival, a time-dependent recapture probability, time- and sex-dependent population entry and sex-dependent population size. The gross population size estimated from the model was 1051.4 individuals, i.e. 512.5 (95% CI: 398.2–626.7) males and 538.9 (421.6–656.1) females. For the autumn cohort, the best model [ $\Psi(\sim \text{time} + \text{sex})p(\sim \text{time} + \text{sex})\text{pent}(\sim \text{time} + \text{sex})N(\sim \text{sex})$ ] included time and sex-dependence for survival probability, recapture probability and population entry, and a sex-dependent population size. The gross population size was 2806.9 individuals, i.e. 1431.1 (1151.1–1711.1) males and 1375.8 (1095.2–1656.3) females.

## Discussion

Based on our survey of natural populations of summer and autumn cohorts of *L. virens*, we provide strong support for elevational cline in the phenology of emergence and reproduction and abundance. The elevational shift of phenology was not equal between the cohorts, i.e. the delay was stronger in the summer cohort than in the autumn cohort. The distance between the temporal distribution of the two cohorts becomes smaller at higher elevations, suggesting potential cohort mixing in high-elevation populations. Both cohorts were fairly abundant at all sites, but the autumn cohort had a higher abundance than the summer cohort and the difference increased with elevation.

### Geographic distribution

Our study reveals new data on the distribution of the species. The autumn cohort was supposed to migrate from low to high elevation to estivate and then come back to low elevation to reproduce (Samraoui, 2009). We showed here that there are successfully reproductive populations of the autumn cohort at high elevation and that the species reproduction is not restricted only to low elevation, but has large elevational distribution. In addition, individuals from the autumn cohort that emerge from high-elevation populations do not carry out massive dispersal but estivate in nearby forests (H. Amari, pers. obs.). This implies that the cohort does not have an obligate migration for maturation or that distinct populations might have different ecological strategies depending on the landscape and environmental requirements of the species. Our results on the distribution of species also suggest that the sympatry of the two cohorts is common in north-east Algeria along a large elevational gradient.



**Fig. 6.** Elevational pattern of the abundance of mature adults of the summer and autumn cohorts of *Lestes virens* in north-east Algeria. The line is a linear regression and the ribbon refers to the standard error. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)].



**Table 3.** Summary results of the linear regression assessing the elevational pattern of density of individuals during the reproductive season of the summer and autumn cohorts of *Lestes virens* in north-east Algeria. Summer cohort and reproductive pair are used as the baseline level for contrast calculation.  $R^2 = 0.24$ . State is a factor with two levels (male or reproductive pair).

	Estimate	SE	<i>t</i> -value	<i>P</i>
Intercept	57.051	13.597	4.196	< 0.0001
Elevation	0.072	0.023	3.095	0.002
Cohort (autumn)	48.014	15.993	3.002	0.003
State (male)	-23.167	19.125	-1.211	0.228
Elevation: group (male)	-0.072	0.033	-2.204	0.029
Cohort (autumn): group (male)	-46.101	22.619	-2.038	0.043

### Phenology

Based on the sampling of teneral, we did not detect any geographic pattern during the emergence season, but there was a strong shift of the phenological distribution across elevation. This elevational cline in the emergence is most likely due to the difference in temperature between low- and high-elevation sites (Hodkinson, 2005). At low elevation, temperature is warmer, which allows the larvae to develop faster and emerge earlier, whereas, at high elevation, it is colder and thus the development rate is slower (Lutz, 1968; Pickup *et al.*, 1984; Pickup & Thompson, 1990). The similarity in the duration of emergence season of the two cohorts across elevation shows that the synchronisation of the population of both cohorts is not altered by the environmental conditions, suggesting that time constraint could dictate the synchronisation of larval development (Johansson *et al.*, 2001).

Similar to the phenology of emergence, the phenology of the reproduction also shifted across elevation for both cohorts, but the cline was steeper in the summer cohort than in the autumn cohort. This corresponds to our second prediction of elevational cline, described in Fig. 2c. The phenology of the summer cohort geographically shifted 3.1 times faster than that of the autumn cohort, which suggests that the environmental cues that trigger the start of the reproduction of each cohort might be different. Knowing that temperature changes quite rapidly across elevation (Colwell *et al.*, 2008), it is likely that the phenology of the reproductive season of the summer cohort is highly dependent on the phenology of emergence, which in turn is influenced by the spring temperature. This spring temperature effects on adult phenology are typical in temperate odonates (Hassall *et al.*, 2007; Dingemans & Kalkman, 2008). The phenology of the reproduction of the autumn cohort, which occurs after a long estivation period of 3–4 months, might not be controlled by the timing of emergence alone, but also by other adaptive mechanisms related to time constraints imposed by the length of the warm season. Winter starts earlier at high elevation than at low elevation. Considering the fact that individuals emerge later at high elevation, they are under time constraint to mature and finish the reproductive season earlier. Such a pattern of seasonal regulation was detected in obligatorily univoltine

odonates (De Block & Stoks, 2004; De Block *et al.*, 2008). The smaller wing length of autumn cohort females at high compared with low elevation is probably a cost of faster development at high elevation (Śniegula *et al.*, 2012). The absence of such a geographic pattern in males should be further investigated.

So what triggers the start of the reproductive season for the autumn cohort? The effect of temperature at the start of the reproductive season is probably minor because it changes considerably from one year to another. The start of the reproduction is probably triggered by photoperiod because it does not change from one year to another or from low to high elevation, which makes it a reliable factor with which to time phenological events such as reproduction (Körner & Basler, 2010). The exact photoperiodic mechanism that triggers the reproductive season is still unknown, but it could be that individuals respond to either a specific day length threshold or to the rate of decline in day length (Norling, 1984; Tauber *et al.*, 1986).

### Abundance

Our results on population size at reproduction show that individuals of the autumn cohort outnumber those of the summer cohort across the entire elevation gradient. It is likely that the difference in population size between summer and autumn cohorts actually results from disparity in the strategy predominantly adopted by *L. virens*. In this case, the origin of such disparity is an interesting question that deserves to be addressed, because it may shed light on the origin of cohort splitting. When we compare the two strategies, they both have advantages and disadvantages. The summer reproduction strategy is characterised by a shorter maturation period (1 month), but a longer period of egg diapause (about 6 months), whereas the autumn reproduction strategy has a long adult maturation period (3 months), but a shorter period of egg diapause (about 2 months). Thus, the optimal strategy should be the one that minimises the overall mortality costs, including immature adult mortality and egg mortality. Immature adults that postpone reproduction (long maturation period) are more likely to be predated than those that do not postpone reproduction (short maturation period). Similarly, eggs with longer diapause periods have higher mortality probability related to biotic factors such as parasitism by parasitoid wasps than those with shorter diapause periods (Reinhardt & Gerighausen, 2001; Harabis *et al.*, 2015). Therefore, if we hypothesise that the dominance of the autumn reproduction strategy is true and not an artefact (differential immature mortality), then the overall mortality, encompassing egg mortality and immature adult mortality, is higher in the summer reproduction strategy than in the autumn reproduction strategy.

There are other hypotheses that might contribute to or exacerbate the difference in the population size between summer and spring populations. For instance, our observations in the field show that livestock eats the green leaves of the oviposition sites in the spring and summer, but this does not occur in the autumn because of the absence of green oviposition supports. Thus, it is likely that a proportion of eggs of the summer cohort are killed regularly (Tscharntke, 1997; Lee Foote & Rice Hornung, 2005; Van Noordwijk *et al.*, 2012), which leads to a bias in population size between cohorts.

Besides the inter-cohort difference in the abundance of individuals, there was an intra-cohort variation across the elevational gradient in both cohorts. The abundance of adults increased with elevation, especially in the autumn cohort. The absence of significant change in the duration of the reproductive season at higher elevation implies that there is no major synchronisation that might influence abundance across the gradient. This geographic pattern of abundance is most likely related to the maturation period. It is predictable that longer maturation period leads to higher mortality (Anholt, 1992) because the likelihood of predation increases with time. Our results regarding the elevational cline in the phenology of emergence and reproduction of the two cohorts show that the shifts in the reproductive phenology of the summer and autumn cohorts were 30% and 80% lower, respectively, than that of emergence. This implies that the maturation period shortens with elevation in both cohorts, particularly in the autumn cohort. This geographic pattern corresponds to that of the abundance of the two cohorts.

#### *Taxonomic reconsiderations*

As we highlighted earlier, the taxonomy of *L. virens* in North Africa should be revisited. To consider the two cohorts as separate species based on temporal segregation, the entire geographic range of the species should be considered. When one visits a single site in low lands, it may seem that the two cohorts are clearly temporally isolated. However, in the context of a metapopulation where dispersal occurs, a high-elevation summer population starting late may meet with a low-elevation autumn population starting early through dispersal, and subsequent cohort mixing can occur (Hughes *et al.*, 1999).

Yet, the data available show no morphological difference, small genetic variation, and potential gene flow between cohorts within the same population (particularly at high elevation) and among populations (mixture between low- and high-elevation populations). Indeed, seasonal regulation may result in a fully isolated population and speciation, but we think that the current available data suggest a single species with different seasonal regulation strategies. Further genetic analyses including multiple populations across the geographic range of the species are needed to shed light on the genetic differentiation and taxonomy.

#### *Future directions*

There are two important questions that need to be addressed in future studies. The first is, when does the cohort splitting happen, at the egg or larval stage? In other damselflies in North Africa where cohort splitting occurs as partial bivoltinism, the main cohort emerges in spring and summer, while a smaller cohort emerges in autumn (Mahdjoub *et al.*, 2015; Khelifa, 2017), and it is most likely that the individual 'decision' is taken at the larval stage. Experimental studies have shown that environmental conditions at the larval stage are a driving force of life-history variation that may lead to cohort splitting (Johansson *et al.*, 2001). In *L. virens*, the egg stage should also be considered because eggs laid in summer encounter different conditions than those laid in autumn. The second question is, does cohort switch

occur? That is, do eggs laid in summer produce only summer reproducers or do they produce both summer and autumn reproducers? This question can be answered with ontogenic experiments in the laboratory and field, in which eggs are held in different conditions and, after emergence, the adults are held in a common environment.

An important question that arises from our study is how climate change could disrupt the maintenance of temporal isolation in the two cohorts at high elevation. If future warming leads to delay in reproduction of the summer cohort (Doi, 2008) and advancement of the autumn cohort, the probability of overlap between the two cohorts will increase. However, as *Lestes* species are known to have egg diapause (Corbet *et al.*, 2006), some refractory processes may hinder the phenological shift in the following years (Harrington *et al.*, 2007; Hassall *et al.*, 2007). Thus the sensitivity of the reproductive season to temperature has to be investigated to carry out predictions of future dynamics in the phenology of the two cohorts.

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#### **Supporting Information**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** The relationship between density of individuals and the estimated abundance of mature adults of the summer and autumn cohorts of *Lestes virens* across elevation. The density of individuals was calculated along a transect of 30 m. The estimated abundance was derived from the POPAN model by estimating the abundance for each sampling occasion.

**Figure S2.** Seasonal pattern of the density of mature adults of the summer and autumn cohorts of *Lestes virens* across elevation in north-east Algeria. The size of the point indicates the number of individuals (both sexes pooled together) recorded within 30-m transect.

**Table S1.** Geographic coordinates and elevation of the study sites

**Table S2.** Summary results of the linear regression between the estimated abundance of adults and the density of individuals in the summer and autumn cohorts of *Lestes virens* at Messmasa.

**Table S3.** Descriptive statistics on body and wing length of the autumn cohort of *Lestes virens* at a low- and a high-elevation site.

**Table S4.** Goodness-of-fit tests of the general capture–mark–recapture model for the summer and autumn cohorts of *Lestes virens*. The non-significance of all tests means that the assumptions of equal catchability and homogeneity in the survival probability among individuals for the estimation of survival and abundance are met.

**Table S5.** Model selection of POPAN models for capture–mark–recapture of the summer and autumn cohorts of *Lestes virens*. The models were ranking by the AICc. The best model is in bold.

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