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Field estimates of fitness costs of the pace-of-life in an endangered damselfly

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Abstract

Theory predicts that within-population differences in the pace-of-life can lead to cohort splitting and produce marked intraspecific variation in body size. Although many studies showed that body size is positively correlated with fitness, many argue that selection for the larger body is counterbalanced by opposing physiological and ecological selective mechanisms that favour smaller body. When a population split into cohorts with different paces of life (slow or fast cohort), one would expect to detect the fitness–size relationship among and within cohorts, that is, (a) slower-developing cohort has larger body size and higher fitness than faster-developing cohort, and (b) larger individuals within each cohort show higher fitness than smaller individuals. Here, we test these hypotheses in capture–mark–recapture field surveys that assess body size, lifespan, survival and lifetime mating success in two consecutive generations of a partially bivoltine aquatic insect, *Coenagrion mercuriale*, where the spring cohort is slower-developing than the autumn cohort. As expected, body size was larger in the slow-developing cohort, which is consistent with the temperature-size rule and also with the duration of development. Body size seasonal variation was greater in slow-developing cohort most likely because of the higher variation in age at maturity. Concordant with theory, survival probability, lifespan and lifetime mating success were higher in the slow-developing cohort. Moreover, individual body size was positively correlated with survival and mating success in both cohorts. Our study confirms the fitness costs of fast pace-of-life and the benefits of larger body size to adult fitness.

KEYWORDS
life history, mating success, odonate, plasticity, survival, temperature-size rule

1 | INTRODUCTION

Several studies agree that there is a trade-off between development rate and size at maturity in ectotherms (Stearns, 1992). Individuals that develop slowly will have larger body size at maturity whereas those that develop quickly will have a smaller body size (Ashton, 2004; Blackburn et al., 1999). As one consequence of this pattern, plasticity in development rate and body size occurs across a species range where individuals from southern populations are smaller than individuals from northern populations (Angilletta, Steury, & Sears, 2004; Partridge & Coyne, 1997; Pincheira-Donoso et al., 2008; Van Voorhies, 1996). Although laboratory studies have documented the trade-off between development rate and fitness (Angilletta et al., 2004), the results derived from the laboratory are not often similar to those observed in the field (Irschick et al., 2008; Warner & Andrews, 2002).

In insects, a positive relationship between female body size and fecundity has been observed in many groups (Berrigan, 1991; Honěk & Kocourek, 1990; Partridge & Farquhar, 1983; Tammaru, Esperk, & Castellanos, 2002; Thornhill & Alcock, 1983) because larger females have the capacity to produce and carry more eggs. In males, larger body size has also been shown to confer mating advantages, particularly in territorial species because larger males are better at acquiring and defending territories (Alcock, 1981; Baker, 1983; Choe & Crespi, 1997). However, there is also evidence of selection for smaller or intermediate body size (Cordero, Carbone, & Utzeri, 1997; Okuyama, Samejima, & Tsubaki, 2015; Rivas-Torres, Sanmartín-Villar, Gabela-Flores, & Cordero-Rivera, 2017; Rivera, 2000; Zamudio, Huey, & Crill, 1995). For instance, larger body might be associated with disadvantages such as longer development time, higher nutritional requirements and lower flight performance (Blanckenhorn, Preziosi, & Fairbairn, 1995; Clutton-Brock, Albon, & Guinness, 1985).

Insects of the temperate region show latitudinal plasticity in voltinism (the number of generations produced per year) (Dmitriew, 2011). Populations have shorter generation time at lower latitudes due to higher temperatures. Thus, univoltine, bivoltine and multivoltine life histories are dominant in hot temperate (southern) areas whereas semi- and partivoltine forms are widespread at cold temperate (northern) areas (Corbet, Suhling, & Soendgerath, 2006; Flenner, Richter, & Suhling, 2010). Some populations display a mixed life-history pattern (e.g. partial semi- or bivoltinism) in which two population cohorts have considerably different development times as a response to different environmental conditions, hence producing groups of individuals with different paces of life (Ricklefs & Scheuerlein, 2002). These individuals typically show variations in behaviour, physiology and life-history traits, which determine their fitness at the adult stage (Réale et al., 2010). Pace of life syndrome (POLS) has been reported in deciduous trees (Vitasse, Porté, Kremer, Michalet, & Delzon, 2009), birds (Gebhardt-Henrich & Richner, 1998), mammals (Lovegrove, 2003) and insects (e.g. beetles) (Singh & Mishra, 2014). Odonates (dragonflies and damselflies) offer a great opportunity for the study of POLS (Debecker, Sanmartín-Villar, de Guinea-Luengo, Cordero-Rivera, & Stoks, 2016) because shifts in life history occur within the same population, leading to cohort splitting (Amari et al., 2019; Watts & Thompson, 2012). In fact, one cohort which reproduces in the spring can produce offspring that develop quickly throughout the summer and emerge during the same year (Ferreras-Romero, 1991; Ferreras-Romero & García-Rojas, 1995; Ingram & Jenner, 1976; Khelifa, 2017).

One indicator of the variance in physiological and behavioural traits in a population is the commonly observed decrease in body size for successive generations over the season (Corbet, 1999), which has long been observed in adult insects (Rowe & Ludwig, 1991). The most common pattern is the decrease in size over the season (Corbet, 1999). This seasonal decline has been well documented, but only a few studies have suggested satisfying explanations. Rowe and Ludwig (1991) suggested that the cost to delaying maturation increases with the season such that late individuals trade off further growth against earlier emergence, which results in a decline of size at emergence across the season. Other studies suggested proximate causes like the seasonal changes in resource availability and/or quality (Forrest, 1987; Palmer, 1984). An alternative explanation is the relationship between the length of the development season and seasonal size variation; in other words, larger individuals are those that spend the longest development time in contrast to smaller individuals which spend the shorter development time. In a context of a cohort-splitting species where most of the population is univoltine and a small cohort is bivoltine, one would expect that the average fitness is different among cohorts. This comes from the fact that the main cohort that emerges in early season mostly consists of individuals that come from the reproduction of the previous spring and those that come from the reproduction of the previous autumn, thus resulting in larger body size in the spring and consequently higher fitness.

In this study, we carried out a field investigation based on an extensive capture–mark–recapture of two consecutive generations of an endangered damselfly *Coenagrion mercuriale* – a partially bivoltine (a large cohort is univoltine but a small cohort is bivoltine) population with a spring and autumn cohort (Mahdjoub, Khelifa, Zebsa, Bouslama, & Houhamdi, 2015). We estimated differences in the body size, lifespan, survival probability and mating success within and among cohorts and determine the relationship among these parameters. Based on the trade-off between development time and body size at emergence and the pattern of life history of the species, we hypothesize that (a) the slower-developing (spring) cohort would have larger body size than the faster-developing (autumn) cohort, (b) due to the longer development time and mixed larval cohorts in the spring compared to the relatively synchronized development of the bivoltine autumn cohort, the seasonal pattern of body should appear in both cohorts, (3) the body size positively affects lifespan, survival probability and mating success in both cohorts.

2 | METHODS

2.1 | Study site

We collected data during 2013 in Old Bridge canal, a shallow 450-m artificial stream that flows into the Seybouse River near Guelma, Northeast Algeria (36°28′ N, 7°22′ E) (Khelifa et al., 2011). *Typha angustifolia* and *Paspalum distichum* dominate the stream where *C. mercuriale* population occurs. No *C. mercuriale* population occurs within 10 km of the study population (Khelifa, Zebsa et al., 2016).

2.2 | Background information

Endangered in most parts of its range (Boudot et al., 2009), *C. mercuriale* has a fragmented distribution over Europe and North Africa (southern and northern latitudinal limit: 30°N–54°N). The species is listed as endangered in most parts of its geographic range (Boudot et al., 2009). The voltinism of the species is plastic across its distribution range with a semivoltine life history at its northern range limits (UK) (Corbet, 1957; Purse & Thompson, 2003) and a

partially bivoltine life history at its southern range limits (North Africa) (Mahdjoub et al., 2015). The larger cohort emerges in early spring and reproduces after a short maturation period of about a week (Mahdjoub et al., 2014). Eggs that are laid during the spring reproductive season hatch in summer, but some of the larvae develop rapidly and emerge in late summer and autumn (hereafter autumn cohort) (Mahdjoub et al., 2015). However, most of the larvae emerge in the next spring where the adult cohort consists of individuals that resulted from spring and autumn reproduction (hereafter spring cohort). Therefore, while there are two adult cohorts (spring and autumn), there are three larval cohorts with different development rates (rapid, intermediate and slow) (Figure 1a,b).

2.3 | Capture–Mark–Recapture protocol

Prior to the study, we conducted daily visits in late March 2013 in order to record the exact date of the start of the flight season. When the flight season started, we carried out a daily capture–mark–recapture between 18 April and 25 May 2013 for spring season and between 19 August and 19 September 2013 for the autumn season. We caught mature individuals along a 120-m transect and marked them with an alphanumeric code on the left hind wing using a paint marker (Edding paint marker 780). To estimate lifespan, we assumed that the day at which an individual was captured for the first time was its first day as a flying adult (Fincke, 1982). This assumption was reasonable since (a) there was no nearby population in the nearest
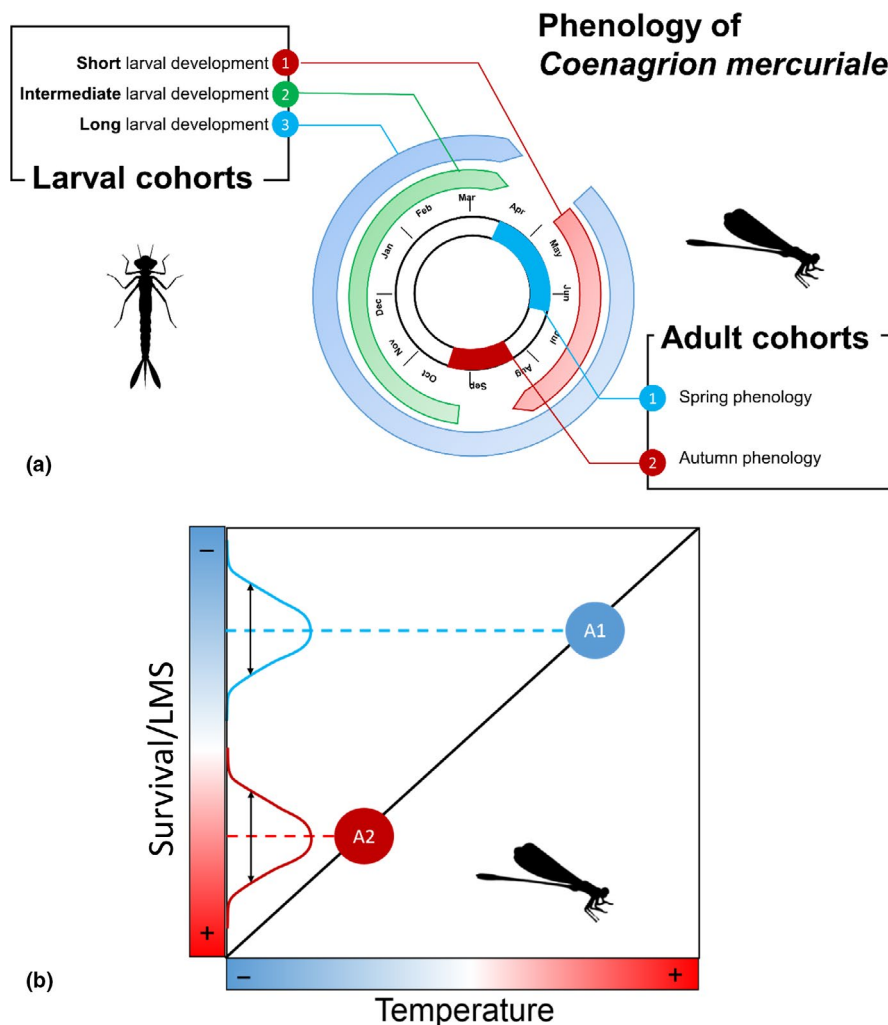

FIGURE 1 A theoretical representation of the partially bivoltine life history of *Coenagrion mercuriale* in Northeast Algeria and the expected fitness for the two adult cohorts. (a) Phenology of the species showing adult and larval cohort splitting. There are two adult cohorts resulting from a partial bivoltinism, that is, a large population that emerges from April to July and a smaller population that emerges from August to October. Due to the absence of maturation delay, this adult phenology produces three larval cohort: (1) a cohort with short larval development period resulting from eggs laid in late spring and emerging in early August (3–4 months of development); (2) a cohort with a intermediate(rate) larval development which comes from the eggs laid in autumn and emergence in the spring (6–7 months of development); and (3) a cohort with long larval development period, resulting from eggs laid in spring from which larvae later hatch and adults emerge the next spring (9–11 months). (b) Expected fitness consequences for each adult cohort. Cohort A1 is expected to have a higher fitness than cohort A2

	Estimate	Std. Error	*t* value	*p*-value
Intercept	34.113	0.577	59.164	<0.0001
Season	−0.022	0.005	−4.322	<0.0001
Sex[Male]	−0.949	0.119	−7.959	<0.0001
Cohort[Autumn]	−6.310	1.311	−4.814	<0.0001
Season: Cohort[Autumn]	0.025	0.007	3.61	0.0003
Sex[Male]:Cohort[Autumn]	0.488	0.169	2.89	0.004

TABLE 1 Summary results of the linear model regressing body length against season, cohort and sex ($R^2 = 0.67$)

Note: Female and spring cohort are the base level for contrast comparisons. Based on the AIC, models including season-by-cohort and the three-way interaction of season-by-sex-by-cohort did not explain more variance than the current model.

10 km (limited immigration) (Purse, Hopkins, Day, & Thompson, 2003), (b) the reproductive sites were limited to 60 m stretch of the watercourse (Mahdjoub et al., 2014), and (c) our surveys were conducted on a daily basis to minimize nondetection. On each sampling occasion, code, sex and the state (single or pairs) were recorded. A pair was noted when a male and a female are physically attached either in (e.g. wheel or oviposition). To assess the lifetime mating success, the number of matings of each individual was assessed by scanning the study area repeatedly during the entire day.

2.4 | Body size

Because body size is known to be correlated with fitness components of individual odonates such as survival, foraging and reproductive success (Sokolovska, Rowe, & Johansson, 2000), we measured two morphological traits that are often used in damselflies (Cordero, 1991, 1992; Raihani, Serrano-Meneses, & Córdoba-Aguilar, 2008). Because the body size of adult odonates does not change with age, we took a single measure of body size during the first capture. For each individual captured, we measured body and wing length using a digital calliper (0.01 mm). The two variables were strongly correlated (Spearman's correlation: $r = 0.64$, $p < 0.0001$ for the spring cohort; $r = 0.52$, $p < 0.0001$ for the autumn cohort), and thus, we decided to work with body length.

2.5 | Statistical analyses

Seasonal pattern of body length was analysed with a multiple linear model including Julian date (day of the first capture), sex and cohort (spring or autumn) as independent variables. To assess the effect of body size on lifespan, we carried out a Poisson model regressing the estimated lifespan (the number of days between the release and last recapture date) against body length, sex and cohort. To analyse the effect of body size on apparent lifetime mating success (LMS: the total number of mating that resulted into oviposition), a Poisson model was carried out using the following independent variables: body length, lifespan, sex, and cohort. Overdispersion of the Poisson model was assessed using the function *dispersiontest* of the R-package AER (Kleiber & Zeileis, 2017), which showed no sign of overdispersion. All statistical analyses were carried out with the R3.5.0 software (R Development Core Team, 2019).

Survival and recapture probabilities were estimated using the Cormack–Jolly–Seber (CJS) model. Survival (Phi) is the probability of surviving from occasion i to $i + 1$, whereas detectability (p) is the probability of encountering an individual conditional on being alive and in the sample. An encounter history was made for each individual as a binary set of "0"s and "1"s representing absence (not observed) and presence (observed), respectively. For instance, an encounter history of "1011" means that the individual was marked and released in day 1, not recaptured on day 2, but observed on days 3 and 4. The fit of the CJS was assessed with the single-state chi-square tests that test for trap dependence and transience (Test2, Test3 and Total) (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009) using the release.gof function in the R-package Rmark (Choquet et al., 2009). Table S1 shows that all the assumptions for the CJS model are met. The parameter estimates of Phi and p were calculated using RMark (Laake, 2013). Candidate models were chosen for Phi and p. First, the effect of Julian date (time) and sex was tested on both Phi and p starting from the simplest model where the parameter is constant (Phi(.) p(.)) to the most complex including two interactions (Phi(sex*time) p(sex*time)). We calculated the variance inflation factor (c-hat) by dividing the overall χ^2 (sum of the TEST2 and TEST3 component tests) by the overall degrees of freedom (Cooch & White, 2006) and found it <1, and thus, no variance adjustment was performed to the models. Model selection was then carried out using the corrected Akaike information criterion (AICc). To assess the effect of body size on survival, body length (linear and quadratic effects) was included as an individual covariate in the survival model. To determine the effect of body size on survival, a model-averaged approach was utilized with the function *covariate.predictions* of the RMark model.

3 | RESULTS

A total of 1092 (815 males and 277 females) and 557 (478 males and 79 females) adults were captured and marked during the spring and autumn cohorts, respectively. The number of measured individuals was 360 (275 males and 85 females) and 508 (432 males and 76 females) during the spring and autumn cohorts, respectively. Regarding the proportion of recapture for each sex, 420 of 815 males (51.5%) were recaptured and 117 of 277 females (42.2%) were recaptured

FIGURE 2 Seasonal pattern of body length of *Coenagrion mercuriale* during the spring (a) and autumn (b) cohort. Julian date is the date at first capture of each individual. The lines are linear regressions, and grey ribbons are standard errors. Orange is female, and green is male
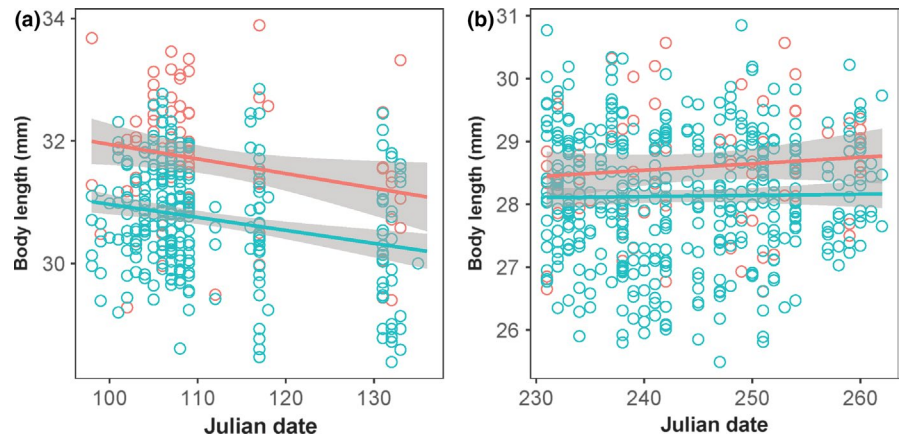
TABLE 2 Model selection of the Cormack–Jolly–Seber for capture–mark–recapture data of *Coenagrion mercuriale* of the spring and autumn cohort

Model	npar	AICc	ΔAICc	weight	Deviance
Spring cohort					
Phi(.) *p*(~sex+time)	56	2354.7	0.000	0.268	1157.0
Phi(~Body) *p*(~sex+time)	57	2355.2	0.413	0.218	2232.8
Phi(~Body+Time) *p*(~sex+time)	58	2355.4	0.602	0.198	2230.7
Phi(~sex) *p*(~sex+time)	57	2356.9	2.119	0.092	1156.8
Phi(~sex+Body) *p*(~sex+time)	58	2357.5	2.71	0.069	2232.8
Phi(~Body+Body²) *p*(~sex+time)	58	2357.5	2.716	0.068	2232.8
Phi(~Body×Time) *p*(~sex+time)	59	2357.7	2.911	0.062	2230.7
Phi(~sex×Body) *p*(~sex+time)	59	2359.8	5.002	0.021	2232.8
Autumn cohort					
Phi(.) *p*(~sex+time)	33	1742.9	0.000	0.268	598.5
Phi(~Body) *p*(~sex+time)	34	1742.9	0.021	0.265	1671.8
Phi(~sex+Body) *p*(~sex+time)	35	1744.7	1.864	0.105	1671.4
Phi(~sex) *p*(~sex+time)	34	1744.9	2.055	0.096	598.4
Phi(~Body+Time) *p*(~sex+time)	35	1744.9	2.084	0.094	1671.6
Phi(~Body+Body²) *p*(~sex+time)	35	1745.1	2.21	0.088	1671.8
Phi(~Body×Time) *p*(~sex+time)	36	1746.5	3.61	0.044	1671.0
Phi(~sex×Body) *p*(~sex+time)	36	1746.8	3.968	0.036	1671.3

Note: Phi is the survival probability, and *p* is the detection probability.

in the spring cohort, and 142 of 478 males (29.7%) were recaptured and 14 of 79 females (17.7%) were recaptured in the autumn cohort.

3.1 | Within- and among-cohort variation in body size

The body size of the two cohorts showed different seasonal patterns (Table 1), revealed by the significant interaction of season-by-cohort. The spring cohort displayed a pattern of decreasing body length, whereas the autumn cohort exhibited no significant pattern (Figure 2). There was a significant sex effect, showing that females were larger than males in both seasons. Also, body length of the spring cohort was on average 20% larger than that of the autumn cohort. The cohort-by-sex interaction indicates that the sexual size

dimorphism (size difference between males and females) declined from spring to autumn cohort.

3.2 | Detection and survival probabilities

In both spring and autumn cohort, we first made a model selection on a set of CJS models excluding individual covariates (body length) and including only time and sex. Table S2 shows the best Cormack–Jolly–Seber models for survival and detectability for the spring and autumn cohort. In the spring cohort, the best model for detection included the additive effect of time and sex. The average detection probability was 0.21 ± 0.007 (±*SE*) for males and 0.14 ± 0.01 for females, and it declined throughout the season. In the autumn cohort, the best model for detection included time.
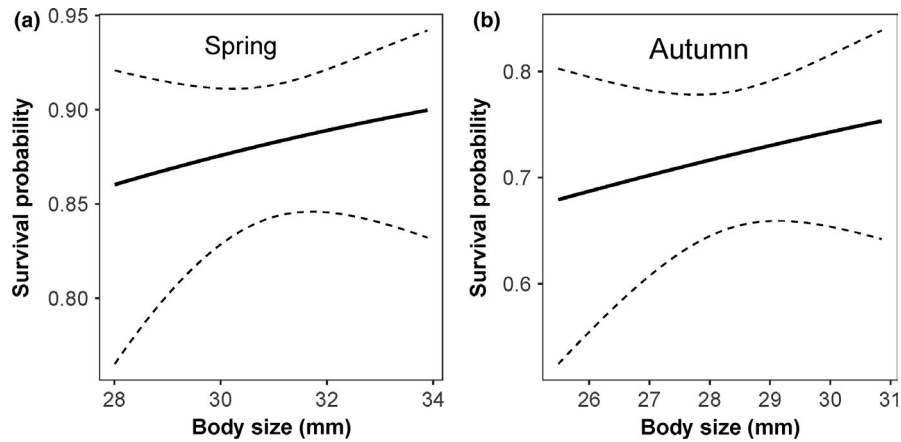
FIGURE 3 The relationship between body length and survival probability for the spring and autumn cohort of *Coenagrion mercuriale*. The regression continuous line was estimated with a model-averaged approach for Cormack–Jolly–Seber models. The dashed lines are 95% confidence intervals

When we do not consider covariates (body size), survival probability of the spring cohort which had an average of 0.85 [95% CI: 0.84–0.86] was best explained by time and showed a seasonal decline. Survival probability of the autumn cohort was best explained by a constant model predicting an average of 0.73 [0.70–0.76]. When we include body length as a covariate in survival models and make a model selection, those including body length were among the top model in both spring and autumn cohort (Table 2). Interestingly, the effect of body length showed the same pattern in both cohorts. Two of the three top models that had a ΔAICc<2 included a positive effect of body length. We estimated the effect of body length using model average approach and found that the probability of survival increased by 0.013 mm^{-1} with an intercept of 0.86 [95% CI: 0.76–0.92] in the spring cohort and by 0.007 mm^{-1} with an intercept of 0.67 [95% CI: 0.52–0.80] in the autumn cohort (Figure 3).

3.3 | Within- and among-cohort variation in apparent lifespan

The average ± *SD* of the lifespan of males and females was 3.72 ± 5.56 days and 2.62 ± 4.47 days for the spring cohort and 1.26 ± 2.21 days and 0.85 ± 2.11 days for the autumn cohort, respectively. The Poisson regression showed that body length positively affected the lifespan of individuals in both sexes and cohorts. Females survived longer than males, and the individuals of the spring cohort survived longer those of the autumn cohort. The nonsignificant effects of the bivariate interactions showed that the pattern of the effect of body length on lifespan for both sexes and the two cohorts was similar (Table 3).

3.4 | Within- and among-cohort variation in apparent lifetime mating success

The average ± *SD* ALRS of the spring cohort was 1.19 ± 0.870 and 0.84 ± 0.91 (oviposition events) in females and males, respectively, whereas that of the second generation was 0.73 ± 0.63 and

TABLE 3 Summary results of the Poisson model regressing lifespan across body length, sex and cohort

	Estimate	Std. Error	z value	p-value
Intercept	−2.670	0.848	−3.146	0.001
Body	0.137	0.024	5.595	<0.0001
Sex[Male]	0.474	0.067	7.009	<0.0001
Cohort[autumn]	−0.725	0.081	−8.902	<0.0001

Note: Female and spring cohort are the base level for contrast comparisons.

0.16 ± 0.38 in females and males, respectively. We tested the effect of body length, sex and cohort on the ALRS (Table 4). First, the significant positive effect of body length and the nonsignificant body-by-cohort interaction reveals that body length had a positive effect on LRS in both cohorts (Figure 4). The significant sex effect shows that female LRS was greater than that of males. Cohort did not show a significant effect, but its interaction with sex was positive, indicating that the difference in LRS was greater in the autumn cohort than the spring cohort.

4 | DISCUSSION

Although experimental studies have shown that POLS occurs in many animal taxa and affects fundamental biological processes involving growth, development and immune system at the juvenile stage (Angilletta et al., 2004; Gotthard, 2001), there have been a few studies that investigated the POLS consequences on survival and mating success at the adult stage, particularly in natural populations. Our study reveals differences in body size and fitness components between and within two cohorts with different life-history paces. We demonstrated that body size was larger in the long- compared to the short-developing cohort and that there was a seasonal decline in size in the slow-developing cohort, but no significant pattern in the fast-developing cohort. The among-cohort analysis showed that survival

TABLE 4 Summary results of the Poisson model regressing apparent lifetime mating success against lifespan, body length, sex and cohort

	Estimate	Std. Error	z value	p-value
Intercept	−3.875	1.529	−2.535	0.011
Lifespan	0.052	0.007	7.798	<0.0001
Body	0.127	0.048	2.650	0.008
Sex[Male]	−0.375	0.121	−3.089	0.002
Cohort[spring]	−0.097	0.218	−0.447	0.655
Sex[Male]:Cohort[spring]	−1.078	0.209	−5.153	<0.0001

Note: Female and spring cohort are the base level for contrast comparisons.

FIGURE 4 The relationship between body length and apparent lifetime mating success for the spring and autumn cohort for females and males of *Coenagrion mercuriale*. The regression lines are derived from a Poisson model. The dashed lines are 95% confidence intervals
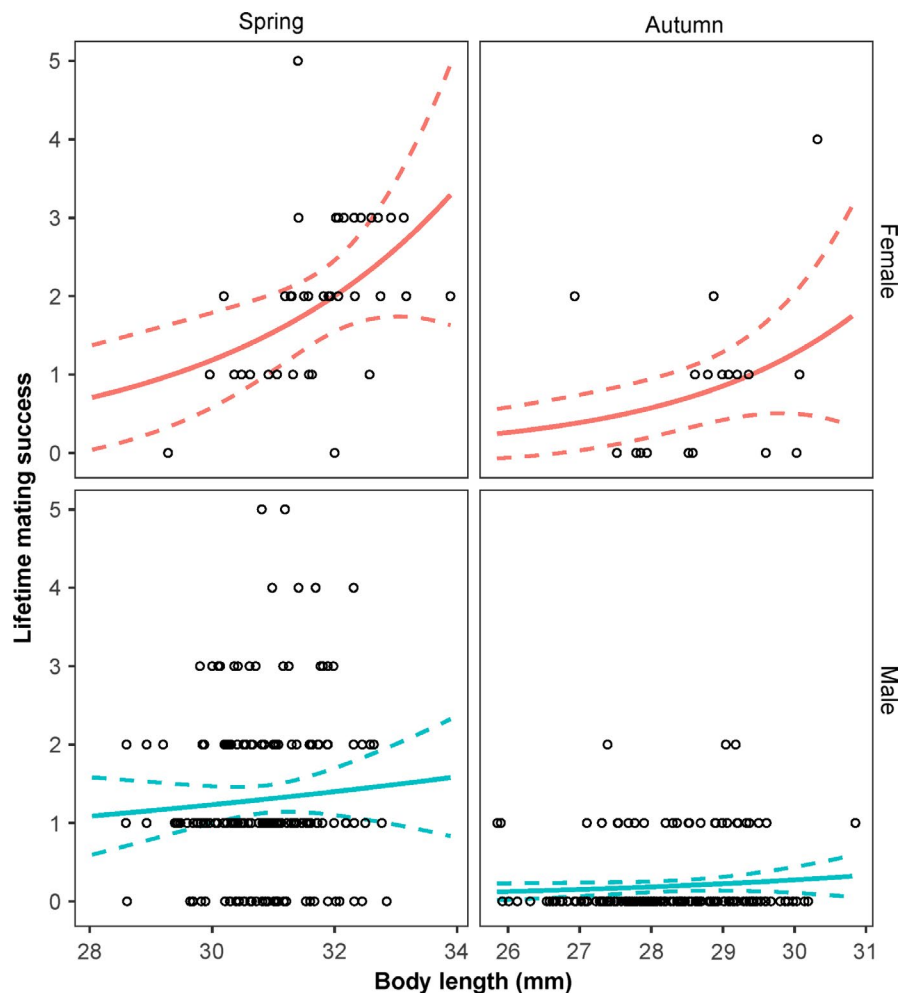
and ALRS were higher in the long- compared to the slow-developing cohort. The within-cohort analysis revealed a positive relationship between body size, survival probability and ALRS in both cohorts.

The relationship between age at maturity (development time) and body size have been well investigated in a wide range of organisms, revealing a positive trend (Kingsolver et al. 2004; Stearns, 1992). Consistent to our study, body size was larger in the spring cohort than in the autumn cohort most likely because the former develops for 6–11 months whereas the latter takes 3–4 months to develop (Mahdjoub et al., 2015). It can be inferred that the development rate was seasonally plastic and depended positively on water temperature (Suhling, Suhling, & Richter,

2015) which was considerably higher in summer, leading to faster development and emergence in the autumn. Many studies have investigated the plastic response of organisms to temperature in a wide range of taxa (Angilletta, 2009) and its consequences on body size (Blanckenhorn, 2000). It is likely that cohort splitting has a genetic basis (Schultheis, Hendricks, & Weigt, 2002) as an adaptive response to environmental variability. In fact, recent studies have shown that North African populations of *C. mercuriale* where bivoltine cohort-split occurs are genetically differentiated from European populations (Ferreira et al., 2016). The plastic and adaptive mechanisms underlying the cohort splitting are still not well understood and require further experimental studies to unravel.

Despite daily sampling of damselflies, the recapture rate of the species was quite low. Such low recapture rates were also recorded in other damselflies (Anholt, Vorburger, & Knaus, 2001; Conrad, Willson, Harvey, Thomas, & Sherratt, 1999; Cordero-Rivera & Stoks, 2008). This might be due to the fact that the population has a wide spatial distribution where adults frequent terrestrial habitat as well as aquatic habitat, which is the case for some damselflies (Khelifa, Mahdjoub, Aouaouche, & Houhamdi, 2016). Sex effect consistently showed in the top models for recapture probability, revealing a slightly higher recapture probability for males. This is consistent with studies on damselflies and dragonflies (Cordero-Rivera & Stoks, 2008). The cryptic behaviour of females is a likely hypothesis to explain this pattern where females spend more time outside reproductive area (far from the water) (Conrad et al., 1999; Stoks, 2001).

Moreover, seasonal variation in body size showed different trends during the spring and the autumn flight season. The spring (slower-developing) cohort showed a decreasing pattern, that is, individuals that reproduce early in the season were larger than those that reproduce later in the season. This is a typical pattern in *C. mercuriale* in particular (Mahdjoub et al., 2015; Purse & Thompson, 2003), other odonates (Banks & Thompson, 1985; Corbet, 1999; Michiels & Dhondt, 1989) and insects in general (Comiskey, Lowrie, & Wesson, 1999; Peckarsky, Cowan, Penton, & Anderson, 1993). On the other hand, the autumn (faster-developing) cohort showed no significant seasonal pattern of body size, which might be explained by the short development period and the low intracohort variation in age at emergence (maturity) in the autumn cohort compared to the spring cohort. The comparative analysis of the two adult cohorts with different paces of life shed some light on the proximate factors that generate the seasonal decline in body size observed in many aquatic insects. Temperature encountered during the larval stage likely plays an important role, in other words, larger individuals that emerge early in the spring season are those that hatched in spring where temperatures are lower and thus development is slower which allow them to accumulate mass and grow bigger whereas the smaller individuals that emerge later in the spring season are those that hatch in summer where temperature is higher and thus development is faster, which results in shorter time spent as larvae and smaller size at emergence (Davidowitz, D'Amico, & Nijhout, 2003). However, other factors such seasonal pattern of food availability (Chapman & Chapman, 1998; Davidowitz et al., 2003), predation (Abrams & Rowe, 1996) and intra- and interspecific competition (Wissinger, 1989) are also to be considered because they could shape mass accumulation, growth and ultimately body size at emergence.

The positive correlation between body size, lifespan and survival probability is consistent with theoretical and empirical studies (Davidowitz et al., 2003; Roff, 2002; Stearns, 1992). Similar results were reported for *Chalcolestes viridis* where variation in survival to maturity was explained by larval time constraint (De Block & Stoks, 2005). Also, an experimental study on the stonefly *Megarcys signata* showed that body mass at emergence was positively correlated with lifespan in both males and females (Taylor, Anderson, & Peckarsky, 1998). There are probably carry-over costs of rapid larval

development that result in lower survival probability at the adult stage (Inness & Metcalfe, 2008; Ricklefs, 2006). We assume that larger individuals that came from slow-developing larvae allocated more resources into biological functions (immunity, flight ability or foraging) that increase lifespan, whereas fast-developing individuals allocated more resources into fast development (Blanckenhorn, 1998). Rolff, Van de Meutter, and Stoks (2004) showed in *Chalcolestes viridis* that time-constrained development can cause suppression of key components of the immune system, which leads to lower longevity. Larger body size may also translate into higher flight ability which confers greater foraging success (Greenleaf, Williams, Winfree, & Kremen, 2007; Van Nieuwstadt & Iraheta, 1996) and higher energy reserve (Arrese & Soulages, 2010; Partridge & Harvey, 1988). The similarity of the positive effect of body size on the lifespan in both cohorts where individuals encounter different abiotic and biotic conditions shows that body size at the cohort and individual level is a good predictor of important fitness components. Our results also suggest that larger individuals did not suffer from higher predation at the adult stage, which is typical for insects and other taxa (Sih, 1982; Wahle, 1992).

Besides survival, mating success was also different among cohorts and body size also showed a positive correlation in both spring and autumn cohorts. The mating system of the species explains the sexual differences in mating success (Fincke, 1982). The reproductive frequency of females depends mainly on their ability to survival longer to produce more eggs (Thompson, 1990), whereas that of males is further limited by their ability to find and copulate with mates (Bangham, Chapman, & Partridge, 2002; Mellal, Bensouilah, Houhamd, & Khelifa, 2018). In species with scramble competition (stay attached to the female during oviposition), the daily mating frequency is mostly binary (either one or zero) (Corbet, 1999). Because there is high (scramble) competition for females in reproductive sites, almost all females with mature eggs find a mate, whereas not all males in the reproductive sites will copulate with a female (Fincke, 1982). This explains the difference in mating frequency between males and females observed in *C. mercuriale*. However, the differences in mating success between spring and autumn cohort might be explained by the pace of life (De Block & Stoks, 2005). This is supported by the positive relationship between body size and mating success at the individual level in both cohorts, which was observed in many odonates (Koenig, 2008; Sokolovska et al., 2000; Thompson & Fincke, 2002) and other insects (Bangham et al., 2002; Blanckenhorn, 2000). In fact, larger individuals may spend more time searching due to their higher energy reserves and thus might be better at finding mates (Otronen, 1995; Yuval, Kaspi, Shloush, & Warburg, 1998). In addition, since larger males had larger survival probability and lifespan, they also had more opportunity to find mates and increase their mating success (Watt, Carter, & Donohue, 1986). Thus, these results corroborate with the survival analysis and the theoretical and empirical studies in animals and plants (Kozłowski, 1992; Stearns, 1992).

So why would individuals emerge in late summer/autumn and pay huge fitness costs? Similar cohort splitting has been observed in other species in North Africa (Khelifa, 2017), which suggests that

this strategy might be an adaptation to the local environment (Lytle & Poff, 2004). Several species of macroinvertebrates have the trailing edge of their distribution in North Africa where drought is usually a common feature of wetlands (Britton & Crivelli, 1993). Although larger individuals might benefit from higher fitness due to their slow development in years where there is no drought, they will suffer high consequences in dry years where fast development is most likely advantageous (Williams, 1996). Thus, in an unpredictable dry environment such as in the North Africa (Cook, Anchukaitis, Touchan, Meko, & Cook, 2016), it is likely that the difference in fitness between cohorts decreases or evens out over the long term due to the slow-development costs of mortality in dry years (Benrey & Denno, 1997). Furthermore, having a flexible life history in an unpredictable environment is particularly beneficial for species persistence, especially in an era of extreme climate change (Conti, Schmidt-Kloiber, Grenouillet, & Graf, 2014). Therefore, we can hypothesize that bigger is evolutionary not always better in fluctuating environments (Blanckenhorn, 2000).

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CONFLICT OF INTEREST

The authors have declared that no competing interests exist.

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REFERENCES

Abrams, P. A., & Rowe, L. (1996). The effects of predation on the age and size of maturity of prey. *Evolution*, *50*, 1052–1061. https://doi.org/10.1111/j.1558-5646.1996.tb02346.x

Alcock, J. (1981). Lek territoriality in the tarantula hawk wasp Hemipepsis ustulata (Hymenoptera: Pompilidae). *Behavioral ecology and sociobiology*, *8*, 309–317. https://doi.org/10.1007/BF00299531

Amari, H., Zebsa, R., Lazli, A., Bensouilah, S., Mellal, M. K., Mahdjoub, H., … Khelifa, R. (2019). Differential elevational cline in the phenology and demography of two temporally isolated populations of a damselfly: Not two but one taxa? *Ecological entomology*, *44*, 93–104. https://doi.org/10.1111/een.12680

Angilletta, M. J. (2009). *Thermal adaptation: A theoretical and empirical synthesis*. Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198570875.001.1

Angilletta, M. J., Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and comparative biology*, *44*, 498–509. https://doi.org/10.1093/icb/44.6.498

Anholt, B. R., Vorburger, C., & Knaus, P. (2001). Mark-recapture estimates of daily survival rates of two damselflies (*Coenagrion puella* and *Ischnura elegans*). *Canadian Journal of Zoology*, *79*, 895–899. https://doi.org/10.1139/z01-053

Arrese, E. L., & Soulages, J. L. (2010). Insect fat body: Energy, metabolism, and regulation. *Annual review of entomology*, *55*, 207–225. https://doi.org/10.1146/annurev-ento-112408-085356

Ashton, K.G. 2004. Sensitivity of intraspecific latitudinal clines of body size for tetrapods to sampling, latitude and body size. *Integrative and Comparative Biology* 44: 403–412.

Baker, R. R. (1983). Insect territoriality. *Annual Review of Entomology*, *28*, 65–89. https://doi.org/10.1146/annurev.en.28.010183.000433

Bangham, J., Chapman, T., & Partridge, L. (2002). Effects of body size, accessory gland and testis size on pre-and postcopulatory success in Drosophila melanogaster. *Animal Behaviour*, *64*, 915–921. https://doi.org/10.1006/anbe.2002.1976

Banks, M. J., & Thompson, D. J. (1985). Lifetime mating success in the damselfly Coenagrion puella. *Animal Behaviour*, *33*, 1175–1183. https://doi.org/10.1016/S0003-3472(85)80178-0

Benrey, B., & Denno, R. F. (1997). The slow-growth–high-mortality hypothesis: A test using the cabbage butterfly. *Ecology*, *78*, 987–999.

Berrigan, D. (1991). The allometry of egg size and number in insects. *Oikos*, *00*, 313–321. https://doi.org/10.2307/3545073

Blackburn, T.M., Gaston, K.J. & Loder, N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* 5: 165–174.

Blanckenhorn, W. U. (1998). Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. *Evolution*, *52*, 1394–1407. https://doi.org/10.1111/j.1558-5646.1998.tb02021.x

Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *The quarterly review of biology*, *75*, 385–407. https://doi.org/10.1086/393620

Blanckenhorn, W. U., Preziosi, R. F., & Fairbairn, D. J. (1995). Time and energy constraints and the evolution of sexual size dimorphism—to eat or to mate? *Evolutionary Ecology*, *9*, 369–381. https://doi.org/10.1007/BF01237760

Boudot, J.-P., Kalkman, V. J., Amorin, A., Bogdanović, T., Rivera, A. C., Degabriele, G., … Jović, M. (2009). Atlas of the Odonata of the Mediterranean and North Africa. *Libellula*, *9*, 1–256.

Britton, R., & Crivelli, A. (1993). Wetlands of southern Europe and North Africa: Mediterranean wetlands. *Wetlands of the world: Inventory, ecology and management*, Vol. *I* (pp. 129–194). Dordrecht, Netherlands: Springer. https://doi.org/10.1007/978-94-015-8212-4

Chapman, R. F., & Chapman, R. F. (1998). *The insects: Structure and function*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511818202

Choe, J. C., & Crespi, B. J. (1997). *The evolution of mating systems in insects and arachnids*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511721946

Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M., & Pradel, R. (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating capture–recapture data. *Ecography*, *32*, 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1985). Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature*, *313*, 131. https://doi.org/10.1038/313131a0

Comiskey, N. M., Lowrie, R. C. Jr, & Wesson, D. M. (1999). Role of habitat components on the dynamics of Aedes albopictus (Diptera: Culicidae) from New Orleans. *Journal of medical entomology*, *36*, 313–320. https://doi.org/10.1093/jmedent/36.3.313

Conrad, K., Willson, K., Harvey, I., Thomas, C., & Sherratt, T. (1999). Dispersal characteristics of seven odonate species in an agricultural landscape. *Ecography*, *22*, 524–531. https://doi.org/10.1111/j.1600-0587.1999.tb00541.x

Conti, L., Schmidt-Kloiber, A., Grenouillet, G., & Graf, W. (2014). A trait-based approach to assess the vulnerability of European aquatic

insects to climate change. *Hydrobiologia*, 721, 297–315. https://doi.org/10.1007/s10750-013-1690-7

Cooch, E., & White, G. (2006). Program MARK: a gentle introduction. Retrieved from http://www.phidot.org/software/mark/docs/book (accessed 26th November 2017).

Cook, B. I., Anchukaitis, K. J., Touchan, R., Meko, D. M., & Cook, E. R. (2016). Spatiotemporal drought variability in the Mediterranean over the last 900 years. *Journal of Geophysical Research: Atmospheres*, 121, 2060–2074.

Corbet, P. S. (1957). The life-history of the emperor dragonfly Anax imperator Leach (Odonata: Aeshnidae). *The Journal of Animal Ecology*, 1–69. https://doi.org/10.2307/1781

Corbet, P. (1999). *Dragonflies: Behaviour and ecology of Odonata*. Colchester, UK: Harley Books.

Corbet, P. S., Suhling, F., & Soendgerath, D. (2006). Voltinism of Odonata: A review. *International Journal of Odonatology*, 9, 1–44. https://doi.org/10.1080/13887890.2006.9748261

Cordero, A. (1991). Fecundity of Ischnura graellsii (Rambur) in the laboratory (Zygoptera: Coenagrionidae). *Odonatologica*, 20, 37–44.

Cordero, A. (1992). Density-dependent mating success and colour polymorphism in females of the damselfly Ischnura graellsii (Odonata: Coenagrionidae). *Journal of Animal Ecology*, 769–780. https://doi.org/10.2307/5630

Cordero, A., Carbone, S. S., & Utzeri, C. (1997). Male mating success in a natural population of Ischnura elegans (Vander Linden)(Odonata: Coenagrionidae). *Odonatologica*, 26, 459–465.

Cordero-Rivera, A., & Stoks, R. (2008). Mark-recapture studies and demography. In A. Córdoba-Aguilar (Ed.), *Dragonflies and damselflies: Model organisms for ecological and evolutionary research* (pp. 7–20). Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199230693.001.0001

Davidowitz, G., D'Amico, L. J., & Nijhout, H. F. (2003). Critical weight in the development of insect body size. *Evolution and Development*, 5, 188–197. https://doi.org/10.1046/j.1525-142X.2003.03026.x

De Block, M., & Stoks, R. (2005). Fitness effects from egg to reproduction: Bridging the life history transition. *Ecology*, 86, 185–197. https://doi.org/10.1890/04-0116

Debecker, S., Sanmartín-Villar, I., de Guinea-Luengo, M., Cordero-Rivera, A., & Stoks, R. (2016). Integrating the pace-of-life syndrome across species, sexes and individuals: Covariation of life history and personality under pesticide exposure. *Journal of Animal Ecology*, 85, 726–738. https://doi.org/10.1111/1365-2656.12499

Dmitriew, C. M. (2011). The evolution of growth trajectories: What limits growth rate? *Biological Reviews*, 86, 97–116. https://doi.org/10.1111/j.1469-185X.2010.00136.x

Ferreira, S., Boudot, J.-P., El Haissoufi, M., Alves, P. C., Thompson, D. J., Brito, J. C., & Watts, P. C. (2016). Genetic distinctiveness of the damselfly Coenagrion puella in North Africa: An overlooked and endangered taxon. *Conservation genetics*, 17, 985–991. https://doi.org/10.1007/s10592-016-0826-5

Ferreras-Romero, M. (1991). Preliminary data on the life history of Cercion lindeni (Selys) in Southern Spain (Zygoptera: Coenagrionidae). *Odonatologica*, 20, 53–63.

Ferreras-Romero, M., & García-Rojas, A. (1995). Life-history patterns and spatial separation exhibited by the odonates from a Mediterranean inland catchment in southern Spain. *Vie et Milieu*, 45, 157–166.

Fincke, O. M. (1982). Lifetime mating success in a natural population of the damselfly, Enallagma hageni (Walsh)(Odonata: Coenagrionidae). *Behavioral Ecology and Sociobiology*, 10, 293–302. https://doi.org/10.1007/BF00302820

Flenner, I., Richter, O., & Suhling, F. (2010). Rising temperature and development in dragonfly populations at different latitudes. *Freshwater Biology*, 55, 397–410. https://doi.org/10.1111/j.1365-2427.2009.02289.x

Forrest, T. (1987). Insect size tactics and developmental strategies. *Oecologia*, 73, 178–184. https://doi.org/10.1007/BF00377505

Gebhardt-Henrich, S., & Richner, H. (1998). Causes of growth variation and its consequences for fitness. *Oxford Ornithology Series*, 8, 324–339.

Gotthard, K. (2001). Growth strategies of ectothermic animals in temperate environments. In D. Atkinson & M. Thorndyke, (Eds.), Environment and animal development , (pp. 287–304). Oxford, UK: Oxford BIOS Scientific Publishers.

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153, 589–596. https://doi.org/10.1007/s00442-007-0752-9

Honěk, A., & Kocourek, F. (1990). Temperature and development time in insects: A general relationship between thermal constants. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, 117, 401–439.

Ingram, B., & Jenner, C. (1976). Life histories of Enallagma hageni (Walsh) and E. aspersum (Hagen)(Zygoptera: Coenagrionidae). *Odonatologica*, 5, 331–345.

Inness, C.L., & Metcalfe, N.B. (2008). The impact of dietary restriction, intermittent feeding and compensatory growth on reproductive investment and lifespan in a short-lived fish. *Proceedings of the Royal Society of London B: Biological Sciences*, 275, 1703–1708. https://doi.org/10.1098/rspb.2008.0357

Irschick, D.J., Meyers, J.J., Husak, J.F. & Le Galliard, J.-F. 2008. How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research 10*: 177–196.

Khelifa, R. (2017). Partial bivoltinism and emergence patterns in the North African endemic damselfly Calopteryx exul: Conservation implications. *African Journal of Ecology*, 55, 145–151. https://doi.org/10.1111/aje.12332

Khelifa, R., Mahdjoub, H., Aouaouche, M. S., & Houhamdi, M. (2016). Reproductive behaviour of a North African endemic damselfly, Platycnemis subdilatata (Odonata: Platycnemididae) and probable senescence effects. *Journal of Odonatology*, 19, 157–167. https://doi.org/10.1080/13887890.2016.1196619

Khelifa, R., Youcefi, A., Kahlerras, A., Alfarhan, A., Al-Rasheid, K. A. S., & Samraoui, B. (2011). L'odonatofaune (Insecta : Odonata) du bassin de la Seybouse en Algérie : Intérêt pour la biodiversité du Maghreb. *Revue d'Écologie (La Terre et la Vie)*, 66, 55–66.

Khelifa, R., Zebsa, R., Amari, H., Mellal, M. K., Mahdjoub, H., & Kahalerras, A. (2016). A hotspot for threatened Mediterranean odonates in the Seybouse River (Northeast Algeria): Are IUCN population sizes drastically underestimated? *International Journal of Odonatology*, 19, 1–11. https://doi.org/10.1080/13887890.2015.1133331

Kingsolver, J.G., Izem, R. & Ragland, G.J. 2004. Plasticity of size and growth in fluctuating thermal environments: comparing reaction norms and performance curves. *Integrative and Comparative Biology* 44: 450–460.

Kleiber, C., & Zeileis, A. (2017). *Package 'AER': Applied Econometrics with R*. New York: Springer-Verlag. *R package version 1.2* 4. Retrieved from https://CRAN.R-project.org/package=AER

Koenig, W. D. (2008). Lifetime reproductive success and sexual selection theory. In A. Córdoba-Aguilar (Ed.), *Dragonflies and damselflies: Model organisms for ecological and evolutionary research* (pp. 153–166). Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199230693.001.0001

Kozłowski, J. (1992). Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology & Evolution*, 7, 15–19. https://doi.org/10.1016/0169-5347(92)90192-E

Laake, J. (2013). RMark: An R Interface for Analysis of Capture–Recapture Data with MARK, AFSC Processed Rep 2013-01. *Alaska Fish. Sci. Cent., NOAA, National Marine Fisheries Service, Seattle, Washington.*

Lovegrove, B. (2003). The influence of climate on the basal metabolic rate of small mammals: A slow-fast metabolic continuum. *Journal of Comparative Physiology B*, *173*, 87–112.

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in ecology & evolution*, *19*, 94–100. https://doi.org/10.1016/j.tree.2003.10.002

Mahdjoub, H., Khelifa, R., Zebsa, R., Bouslama, Z., & Houhamdi, M. (2015). Bivoltinism in Coenagrion mercuriale (Zygoptera: Odonata) in the southern margin of its distribution range: Emergence pattern and larval growth. *African Entomology*, *23*, 59–67. https://doi.org/10.4001/003.023.0120

Mahdjoub, H., Khelifa, R., Zebsa, R., Mellal, M. K., Bouslama, Z., & Houhamdi, M. (2014). Aspects of reproductive biology and ecology of *Coenagrion mercuriale* at its southern range margin. *International Journal of Odonatology*, *17*, 173–180. https://doi.org/10.1080/13887890.2014.958580

Mellal, M. K., Bensouilah, M., Houhamd, M., & Khelifa, R. (2018). Reproductive habitat provisioning promotes survival and reproduction of the endangered endemic damselfly Calopteryx exul. *Journal of Insect Conservation*, *22*, 563–570. https://doi.org/10.1007/s10841-018-0085-5

Michiels, N. K., & Dhondt, A. A. (1989). Effects of emergence characteristics on longevity and maturation in the dragonflySympetrum danae (Anisoptera: Libellulidae). *Hydrobiologia*, *171*, 149–158. https://doi.org/10.1007/BF00008175

Okuyama, H., Samejima, Y., & Tsubaki, Y. (2015). Smaller damselflies have better flight performance at lower body temperature: Implications for microhabitat segregation of sympatric Mnais damselflies. *International Journal of Odonatology*, *18*, 217–224. https://doi.org/10.1080/13887890.2015.1065517

Otronen, M. (1995). Energy reserves and mating success in males of the yellow dung fly, Scathophaga stercoraria. *Functional Ecology*, 683–688. https://doi.org/10.2307/2390161

Palmer, J. O. (1984). Environmental determinants of seasonal body size variation in the milkweed leaf beetle, Labidomera clivicollis (Kirby) (Coleoptera: Chrysomelidae). *Annals of the Entomological Society of America*, *77*, 188–192. https://doi.org/10.1093/aesa/77.2.188

Partridge, L. & Coyne, J.A. 1997. Bergmann's rule in ectotherms: is it adaptive? *Evolution 51*: 632–635.

Partridge, L., & Farquhar, M. (1983). Lifetime mating success of male fruitflies (Drosophila melanogaster) is related to their size. *Animal Behaviour*, *31*, 871–877. https://doi.org/10.1016/S0003-3472(83)80242-5

Partridge, L., & Harvey, P. H. (1988). The ecological context of life history evolution. *Science*, *241*, 1449–1455. https://doi.org/10.1126/science.241.4872.1449

Peckarsky, B. L., Cowan, C. A., Penton, M. A., & Anderson, C. (1993). Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology*, *74*, 1836–1846. https://doi.org/10.2307/1939941

Pincheira-Donoso, D., Hodgson, D.J. & Tregenza, T. 2008. The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? *BMC Evolutionary Biology 8*: 68.

Purse, B. V., Hopkins, G. W., Day, K. J., & Thompson, D. J. (2003). Dispersal characteristics and management of a rare damselfly. *Journal of applied ecology*, *40*, 716–728. https://doi.org/10.1046/j.1365-2664.2003.00829.x

Purse, B. V., & Thompson, D. J. (2003). Emergence of the damselflies, Coenagrion mercuriale and Ceriagrion tenellum (Odonata: Coenagrionidae), at their northern range margins, in Britain. *European Journal of Entomology*, *100*, 93–100. https://doi.org/10.14411/eje.2003.018

R Development Core Team (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raihani, G., Serrano-Meneses, M., & Córdoba-Aguilar, A. (2008). Male mating tactics in the American rubyspot damselfly: Territoriality, nonterritoriality and switching behaviour. *Animal Behaviour*, *75*, 1851–1860. https://doi.org/10.1016/j.anbehav.2007.11.002

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*, 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Ricklefs, R.E. (2006). Embryo development and ageing in birds and mammals. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*, 2077–2082. https://doi.org/10.1098/rspb.2006.3544

Ricklefs, R. E., & Scheuerlein, A. (2002). Biological implications of the Weibull and Gompertz models of aging. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *57*, B69–B76. https://doi.org/10.1093/gerona/57.2.B69

Rivas-Torres, A., Sanmartín-Villar, I., Gabela-Flores, M., & Cordero-Rivera, A. (2017). Demographics and behaviour of Heteragrion cooki, a forest damselfly endemic to Ecuador (Odonata). *International Journal of Odonatology*, *20*, 123–135. https://doi.org/10.1080/13887890.2017.1336495

Rivera, A. C. (2000). An analysis of multivariate selection in a non-territorial damselfly (Odonata: Coenagrionidae). *Etología*, *8*, 37–41.

Roff, D. (2002). *Life history evolution*. Sunderland, MA: Sinauer Associates Google Scholar. https://doi.org/10.2307/3544887

Rolff, J., Van de Meutter, F., & Stoks, R. (2004). Time constraints decouple age and size at maturity and physiological traits. *The American Naturalist*, *164*, 559–565. https://doi.org/10.1086/423715

Rowe, L., & Ludwig, D. (1991). Size and timing of metamorphosis in complex life cycles: Time constraints and variation. *Ecology*, *72*, 413–427. https://doi.org/10.2307/2937184

Schultheis, A. S., Hendricks, A. C., & Weigt, L. A. (2002). Genetic evidence forleaky'cohorts in the semivoltine stonefly Peltoperla tarteri (Plecoptera: Peltoperlidae). *Freshwater Biology*, *47*, 367–376. https://doi.org/10.1046/j.1365-2427.2002.00807.x

Sih, A. (1982). Foraging strategies and the avoidance of predation by an aquatic insect, Notonecta hoffmanni. *Ecology*, *63*, 786–796. https://doi.org/10.2307/1936799

Singh, N., & Mishra, G. (2014). Does temperature modify slow and fast development in two aphidophagous ladybirds? *Journal of Thermal Biology*, *39*, 24–31. https://doi.org/10.1016/j.jtherbio.2013.11.003

Sokolovska, N., Rowe, L., & Johansson, F. (2000). Fitness and body size in mature odonates. *Ecological Entomology*, *25*, 239–248. https://doi.org/10.1046/j.1365-2311.2000.00251.x

Stearns, S. C. (1992). *The evolution of life histories*. Oxford, UK: Oxford University Press.

Stoks, R. (2001). Male-biased sex ratios in mature damselfly populations: Real or artefact? *Ecological Entomology*, *26*, 181–187. https://doi.org/10.1046/j.1365-2311.2001.00301.x

Suhling, F., Suhling, I., & Richter, O. (2015). Temperature response of growth of larval dragonflies–an overview. *International Journal of Odonatology*, *18*, 15–30. https://doi.org/10.1080/13887890.2015.1009392

Tammaru, T., Esperk, T., & Castellanos, I. (2002). No evidence for costs of being large in females of Orgyia spp. (Lepidoptera, Lymantriidae): larger is always better. *Oecologia*, *133*, 430–438. https://doi.org/10.1007/s00442-002-1057-7

Taylor, B. W., Anderson, C. R., & Peckarsky, B. L. (1998). Effects of size at metamorphosis on stonefly fecundity, longevity, and reproductive success. *Oecologia*, *114*, 494–502. https://doi.org/10.1007/s004420050473

Thompson, D. J. (1990). The effects of survival and weather on lifetime egg production in a model damselfly. *Ecological Entomology, 15*, 455–462. https://doi.org/10.1111/j.1365-2311.1990.tb00828.x

Thompson, D. J., & Fincke, O. M. (2002). Body size and fitness in Odonata, stabilising selection and a meta-analysis too far? *Ecological Entomology, 27*, 378–384. https://doi.org/10.1046/j.1365-2311.2002.00419.x

Thornhill, R., & Alcock, J. (1983). *The evolution of insect mating systems.* Cambridge, MA: Harvard University Press. https://doi.org/10.4159/harvard.9780674433960

Van Nieuwstadt, M., & Iraheta, C. R. (1996). Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie, 27*, 219–228. https://doi.org/10.1051/apido:19960404

Van Voorhies, W.A. 1996. Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Evolution 50*: 1259–1264.

Vitasse, Y., Porté, A. J., Kremer, A., Michalet, R., & Delzon, S. (2009). Responses of canopy duration to temperature changes in four temperate tree species: Relative contributions of spring and autumn leaf phenology. *Oecologia, 161*, 187–198. https://doi.org/10.1007/s00442-009-1363-4

Wahle, R. A. (1992). Body-size dependent anti-predator mechanisms of the American lobster. *Oikos, 65*, 52–60.

Warner, D.A. & Andrews, R.M. 2002. Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biological Journal of the Linnean Society 76*: 105–124.

Watt, W. B., Carter, P. A., & Donohue, K. (1986). Fe males' choice of "good genotypes" as mates is promoted by an insect mating system. *Science, 233*, 1187–1190. https://doi.org/10.1126/science.3738528

Watts, P., & Thompson, D. (2012). Developmental plasticity as a cohesive evolutionary process between sympatric alternate-year insect cohorts. *Heredity, 108*, 236. https://doi.org/10.1038/hdy.2011.63

Williams, D. D. (1996). Environmental constraints in temporary fresh waters and their consequences for the insect fauna. *Journal of the North American Benthological Society, 15*, 634–650. https://doi.org/10.2307/1467813

Wissinger, S. A. (1989). Seasonal variation in the intensity of competition and predation among dragonfly larvae. *Ecology, 70*, 1017–1027. https://doi.org/10.2307/1941370

Yuval, B., Kaspi, R., Shloush, S., & Warburg, M. S. (1998). Nutritional reserves regulate male participation in Mediterranean fruit fly leks. *Ecological Entomology, 23*, 211–215. https://doi.org/10.1046/j.1365-2311.1998.00118.x

Zamudio, K. R., Huey, R. B., & Crill, W. D. (1995). Bigger isn't always better: Body size, developmental and parental temperature and male territorial success in Drosophila melanogaster. *Animal Behaviour, 49*, 671–677.

SUPPORTING INFORMATION

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