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Life-history variation in relation to time constraints in a damselfly

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Abstract Although variation within populations in plasticity to time constraints is expected with regard to hatching date, empirical studies are largely lacking. We studied life-history responses to time constraints manipulated by photoperiod and associated with hatching date in larvae of the damselfly *Lestes viridis* for two populations with a different hydroperiod. In a common garden experiment, early- and late-hatched larvae from both populations were reared at two photoperiods mimicking the start and the end of the egg-hatching season. In a reciprocal transplant experiment, early- and late-hatched larvae from both populations were reared in both ponds. In all these experiments, larvae were reared from egg hatching until adult emergence. Within both populations, larvae reared at the photoperiod indicating a late time point in the growing season, reduced development time to compensate for their perceived shorter development period. Growth rate, however, did not respond to photoperiod, resulting in a lower mass at emergence. As expected, both in the laboratory and in the field, larvae from eggs that hatched later in the season generally had a shorter development time and a faster growth rate, resulting in a higher mass at emergence compared to early-hatched larvae. This may explain the intriguing seasonal increase in mass at emergence in this species, and affect the predictions of optimality models. None of these life-history responses differed between the two populations, despite clear differences in time constraints linked to hydroperiod, suggesting the robustness of the observed patterns. Given the ubiquity of asynchronous hatching in nature, and the adaptive value of the observed differences between early- and late-hatched larvae, we expect the effects of hatching date on life-history plasticity to be widespread.

Keywords Environmental stress · Damselfly larvae · Hatching date · Hydroperiod · Life-history plasticity

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Introduction

Trading-off early maturation against large size is a useful framework to understand the variation in age and size at a life-history transition (Roff 1992, 2002; Stearns 1992; Abrams and Rowe 1996). In animals with a complex life-cycle, time constraints like those imposed by seasonality or by pond drying may play an important role in balancing these conflicting demands (Rowe and Ludwig 1991; Abrams et al. 1996). There may be considerable within-population variation in time constraints between early- and late-hatched animals (Carrière et al. 1996). In response to variation in time constraints, animals are expected to exhibit variation both in baseline life-history traits and in plasticity to time constraints (Travis 1994; Via et al. 1995).

Only a few studies have considered life-history differences between early- and late-hatched individuals, although hatching dates can vary considerably within a population, resulting in large differences in the available length of the growth season. The limited empirical work on this topic showed a shorter development time in late-hatched individuals than in early-hatched individuals, which is consistent with the shorter period available for development in the former (e.g. Abrams et al. 1996). Carrière et al. (1996) reported shorter development times but decreased growth rate, resulting in smaller adults, in experimentally delayed nymphs of the cricket *Gryllus pennsylvanicus*. Altwegg (2002) found that late-hatched *Rana lessonae* tadpoles had shorter development times, but only in the presence of a caged predator. To our knowledge there are, however, no studies so far that have

looked at whether late-hatched individuals also had a different plasticity to time constraints than early-hatched individuals. Given their already shorter development period, late-hatched individuals may react more to an extra-imposed time constraint than early-hatched individuals. Alternatively, they may already grow at their physiological maximum and not show a plastic response to time constraints.

Here we test for variation in larval life-history responses to time constraints (seasonality) in the damselfly *Lestes viridis* Vander Linden. This species has populations both in temporary and permanent water bodies and is strictly univoltine (Jödicke 1997). Eggs are laid in summer and embryonic development stops when they reach a diapausing stage during winter. In early spring, after a post-diapause embryonic development period, eggs hatch and larvae complete their development in about 3 months in spring-early summer (Jödicke 1997). The three key life-history variables under study, mass at emergence, development time and growth rate, have been shown to possess genetic variation in *L. viridis* or other *Lestes* (De Block and Stoks 2003; R. Stoks, unpublished data). In a previous study, we have shown that larvae from a permanent pond population of this species reduced development time in response to time constraints imposed by photoperiod (De Block and Stoks 2003, 2004). Here we test two key predictions based upon the above-mentioned adaptive scenarios with regard to temporal variation in time constraints: (1) late-hatched larvae should reduce development time and, if possible, increase growth rate compared to early-hatched larvae, and (2) this effect will be stronger under time constraints imposed by photoperiod unless larvae have reached their physiological maximum. We studied these predictions in two populations: one from a permanent pond and one from a temporary pond. This allowed us to test for population differentiation using populations that differ in time constraints linked to hydroperiod. To distinguish between environmentally and genetically induced variation in life history between the populations from both ponds, we performed both a common garden and a reciprocal transplant experiment. Performing both laboratory and field experiments with two populations allows us to combine rigorous manipulation of rearing conditions with experimental data obtained under more natural conditions, to assess the robustness of the observed life-history patterns.

Materials and methods

Common set-up experiments

To look for temporal variation in larval life history with regard to time constraints, we compared the life history of larvae that hatched early versus late in the season. Dates were chosen based on an intensive monitoring of egg-hatching dates in our study populations (M. De Block, unpublished data). Early-hatched larvae were those collected when ca. 20% of the eggs had hatched (i.e. 22 April) and late-hatched larvae were those collected when more than 95% of the larvae had hatched (i.e. 7 May for the reciprocal transplant experiment in 2000 and 12 May for the common garden experiment in 2001). Hereafter, these egg-hatching dates will be called date 1 and date 2, respectively. For both experiments, we evaluated this temporal variation in life-history plasticity in larvae from two ponds with contrasting hydroperiod. Both ponds were situated in northern Belgium. The temporary pond (TP) is located in Wilrijk and shows considerably reduced water levels each year. During the last 10 years that we have monitored it, this pond dried up completely four times, resulting in the death of the larvae that did not complete larval development before drying. The permanent pond (PP) is located in Brasschaat, about 30 km to the north of the temporary pond, and does not show large fluctuations in water level.

L. viridis lays eggs in branches of trees at the waterside. When these eggs hatch, larvae fall from the trees into the pond. Freshly hatched (1-day old) larvae were collected from both the temporary and the permanent pond by attaching to trees funnels (diameter=50 cm) with a removable plastic cup (diameter=8 cm, height=11.5 cm) filled to a height of 4 cm with pond water. For the reciprocal transplant experiment in 2000, these larvae were collected in situ, while for the common garden experiment in 2001, these larvae were collected from a common garden egg-hatching experiment in the experimental garden of the University of Antwerp (M. De Block, unpublished data). By using larvae from the egg-hatching experiment we could, to some extent, control for differences in environmental conditions during embryonic development when comparing larvae from both populations that hatched early or late.

For both experiments, larvae were reared from egg hatching until adult emergence and three larval life-history variables were scored. Development time was calculated as the number of days from egg hatching until emergence. Mass at emergence (=dry mass) was determined by drying individuals for 48 h at 60°C and then weighing them to the nearest 0.01 mg using an electronic microbalance. Growth rate was calculated as $\log_e$ (dry mass) divided by development time (see Johansson et al. 2001).

Common garden experiment

In the common garden experiment, a time constraint was imposed on larvae from all four combinations of source site and hatching date by manipulating light regimes (see Nylin et al. 1996; Johansson et al. 2001). This gave a randomised full factorial 2×2×2 design with two levels of hatching date (date 1/date 2), photoperiod (early/late), and source site (TP/PP). Each treatment combination was replicated 20 times.

On each hatching date, 40 larvae from both source sites were brought to the laboratory (in total 160 larvae) and randomly divided into 2 groups. Each group was allocated to one of two adjacent walk-in climate rooms. Room temperature was kept at 18±1°C. Photoperiods in the two rooms were set to simulate those that would be experienced by early- and late-hatched larvae at both study ponds. For the larvae collected on date 1, one room started with the photoperiod of 20 April (L:D 14:10; early photoperiod) and the other room with the photoperiod of 1 June (L:D 16:8; late photoperiod). Throughout the experiment, photoperiods were adjusted every 10 days to simulate the natural progress of the light cycle. The larvae collected on date 2 were reared in the same two climate rooms as the larvae from date 1. At the moment of collection of these late-hatched larvae, the photoperiods indicating early and late time points in the growth season in the climate rooms were those of 10 May (L:D 15.5:8.5) and 20 June (L:D 16.5:7.5), respectively. To minimise potential confounding differences between the two climate rooms, larvae and their respective photoperiod were rotated between climate rooms every 10 days (see Johansson et al. 2001). Larvae were reared individually in white, plastic cups (diameter=5 cm, height=9 cm) filled to a height of 4 cm with filtered pond water and were fed laboratory-reared brine shrimp each day of the week, except Sunday. The mean food portion fed to a single larva on each feeding occasion contained 166 shrimps (SE: 5, n=6).

Effects of hatching date, photoperiod and source site on life history (development time, growth rate, and mass at emergence) were evaluated by performing univariate analysis of variance (ANOVAs) in PROC GLM in SAS 8.02 (SAS Institute 2000). We included sex in the analyses but as differences in responses between sexes were not relevant to our hypotheses, we only explicitly report effects of our focal variables (hatching date, photoperiod and source site) and eventual interactions with sex. We initially started with a full factorial model and proceeded with stepwise simplification of the model by sequentially removing the highest-factor term that was not statistically significant (Verbeke and Molenberghs 1997).

Reciprocal transplant experiment

A reciprocal transplant experiment was conducted at the same two ponds, giving four combinations of source site and transplant site. For spatial combination, we tested larvae of both hatching dates. This gave a randomised full factorial 2×2×2 design with two levels of hatching date (date 1/date 2), source site (TP/PP) and transplant site (TP/PP).

On each hatching date, 120 larvae from both source sites were transported to the laboratory to give them a similar transport treatment. The same day, 60 randomly picked larvae from each source site were returned to their native pond and randomly assigned to 2 field enclosures (30 per enclosure). Simultaneously, 60 other larvae of each source site were transported to their non-native pond and likewise randomly assigned to 2 field enclosures. In total, 480 larvae were reared in 16 cylindrical enclosures (diameter=25 cm, height=90 cm) made of a frame of coated iron wire (mesh size: 7.5×10 cm) covered with nylon netting (mesh size: 0.3×0.3 mm). They were sealed at the bottom with a plastic dish containing approximately 4 cm of sediment. The eight enclosures at each transplant site were linearly arranged and extended 30 cm out of the water. The tops were covered with transparent bee-netting (mesh size: 2×7 mm) to avoid predators entering the enclosures and to collect emerged damselflies. To provide structure within the enclosures, we added four strips of green netting (6×90 cm, mesh size: 2×2 mm) that were attached with one side 30 cm below the top. Four enclosures per pond were placed on 15 April (for date 1) and on 30 April (for date 2) so that prey could colonise the enclosures for 1 week before the addition of the damselfly larvae. Growth rates in such enclosures are similar to those obtained in natural field populations for coenagrionid damselfly larvae (McPeek 1998).

When larvae were 47 days old (7 and 22 June for dates 1 and 2, respectively), the enclosures were removed from the ponds and carefully transferred to cylindrical containers filled to a height of 20 cm with pond water. The containers were transported to the laboratory where the content of the enclosures was sieved. Surviving damselfly larvae were counted. To allow larger prey to colonise the cages, the nylon netting of the enclosures was replaced by one with mesh size 1×1 mm. The enclosures with the surviving larvae were placed back in their respective transplant sites. Starting 1 week later, the enclosures were checked every 2nd day for emerging adults.

We first analysed the effects of hatching date, source site and transplant site on the number of larvae that emerged from each enclosure with an ANOVA in PROC GLM in SAS 8.02 (SAS Institute 2000). The effects of hatching date, source site and transplant site on the life-history variables growth rate, development time and mass at emergence were analysed with separate mixed-model analyses of variance using PROC MIXED in SAS 8.02 (SAS Institute 2000). As for the common garden experiment, we included sex in the analyses but only explicitly report effects of our focal variables (hatching date, source and transplant site) and eventual interactions with sex. Enclosure, nested in hatching date×source site×transplant site, was included in the model as a random variable. Because densities may affect life-history variables and may change differentially among treatments during the experiment, we initially also included the number of surviving larvae at day 47 and at emergence as covariates in the model. These were, however, never significant and did not affect the significance of the treatment effects and were dropped from the model. We initially started with a full factorial model and proceeded with stepwise simplification of the model by sequentially removing the highest-factor term that was not statistically significant (Verbeke and Molenberghs 1997). Correct degrees of freedom were obtained with the Satterthwaite option (Verbeke and Molenberghs 1997).

Results

Common garden experiment

Larvae from eggs that hatched late (date 2) had shorter development times than larvae from eggs that hatched early (date 1) (Table 1). This was more pronounced for larvae reared at the photoperiod indicating an early time

Table 1 Summary of ANOVAs on the effects of hatching date (date 1, date 2), photoperiod (early, late), source site (temporary pond, permanent pond), and sex on larval development time, growth rate and mass at emergence in the common garden experiment

	Development time			Growth rate			Mass at emergence		
R^2 final model	0.39			0.46			0.51		
Source	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Hatching date (HD)	1,141	44.18	**<0.001**	1,143	127.32	**<0.001**	1,139	107.22	**<0.001**
Photoperiod (PH)	1,141	32.54	**<0.001**	1,143	0.02	0.899	1,139	31.25	**<0.001**
Source site (SS)	1,141	0.77	0.380	1,143	0.68	0.410	1,139	0.31	0.576
Sex (S)	1,141	0.37	0.546	1,143	4.43	**0.037**	1,139	19.61	**<0.001**
HD×PH	1,141	4.28	**0.040**	1,138	0.16	0.686[a]	1,136	0.23	0.635[a]
HD×SS	1,140	0.01	0.931[a]	1,140	0.87	0.352[a]	1,138	1.14	0.288[a]
HD×S	1,139	0.18	0.670[a]	1,137	0.08	0.784[a]	1,137	0.25	0.618[a]
PH×SS	1,141	6.94	**0.009**	1,142	2.15	0.145[a]	1,139	0.57	0.450
PH×S	1,141	0.54	0.465	1,141	1.07	0.303[a]	1,139	3.58	0.061
SS×S	1,141	0.049	0.826	1,139	0.22	0.637[a]	1,139	0.02	0.901
HD×PH×SS	1,138	0.06	0.808	1,135	0.43	0.513[a]	1,134	1.21	0.273[a]
HD×PH×S	1,136	0.01	0.911[a]	1,136	1.26	0.263[a]	1,135	1.32	0.252[a]
HD×SS×S	1,137	0.01	0.910[a]	1,134	0.25	0.621[a]	1,133	0.37	0.543[a]
PH×SS×S	1,141	4.62	**0.033**	1,133	0.20	0.659[a]	1,139	4.95	**0.028**
HD×PH×SS×S	1,135	0.90	0.343[a]	1,132	1.18	0.280[a]	1,132	0.14	0.713[a]

[a]Factors were removed in a backward selection procedure. Note that this causes changes in the degrees of freedom

point in the growth season, giving an interaction between hatching date and photoperiod (Fig. 1a,b). Overall, larvae from both source sites had a shorter development time when reared at a photoperiod indicating a late time point in the growth season than when reared at a photoperiod indicating an early time point in the growth season. In females, however, the photoperiod-induced reduction in development time was only true for larvae from TP (Fig. 1b), while in males this reduction was similar for larvae from both source sites (Fig. 1a) This yields a significant three-way interaction between photoperiod, source site and sex (Table 1).

Growth rate was higher in larvae from date 2 than in larvae from date 1 (Table 1; Fig. 1c,d). Neither photoperiod nor source site affected growth rate.

Mass at emergence was higher in larvae from date 2 than in larvae from date 1 (Table 1; Fig. 1e,f). Overall, mass at emergence was lower in larvae reared at the photoperiod indicating a late time point in the growth season than when reared at a photoperiod indicating an early time point in the growth season. In males, however, the photoperiod-induced reduction in mass was only true for larvae from PP (Fig. 1e), while in females this reduction was significant for larvae from both source sites

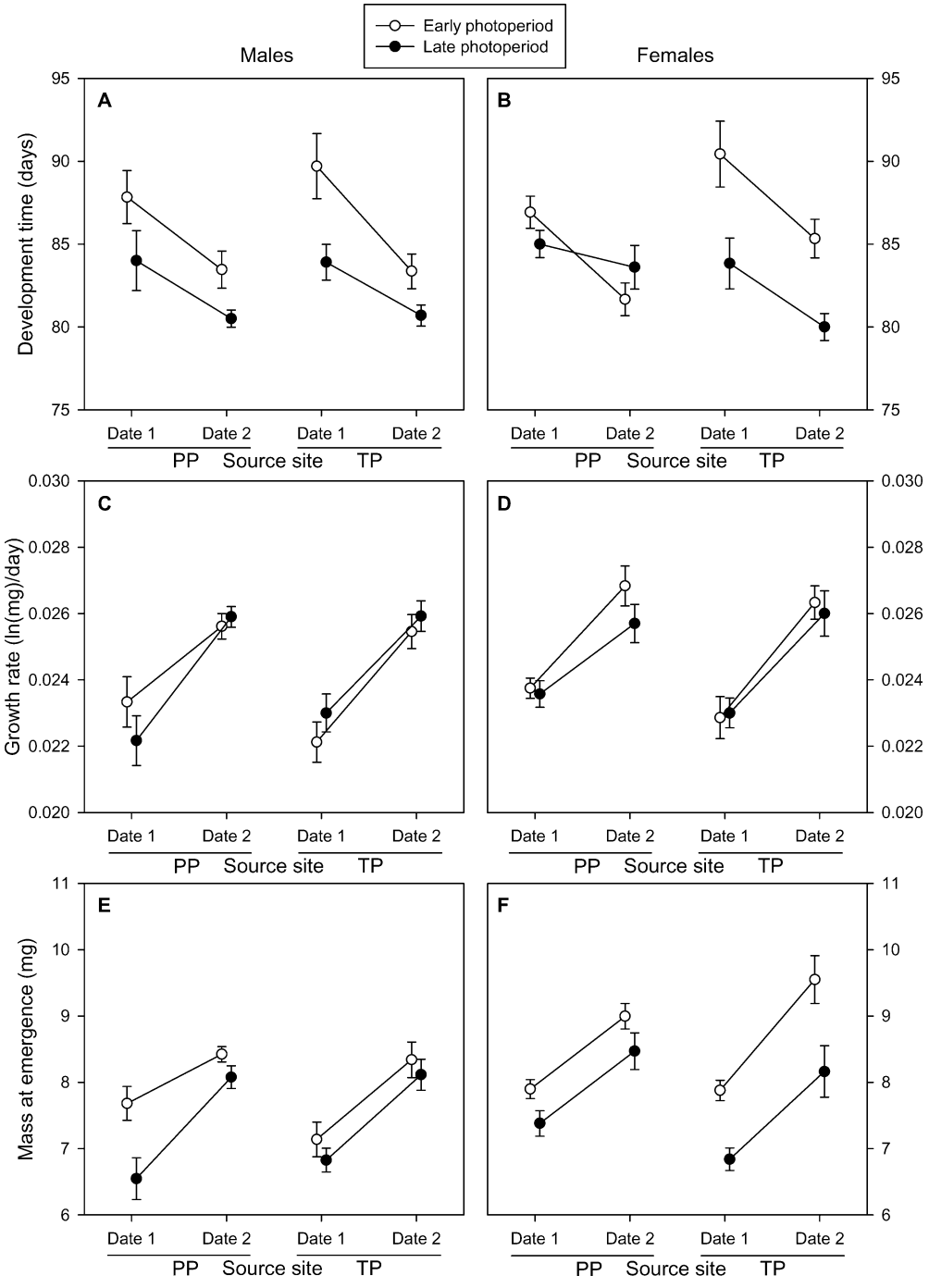

Fig. 1a–f The effect of hatching date, photoperiod, source site and sex on life-history variables in *Lestes viridis*: **a,b** development time; **c,d** growth rate; **e,f** mass at emergence. Means are given ±1 SE. Early (late) photoperiod refers to a photoperiod indicating an early (late) time point in the growth season. Sample sizes for group means range between 6 and 14

(Fig. 1f). This yields a significant three-way interaction between photoperiod, source site and sex (Table 1).

Reciprocal transplant experiment

The percentage of individuals that emerged from the enclosures ranged from 23 to 77%. More adults emerged from enclosures with larvae from eggs hatched at date 1 (51.67±6.01%) than from enclosures with larvae from eggs hatched at date 2 (36.67±5.12%; ANOVA, $F_{1,8}$=8.76, P=0.018). More adults emerged from enclosures at the transplant site TP (56.25±5.36%) than from enclosures at the transplant site PP (32.08±2.81%; $F_{1,8}$=22.73, P=0.0014).

There was no effect of source site on development time (Table 2). Overall, larvae had a shorter development time in transplant site TP than in PP (Fig. 2a,b). In TP, larvae from date 2 in general had a shorter development time than larvae from date 1 (Fig. 2a,b). In PP, however, males did not show such difference in development time between both hatching dates (Fig. 2a), and females even had a longer development time when hatched later in the season (Fig. 2b). This resulted in a significant three-way interaction between hatching date, transplant site and sex (Table 2).

Growth rate was, overall, higher in the transplant site TP than in PP (Table 2; Fig. 2c,d). In TP, larvae from date 2 had a higher growth rate than larvae from date 1 (Fig. 2c, d), but in PP there were no differences in growth rate between hatching dates (Fig. 2c,d). This resulted in a significant two-way interaction between hatching date and transplant site (Table 2). Source site and transplant site interacted in shaping growth rate, with the general pattern being that, in a given transplant site, larvae had a higher growth rate when this was also their source site (Table 2; Fig. 2c,d). More specifically, in TP, larvae from TP had a higher growth rate than those from PP, and in PP, however, larvae from PP had a higher growth rate than those from TP.

Overall, mass at emergence was higher in transplant site TP than in PP (Table 2; Fig. 2e,f). In TP, larvae from date 2 had a higher mass at emergence than larvae from date 1 (Fig. 2e,f), but in PP there were no differences in mass at emergence between hatching dates (Fig. 2e,f). This resulted in a significant two-way interaction between hatching date and transplant site (Table 2). As for growth rate, source site and transplant site interacted in shaping mass at emergence, with the general pattern being that in a given transplant site, larvae had a higher mass at emergence when this was also their source site (Table 2; Fig. 2e,f). More specifically, in TP, larvae from TP had a higher mass than those from PP, and in PP, however, larvae from PP had a higher mass than those from TP.

Discussion

As predicted by optimality models (e.g. Rowe and Ludwig 1991; Abrams et al. 1996) and consistent with previous studies on *Lestes* damselflies (Johansson and Rowe 1999; Johansson et al. 2001) including the study species (De Block and Stoks 2003), larvae reared at a photoperiod indicating a late time point in the growth season had shorter development times than larvae reared at a photoperiod indicating an early time point in the growth season. In contrast with our prediction, the shorter development time in larvae reared at the photoperiod indicating a late time point was more pronounced for early-hatched larvae. At the photoperiod indicating an early time point, development time was already much shorter in the late-hatched larvae than in the early-hatched larvae (Fig. 1a,b). Therefore, at the photoperiod indicating a late time point, late-hatched larvae probably could not decrease development time to the same extent as did early-hatched larvae under the photoperiod-induced time stress because they

Table 2 Summary of mixed-model ANOVAs on the effects of hatching date (date 1, date 2), source site (temporary pond, permanent pond), transplant site (temporary pond, permanent pond) and sex on larval development time, growth rate and mass at emergence in the reciprocal transplant experiment. Note that enclosure, nested in hatching date×source site×-transplant site, was included in the model as a random variable, but not shown in this table

[a]Factors were removed in a backward selection procedure. Note that this causes changes in the degrees of freedom

[b]Degrees of freedom were obtained after Satterthwaite correction

Source	Development time			Growth rate			Mass at emergence		
	df[b]	*F*	*P*	*df*[b]	*F*	*P*	*df*[b]	*F*	*P*
Hatching date (HD)	1,16.9	0.01	0.938	1,11.3	6.37	**0.028**	1,13.3	5.82	**0.031**
Source site (SS)	1,11.1	2.60	0.135	1,9.28	0.47	0.510	1,10.9	0.10	0.754
Transplant site (TS)	1,16.9	119.41	<**0.001**	1,10.7	283.26	<**0.001**	1,12.1	86.49	<**0.001**
Sex (S)	1,193	9.40	**0.0025**	1,178	30.46	<**0.001**	1,176	25.05	<**0.001**
HD×SS	1,9.35	1.22	0.297[a]	1,7.5	0.55	0.480[a]	1,8.4	0.89	0.371[a]
HD×TS	1,16.9	11.70	**0.0033**	1,10.9	35.43	<**0.001**	1,13.3	7.42	**0.017**
HD×S	1,191	1.53	0.218	1,175	0.55	0.459[a]	1,175	4.11	**0.044**
SS×TS	1,10.6	1.11	0.315[a]	1,9.08	6.15	**0.035**	1,10.9	5.11	**0.045**
SS×S	1,191	0.97	0.327[a]	1,175	1.85	0.176[a]	1,174	0.05	0.823[a]
TS×S	1,191	5.46	**0.021**	1,173	0.00	0.958[a]	1,176	3.91	0.050
HD×SS×TS	1,11.6	0.83	0.382[a]	1,10.4	0.03	0.867[a]	1,10.6	0.01	0.917[a]
HD×SS×S	1,188	0.74	0.391[a]	1,171	0.11	0.740[a]	1,171	0.32	0.569[a]
HD×TS×S	1,191	4.82	**0.029**	1,172	1.67	0.198[a]	1,172	1.14	0.288[a]
SS×TS×S	1,180	1.82	0.179[a]	1,158	2.72	0.101[a]	1,164	1.69	0.195[a]
HD×SS×TS×S	1,183	1.03	0.311[a]	1,166	00.01	0.913[a]	1,167	0.13	0.721[a]

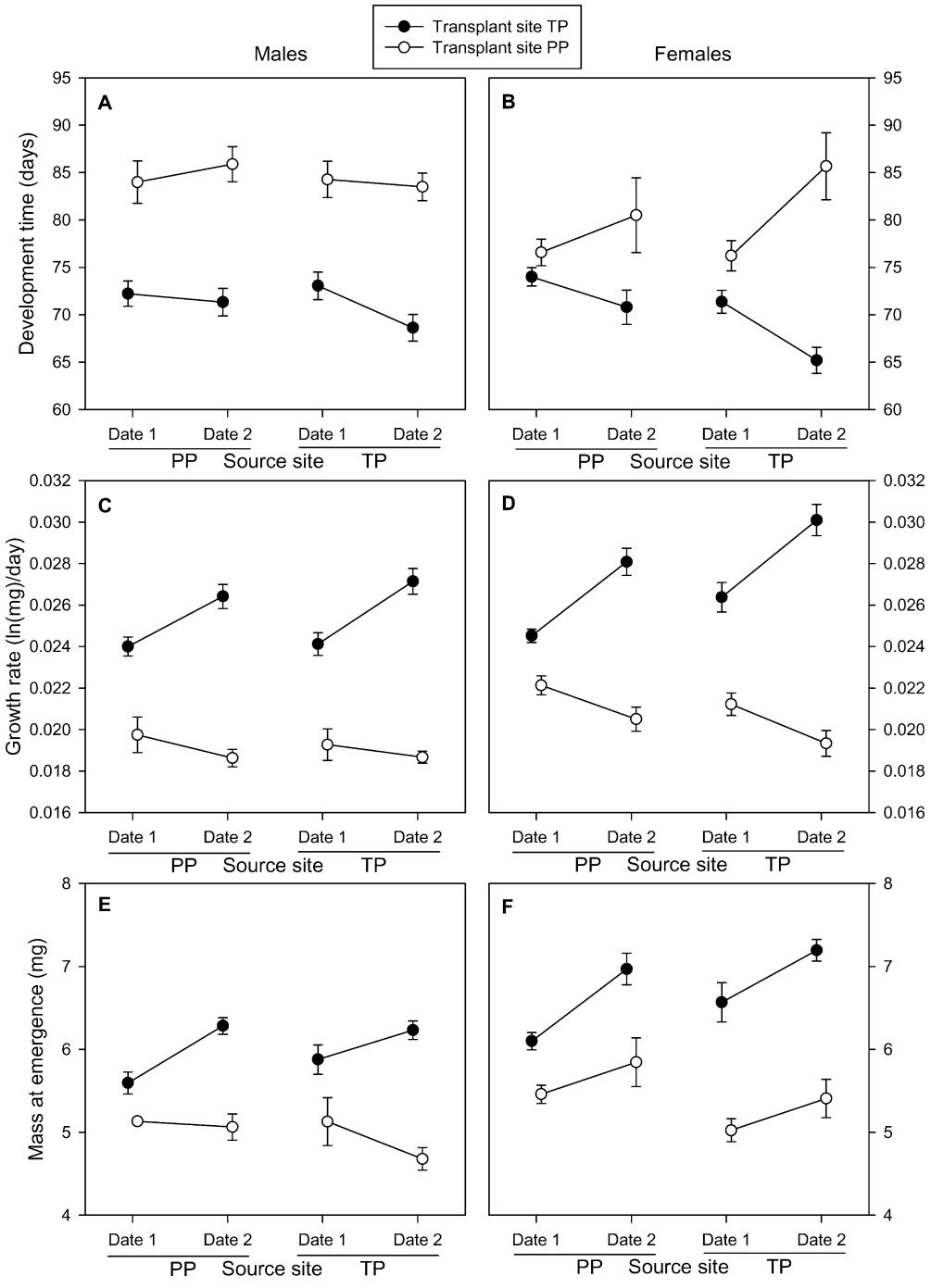

Fig. 2a–f The effect of hatching date, source site, transplant site and sex on life-history variables in *Lestes viridis*: **a,b** development time; **c,d** growth rate; **e,f** mass at emergence. Means are given ±1 SE. Sample sizes for group means range between 12 and 31

reached their physiological maximum under the given rearing conditions. Growth rate was not affected by photoperiod, as we also found in another study on the damselfly *L. viridis* (De Block and Stoks 2003). As a result of the decrease in development time, while growth rate did not change at the photoperiod indicating a late time point in the growth season, mass at emergence was lower under this condition.

We found, both in the laboratory and in the field, the expected within-population variation in larval life history with regard to time constraints imposed by hatching date. In general, larvae that hatched late in the season had a shorter development time and faster growth rate than larvae that hatched early (Figs. 1a–d, 2a–d). In the common garden experiment, this was true for all eight possible combinations of photoperiod, source site and sex. In the reciprocal transplant experiment this was, however, only true for larvae reared in the transplant site TP. Probably, PP provided a bad growth environment for the larvae, and so late-hatched larvae were not able to reduce development time and increase growth rate in this environment. This is supported by the fact that mass at emergence in PP was the lowest one that we observed in

both larval rearing experiments. Moreover, the proportion of surviving larvae was about 2 times lower than in TP.

In accordance with the two other studies so far (Carrière et al. 1996; Altwegg 2002), the shorter development time in late-hatched larvae is in agreement with the fact that larvae that hatch later in the season experience a higher natural time constraint. By also increasing growth rate, *L. viridis* larvae seemed to be able to compensate for the shorter development time. In fact they overcompensated, as mass at emergence was, if anything, higher for larvae that hatched at date 2 than for larvae that hatched at date 1. Although at first sight surprising, similar overcompensation in growth has been shown in animals after a starvation period, and a recent theoretical model showed it is to be expected when animals increase food intake and increase their allocation of assimilated food into body mass (Gurney et al. 2003). Both premises have been shown to occur in another *Lestes* species under time stress (R. Stoks, M. De Block, F. Van de Meutter, F. Johansson, in review). This reduced development time and faster growth rate of late-hatched larvae is unlikely to be a plastic response to photoperiod. For example, in the common garden experiment, photoperiod did not affect growth rate while late-hatched larvae, irrespective of photoperiod, had much higher growth rates than early-hatched larvae (Fig. 1c,d) and this despite a smaller difference in day lengths between both hatching dates (ca. 3 weeks) than between both photoperiod regimes (ca. 6 weeks). This suggests that these life-history differences between early- and late-hatched larvae may have a genetic basis or are maternally determined.

In the reciprocal transplant experiment, there was a strong transplant-site effect on all three life-history variables. Development time was shorter and growth rate was higher in the temporary than in the permanent pond, which is consistent with an adaptive scenario between both pond types (Wellborn et al. 1996). This differentiation between transplant sites was, however, determined by local environmental conditions and not genetically underpinned. Apparently, conditions for development were better in the temporary pond than in the permanent pond (see above). Larvae had a slightly higher growth rate and mass at emergence when they were reared in their pond of origin (Fig. 2c–f), which may suggest a weak adaptation to the local conditions. Note, however, that this effect was only marginally significant.

The within-population variation in larval life history with regard to time constraints imposed by hatching date was strikingly similar in both populations, despite their differences in the period available for growth. This lack of population differentiation to time constraints is somewhat surprising given the higher fitness costs of not adequately reacting to such constraints in a temporary pond (death by desiccation). Apparently, the generalist strategy of *L. viridis,* with high plasticity in development time to photoperiod coupled with a faster growth rate and shorter development times of late-hatched larvae, is enough to maintain populations in at least some temporary ponds. Furthermore, as suggested by the strong transplant-site effect in the reciprocal transplant experiment, *L. viridis* may only occur successfully in temporary ponds where local conditions are favourable for rapid development. This absence of pronounced population differentiation may be linked with the frequent population extinctions due to pond drying and gene flow from permanent ponds toward the temporary ponds, which may act as sinks (M. De Block, K. Jordaens, S. Geenen, R. Stoks, unpublished work).

Taken together, the striking similarity of the effects of hatching date on life history across both study populations in the field and in the laboratory suggests these effects are strong and general within *L. viridis*. Given their adaptive value and the ubiquity of variation in hatching date within populations, they may be widespread in other taxa. Late-hatched *L. viridis* larvae apparently overcompensated for the shorter period available for growth by emerging at a higher mass. This may explain the unexpected finding that mass at emergence increased with emergence date in four monitored natural populations of *L. viridis* (M. De Block, unpublished data). In general, size decreases with emergence date in insects, and this has been theoretically explained by differentially trading-off further mass increase during the larval stage against development time in function of the progress of the emergence season (Ludwig and Rowe 1990; Rowe and Ludwig 1991). Obviously, if present, fixed higher growth rates in late-hatched larvae may cause mismatch with predictions of current optimality models that do not include differences between early- and late-hatched individuals (Ludwig and Rowe 1990; Rowe and Ludwig 1991). As also shown, in both study populations, life-history plasticity to photoperiod differed between early- and late-hatched larvae. This has been ignored so far in empirical and theoretical work on life-history plasticity, and evaluating its occurrence and exploring its genetic underpinnings may increase further realism to life- history theory.

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