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ORIGINAL ARTICLE

North vs. South: Contrasting patterns in the phenotypic plasticity of the firebug *Pyrrhocoris apterus* (Hemiptera: Pyrrhocoridae) at the latitudinal extremes of its distribution range*

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Abstract. In widely distributed insects, some life-history traits are conserved across the whole distribution range and are considered species-specific while other such traits differ geographically. This interplay of geographic variation and phenotypic conservatism is poorly understood even in relatively well-studied model species. Furthermore, a careful study may reveal that conventionally stable traits, such as the lower temperature threshold for development and the sum of degree-days, are both geographically variable and environmentally plastic. We studied how photoperiodic conditions and temperature jointly affect immature development, adult body size and wing polymorphism in two populations of the firebug from the opposite latitudinal margins of this species' range. All the three traits rarely clearly differ under short-day and long-day conditions or between north and south. Instead, we find prevalent temperature-by-photoperiod and temperature-by-origin interactions, which emphasize that it is not only the absolute values of these traits but the degree of their temperature-dependence, or thermal plasticity, that varies in time (in response to seasonal changes in day length) and in space (along latitudinal gradients). These results indicate that caution should be exercised when extrapolating any life-history traits in *P. apterus* beyond the season when and the location where these were measured. In particular, the use of a constant lower temperature threshold coupled with a constant sum of degree-days is likely to oversimplify the diversity of current and projected phenological patterns in this species.

INTRODUCTION

Many Eastern European insects are widely encountered from the boreal-forest zone to forest-steppes and even penetrate farther north and south. The vastness of their distribution ranges is at least partially explained by the relatively flat terrain in this area, which, together with a moderate Atlantic influence, has resulted in a gentle climatic gradient that spans a vast stretch of land from the Mediterranean to Fennoscandia. These widespread insect species have long been used as models for studying local adaptation and continuous latitudinal clines (Maslennikova & Mustafaeva, 1971; Vinogradova, 1975; Druzhelyubova, 1976; Imasheva et al., 1994; Elmes et al., 1999). Even after decades of dedicated research, adaptive differences observed across geographic space remain a recurrent theme in ecology because these differences ultimately shed light on the selective pressures that have acted over the evolutionary time.

One such common European insect is the firebug *Pyrrhocoris apterus* (Linnaeus, 1758). This is a Palaearctic member of the predominantly tropical heteropteran family Pyrrhocoridae. The distribution range of this species encompasses much of Europe (except the northernmost regions), the North-African coast of the Mediterranean Sea, and parts of Asia eastward to Mongolia and India (Puchkov, 1974). There are several instances of the introduction of the firebug in North America and it is now locally established on that continent (Oviedo Rojas & Jackson, 2018). Also, since the first sporadic occurrences in 2018, *P. apterus* has been rapidly spreading in south eastern Australia (Mata et al., 2021).

Detailed accounts of the biology and ecology of *P. apterus* can be found in Puchkov (1974) and Socha (1993). In summary, this is a flightless insect of forests, parks, fallows, hillslopes, and roadsides. As typical of pyrrhocorids, nymphs and adults of *P. apterus* feed primarily on the ripe seeds of Malvales but they will also consume other seeds, plant sap, and dead animal matter. Polyphagy is thought to have contributed to the firebug's wide occurrence and invasive potential (Socha, 1993). Adults overwinter in leaf

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litter, under bark, and in crevices of buildings. Copulation and oviposition begin early in spring. Nymphs pass through five instars. During the latter half of their nymphal life, firebugs become sensitive to photoperiodic cues that control reproductive activity in the adult (Hodek, 1971; Volkovich & Goryshin, 1979). Such sensitivity is also retained in the adult firebug (Hodkova, 2015). Short-day conditions induce reproductive arrest, or diapause, in the adult stage whereas long-day conditions promote oviposition (Hodek, 1968, 1971; Volkovich & Goryshin, 1979; Saunders, 1983). The critical daylength for diapause induction increases northward (Saunders, 1983; Socha et al., 2001), which is typical of temperate insects in the Northern Hemisphere and ensures a timely onset of dormancy before winter (Danilevskii, 1965). This qualitative photoperiodic response depends on the thermal conditions such that chronic or periodic exposure to low temperatures increases the critical photoperiod and, effectively, bolsters the tendency to diapause (Numata et al., 1993). Reproductive arrest in *P. apterus* is thus facultative and the species is potentially multivoltine (Socha, 1993). In the central parts of the firebug's range, such as the South Bohemian Region of the Czech Republic (Socha & Šula, 1992; Koštál & Šimek, 2000) and Belgorod and Ryazan regions of Russia (Saulich & Musolin, 1996; Orlova et al., 2009), females from early-season clutches commence reproduction in midsummer and so at least a partial second generation is possible, especially in warmer years and at better-insolated sites. The current rise in global temperatures will likely increase the opportunity for bivoltinism in *P. apterus* populations (Honek et al., 2020). We are not aware of any formal phenological studies on the firebug in the south of its range but extensive GBIF observations of this species (GBIF Secretariat, 2021) show that, e.g., in Israel, nymphs have been photographed in the field in every month from April through to December, indicating a multivoltine cycle with winter diapause.

Despite the species name, the degree of wing development in *P. apterus* is variable and depends on both genetic and environmental factors (Socha, 1993). The two most common morphs are macropters with both pairs of wings fully developed, albeit non-functional (Socha & Zemek, 2000), and brachypters with reduced forewing membranes and rudimentary hindwings (Socha, 1993). In the firebug populations from the Czech Republic, the highest proportion of the macropterous morph, up to 11–14%, can be obtained by rearing the nymphs under long-day conditions (> 16 h of light per day, or > 16L : 8D) at moderately high temperatures (24–27°C), as opposed to short-day photoperiods and cooler temperatures, which promote brachyptery (Honěk, 1995). From an eco-physiological standpoint, these macropters are characterized by slightly longer immature development times at 24–26°C, larger body size, enhanced walking activity, decreased male mating propensity, and delayed oviposition as compared with their brachypterous counterparts (Honěk, 1985, 1987, 1995; Socha & Zemek, 2003; Socha, 2004). The incidence of macroptery increases southward while the daylength at which this incidence is highest decreases: for an Israeli population, up to 35% of firebugs reared under the short-day photoperiod of 12L : 12D are macropterous (Socha & Šula, 1996; Socha, 2001). The effect of thermal conditions on wing polymorphism in a southern population of *P. apterus* remains to be tested as the cited experiments were only carried out at 26°C.

While the qualitative photoperiodic responses in *P. apterus* (i.e., induction and termination of diapause and percentage of macropters) are studied in great detail, much less attention has been paid to the parallel quantitative responses, namely, the effects of photoperiod on immature developmental rate and adult body mass at eclosion (but see Honěk, 1983, 1987; Saunders, 1983). In a previous study (Lopatina et al., 2007), the simultaneous effects of temperature and photoperiod on immature development in four *P. apterus* populations from Central Russia, i.e., from the interior of its geographic distribution, are reported. This study revealed a strong photoperiod-by-temperature interaction whereby short-day conditions accelerated nymphal development at low temperatures and long-day conditions at high temperatures.

This communication presents the results of eco-physiological laboratory experiments with two more populations of the firebug that were sampled at the opposite latitudinal ends of this species' range three thousand kilometres from each other. We measured immature development time, adult body mass at emergence and the frequency of the wing-morphs under various combinations of constant temperature and constant photoperiod. This multifactorial design allowed the comparison not only of the mean trait values between the two populations but also the plasticity of these traits in response to temperature and photoperiod.

MATERIALS AND METHODS

Sources of material and maintenance of parental individuals

The experiments were carried out on two geographically distant populations of *P. apterus*, one from the village of Podlipye (58°27´N, 27°50´E, Pskov Oblast, the extreme northwest of the European part of Russia) and the other from the city of Tel Aviv (32°4´N, 34°50´E, Israel). The former locality has a temperate humid continental, or hemi boreal, climate with warm summers and freezing cold winters. The latter locality has a hot-summer Mediterranean climate. These two populations are hereinafter referred to as northern and southern, respectively.

Adults of the northern population were collected by hand from leaf litter under linden trees on May 13, transported to St. Petersburg the same day and the experiment started immediately. Groups of bugs were maintained in the laboratory in half-litre plastic containers with a paper sheet on the bottom and pieces of accordion-folded paper as shelter. The bugs were supplied with food (fruit of linden *Tilia platyphyllos* Scop., which were split to facilitate access to the seed) and water (Eppendorf tubes filled with water and plugged with cotton wool), which were replenished as needed. The containers were kept in an environmental chamber at a temperature of 25°C under a 20L : 4D photoperiod.

The southern population resumes activity earlier in the season and, accordingly, the experiment was also carried out earlier in order to ensure that the parental individuals of both populations were in more or less equivalent physiological states. Adults and nymphs were collected in urban parks in early November, transported by air to St. Petersburg and kept in the same manner as the northern population except that the environmental chamber was set to 25°C and a 12L : 12D photoperiod and linden seed was supplemented with dry seed of hollyhock *Alcea rosea* L. The remaining nymphs were allowed to complete development and accumulate reserves for overwintering. Then the rearing temperature and daylength were gradually decreased over several weeks and the bugs were eventually transferred to a cool dark room with a temperature of 4°C where they were stored until late January when the experiment began. Overwintered adults were kept in an environmental chamber in which the temperature was gradually increased to 22°C and the daily light-dark cycle, to 16L : 8D.

At the start of the experiment, firebugs were divided into male-female pairs. Each pair was confined in a 9 cm Petri dish with a paper disc on the bottom and provided with food and water. In total, there were 28 northern and 42 southern pairs. Eggs laid by females of both populations were collected daily and transferred to small plastic Petri dishes (40 mm in diameter) which were kept in larger dishes (100 mm in diameter) on a layer of damp cotton wool to prevent desiccation. Thus, the experiment in both cases used the first laboratory generation obtained from overwintered field-collected parents. Eggs were laid by 25 of 28 northern and 24 of 42 southern females. Lower oviposition rates in the latter population were presumably due to incomplete reactivation from diapause.

Experimental procedures

Clutches of eggs (whole or divided into two, depending on size) were randomized among several combinations of constant temperature and photoperiod, with one environmental chamber per treatment. With the northern population, ten such combinations were used, comprising five temperatures (20, 22, 24, 26 and 28°C) and two photoperiods (short-day 12L : 12D and long-day 22L : 2D). With the southern population, the same five temperatures were used in combination with one of three constant photoperiods (short-day 10L : 14D, long-day 16L : 8D and extremely long-day 22L : 2D). Hatching was recorded daily. As hatchlings emerged synchronously within each clutch, all eggs that remained after mass emergence were considered non-viable. The initial median number of egg batches per treatment was 11.5 (minimum–maximum: 8–17) for the northern and 8 (5–17) for the southern populations, with fewer clutches incubated at higher temperatures where survival to the adult stage was expected to be better. None of the females laid sufficient eggs for its progeny to be included in all of the temperature-photoperiod combinations; the median number of treatments per parental female was 5 (minimum–maximum: 2–8 for the northern and 1–14 for the southern population). However, the distribution of clutches across the treatments was random and every treatment contained a diverse subsample of either population. The incompleteness of our experimental design with respect to parentage was later taken into consideration in the statistical analyses.

Newly hatched nymphs were transferred to 90 mm Petri dishes on the day of hatching and to 250 ml containers after moulting to the third instar. Nymphs were supplied with food and water in the same manner as the adults. Newly emerged adults were recorded daily and weighed on a digital analytical balance (Gosmetr VL-210 with 0.1 mg precision in the earlier experiment on the southern population and a Discovery DV215CD with 0.01 mg precision in the later experiment on the northern population). Wing morph was determined by examining the posterior abdominal tergites, which were exposed in brachypterous individuals and hidden under velvety-black forewing membranes in macropterous ones. Sexes were distinguished by the shape of the last abdominal sternite.

Temperature in the environmental chambers was maintained within ± 0.4°C of the desired level via a software-controlled balance of heating and cooling (RLDataView 1.03) and was automatically recorded every 10 s. Average rearing temperatures

Table 1. Mean (± SD) duration (days) of nymphal development recorded for the northern population of *P. apterus* reared at five constant temperatures and under two photoperiods. Values in brackets refer to the number of macropterous ('macro') and brachypterous ('brachy') adults reared.

Daylength (h)	Morph	Sex	Temperature (°C)				
			20.0	21.9	24.0	25.9	27.8
12	macro	♀	—	—	—	30.7 ± 0.72 (2)	26.2 ± 0.88 (5)
		♂	—	—	—	—	27.7 ± 0.62 (6)
		♀+♂	—	—	—	30.7 ± 0.72 (2)	27.0 ± 1.09 (11)
	brachy	♀	54.7 ± 2.81 (52)	41.8 ± 1.78 (71)	34.0 ± 2.43 (81)	28.8 ± 2.84 (70)	24.9 ± 2.93 (62)
		♂	55.8 ± 1.61 (28)	43.3 ± 1.77 (58)	34.2 ± 1.94 (88)	28.9 ± 2.60 (74)	25.6 ± 2.55 (44)
		♀+♂	55.1 ± 2.50 (80)	42.5 ± 1.93 (129)	34.1 ± 2.18 (169)	28.9 ± 2.71 (144)	25.2 ± 2.78 (106)
			19.9	22.0	23.7	25.9	27.8
22	macro	♀	—	54.4 ± 7.70 (2)	39.0 ± 0.99 (3)	30.0 ± 2.22 (7)	25.3 ± 1.43 (5)
		♂	—	57.5 ± 4.92 (2)	42.0 (1)	30.1 ± 0.80 (4)	25.5 ± 1.03 (8)
		♀+♂	—	56.0 ± 7.17 (4)	39.8 ± 2.23 (4)	30.0 ± 1.38 (11)	25.4 ± 0.82 (13)
	brachy	♀	75.4 ± 5.81 (51)	54.3 ± 5.62 (82)	38.2 ± 4.24 (64)	27.0 ± 2.08 (58)	21.8 ± 1.20 (70)
		♂	76.7 ± 6.78 (63)	55.6 ± 5.04 (55)	40.4 ± 4.23 (52)	28.5 ± 2.98 (62)	22.8 ± 1.98 (60)
		♀+♂	76.1 ± 6.38 (114)	54.8 ± 5.41 (137)	39.2 ± 4.30 (116)	27.8 ± 2.67 (120)	22.3 ± 1.67 (130)

slightly deviated from the set values and are given in Tables 1 and 2. The chosen long-day photoperiods of 22L : 2D and 16L : 8D approximately corresponded to midsummer daylength, including civil twilight, at the collection sites. Although the southern population never experiences more than 16 h of light per day, the experimental design with this population did include the 22L : 2D photoperiod so that the southern reaction norm could be directly compared with its exact northern counterpart. The short-day photoperiod for the southern population had a shorter photo phase than that for the northern one because the former was expected to experience a broader range of daylengths in nature owing to a mild, frost-free winter in its Mediterranean habitat.

Statistical analyses

Statistical analyses were done using R version 4.2.1 with RStudio 2022.07.1+554 (RStudio Team, 2022; R Core Team, 2022). The influence of temperature and photoperiod on the characters that could be expressed as binary variables (survival rate, sex ratio and wing morph ratio) was tested with lme4 package (Bates et al., 2015) using generalized linear mixed-effects models with a logit link and binomial error structure. Maternal identity was included in the models as a random intercept term. The two wing-morphs were compared in terms of development time and body mass using one-way ANOVA followed by Tukey's HSD pairwise comparisons test.

A full analysis of the effects of temperature and photoperiod on developmental rate and body mass was only done for brachypterous bugs because these were present in all of the experimental treatments. In this analysis, actual incubation temperature was treated as a continuous predictor and photoperiod as a categorical predictor. The durations (*D*) of the egg and nymphal stages were transformed into rates ($R = 1/D$). The effects of temperature, photoperiod and sex on developmental rate and adult body mass were tested for significance by fitting maximum-likelihood linear models implemented in the R package nlme (Pinheiro et al., 2022) as this package allowed the specification of the variance associated with each temperature level in order to overcome heteroscedasticity. Egg data were analysed using fixed-effects models because nymphs hatched synchronously and thus there was only one developmental rate for the egg stage per group reared. For nymphs, individual developmental rates were available, and so mixed models were fitted to nymphal data. In the mixed models, the random effects term was specified as rearing density nested in maternal identity. Density was expressed as the final, not initial, sample size (number of adults that emerged per group), because most growth took place during the later nymphal instars, whereas most

Table 2. Mean (± SD) duration (days) of nymphal development recorded for the southern population of *P. apterus* at five constant temperatures and under three photoperiods. Values in brackets refer to the number of macropterous ('macro') and brachypterous ('brachy') adults reared.

Daylength (h)	Morph	Sex	Temperature (°C)				
			20.6	22.1	23.7	25.5	28.4
10	macro	♀	—	52.5 ± 2.06 (2)	38.4 ± 1.46 (11)	31.2 ± 1.59 (27)	24.1 ± 0.82 (4)
		♂	—	—	38.1 ± 1.60 (6)	31.5 ± 1.09 (20)	25.0 ± 0.89 (17)
		♀+♂	—	52.5 ± 2.06 (2)	38.3 ± 1.47 (17)	31.3 ± 1.39 (47)	24.8 ± 0.93 (21)
	brachy	♀	72.1 ± 4.86 (16)	50.8 ± 2.63 (35)	39.4 ± 3.65 (11)	31.0 ± 1.87 (8)	22.0 ± 0.84 (14)
		♂	70.1 ± 4.29 (28)	51.3 ± 3.07 (35)	41.5 ± 5.23 (9)	31.7 ± 1.89 (26)	23.2 ± 1.57 (15)
		♀+♂	70.8 ± 4.56 (44)	51.0 ± 2.85 (70)	40.3 ± 4.44 (20)	31.5 ± 1.88 (34)	22.6 ± 1.38 (29)
			20.1	21.8	23.8	26.3	27.8
16	macro	♀	—	58.0 ± 6.57 (3)	39.0 ± 1.14 (3)	—	25.2 ± 1.05 (22)
		♂	—	—	—	—	25.8 ± 1.32 (13)
		♀+♂	—	58.0 ± 6.57 (3)	39.0 ± 1.14 (3)	—	25.5 ± 1.18 (35)
	brachy	♀	68.7 ± 3.62 (24)	49.5 ± 3.71 (16)	35.4 ± 1.31 (48)	27.5 ± 2.04 (13)	22.8 ± 1.69 (11)
		♂	68.2 ± 3.22 (16)	50.6 ± 2.84 (20)	36.3 ± 1.56 (45)	27.3 ± 1.65 (28)	23.8 ± 1.92 (21)
		♀+♂	68.5 ± 3.43 (40)	50.1 ± 3.26 (36)	35.9 ± 1.50 (93)	27.4 ± 1.76 (41)	23.5 ± 1.87 (32)
			20.3	21.8	23.8	25.7	28.2
22	macro	♀	78.4 ± 0.75 (2)	49.5 ± 4.57 (4)	40.6 ± 1.93 (5)	—	—
		♂	74.5 ± 2.07 (5)	49.0 ± 3.83 (12)	40.0 ± 2.83 (2)	—	—
		♀+♂	75.6 ± 2.57 (7)	49.2 ± 3.87 (16)	40.4 ± 1.97 (7)	—	—
	brachy	♀	68.8 ± 3.64 (9)	48.9 ± 2.99 (28)	36.4 ± 2.48 (39)	28.8 ± 1.83 (22)	21.8 ± 1.51 (36)
		♂	69.5 ± 3.60 (13)	49.7 ± 4.06 (31)	36.3 ± 2.87 (30)	29.4 ± 1.67 (22)	22.8 ± 1.58 (57)
		♀+♂	69.2 ± 3.54 (22)	49.3 ± 3.59 (59)	36.3 ± 2.64 (69)	29.1 ± 1.75 (44)	22.4 ± 1.62 (93)

mortality occurred during the earlier instars (pers. obs.). In addition to including rearing density in all models as a random effect, Pearson's correlation coefficients of the analyses of the number of adults reared per group and temperature were computed. Model assumptions of linearity and normality of residuals were verified by visual inspection of residuals plots. The significance of differences was determined with *F*-tests in fixed-effects models and log-likelihood ratio (LLR) chi-squared tests in mixed models. Regardless of Akaike's criterion differences and *p*-values, terms were not removed, except for the factor sex (see below) and the reported statistics refer to full models. However, to visualize the effects of photoperiod and geographic origin on the thermal reaction norms for developmental rate, a separate linear mixed model was fitted for each combination of origin and photoperiod, with temperature as the only fixed effect. Thus, temperature-dependent development was described assuming a linear regression between the rate of development (R) and temperature (T): $R = a + b \times T$. The parameters a and b with their standard errors were taken from the model's output and used to calculate the sum of degree-days (SDD) as $1/b$ and the lower temperature threshold (LTT) as $–a/b$ (Campbell et al., 1974).

RESULTS

Survival rate

The median initial number of eggs per dish was 20 (minimum 4 and maximum 34) and the median final group size, i.e., the number of adults per rearing group, was 11 (minimum 1, maximum 27). Overall, firebugs from the northern population survived better under our experimental conditions than their southern conspecifics (eggs: LLR $\chi^2(1) = 30.2$, $p < 0.0001$; nymphs: LLR $\chi^2(1) = 12.1$, $p = 0.0005$; Fig. 1). Egg hatch in both populations was significantly affected by temperature (northern: LLR $\chi^2(1) = 9.3$, $p = 0.002$; southern: LLR $\chi^2(1) = 33.9$, $p < 0.0001$) but not photoperiod (northern: LLR $\chi^2(1) = 0.6$, $p = 0.4$; southern: LLR $\chi^2(1) = 2.4$, $p = 0.1$). In general, hatchability was better in warm conditions and declined at low temperatures (Fig. 1A). The effect of temperature on nymphal survival mirrored that for eggs (northern: LLR $\chi^2(1) = 156.2$, $p < 0.0001$; southern: LLR $\chi^2(1) = 229.3$, $p < 0.0001$). As a result, the final size of the groups was greater at high temperatures (northern: Pearson's $r = 0.38$, $p = 0.0002$; southern: $r = 0.35$, $p = 0.0009$). There was also a significant effect of photoperiod on nymphal survival (northern: LLR $\chi^2(1) = 10.8$, $p = 0.001$; southern: LLR $\chi^2(1) = 10.5$, $p = 0.001$). Overall, the survival rates of nymphs were lower under short-day conditions, but the difference was small and not consistent across temperatures (Fig. 1B, C).

Sex ratio

The occurrence of males and females did not significantly depend on either temperature (LLR $\chi^2(1) = 1.5$, $p = 0.2$) or photoperiod (LLR $\chi^2(1) = 0.09$, $p = 0.8$), although it did differ significantly between the two populations (LLR $\chi^2(1) = 4.8$, $p = 0.03$). On average across all treatments, the female to male ratio was 1.16 for the northern population (1.20 for macropterous and 1.13 for brachypterous individuals, or short-winged ones) and 0.92 for the southern population (1.11 for macropterous and 0.83 for brachypterous

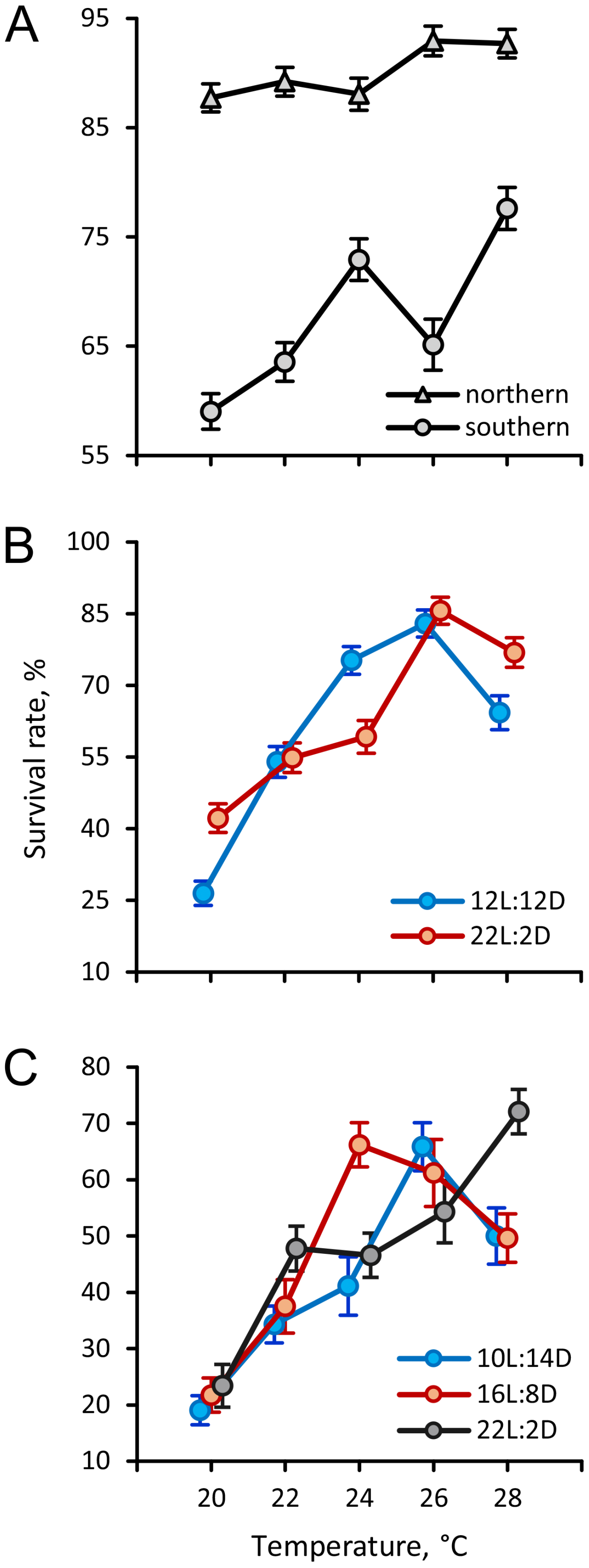

Fig. 1. Survival rates of (A) eggs, (B) nymphs of the northern population and (C) nymphs of the southern population under different rearing conditions. Egg data recorded under different photoperiods are combined. Symbols are slightly set apart along the temperature axis for clarity. Vertical bars denote SE.

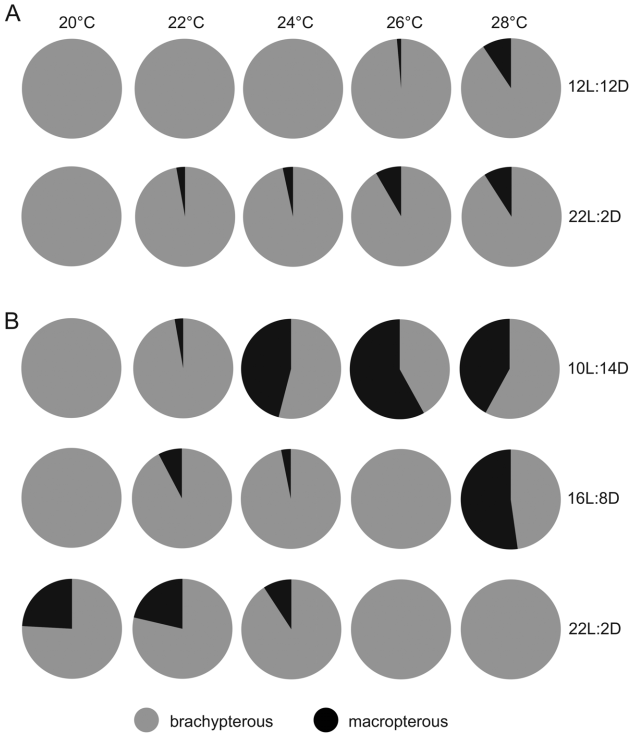

Fig. 2. Proportions of the two wing-morphs recorded for (A) the northern and (B) the southern population of *P. apterus* reared under different combinations of temperature and photoperiod.

individuals). The absolute numbers of males and females are in Tables 1 and 2.

Wing polymorphism

For both populations of *P. apterus*, there was a significant effect of temperature on the occurrence of wing-morphs (northern: LLR $\chi^2(1) = 22.6$, $p < 0.0001$; southern: LLR $\chi^2(1) = 16.0$, $p < 0.0001$). High temperatures favored a higher occurrence of the macropterous morph, especially for the bugs of southern origin (Fig. 2). The effect of photoperiod was temperature- and origin-dependent, as reflected in the significant triple interaction (temperature by photoperiod by population: LLR $\chi^2(1) = 18.0$, $p = 0.01$). Most northern macropterous individuals emerged under long-day conditions (22L : 2D) and most southern macropterous individuals, under short-day conditions (10L : 14D) (Fig. 2). Interestingly, for the southern population reared under the ecologically relevant long-day photoperiod of 16L : 8D, a small proportion of macropterous individuals emerged at low temperatures, which became more prominent under the longest daylength (22L : 2D) (Fig. 2).

The macropterous morph

This morph occurred disproportionately with regard to all of the three factors studied: rearing temperature (more common at high temperatures), photoperiod (more common under either short- or long-day conditions), and geographic origin of the firebugs (more common in those of southern origin). To simplify the analysis and interpretation of the results, the findings for the two morphs are presented separately.

In general, macropterous individuals took somewhat longer to develop than brachypterous individuals (Tables 1 and 2). This difference in development time between the two morphs was significant, e.g., in the northern population at 28°C (ANOVA, effect of morph: $F_{1,256} = 28.3$, $p < 0.0001$; Tukey's HSD test: $p = 0.04$ under the 12L : 12D photoperiod and $p < 0.0001$ under 22L : 2D). An interesting exception was the effect of morph on development time in the southern population under 10L : 14D at 24–28°C. This effect was not significant per se ($F_{1,162} = 0.02$, $p = 0.9$) but the interaction of the factors of morph and temperature was highly significant ($F_{2,162} = 11.4$, $p < 0.0001$) and the Tukey's test showed that, at 28°C, macropterous individuals had a significantly longer developmental time ($p = 0.004$); at 26°C, the development times of the two morphs were not significantly different ($p = 1.0$), while at 24°C, macropterous individuals developed significantly faster than brachypterous individuals ($p = 0.004$).

The macropterous morph also tended to attain a slightly greater body mass than its brachypterous counterpart (Fig. 3). However, this difference was not consistent throughout the experimental conditions and was rarely significant. In the northern population at 28°C, there was no significant difference in body mass between the wing-morphs ($F_{1,256} = 0.8$, $p = 0.4$). In the southern population under the 10L : 14D photoperiod, there was a significant interaction of the factors morph and temperature ($F_{2,162} = 6.9$, $p = 0.002$) and the Tukey's HSD test indicated that macropterous individuals were only significantly heavier than brachypterous ones at 26°C ($p = 0.001$). On average across all the rearing treatments, mean body mass (± SD) of southern macropterous individuals was 39.2 ± 5.48 mg and of southern brachypterous individuals 33.9 ± 5.48 mg.

Unfortunately, it proved difficult to carry out formal comparisons in many cases due to very different sample

Table 3. Parameters of linear thermal reaction norms for the rate of development of the brachypterous morph of *P. apterus* (output of mixed-effects models, fit by maximum likelihood): *a* and *b* – parameters of linear regression; LTT – lower temperature threshold; SDD – sum of degree-days.

Population	Stage and day length	*a* (d^{-1})	*b* (°C^{-1} × d^{-1})	LTT (°C)	SDD (°C × d)
northern	Eggs, 12 h + 22 h	–0.1673 ± 0.00375	0.0120 ± 0.00017	13.9	83.2
	Nymphs, 12 h	–0.0394 ± 0.00142	0.0029 ± 0.00006	13.8	349.6
	Nymphs, 22 h	–0.0699 ± 0.00262	0.0041 ± 0.00011	17.1	245.4
southern	Eggs, 10 h + 16 h	–0.1907 ± 0.00634	0.0125 ± 0.00028	15.3	80.1
	Nymphs, 10 h	–0.0595 ± 0.00216	0.0036 ± 0.00009	16.5	277.3
	Nymphs, 16 h	–0.0621 ± 0.00253	0.0038 ± 0.00011	16.4	263.5
	Nymphs, 22 h	–0.0642 ± 0.00250	0.0039 ± 0.00011	16.4	255.6

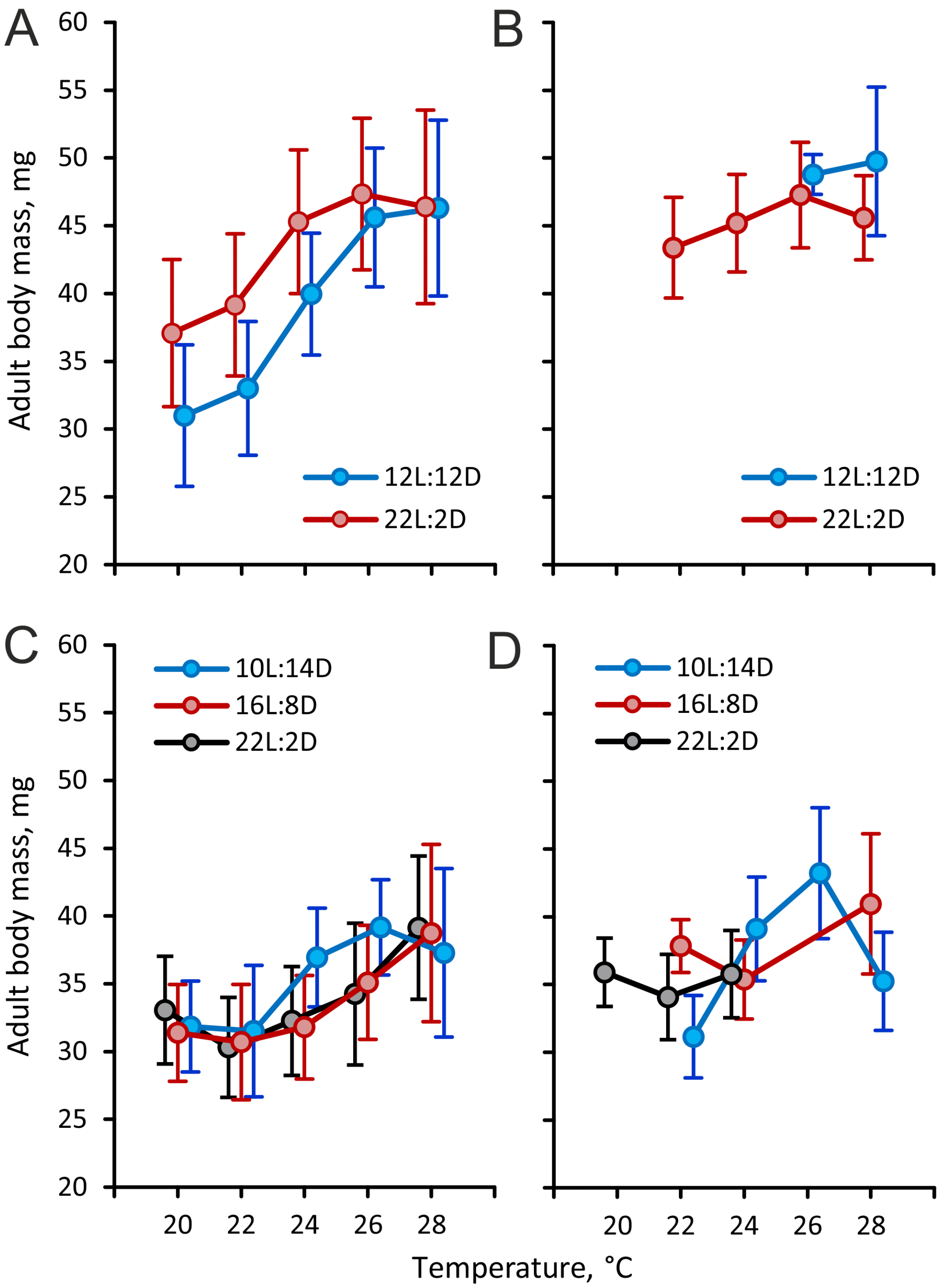

Fig. 3. Mean adult body mass at eclosion recorded for (A) northern brachypterous, (B) northern macropterous, (C) southern brachypterous, and (D) southern macropterous *P. apterus* after rearing at different combinations of temperature and photoperiod. Symbols are slightly shifted along the temperature axis for clarity. Vertical bars denote SD.

sizes and patchy distribution of macropterous individuals across the treatments. The sections below deal with the temperature and photoperiodic responses of eggs and nymphs that developed into the brachypterous morph.

Development and body mass recorded for the northern population

Developmental rates significantly depended on rearing temperature (egg batches: $F_{1,113} = 5131.9$, $p < 0.001$; nymphs: LLR $\chi^2(1) = 44.0$, $p < 0.0001$; Table 1, Fig. 4). There was no significant influence of photoperiod on the developmental rate of eggs ($F_{1,113} = 1.9$, $p = 0.2$). In contrast, photoperiodic conditions significantly affected the rate of nymphal development, both as a main effect (LLR $\chi^2(1) = 98.9$, $p < 0.0001$) and in interaction with temperature (LLR $\chi^2(1) = 95.5$, $p < 0.0001$). At low experimental temperatures, nymphal development was faster under the short-day photoperiod of 12L : 12D than under 22L : 2D, whereas at high temperatures, the pattern was reversed (Fig. 4B). In general, development under short-day condi-

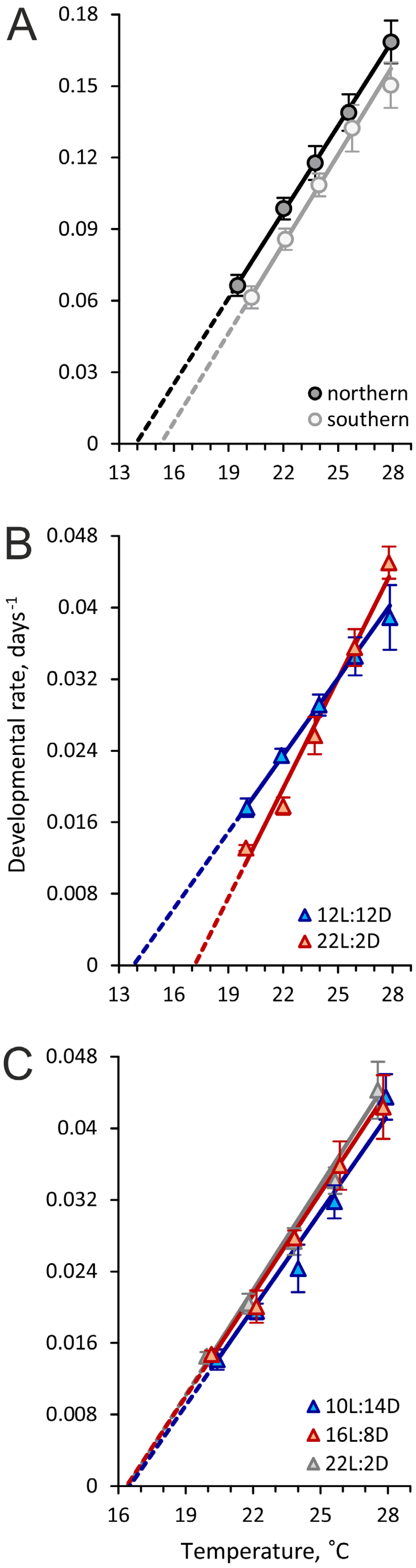

Fig. 4. Linear thermal reaction norms for development estimated for (A) eggs, (B) nymphs of the northern population, and (C) nymphs of the southern population of *P. apterus*. Symbols with bars refer to group means ± SD; their position on the temperature axis matches the temperatures measured in the rearing chambers.

tions was characterized by a flatter thermal reaction norm (one with a shallower slope, i.e., smaller regression coefficient *b*) and a smaller value of the lower temperature threshold (Table 3). Adult body mass depended on both developmental temperature (LLR $\chi^2(1) = 35.8$, $p < 0.0001$) and photoperiod (LLR $\chi^2(1) = 11.4$, $p = 0.0007$); the temperature by photoperiod interaction was also significant (LLR $\chi^2(1) = 7.3$, $p = 0.007$). Northern firebugs grew to a larger size at high temperatures, especially under short-day conditions (Fig. 3A).

The effect of sex on developmental rate was unclear. Overall, northern females developed slightly but consistently faster than males (Table 1). However, the significance of this effect varied greatly depending on how variances were modeled and whether (and which) interaction terms were included or not. In the final model, which contained all main effects and double interactions, the effect of sex alone was non-significant (LLR $\chi^2(1) = 1.1$, $p = 0.3$), but weakly significant in some interactions. Similarly, there was no difference in body mass between freshly emerged males (mean ± SD across all treatments: 41.3 ± 6.61 mg) and females (41.5 ± 8.46 mg) (LLR $\chi^2(1) = 0.03$, $p = 0.9$). As the main focus of this analysis was the photoperiodic responses in a geographic context, the preferred option was to disregard the minor difference in developmental time between males and females, as it did not alter the overall picture.

Development and body mass recorded for the southern population

Developmental rates of southern firebugs significantly depended on rearing temperature (egg batches: $F_{1,127} = 3492.8$, $p < 0.0001$; nymphs: LLR $\chi^2(1) = 183.2$, $p < 0.0001$; Table 2, Fig. 4). There was no significant effect of photoperiod on developmental rate of eggs when the data for the 22L : 2D treatment were removed from the dataset ($F_{1,85} = 0.02$, $p = 0.9$). However, inclusion of these data resulted in a significant effect of photoperiod ($F_{1,127} = 6.5$, $p = 0.01$) and significant temperature by photoperiod interaction ($F_{1,127} = 33.1$, $p < 0.0001$). Compared with the ecologically relevant 16-h photoperiod, in the very long-day treatment, egg development was slightly faster at the three low temperatures and slightly retarded at the higher two. Photoperiodic conditions also significantly affected the rate of nymphal development, both as a main effect (LLR $\chi^2(1) = 21.1$, $p < 0.0001$) and in interaction with temperature (LLR $\chi^2(1) = 29.1$, $p < 0.0001$). However, after the removal of the 22L : 2D data, the effect of photoperiod became non-significant (LLR $\chi^2(1) = 0.01$, $p = 0.9$) and the interaction disappeared (LLR $\chi^2(1) = 0.4$, $p = 0.5$), likely due to a reduction in sample size because otherwise the response to both long-day treatments was very similar (Fig. 4C). In general, southern nymphs developed more slowly and had a shallower thermal reaction norm under the 10L : 14D photoperiod than under either of the long-day photoperiods (Tables 2 and 3). All three regression lines for developmental rate on temperature crossed near the LTT (Fig. 4C). As with the northern firebugs, there was no difference in body mass of freshly emerged males (mean ± SD across all treatments: 34.0 ± 5.35 mg) and females (33.9 ± 5.63 mg), and so the data for both sexes were pooled. Adult body mass in the southern population significantly depended only on developmental temperature (LLR $\chi^2(1) = 5.6$, $p = 0.02$): the firebugs tended to attain a larger size in warmer conditions (Fig. 3C).

Geographic differences

Eggs of the northern population developed significantly faster ($F_{1,221} = 331.8$, $p < 0.0001$) than those of the southern population and their low temperature threshold was lower (Fig. 4A, Table 3; the southern 22L : 2D data were not included in the regression analysis). In particular, mean egg development times at the temperatures from 20 to 28°C were 15.1, 10.1, 8.5, 7.2, and 5.9 d for the northern population and 16.3, 11.7, 9.2, 7.6, and 6.7 d for the southern one. Under short-day conditions, nymphs from the northern population developed significantly faster than southern ones at temperatures below 26°C and slower than those at the highest temperature (main effect of geographic origin: LLR $\chi^2(1) = 49.3$, $p < 0.0001$; interaction with temperature: LLR $\chi^2(1) = 42.3$, $p < 0.0001$). There was no significant difference in the temperature-dependent development of the two populations under long-day conditions, regardless of how they were compared: under 22L : 2D only or under 22L : 2D vs 16L : 8D. Firebugs from the northern population had a significantly greater body mass (LLR $\chi^2(1) = 13.6$, $p = 0.0002$), especially at high temperatures (interaction: LLR $\chi^2(1) = 10.2$, $p = 0.001$) and under the long-day photoperiod (interaction: LLR $\chi^2(1) = 41.3$, $p < 0.0001$).

DISCUSSION

The firebug *P. apterus* is an extraordinarily diverse species with broad inter- and intrapopulation variation (Socha, 1993; Lopatina et al., 2007; Pivarciova et al., 2016; Ditrich et al., 2018). The results presented show that the northern (temperate) and southern (subtropical) populations of *P. apterus* studied differ not only in the absolute values of wing-morph occurrence, rate of immature development and adult body mass, but also in the thermal and photoperiodic plasticity of these traits.

Both populations are clearly thermophilic and perform better at high constant temperatures of 24–28°C, which is manifested in higher survival rates and bigger body size than at 20–22°C (Figs 1 and 3). There is a marked tendency for both northern and southern firebugs to be macropterous at high temperatures (Fig. 2). In both populations, there is no pronounced sexual size dimorphism, sex ratio is independent of temperature and photoperiod and both sexes respond to these factors in a similar way. While sharing these features, by and large the northern and the southern populations differ markedly in their responses to temperature and photoperiod, which was anticipated because the climate in their habitats is very different.

The northern population is less prone to be macropterous and long-winged individuals primarily emerge under long-day conditions at high temperatures. The southern population had a higher proportion of macropterous individuals, especially under short-day conditions, and also produced these at low temperatures (Fig. 2). There is no consensus on the adaptive significance of wing polymorphism in *P. apterus* (Socha, 1993; Honěk, 1995). Macroptery may be associated with greater dispersal capacity (Socha & Zemek, 2003) or, alternatively, may merely represent a neutral vestigial trait in the process of transition to complete brachyptery (Seidenstücker, 1953; Honěk, 1995). Our results corroborate previous findings (Honěk, 1987; Socha & Šula, 1996; Socha, 2001) that geographic populations of *P. apterus* differ not only in the incidence but also in the environmental control of macroptery. For example, Honěk (1987) reports an unusually low percentage of macropterous individuals in a population from Istanbul, Turkey, reared under a long-day photoperiod at 26°C; comparing his result with ours (Fig. 2B), it is likely that the fraction of macropterous individuals in that population would have been higher under short-day conditions. However, the high percentage of macropterous individuals (about 23%) reported by this author for a population from Almaty, Kazakhstan, reared under the same conditions, clearly indicates that not all southern populations are similar in this regard. Thus, if there is an adaptive scenario for the occurrence of macroptery in *P. apterus*, it is likely to be complex and incorporate the thermal and photoperiodic plasticity of wing-morphs.

We do not have a good explanation for why the sex ratio at adult eclosion is slightly female-biased in the north and male-biased in the south. One possible mechanism for this could be sex-biased mortality during the immature period. Overall, the southern population survived worse under our experimental conditions and were smaller, which might have been due to feeding them on the seed of linden, a plant genus common in Europe but not native to Israel.

Egg development recorded for the northern population is faster and more tuned to low temperatures (Figs 1A, 4A). However, when egg batches of the southern population were kept under the 22L : 2D photoperiod, hatchlings emerged relatively earlier at low temperatures, i.e., at least superficially they appear to be similar to their northern conspecifics. It is unlikely, however, that photoperiod could directly affect embryonic development in *P. apterus*. The significant effect of the 22L : 2D photoperiod on egg development in the southern population is presumably due to the disruption of a circadian hatching rhythm. As the postglacial northward expansion of *P. apterus* implies adaptation to low temperatures and long days, it would be interesting to examine in detail whether there are any latitudinal differences in the firebugs' daily hatching patterns. Our results hint at a possibility of such geographic variation in this species.

The photoperiodic responses of the nymphs of the brachypterous morph are markedly different in the two populations. The northern population has a strong photoperiod-by-temperature interaction controlling the rate of development (Fig. 4B) and in this respect it is very similar to the partially bivoltine, more southerly populations from Ryazan and Belgorod (Lopatina et al., 2007). In all these populations, long-day conditions accelerate nymphal development at high, but not low, temperatures. Together with basking behavior, which is well documented in *P. apterus* (Honek & Martinkova, 2019), this response may expedite maturation in firebugs in summer and facilitate bivoltinism. Conversely, short-day conditions accelerate nymphal development when combined with low temperatures. Even at the expense of a smaller final body mass (Fig. 3A), this response is likely to be advantageous late in the season in terms of the timely completion of development before winter. The southern population exhibits only a weak response to photoperiod such that long-day conditions slightly accelerate nymphal development over the whole temperature range studied (Fig. 4C). The firebugs from Israel share this type of quantitative photoperiodic response with many other subtropical and tropical insects, including the sympatric pyrrhocorid bug, *Scantius aegyptius* (Kutcherov et al., 2018).

The phylogenetic tree for *P. apterus* reported by Pivarciova et al. (2016) consists of three distinct and well-supported clades: Western European + (Israeli + Eastern European). Thus far, the emerging geographic pattern in the photoperiodic responses of nymphs is consistent with this topology as the *P. apterus* population from Israel has a markedly different response compared with that of Eastern European populations (Lopatina et al., 2007 and the present study). Unfortunately, the absence of such data for Western European populations prevents a broader generalization. What can be stated is that the short-day thermal reaction norm exhibits more geographic variation than its long-day counterpart as the former becomes considerably shallower northward and intersects the temperature axis at a comparatively low threshold value of 13.7°C (Fig. 4B, C; Table 3). Effectively, under short-day conditions, nymphs of northern origin develop significantly faster than southern nymphs at low temperatures (the sign of the difference is opposite at 28°C due to a strong genotype-by-environment interaction, i.e., an intersection of reaction norms). In contrast, under long-day conditions, southern nymphs at low temperatures outperform northern ones, but only slightly.

From a physiological standpoint, photoperiod does not influence the rate of development, but rather the thermal reaction norm for development, including both the SDD and LTT. It should be stressed that SDDs calculated from different LTTs are not a proxy of development time and, generally, are not comparable. For example, in our experiments, nymphs of the northern population have a shallower yet more elevated reaction norm under short-day conditions, i.e., they develop on average faster than those under the long-day photoperiod, despite having a greater SDD (Table 3). Although our experimental design is static (the photoperiods are kept constant throughout development), previous results (Lopatina et al., 2007) indicate that this response to photoperiod may be more or less gradual. In other words, the LTT and SDD in *P. apterus* are not constant and change as the season progresses in the field, which is especially conspicuous in the northern population. Similarly, it is not possible to say which of the two populations, the northern one or the southern one, develops more rapidly during the nymphal stages as the answer will depend on the combination of temperature and photoperiod under which the comparison is made. A possible confounding factor that may have contributed to the geographic disparities in our experiments is different parental overwintering history (natural overwintering in the northern population and simulated in the southern one). Such transgenerational effects are rather small in magnitude in *P. apterus* (Balashov et al., 2007), but add another dimension to the variation in thermal reaction norms. Also, our experiments were not designed to explicitly test for the effects of rearing density (which is a nuisance variable here, treated as a random-effect term), and yet, temperature-dependent mortality resulted in larger groups at higher temperatures where nymphs might have developed faster, achieved a bigger size (Schmuck, 1995) and switched to the macropterous phenotype more frequently than under the influence of high temperature alone. The precise contribution of the factor group density remains to be quantified in future studies.

Arguably, caution should be exercised when extrapolating any life-history traits in *P. apterus* beyond the season when and the location where these were experimentally measured. For example, the LTT and SDD can vary both in time (seasonally) and in space (geographically) (Table 3). The use of a constant LTT coupled with a constant SDD likely oversimplifies the diversity of current and projected phenological patterns in this species. Taking this variation into account, however daunting it may seem, will undoubtedly improve the accuracy of phenological forecasts.

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