

# Sex-specific phenotypic plasticity in response to the trade-off between developmental time and body size supports the dimorphic niche hypothesis

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Female-biased sexual size dimorphism (SSD) is widespread in many invertebrate taxa. One hypothesis for the evolution of SSD is the dimorphic niche hypothesis, which states that SSD evolved in response to the different sexual reproductive roles. While females benefit from a larger body size by producing more or larger eggs, males benefit from a faster development, which allows them to fertilize virgin females (protandry). To test this hypothesis, we studied the influence of temperature and intraspecific density on the development of the grasshopper, *Chorthippus montanus*. We reared them in monosexual groups under different conditions and measured adult body size, wing length, nymphal mortality, and development time. The present study revealed an inverse temperature–size relationship: body size increased with increasing temperature in both sexes. Furthermore, we found intersexual differences in the phenotypic response to population density, supporting the dimorphic niches hypothesis. At a lower temperature, female development time increased and male body size decreased with increasing density. Because there was no food limitation, we conclude that interference competition hampered development. By contrast to expectations, mortality decreased with increasing density, suggesting that interference did not negatively affect survival. The present study shows that sex-specific niche optima may be a major trigger of sexual dimorphisms. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**, 48–57.

**ADDITIONAL KEYWORDS:** Bergmann's rule – crowding – density dependence – latitudinal compensation hypothesis – life-history traits – orthoptera – sexual size dimorphism – temperature–size rule.

## INTRODUCTION

It is a well-known phenomenon that the sexes of most biota differ fundamentally in morphology, ecology, and behaviour (Darwin, 1859). Sexual differences in size (i.e. sexual size dimorphism; SSD), are particularly widespread among animal species (Hedrick & Temeles, 1989; Honěk, 1993; Fairbairn, 1997; Davidowitz & Nijhout, 2004). In most cases, SSD is female-biased, although exceptions occur (particularly among birds and mammals; Andersson, 1994; Blanckenhorn, 2005). There are several hypotheses explaining the evolutionary origin of SSD (Lande, 1980; Slatkin, 1984; Hedrick & Temeles, 1989; Shine, 1989; Temeles *et al.*, 2000). The most widely studied one is the sexual selection hypothesis, which proposes

that sexual dimorphism emerges as a result of competition for mates or mate choice (Hedrick & Temeles, 1989). It is assumed that sexual selection generally favours male-biased SSD based on the competition advantages for larger males during mate acquisition. Although female-biased SSD may also be a result of sexual selection (e.g. male preferences for larger females), ecological factors could also result in natural selection for sexual size dimorphism (Shine, 1989; Crowley, 2000; Blanckenhorn, 2005).

The role of natural selection for SSD is highlighted by the dimorphic niche hypothesis (or reproductive role hypothesis), which states that the differential reproductive roles of the sexes are associated with differential energetic costs (Savalli & Fox, 1998), leading to different fitness optima (Slatkin, 1984; Hedrick & Temeles, 1989; Shine, 1991; Hochkirch, Gröning & Krause, 2007). These different optima are described by differential equilibria of the three major

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selective forces: sexual selection, fecundity selection, and viability selection (Blanckenhorn, 2005). In females of most invertebrate species, fecundity selection is considered to select for larger individuals, favouring larger clutch size, egg size or offspring size (Honěk, 1993; Reeve & Fairbairn, 1999). Males may benefit from a smaller body size, favouring sooner adult emergence (i.e. protandry), which increases the potential to fertilize virgin females (Bidau & Martí, 2007; Hochkirch & Gröning, 2008). Other advantages for small males may be reduced ecological competition with females or greater mobility and agility facilitating the search for mates (Kelly, Bussière & Gwynne, 2008), as well as decreased predation risk and lower food requirements (Blanckenhorn, 2000). By contrast, sexual selection usually favours larger males (Wiklund & Kaitala, 1995; Savalli & Fox, 1998). The effect of viability selection on SSD remains poorly studied, although size-specific effects of predation, thermoregulation, etc., are often assumed to be important for constraining the potential size differences between the sexes (Bouteiller-Reuter & Perrin, 2005; Cox & Calsbeek, 2009). Hence, the differential effects of fecundity selection are usually considered to be the predominating power behind female-biased SSD (Reeve & Fairbairn, 1999; Cox & Calsbeek, 2009), whereas sexual selection is considered to support male-biased SSD (Blanckenhorn, 2005; Stillwell *et al.*, 2010). Female-biased SSD is common in a majority of insect species and in 95% of Orthoptera species (Hochkirch & Gröning, 2008; Stillwell *et al.*, 2010).

Body size is generally a plastic character, being strongly affected by environmental factors, as well as genetic preconditions (Honěk, 1993). Food quantity and quality, as well as temperature, affect growth and development (Atkinson, 1994; Angilletta Jr & Dunham, 2003; Davidowitz & Nijhout, 2004). The temperature–size rule states that, at lower temperatures, ectothermic individuals grow slower but attain larger body sizes than at higher temperatures (Angilletta Jr & Dunham, 2003; Davidowitz & Nijhout, 2004). Therefore, insects face a trade-off and may respond to energetic limitations either by reducing their body size or by undergoing a prolonged developmental time. Phenotypic plasticity of body size can vary substantially between the sexes and can cause intraspecific variation (Teder & Tamaru, 2005; Stillwell *et al.*, 2010). Given that the dimorphic niche hypothesis applies, one would expect that the sexes differ in their response towards environmental stresses, such as competition or limited energy supply to maximize their fitness (Blanckenhorn, 2005). Although females should aim to reach a maximum body size also under energetic limitation (which they may only reach by a longer developmental time),

males should reduce body size to reach adulthood earlier.

We tested this hypothesis by raising single-sex groups of the water meadow grasshopper, *Chorthippus montanus* (Charpentier, 1825), in the laboratory under two different temperature regimes and three different densities. We measured adult body size, wing length, nymphal mortality, and developmental time aiming to investigate whether density and temperature affect nymphal development of the sexes differentially. Similar to most other grasshopper species, *Ch. montanus* is graminivorous but not further specialized in its diet. Because grasses are generally abundant in its habitat, we assumed that the species is not limited in food supply. Therefore, we assumed that these insects are mainly affected by interference competition and provided a sufficient food and water supply. We expected that, if the dimorphic niche hypothesis applies, males would attain a lower adult body size under the lower temperature regime and higher densities, whereas females would require a longer time to reach adulthood.

## MATERIAL AND METHODS

### STUDY SPECIES

*Chorthippus montanus* is a univoltine, hygrophilous grasshopper species, which occurs in wet habitat types, such as marshes, peat bogs, wet grassland, and water meadows (Ingrisch, 1983; Froehlich, 1994; Kleukers *et al.*, 1997). Nymphs hatch in April and May and become adult from end of July to end of September (Weyer, Weinberger & Hochkirch, 2012). It is widely distributed over Eurosiberia from Western Europe to Kamtchatka (Kleukers *et al.*, 1997). In the study region, it is restricted to wet grasslands and bogs at elevations above 400 m (Weyer *et al.*, 2012). As is typical for most grasshopper species (Hochkirch *et al.*, 2008), *Ch. montanus* shows a pronounced sexual size dimorphism: males reach an entire body length of 13–16 mm and females reach 17–24 mm (Maas, Detzel & Staudt, 2002).

### SAMPLING

A total of 478 first- and second-instar nymphs of *Ch. montanus* was collected from 19 June to 3 July near Hundheim (49°50'3.96"N; 07°09'57.37"E) and Muhl (49°40'8.73"N; 07°02'27.12"E) in the Hunsrueck mountains (Rhineland-Palatinate, Germany). To avoid any possibility of confusion with nymphs of the closely-related grasshopper *Chorthippus parallelus*, nymphs were sampled only at localities, where *Ch. parallelus* did not occur (based upon studies in the preceding years). They were sorted by sex and kept in

plastic terraria (19.5 × 30 × 20.5 cm) containing grass for transport.

#### EXPERIMENTAL DESIGN

We performed a full factorial experiment with two factors: temperature (two factor levels: 22 °C and 27 °C) and population density (three factor levels: two, four, and eight individuals). The grasshoppers were separated by sex but, because of uneven sample size, it was not possible to achieve an equal number of replicates for both sexes (Table 1). Initially, we started the experiment with 16 replicates per temperature and density, aiming to sustain ten replicates after replacement of dead individuals. Whenever the initial density decreased as a result of mortality, dead insects were removed and replaced by grasshoppers from a terrarium of the corresponding factorial combination (i.e. similar temperature and population density), which was subsequently excluded. The final number of replicates for each factor level combination varied between twelve and 15.

Experimental terraria (15.3 × 23 × 16.5 cm) were covered with soil with grass seeds and sand for oviposition. The aeration was ensured with a mesh lid. Seed propagation took place under standardized conditions in climate chambers (22 °C and 65% relative humidity) with daily watering. The experiment took place in two climate chambers (Kälte Kamrath) under a 17 : 7 h light/dark cycle at constant temperature (22 °C or 27 °C) and a relative humidity of 65%. Each terrarium was illuminated by two ultraviolet and visible-emitting fluorescent tubes (Osram Biolux L36W/965). The terraria were inspected daily (except on one day) until all specimens were adult (total of 51 days). Grass was cultivated in each terrarium and, additionally, fresh grass was added every second day to avoid food limitation. The number of individuals (dead insects, number of final molts) was noted. After final molt, body size (the length of the insect from the frontal ridge to the tip of the abdomen) and wing length (length of the elytron) of each grasshopper were measured using a caliper

**Table 1.** Initial number of replicates (terraria) per density (two, four or eight individuals per terraria) and temperature (22 °C and 27 °C) sorted by sex

	22 °C		27 °C	
Density/sex	Male	Female	Male	Female
2	8	9	7	7
4	8	9	8	9
8	7	10	6	10
Sum	23	28	21	26

(with an accuracy of 0.01 mm/0.0005). For subsequent analysis, we calculated the mean values for each terrarium. It was also noted whether a specimen was macropterous (i.e. had fully developed fore and hind wings).

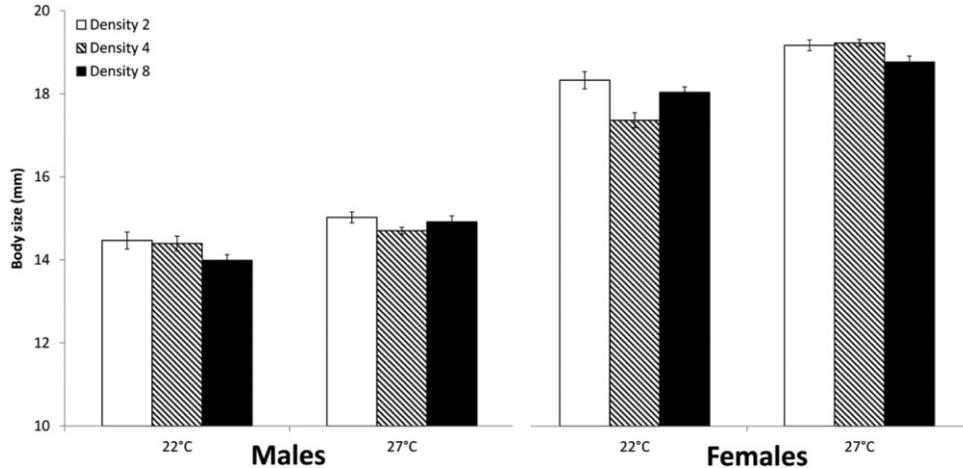
#### STATISTICAL ANALYSIS

Three-way analyses of variance (ANOVA) were used to analyze the influence of the explanatory variables temperature, density, and sex on the response variables body size, wing length, relative wing length (wing length/body size), and time of nymphal development. The time of nymphal development was defined as the time from collecting to the final molt. To analyze the effect of temperature and density on SSD, we chose terraria randomly and calculated the ratio of mean female length to mean male length for these terraria combinations (resulting in six to eight replicates per temperature–density combination). All response variables were Box-Cox transformed using the MASS library for R to infer the optimal lambda (i.e. the exponent for each variable) to achieve an optimal data distribution for ANOVAs (Venables, 2002). We stepwise simplified the ANOVA models using the step function in R, which uses the Akaike information criterion to remove non-informative interaction terms. When significant interactions with sex occurred, we also analyzed the data for each sex separately in ANOVAs. To illustrate potential correlations between variables, we performed two principal component analyses (PCA) in R using the VEGAN package, version 2.0-10 (Oksanen *et al.*, 2013). The PCAs were performed for each sex separately because the major body size differences between sexes would otherwise mask the effects of temperature and density. We scaled each factor by their proportional eigenvalue because of the strong variability of the scales of our data (development time, body size). We also included a rough measure of growth rate by dividing body size by development time. Correlations of the explanatory variables (density, temperature) with the PCA functions were tested for significance using environmental fitting with 1000 permutations. To test, whether the occurrence of macropterous individuals was affected by temperature or density, we used two- or three-sample tests for equality of proportions with continuity correction, respectively. All tests were carried out in R, version 3.0.2 (R Development Core Team, 2014).

## RESULTS

### BODY SIZE AND WING LENGTH

As is typical for grasshoppers, females were significantly larger than males (ANOVA,  $\lambda = -1.42$ ,



**Figure 1.** Mean adult body size of males and females of *Chorthippus montanus* at rearing temperatures of 22 °C and 27 °C and at densities of two, four or eight individuals per terrarium. Error bars indicate the SE.

$F_{1,86} = 983.0$ ,  $P < 0.001$ ). Furthermore, temperature significantly influenced body size (ANOVA,  $\lambda = -1.42$ ,  $F_{1,86} = 44.0$ ,  $P < 0.001$ ). At higher temperatures (27 °C), individuals reached significantly larger sizes than at lower temperatures (Fig. 1). We found no significant main effect of density on body size but a near-significant trend (ANOVA,  $\lambda = -1.42$ ,  $F_{2,86} = 2.88$ ,  $P = 0.062$ ) and a significant interaction between sex, density, and temperature (ANOVA,  $\lambda = -1.42$ ,  $F_{2,86} = 4.38$ ,  $P = 0.015$ ) (Fig. 1). While male body size was negatively affected by density at low temperatures, females showed no effect of density on body size (Fig. 1). Wing length followed the same pattern as body size. For relative wing length, we only found a significant difference between the sexes (ANOVA,  $\lambda = 1.25$ ,  $F_{1,95} = 557.6$ ,  $P < 0.001$ ), which is typical for many brachypterous Orthoptera species. There was a near-significant trend for smaller relative wing lengths at higher temperatures (ANOVA,  $\lambda = 1.25$ ,  $F_{1,95} = 3.2$ ,  $P = 0.077$ ). Only four macropterous individuals were found in the present study, all of which were females. Because of the small number of macropters, these individuals were excluded from the analysis of the wing length. Sexual size dimorphism showed no significant response to the two explanatory variables, although there was a slight tendency of larger SSD at higher temperatures (22 °C: mean  $\pm$  SE:  $1.26 \pm 0.02$ ; 27 °C: mean  $\pm$  SE:  $1.29 \pm 0.01$ ; ANOVA,  $\lambda = 3.9$ ,  $F_{1,42} = 2.526$ ,  $P = 0.12$ ).

The PCAs for both sexes were highly similar (Fig. 2; but note that the loadings are reversed). The first function was mainly explained by growth rate (male score: 1.58; female score:  $-1.71$ ), body size (male: 1.23; female:  $-1.55$ ), and development time (male:  $-1.51$ ; female: 1.61), whereas the second function was mainly explained by wing length (male: 1.62; female:

$-1.74$ ) and relative wing length (male: 1.55; female:  $-1.67$ ). The two first principal components explained 81% (males) and 88% (females) of the variance. Only temperature correlated significantly with both PCAs (environmental fitting:  $P < 0.001$ ).

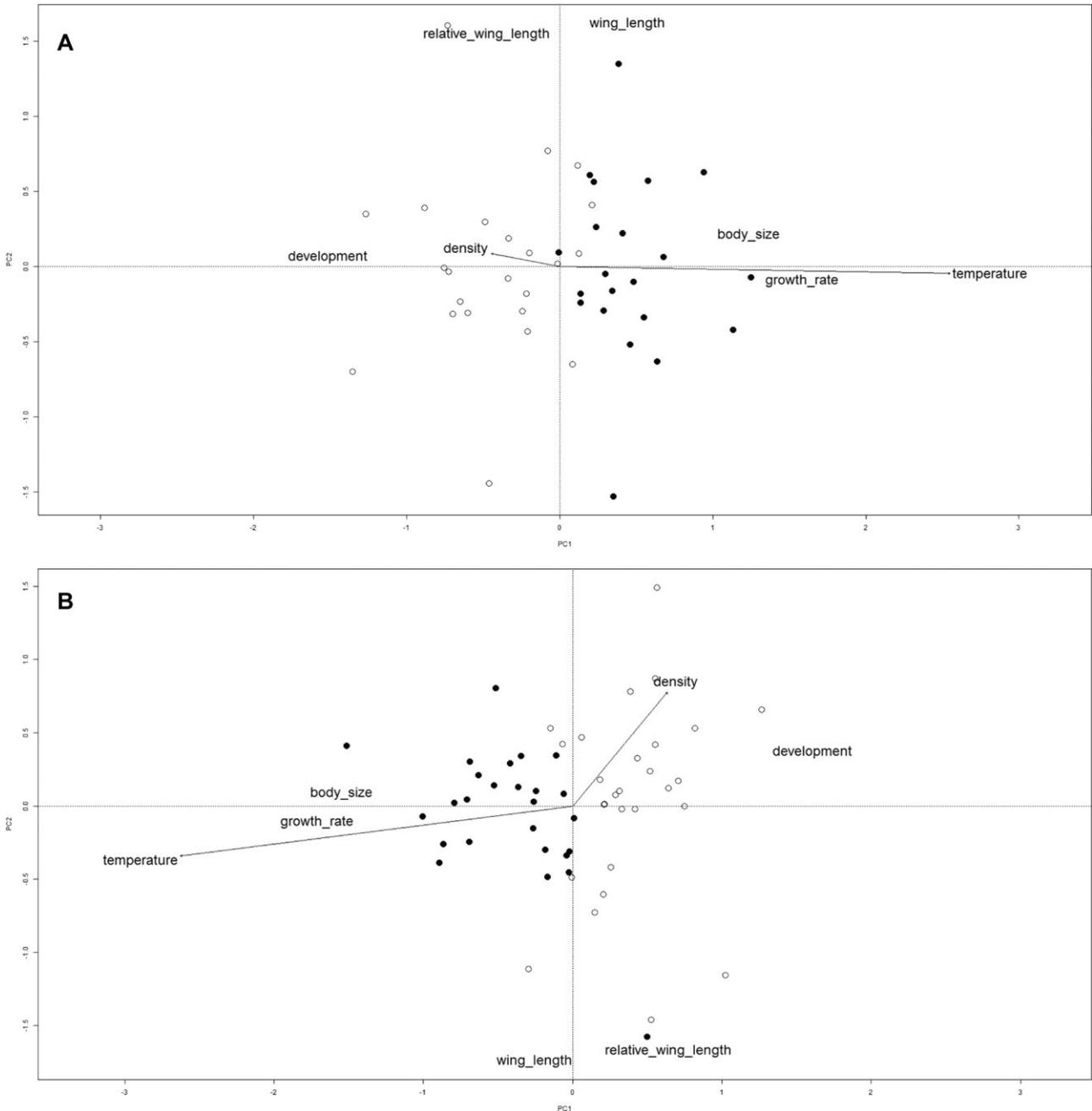
#### EFFECTS ON TIME OF NYMPHAL DEVELOPMENT AND MORTALITY

In both sexes, the developmental time took significantly longer at 22 °C than at 27 °C (ANOVA,  $\lambda = 0$ ,  $F_{1,93} = 113.8$ ,  $P < 0.001$ ), although males generally developed faster than females, on average by 2.5 days (ANOVA,  $\lambda = 0$ ,  $F_{1,93} = 9.91$ ,  $P = 0.002$ ) (Fig. 3). Furthermore, we found a near-significant trend that developmental time increased with increasing density (ANOVA,  $\lambda = 0$ ,  $F_{2,93} = 2.51$ ,  $P = 0.087$ ). When the sexes were tested separately, this effect was significant for females (ANOVA,  $\lambda = 0$ ,  $F_{2,48} = 4.54$ ,  $P = 0.016$ ) but not for males (ANOVA,  $\lambda = 0$ ,  $F_{2,38} = 0.03$ ,  $P = 0.97$ ) (Fig. 2).

Mortality decreased significantly with increasing density (ANOVA,  $\lambda = 0.35$ ,  $F_{1,91} = 23.90$ ,  $P < 0.001$ ) (Fig. 4), although this effect was smaller at the lower temperature regime resulting in a significant interaction between temperature and density (ANOVA,  $\lambda = 0.35$ ,  $F_{1,91} = 6.58$ ,  $P = 0.012$ ). Furthermore, mortality was significantly higher among females than among males but independent of experimental treatment (ANOVA,  $\lambda = 0.35$ ,  $F_{1,91} = 4.09$ ,  $P = 0.046$ ) (Fig. 4).

#### DISCUSSION

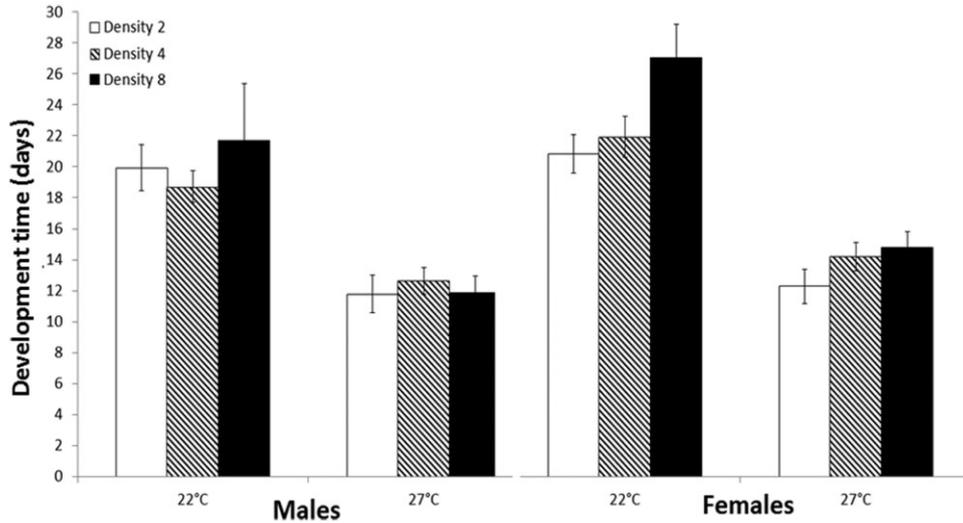
The results of the present study show that the sexes respond differentially to increasing intrasexual



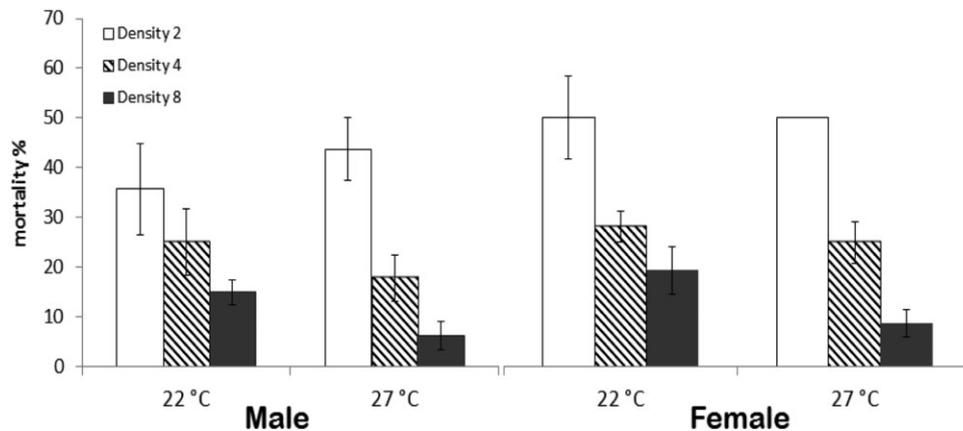
**Figure 2.** Plot of the first two functions of the principal component analyses (PCA) on the variables body size, development time, growth rate, wing length, and relative wing length for males (A) and females (B), explaining 81% and 88% of the total variance for males and females, respectively. Each point represents one individual (black points: 27 °C; white circles: 22 °C). Arrows show the correlation of density and temperature using environmental fitting.

density. By contrast to the temperature–size rule, the insects became generally larger but, in line with the rule, developmental time became shorter at higher temperatures. Females generally took longer to reach adulthood when intrasexual density was higher, whereas, in males, developmental time was not affected by density. Instead, they obtained a smaller

adult body size at high densities but only when the temperature regime was lower (22 °C). These results differ from those obtained by Wall & Begon (1987a), who showed that both sexes of *Ch. brunneus* have a prolonged development time and smaller weight at higher densities. Our results support the dimorphic niche hypothesis, which states that the major drivers



**Figure 3.** Developmental time of males and of females of *Chorthippus montanus* at rearing temperatures of 22 °C and 27 °C and at densities of two, four or eight individuals per terrarium. Error bars indicate the SE.



**Figure 4.** Relative mortality of males and females of *Chorthippus montanus* at rearing temperatures of 22 °C and 27 °C and at densities of two, four or eight individuals per terrarium. Error bars indicate the SE.

of SSD are the different fitness optima of the sexes (Slatkin, 1984; Hedrick & Temeles, 1989; Hochkirch *et al.*, 2007). The sexes differ in their response to the trade-off between developmental time and body size and exhibit a sex-specific phenotypic plasticity. Females are considered to benefit from a large body size, which is necessary to produce a higher number of eggs and/or larger eggs, as has been shown by Hassall *et al.* (2006) for *Ch. brunneus*. They respond to competition by a prolonged nymphal development allowing them to attain an optimal body size for reproduction. This is in line with the results of Wall & Begon (1987b), who showed that, at higher densities, females benefit from larger body size by a higher reproductive success, whereas they did not find such a correlation at low densities. Furthermore, it was

hypothesized that nymphal experience is more important than adult experience, which is in line with the results of the present study. By contrast, males may profit from a short nymphal development (protandry) and this allows them to fertilize virgin females at the beginning of the season. Hence, they respond to competition by reducing their body size to avoid a belated adulthood. It has been shown for other *Chorthippus* species (e.g. *Chorthippus biguttulus*) that females are highly reproductive during the first week of adulthood and often do not re-mate in their lifetime (Kriegbaum, 1988). This may differ in *Ch. montanus*, although females of its sibling species *Ch. parallelus* (which re-mate frequently) do not require fresh sperm to fertilize their eggs (Reinhardt, Köhler & Schumacher, 1999).

## COMPETITION

Because there was no food limitation in the present study, it is likely that interference competition (Case & Gilpin, 1974; Schoener, 1983) was the major factor driving the observed pattern. The effects of interference are mainly attributed to behavioural changes that ultimately lead to differences in energy and time management, which may be negatively correlated with growth (Goss-Custard, 1980; Huntingford & Turner, 1987). In our case, density negatively affected nymphal growth in both sexes, although only females delayed development. The underlying behavioural interactions remain somewhat dubious because, in contrast to dragonfly larvae (Johnson *et al.*, 1985), grasshopper nymphs are not territorial. Because we kept the sexes separated, it is also unlikely that the nymphs already showed sexual interest in other individuals (although one might suspect some incipient rivalry among male nymphs). Furthermore, the tested densities were probably not sufficiently high to invoke crowding effects in a strict sense, although it should be noted that crowding effects are typically graded (Applebaum & Heifetz, 1999). However, the observed response was the reverse of the crowding effects known from two other grasshopper species in which crowding accelerated development rather than slowing it down (Uvarov, 1977). We assume that the negative effects of density on nymphal development stem from the energetic costs of direct interactions and the associated loss of time left for feeding. Interestingly, mortality decreased with increasing density, whereas the opposite would be expected under typical crowding conditions (Wall & Begon, 1986; Joshi, Wu & Mueller, 1998). It might be suggested that the observed changes in the development of *Ch. montanus* compensate for the negative effects of interference, and even lead to overcompensation. This is supported by Abrams *et al.* (1996), who found that increased growth rate might be associated with greater juvenile mortality.

## CONVERSE TEMPERATURE–SIZE RULE

In the present study, the general effects of temperature were similar for both sexes (i.e. the insects became larger and developmental time became shorter at higher temperatures). These results support previous studies indicating that most Orthoptera species follow a converse temperature–size rule (Whitman, 2008; Laiolo, Illera & Obeso, 2013; Eweleit & Reinhold, 2014; Parsons & Joern, 2014). This is in line with the latitudinal compensation hypothesis (Blanckenhorn & Demont, 2004; Parsons & Joern, 2014), stating that a smaller body size at colder temperature is a response to time constraints for development as a result of short seasons

(i.e. the insects need to complete their life cycle within one season). Higher temperatures allow a faster growth rate, shorter development time, and an earlier oviposition (Roff, 1980; Walters & Hassall, 2006). Another proximate explanation given by Walters & Hassall (2006) is that the performance of the temperature–size rule or its converse depends upon the minimum temperature thresholds for growth versus development. However, it is probably more appropriate to suggest differences in the temperature relationships for both factors. If we compare the growth rates in our experimental treatments (by dividing adult body size by developmental time), it becomes obvious that growth rate is substantially reduced at lower temperature (by 43% across all densities and sexes) and higher density (up to 24% for females when comparing the highest and lowest densities at the low temperature regime). Our results differ from those modelled by Abrams *et al.* (1996), who suggested that an increase in available time would result in an increased growth rate and/or reduced adult body size. However, because developmental time was strongly determined by temperature in the present study, the direct effects of temperature are difficult to separate from those mediated through developmental time. *Chorthippus montanus* thus follows a typical compensatory life-history strategy, focusing on completing development within one season (Parsons & Joern, 2014), whereas expansion of the growth rate is only possible at higher temperatures. This is probably an adaptation to its cold environment. The species occurs in wet grasslands (with a permanently high water table) and also at higher latitudes (Kleukers *et al.*, 1997) and has one of the latest adult emergence periods among Central European grasshoppers (Weyer *et al.*, 2012). In such a case, strong selection towards completing the life cycle is likely. Indeed, other species of the genus *Chorthippus* also show a decrease in body size with increasing temperature (Laiolo *et al.*, 2013). Walters & Hassall (2006) suggest that the variable responses of ectothermic species are based on their enzyme kinetics associated with growth rate and development rate. Univoltine populations may benefit from an increasing body size with temperature as a result of direct fitness benefits in female fecundity (Laiolo *et al.*, 2013).

## MACROPTERY

By contrast to other studies (Köhler, 2002; Poniatowski & Fartmann, 2009), we found no effects of density on the number of macropters. Although our maximum densities were slightly lower than in the previous studies, they were considerably higher than under natural conditions, with 229 ind. m<sup>-2</sup> in the

present study versus 0.1–7.3 ind. m<sup>-2</sup> in the field (Ingrisch & Köhler, 1998; Weyer *et al.*, 2012). In Orthoptera, the most important phase during which macropterism is determined comprises the first two nymphal instars (Köhler, 2002). Because we caught the specimens during this phase, it is unlikely that we missed the sensitive period of the nymphs, although it cannot be completely excluded. An alternative explanation for the lack of density-induced macroptery in the present study might be found in the strong habitat specialization of *Ch. montanus*. Macropterous individuals have a low probability of colonizing suitable habitats as these are scarce and naturally fragmented (at least in Central Europe). Moreover, macropterous morphs typically have a lower fertility (Roff & Fairbairn, 1991; Crnokrak & Roff, 1995; Fairbairn & Preziosi, 1996; Köhler, 2002). The combination of these two properties may decrease the benefits of macropterism. However, in another habitat specialist, *Metrioptera brachyptera*, density-induced macroptery has been documented (Poniatowski & Fartmann, 2009), even though macropters are rarely found in nature in this species (Poniatowski & Fartmann, 2011).

Despite the low propensity of *Ch. montanus* to develop into a macropterous morph, such alate specimens are regularly found in natural populations and, also in the present study, four individuals became macropterous. We thus hypothesize that genetic effects play a more important role for wing dimorphism in this species than environmental factors. The importance of a genetic propensity for macroptery has also been proposed for species that show a strong density-response of macropterism (Simmons & Thomas, 2004). Zera & Denno (1997), therefore assume that both genetics and environmental conditions are equally important for macroptery. However, it is likely that the response to environmental factors is highly variable among species and probably even among individuals.

#### CONCLUSIONS

The results of the present study show that nymphal development of *Ch. montanus* is strongly influenced by temperature and population density. *Chorthippus montanus* follows the converse temperature–size relationship, as do other Orthoptera, which might represent an adaptation to its cool habitat and northern distribution. The differential response of the sexes to increasing population density at low temperatures is in line with the dimorphic niche hypothesis and provides evidence for a sex-specific phenotypic plasticity in *Ch. montanus*. Although males attained smaller body sizes when reared at high densities, the females responded by a prolonged development. We hypoth-

esize that this response maintains maximum fecundity, allowing females to produce a high number of eggs per clutch or larger egg sizes and males to become adult before female final molt with a higher chance of fertilizing virgin females.

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