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Environmental effects on sexual size dimorphism of a seed-feeding beetle

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Abstract Sexual size dimorphism is widespread in animals but varies considerably among species and among populations within species. Much of this variation is assumed to be due to variance in selection on males versus females. However, environmental variables could affect the development of females and males differently, generating variation in dimorphism. Here we use a factorial experimental design to simultaneously examine the effects of rearing host and temperature on sexual dimorphism of the seed beetle, *Callosobruchus maculatus*. We found that the sexes differed in phenotypic plasticity of body size in response to rearing temperature but not rearing host, creating substantial temperature-induced variation in sexual dimorphism; females were larger than males at all temperatures, but the degree of this dimorphism was smallest at the lowest temperature. This change in dimorphism was due to a gender difference in the effect of temperature on growth rate and not due to sexual differences in plasticity of development time. Furthermore, the sex ratio (proportion males) decreased with decreasing temperature and became female-biased at the lowest temperature. This suggests that the temperature-induced change in dimorphism is potentially due to a change in non-random larval mortality of males versus females. This most important implication of this study is that rearing temperature can generate considerable intraspecific variation in the degree of sexual size dimorphism, though most studies assume that dimorphism varies little within species. Future studies should focus on whether sexual differences in phenotypic plasticity of body size are a consequence of adaptive canalization of one sex against environmental variation in temperature or whether they simply reflect a consequence of non-adaptive developmental differences between males and females.

Keywords Sexual size dimorphism · Phenotypic plasticity · Body size · Differential-plasticity hypothesis · Seed beetles

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Introduction

Most animals show some degree of sexual size dimorphism, but the direction and magnitude of this dimorphism varies substantially among species, and often among populations within species (Anderson 1994; Teder and Tammaru 2005; Blanckenhorn et al. 2006). This variation in dimorphism among animals has a common pattern in nature: sexual size dimorphism tends to increase with increasing overall body size when males are the larger sex and decreases with body size when females are the larger sex, a pattern known as Rensch's rule (Fairbairn 1997). Though Rensch's rule was originally meant to explain variation in sexual dimorphism among species, it has since been applied to studies of intraspecific variation in dimorphism (Blanckenhorn et al. 2006). Much of this variation in dimorphism among populations is likely due to variation in the magnitude of selection (Fairbairn 1997), often sexual selection due to variance in sex ratio. Alternatively, the effects of climate or other ecological and environmental variables may have different effects on males versus females, either because the fitness consequences of large versus small body size differs between the sexes or because

the sexes differ in the degree of plasticity they exhibit in response to climatic or ecological variables (Fairbairn 2005; Blanckenhorn et al. 2006). Many studies have examined how environmental factors, such as temperature, affect phenotypic plasticity in body size (Stillwell and Fox 2005) but few have examined how environmental factors affect sexual size dimorphism and the traits that mediate selection on male versus female body size (Fox and Czesak 2006).

Two of the most important environmental variables that induce substantial phenotypic plasticity in body size of ectothermic animals are diet and temperature. In general, animals reared on lower quality diets mature smaller (Berrigan and Charnov 1994; Nylin and Gotthard 1998) and animals reared at lower developmental temperatures mature larger (Atkinson 1994; Angilletta and Dunham 2003). Variation in sexual size dimorphism can result when males and females respond differently to diet or temperature (differential-plasticity hypothesis; Fairbairn 2005). The differing responses of the sexes could be caused by adaptive canalization of one sex against environmental variation in temperature (Fairbairn 2005) or sexual differences in dietary requirements (Teder and Tammaru 2005). Because variation in dimorphism mediated by differences in plasticity between the sexes has rarely been the focus of plasticity studies, it is difficult to determine the generality of these patterns, much less what causes them.

In this study, we use two populations of the seed beetle, *Callosobruchus maculatus*, that exhibit female-biased sexual size dimorphism, as a model system to explore the impact of larval rearing diet (host species) and temperature on adult sexual size dimorphism. Both host species (Chandrakantha and Mathavan 1986; Van Huis and de Rooy 1998; Stillwell et al. 2007) and temperature (Chandrakantha and Mathavan 1986; Guntrip et al. 1997; Stillwell et al. 2007) affect body size of *C. maculatus*, but how dimorphism varies as a result of differences in phenotypic plasticity between the sexes has not previously been explored. Also, to our knowledge, no study has simultaneously examined how temperature and diet influence intraspecific variation in size dimorphism. Here, using a factorial experimental design we test whether males and females of *C. maculatus* differ in plasticity of body size in response to rearing host and temperature, thus creating intraspecific variation in sexual size dimorphism.

Materials and methods

Natural history and study populations

The seed beetle, *Callosobruchus maculatus* (Coleoptera: Chrysomelidae: Bruchinae), is a generalist seed herbivore of storage legumes, but in nature uses primarily species in the genus *Vigna*. The life cycle of *C. maculatus* revolves around seeds. Females cement their eggs directly onto the seeds of their host plant. Eggs hatch and larvae burrow directly underneath the egg into the seed. Larval growth and pupation take place entirely within a single seed. Upon emergence from the seed, adults mate and females begin to lay eggs within hours. *C. maculatus* needs only the resources inside of a single seed to complete development and reproduce; additional food and water are not necessary (Fox et al. 2004a, b). Because of the ease with which it is reared in the laboratory, *C. maculatus* is a widely used model system for life history, behavior and genetic studies (Bieri and Kawecki 2003; Fox et al. 2004b; Messina 2004a, b; Arnqvist et al. 2005; Vamosi 2005).

We examine differences in plasticity of body size between males and females in two populations of *C. maculatus* that differ substantially in body size and in their response to rearing host and temperature (Stillwell et al., 2007). The South India (SI) population was collected in 1979 from infested pods of mung bean, *Vigna radiata* (L.) Wilczek, and the closely related black gram, *V. mungo* (L.) Hepper, in Tirunelveli, India (Mitchell 1991). The Burkina Faso (BF) population was collected in 1989 from infested pods of cowpea, *V. unguiculata* (L.) Walp., in Ouagadougou, Burkina Faso (Messina 1993). These two populations differ in a large number of traits including body size, adult lifespan, larval competitiveness, oviposition behavior and the amount of paternal investment into reproduction (Fox et al. 2004a, b, c; Savalli et al. 2000), many of which have likely evolved due to differences in the properties of their host species (Messina and Karren 2003; Messina 2004a). Both populations were maintained in laboratory growth chambers on seeds of *V. radiata* (SI) or *V. unguiculata* (BF) at >1,000 adults per generation for >100 generations (BF) or >200 generations (SI) prior to this experiment.

Experimental design

We used a multifactorial experimental design (two populations × three hosts × four temperatures) to simultaneously examine the effects of host plant species and temperature on sexual size dimorphism, development time dimorphism and growth rate dimorphism in the BF and SI populations of *C. maculatus*. In short, larvae of full-sib families were reared on three host plants (mung; *V. radiata*, azuki; *V. angularis* and cowpea; *V. unguiculata*) and at four rearing temperatures (20, 25, 30 and 35°C; all at 15:9 h, light:dark; though this is a long daylight cycle for tropical beetles, the photoperiod was the same for all treatments and populations) yielding 12 treatment combinations for each population. These temperatures and light cycle are identical to rearing protocols used in other studies for normal

growth, development and reproduction of *C. maculatus* (Chandrakantha and Mathavan 1986; Chandrakantha et al. 1987; Fox et al. 2004a, b, c; Mbata et al. 2005). Offspring of each full-sib family were reared on only one host (i.e., no split-brood design) but siblings were divided equally among the rearing temperature treatments creating a spilt-brood design for rearing temperature. The purpose of the split-brood design was to examine the genetic architecture of plasticity (Stillwell et al. 2007) but here we focus only on sexual dimorphism.

Species of *Vigna* vary considerably in the quality (nutrient content, allelochemicals, etc.) and size of seeds they produce (Bisht et al. 2005). We chose three hosts that were representative of this variation and are the most commonly used hosts of *C. maculatus*. Cowpea and mung are the native hosts for the BF and SI populations, respectively, and azuki is an intermediate-sized host to which neither is adapted. Mung has the highest protein and energy content per gram, whereas azuki has the lowest (United States Department of Agriculture National Nutrient Database for Standard Reference, Release 19; http://www.ars.usda.gov/ba/bhnrc/ndl) but the major difference among these hosts is the size of their seeds (cowpea seeds are the largest whereas mung are the smallest) which affects larval competition in nature (Credland et al. 1986; Messina 1991). However, in this study we reared larvae at a density of one larva per seed to eliminate larval competition and individual seeds are large enough to support a single beetle through development. Thus, any effect of rearing host on sexual size dimorphism that we observe is likely due to sexual differences in the effect of seed quality on body size. Body size, development time and growth rate are all significantly affected by rearing on these hosts; BF beetles generally have the shortest development time, are the largest and grow faster when reared on cowpea, whereas SI beetles have the shortest development time, are the largest and grow faster when reared on azuki and mung (Stillwell et al. 2007). The temperatures we used are within the normal range of temperatures at which *C. maculatus* can develop and reproduce (Chandrakantha and Mathavan 1986; Chandrakantha et al. 1987; Mbata et al. 2005).

To create families, seeds bearing eggs were randomly selected from our laboratory colonies and isolated in 35-mm petri dishes (one seed per dish, one egg per seed). Adults emerging from these seeds were used as parents to generate full-sib families by randomly pairing virgin males and females within each population. Each pair was randomly assigned to one of three rearing hosts (60-mm dishes containing 30 seeds of cowpea, 35-mm dishes containing 40 seeds of mung or 35-mm dishes containing 30 seeds of azuki) and placed in a growth chamber to lay eggs (25°C; 15:9 h, light:dark). Dishes were checked for eggs twice per day until females laid eggs on ~32 seeds (seeds bearing eggs were replaced at each check) after which adults were discarded. Seeds containing eggs were scraped to one egg/seed (to eliminate larval competition) and placed individually in 35-mm petri dishes. Egg-bearing seeds were randomly assigned to one of the four rearing temperature treatments within 12 h of being laid, such that offspring from each family were divided evenly among the four treatments (split-brood design) with approximately eight offspring per temperature treatment. All offspring were reared inside temperature-controlled growth chambers. Developing larvae were rotated daily throughout the chamber to control for spatial variation within the chambers.

Emerging adult beetles were collected twice daily. Subsamples of six offspring per family per rearing temperature were weighed on an electronic balance (AT261 Delta Range; Mettler Toledo, Columbus, Ohio) to the nearest 0.1 mg. These six offspring were randomly selected at the egg stage and their dish marked.

We tested whether gender differences in plasticity of body size were due to: (1) gender differences in plasticity of development time, or (2) gender differences in plasticity of growth rate. Growth rate was estimated as log(body mass)/larval development time. Because our measure of development time includes the duration of the pupal period, in which growth is not taking place, we first subtracted the average interval of the pupal period. Though growth rate is not independent of body mass and development time (because it includes both) it is useful in that it allows us to test whether gender differences in development time are adequate to explain size dimorphism.

In total, 9,785 adults from 387 full-sib families were raised to adult roughly evenly divided among the three rearing hosts, and 7,658 adults were weighed.

Statistical analyses

Sexual size dimorphism was estimated using the Lovich and Gibbons (1992) index, in which sexual size dimorphism = (size of the larger sex/size of the smaller sex) − 1, made positive when females are the larger sex and negative when males are the larger sex. This index has the best statistical properties of all dimorphism indices that have been proposed (Lovich and Gibbons 1992; Smith 1999). Because *C. maculatus* females are always larger than males, we calculated sexual size dimorphism as (mean female size/mean male size) − 1 for each full-sib family at each temperature. Sexual differences in development time and growth rate were estimated using the same methodology. For simplicity, we refer to sexual differences in development time and growth rate also as "dimorphism" though these traits are not morphological traits. We used these indices for measuring dimorphism instead of sex-by-environment interactions in ANOVA because these interactions

are biased by scale effects (Dobson and Wigginton 1996; Blanckenhorn et al. 2006).

Statistical analyses were done with SAS 9.1 (SAS Institute, Cary, N.C.) using ANOVA (type III sums of squares). All three dimorphism indices were normally distributed and were thus not transformed prior to analysis. For our ANOVAs we included population, host and temperature as main effects. ANOVAs were first performed using the full model with all possible interaction terms present; the non-significant three-way term (population-by-host-by temperature) was dropped from the final models in the analyses.

Results

As expected, females were substantially larger than males (Fig. 1; sexual size dimorphism estimates >0 for all treatment combinations) consistent with other studies showing female-biased size dimorphism in this species (Fox et al. 2007). Females were larger not because they had substantially longer development times (the difference in development time between females and males was <1%) but because they gained mass faster (i.e., females had much higher growth rates; Fig. 2; growth rate dimorphism estimates >0 for all treatment combinations). The magnitude of the female-biased dimorphism in body size and growth rate was largest in SI beetles (Figs. 1, 2; population effect for size dimorphism, $F_{1,1350} = 37.1$, $P < 0.0001$; growth rate dimorphism, $F_{1,1350} = 7.05$, $P = 0.008$; development time dimorphism, $F_{1,1350} = 1.62$, $P = 0.20$).

Rearing host had no effect on sexual dimorphism (size dimorphism, $F_{2,1350} = 1.63$, $P = 0.20$; growth rate dimorphism, $F_{2,1350} = 2.53$, $P = 0.08$; development time dimorphism, $F_{2,1350} = 1.13$, $P = 0.32$). However, sexual size dimorphism did change with rearing temperature—male body mass varied across rearing temperatures substantially more than did female body mass (Tables 1, 2; $F_{3,1350} = 139$, $P < 0.0001$). This created a large change in the magnitude of sexual size dimorphism with rearing temperature; dimorphism was greatest at 30°C and lowest at 20°C (Fig. 1).

The effect of temperature on size dimorphism was not due to a difference between the sexes in development time; though temperature did affect development time dimorphism ($F_{3,1350} = 4.96$, $P = 0.002$), the temperature effect on size dimorphism persists after correcting for development time (analysis of covariance, $F_{3,1349} = 165$, $P < 0.0001$). The effect of temperature on size dimorphism was instead due to an effect of temperature on growth rate dimorphism (Fig. 2; $F_{3,1350} = 67.2$, $P < 0.0001$); on average females grew 9% faster than males when reared at 20°C but grew 25% faster than males at 30°C (Fig. 2). This resulted in a large change of the relative difference in growth rate between males and females; growth rate of females relative to males was greatest at 30°C and smallest at 20°C (Fig. 2).

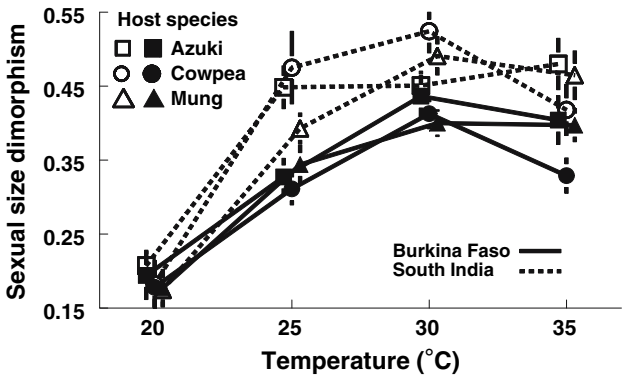

Fig. 1 Sexual size dimorphism of the Burkina Faso (*filled symbols*) and South India (*open symbols*) populations of adult *Callosobruchus maculatus* in response to rearing on azuki, cowpea and mung at four different temperatures (mean ± 1 SEM). Sexual dimorphism was estimated as (mean female mass (mg)/mean male mass (mg)) − 1 for each full-sib family at each temperature

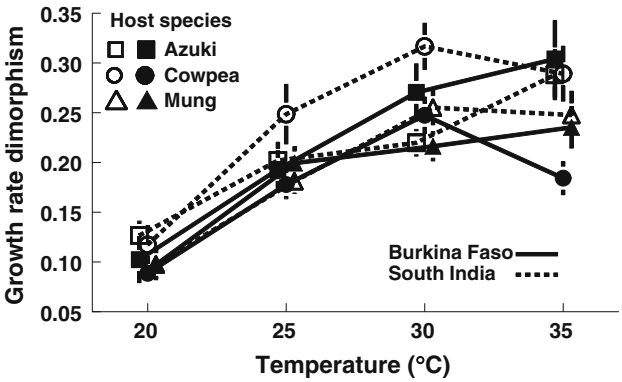

Fig. 2 Growth rate dimorphism of the Burkina Faso (*filled symbols*) and South India (*open symbols*) populations of *C. maculatus* in response to rearing on azuki, cowpea and mung at four different temperatures (mean ± 1 SEM). Growth rate was calculated as the log base 10 of mass (mg) divided by larval development time (days). Growth rate dimorphism was estimated as (mean female growth rate/mean male growth rate) − 1 for each full-sib family at each temperature

Table 1 Female and male body mass (mg; mean ± 1 SEM)[a] of the Burkina Faso and South India populations of *Callosobruchus maculatus*

	Burkina Faso		South India	
	Females	Males	Females	Males
20°C	6.46 ± 0.09	5.58 ± 0.10	7.76 ± 0.11	6.51 ± 0.10
25°C	5.96 ± 0.07	4.52 ± 0.07	6.96 ± 0.08	4.94 ± 0.07
30°C	5.46 ± 0.07	3.88 ± 0.05	6.08 ± 0.08	4.12 ± 0.05
35°C	4.98 ± 0.07	3.64 ± 0.05	5.33 ± 0.08	3.78 ± 0.06

[a] Because there is no effect of rearing host on sexual size dimorphism ($F_{2,1350} = 1.63$, $P = 0.20$), means were averaged across rearing hosts to illustrate responses to rearing temperature

Table 2 A matrix showing the percentage increase in mass of female (*above diagonal*) and male (*below diagonal*) *C. maculatus* when reared at a low temperature relative to a higher temperature ($mass_{low\ temperature} - mass_{high\ temperature} / mass_{high\ temperature}$) for each pair of temperatures[a]

	Burkina Faso				South India			
	20°C	25°C	30°C	35°C	20°C	25°C	30°C	35°C
20°C	–	8%	18%	30%	–	11%	28%	46%
25°C	23%	–	9%	20%	32%	–	14%	31%
30°C	44%	16%	–	10%	58%	20%	–	14%
35°C	53%	24%	7%	–	72%	31%	9%	–

[a] For example, South India males reared at 20°C are 72% larger than South India males reared at 35°C, 58% larger than males reared at 30°C and 32% larger than males reared at 25°C. Likewise, South India females reared at 20°C are 46% larger than South India females reared at 35°C, 28% larger than females reared at 30°C and 11% larger than females reared at 25°C

All interactions were non-significant ($F < 2.03$, $P > 0.06$) with one exception: growth rate dimorphism of SI beetles was generally greatest when reared on cowpea, while growth rate dimorphism of BF beetles was greatest when reared on azuki (Fig. 2; significant population-by-host interaction; $F_{2,1350} = 7.27$, $P = 0.0007$).

Temperature-induced variation in size dimorphism might be attributed to non-random larval mortality of males versus females (Blanckenhorn 1997). Rearing temperature had a highly significant effect on the sex ratio of emerging adults (logistic regression, $\chi^2_3 = 14.0$, $P = 0.003$); the sex ratio (proportion males) declined with decreasing temperature and became female-biased at 20°C (Fig. 3). This suggests that the pattern of dimorphism we observed may be due to differences between the sexes in mortality of large versus small beetles at high versus low temperature. There was no host ($\chi^2_2 = 0.85$, $P = 0.66$) or population ($\chi^2_1 = 2.35$, $P = 0.13$) effect on the sex ratio.

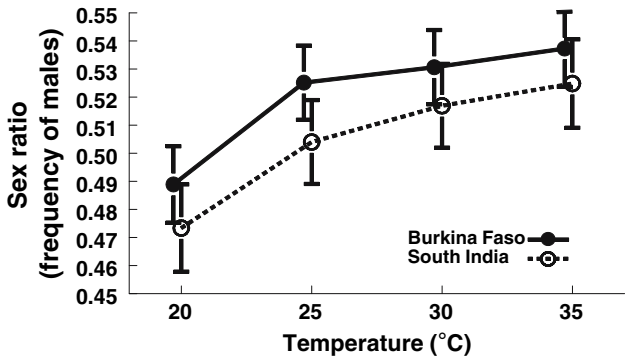

Fig. 3 Sex ratio (frequency of males) of the Burkina Faso and South India populations of *C. maculatus* reared at four different temperatures (mean ± 1 SD). For simplicity, the sex ratio was averaged across hosts because there was no host effect on the sex ratio ($\chi^2_2 = 0.85$, $P = 0.66$)

Discussion

The most important finding of our study is that males and females of the seed beetle, *Callosobruchus maculatus*, differ in plasticity of body size in response to rearing temperature but not rearing host. This gender difference in plasticity generates substantial temperature-induced variation in sexual size dimorphism. We discuss the general implications and potential causes of this pattern below.

Gender differences in phenotypic plasticity and variation in sexual size dimorphism

Sexual size dimorphism is often assumed to be invariant within species (Teder and Tammaru 2005) but recent studies have revealed that males and females can exhibit different responses to temperature (Blanckenhorn 1997; Morin et al. 1999; Fischer and Fiedler 2000, 2001; Fairbairn 2005; Teder and Tammaru 2005) and/or food quality/quantity (Mackauer 1996; Teder and Tammaru 2005) generating considerable intraspecific variation in dimorphism. A recent meta-analysis of the insect literature found that females are generally more sensitive to environmental conditions than are males (Teder and Tammaru 2005), but the opposite pattern has also been observed (Mackauer 1996; Blanckenhorn 1997; Morin et al. 1999). We found that body size of male *C. maculatus* is more sensitive to rearing temperature than is female body size, creating temperature-induced variation in sexual size dimorphism, with dimorphism being greatest at one of the intermediate temperatures (30°C) and smallest at the lowest temperature (20°C; Fig. 1). Though the degree of dimorphism changed substantially with rearing temperature, the direction did not, consistent with other studies (Teder and Tammaru 2005). However, incorporation of an increased range of temperatures could possibly change the direction of sexual dimorphism. For example, we detected the lowest degree of dimorphism at the coldest temperature but rearing at even colder temperatures, such as 15 or 10°C, could possibly change the direction of the dimorphism in *C. maculatus* if larvae are capable of surviving to adult at such low temperatures.

Environmental variation in sexual dimorphism may be generated by developmental canalization of traits of one sex against the effects of rearing temperature. For example, water striders show temperature-induced variation in dimorphism caused by sex-specific canalization of traits that are most closely associated with fitness; abdomen length in females and genital length in males (Fairbairn 2005). Similarly, temperature-induced dimorphism in *Lycaena* butterflies is caused by greater canalization of female body size, which is directly related to the female's fitness via fecundity selection (Fischer and Fiedler 2000, 2001). In contrast, male development time is more

canalized than female development time in *Lycaena*, likely because development time is more directly related to the male's fitness through selection for rapid development (protandry). In *C. maculatus*, female body size has a large effect on female fitness through fecundity selection for large females (large females lay more eggs). However, male size has less effect on adult male fitness (Savalli and Fox 1999). Because male body size exhibited more plasticity in response to rearing temperature than did female body size, it is possible that the pattern of dimorphism we observed is created by developmental canalization of female size against the effects of temperature. However, in contrast to *Lycaena*, there was no detectable sex difference in development time indicating there is no increase in canalization of development time of males relative to females against variation in temperature. Interestingly, sexual size dimorphism does not appear to vary with temperature in the seed beetle *Stator limbatus* (Stillwell and Fox 2005), a species for which body size has large effects on fitness of both males and females, consistent with the prediction of the adaptive canalization hypothesis.

Alternatively, temperature-induced variation in dimorphism of *C. maculatus* could be generated by sex-specific responses to physiological stress. The temperatures we chose were based on prior studies indicating that development and reproduction are normal at these temperatures (Chandrakantha and Mathavan 1986; Chandrakantha et al. 1987; Mbata et al. 2005). However, at the lowest (20°C) and highest (35°C) temperatures both egg-to-adult survivorship and female lifetime fecundity were lowest (Stillwell et al. 2007) suggesting that these temperatures are physiologically stressful. The degree of dimorphism was likewise smallest at the lowest (20°C) and highest (35°C) temperatures. This suggests that females may be more sensitive to developmental stress and thus may be unable to reach their target body size when reared at the lowest and highest temperatures. Such patterns could also be caused by sexual differences in larval mortality in response to temperature (Blanckenhorn 1997). Consistent with this prediction, the temperature effect we observed on sex ratio (the proportion of male emergers declined with decreasing temperature and became female-biased at the lowest temperature) indicates that at the lowest temperature (where dimorphism was smallest) males experienced greater mortality than females. This cannot be due to differences in the sex ratio at fertilization because all females laid eggs in a common oviposition environment (see Materials and methods). Thus, temperature-induced variance in sexual dimorphism may be due to smaller males experiencing greater mortality than large males at the lowest temperature. Interestingly, both size dimorphism and sex ratio decrease with increasing rearing temperature in dung flies, changing from male-biased at low temperature to female-biased at high temperature (Blanckenhorn 1997). This suggests that the effect of temperature on size-selective mortality may differ substantially between males and females, and may be responsible for generating temperature-induced patterns of dimorphism.

The difference between males and females in their sensitivity to temperature could also reflect the non-adaptive consequences of developmental differences between the sexes. Sex-specific differences in growth duration and/or growth rate during ontogeny are required to generate adult sexual size dimorphism (Badyaev 2002). The temperature-induced variation in size dimorphism we observed was matched by an identical pattern in growth rate dimorphism (and not development time) implying that the sexes achieve differences in size through diverging growth rates, a pattern that is common in arthropods (Blanckenhorn et al. 2007). However, the intricacies of how the sexes achieve such diverging growth patterns are poorly understood (Badyaev 2002). Further work is required to understand the developmental processes that produce this pattern.

The environmental dependence of Rensch's rule

A common observation in nature is that sexual size dimorphism tends to increase with increasing overall body size when males are the larger sex and decrease with body size when females are the larger sex (Fairbairn 1997); i.e., variation in male body size is greater than variation in female body size among species, or among populations within species. This pattern, called Rensch's rule, is typically assumed to be due to differential selection on males versus females, with the focus on sexual selection (Fairbairn 2005). Alternatively, variation in sexual size dimorphism consistent with Rensch's rule could be generated by differences between males and females in environmental sensitivity of traits. Though this point has been made before (Fairbairn 2005) our data illustrate this quite well. In Fig. 4 we have plotted male size versus female size with lines connecting our temperature treatments. The grey line represents isometry between male and female size. Imagining that these are populations in nature that differ only in environmental experiences and not genetic body size we would conclude that Rensch's rule is upheld when the slope of the male–female regression (reduced major axis regression) is steeper than the grey line (i.e., when $\beta > 1$) and would reject Rensch's rule when the slope is less than 1 (Fairbairn 1997; Fairbairn 2005). Note that if our field populations varied in developmental temperature only from 30 to 35°C (the smallest beetles, left end of the figure) we would conclude that the slope of the regression is less than 1 (average slope = 0.66) and thus reject Rensch's rule. In contrast, if our range of temperatures experienced in nature is typically <25°C (large beetles, right end of the figure) we would conclude that the slope is greater than 1 (average

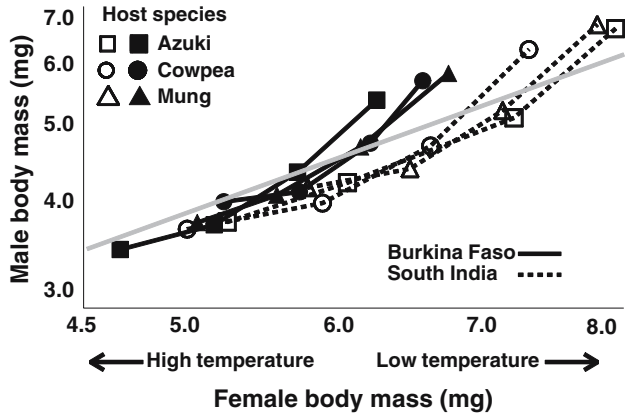

Fig. 4 Reduced major axis regression of male body mass (log scale) on female body mass (log scale) of the Burkina Faso (*filled symbols*) and South India (*open symbols*) populations of *C. maculatus* in response to rearing on azuki, cowpea and mung at four different temperatures. Lines connect the four temperature treatments, with a separate line for each rearing host species. Small beetles (*left-most points*) are those reared at high temperature and large beetles (*right-most points*) are those reared at low temperature. The *grey line* reflects a reduced major axis regression slope of 1.0

slope = 2.62) and thus Rensch's rule is upheld. Thus, as emphasized by Fairbairn (2005), it is necessary to perform common garden experiments before interpreting field patterns of dimorphism as either consistent with, or inconsistent with, Rensch's rule, especially when populations are known or expected to experience different environmental conditions in nature.

Conclusion

We found that males and females of *C. maculatus* differed in their developmental response to rearing temperature. The most important implication of our study is that environmental variables can create substantial variation in sexual size dimorphism within a species. Future studies should focus on whether this variation can be attributed to adaptive canalization of one sex against environmental variation in temperature or whether it reflects a consequence of non-adaptive developmental differences between the sexes.

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