Variation in selection, phenotypic plasticity, and the ecology of sexual size dimorphism in two seed-feeding beetles

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8.1 Introduction

Most animals show some degree of sexual size dimorphism. However, the degree and direction of dimorphism vary substantially among taxa and even among populations within species. Major progress has been made in the study of sexual size dimorphism in the last decade. Yet detailed studies on the proximate and ultimate causes of sexual size dimorphism in a single animal taxon are few (e.g. Chapters 9–20 in this volume). In this chapter we examine sexual size dimorphism in two well-studied species of seed beetle that differ in the direction of dimorphism (female-biased and male-biased) and that show substantial variation in dimorphism among populations within species. Seed beetles are an excellent system for studies of evolutionary biology because of their ease of laboratory rearing, allowing for large-scale studies that are impractical with many other organisms. We review studies on the sources of selection on body size, how this selection varies between species and among populations, and the consequences of this variation for the evolution of sexual size dimorphism.

8.2 Selection on male body size in *Stator limbatus* and *Callosobruchus maculatus*

In most insects, including seed beetles in the genus *Callosobruchus*, females are larger than males, presumably because of substantial fecundity selection on females. For insect species where males are larger than females the male-biased size dimorphism is typically associated with male–male interference competition that imposes selection for large male size. However, males are larger than females in the genus *Stator* despite an absence of direct male–male conflict. Laboratory experiments (Savalli and Fox 1998b) show that, when presented simultaneously with both large and small males, females are more likely to mate with the large male, but the effect is small and appears to be due to scramble competition among males rather than active female choice. However, this slight advantage of large males in scramble competition is likely offset by scramble competition favoring small males when flying (see the discussion on temperature, below).

So why are males larger than females in *Stator limbatus*? We have identified two sources of selection favoring large males: fecundity selection mediated via nuptial gifts, and effects of male body size on female receptivity to future matings.

8.2.1 Fecundity selection

Like many insects, male seed beetles transfer nuptial gifts to females in the form of a large volume of seminal fluid (Takakura 1999). In *Callosobruchus maculatus*, virgin males contribute 6–10% of their body mass to females during mating (Fox 1993a; Savalli and Fox 1998a), although the proportion of their mass transferred declines

substantially in subsequent matings (Fox *et al.* 1995; Savalli and Fox 1999b). Male *S. limbatus* produce similar-sized ejaculates, averaging approximately 7% of their mass (Moya-Laraño and Fox 2006). For all seed-beetle species in which nuptial gifts have been studied, substances in male ejaculates are incorporated into female eggs and somatic tissues (e.g. Boucher and Huignard 1987). Females treat these male-derived nutrients as a food source: females with limited access to food, or access to only low-quality food, increase their mating rate (Takakura 2004). Male ejaculates can also be a source of water for females (Arnqvist *et al.* 2005). These male nuptial gifts appear to have positive effects on female reproduction. For example, studies manipulating female mating frequency generally demonstrate that multiply mating females have higher fecundity (Fox 1993b; Savalli and Fox 1999a; Wilson *et al.* 1999; but see Arnqvist *et al.* 2005), increased adult lifespan (Fox 1993b; but see Savalli and Fox 1999a), and their egg size declines more slowly with age (Wasserman and Asami 1985; Fox 1993a), all consistent with females using materials in male nuptial gifts for egg production and somatic maintenance. Also, females that mate with non-virgin males (which produce smaller ejaculates than virgin males) have lower fecundity and are more likely to remate than are females that mate with virgin males (Savalli and Fox 1999a), an effect not likely due to sperm limitation.

Male nuptial gift size is positively correlated to male body size in *S. limbatus*, driving substantial fecundity selection on male body size (Savalli and Fox 1998b; Moya-Laraño and Fox 2006). Females mated to large males lay more eggs than do females mated to small males, and the effect of male body size on female fecundity is nearly as great as the effect of female body size on her own fecundity (partial R^2 is approximately 75% for both effects; Savalli and Fox 1998b). When pairs are confined together until death the total mass lost through a male's lifetime explains 32% of the variance in female fecundity, whereas female mass loss explains 36% of female fecundity, suggesting that males are contributing much of the biomass used by females to make eggs. However, the relative effects of male and female size on female fecundity varies among oviposition hosts (Czesak

and Fox 2003; Fox and Czesak 2006) and among studies. This fecundity selection on male size is clearly mediated by the size of the male nuptial gift. Using path analysis, Moya-Laraño and Fox (2006) showed that first male size has no direct effect on female fecundity. Instead, the entire effect is via the body size → ejaculate size → female fecundity pathway. Thus, in contrast to many species (but see Vahed 1998) fecundity selection acts quite substantially on male *S. limbatus* via nuptial gifts and this fecundity selection on males is similar in intensity to fecundity selection acting on females.

Although male nuptial gift size is also large and positively correlated to male body size in *C. maculatus* (Savalli and Fox 1998a), fecundity selection on male body size appears to be much weaker in *C. maculatus* than in *S. limbatus*. For example, the partial R^2 for the male size effect is only about one-third as large as that for the effect of female size on her own fecundity (Savalli and Fox 1999b). Using a different population of *C. maculatus*, Eady and Brown (2000) found a negative relationship between male size and female fecundity, whereas two further studies failed to find any relationship between male body size or nuptial gift size and female fecundity (Edvardsson and Tregenza 2005; Fox *et al.* 2007). Although nuptial gift size likely affects female reproduction and adult survival in *C. maculatus*, variation in gift size does not appear to mediate strong fecundity selection on male body size. This potentially explains the large difference in sexual dimorphism between *S. limbatus* and *C. maculatus* but raises the intriguing question of why *S. limbatus* males experience substantial fecundity selection and male *C. maculatus* do not when both species produce similarly sized ejaculates that are positively correlated with body size.

8.2.2 Female receptivity to remating

A second source of selection on male body size in *S. limbatus* is through effects of male size on female post-mating behavior. Although females show no active preference for large over small males during their first mating, females that mate with larger males are less likely to accept a second mate and have a longer refractory period before remating (Savalli and Fox 1998b; Moya-Laraño and

Fox 2006). Although sperm competition has not been studied in *S. limbatus*, second-male sperm precedence is very high in other seed beetles (Eady 1994, 1995; Eady *et al.* 2004). Thus, smaller males are likely to get fewer fertilizations than are larger males. However, a recent analysis demonstrated that nuptial-gift size has little effect on female receptivity: females were more likely to remate if the first male was small or the second male large, regardless of the size of the nuptial gift (Moya-Laraño and Fox 2006). Moreover, females mating with larger second males laid more eggs independently of the ejaculate size transferred by these males, suggesting some kind of post-mating sexual selection acting on male body size (Moya-Laraño and Fox 2006).

In contrast to *S. limbatus*, receptivity of female *C. maculatus* is not influenced by male body size (Savalli and Fox 1999b). Females are more likely to remate after mating with a non-virgin male (suggesting that male nuptial gifts do indeed affect female behavior; Savalli and Fox 1999a), if their initial copulation is short (and thus the amount of ejaculate transferred is small; Edvardsson and Canal 2006), and when food is restricted (Savalli and Fox 1999b). However, we have no evidence that this foraging for ejaculates translates into significant selection on male nuptial gift size or male body size.

8.3   Within-species variation in sexual size dimorphism

The difference in sexual size dimorphism between *Stator* and *Callosobruchus* appears to be due, at least in part, to differences in (1) fecundity selection and (2) sexual selection on male body size. However, sexual dimorphism and body size also vary substantially among populations within species (Kraushaar and Blanckenhorn 2002; Blanckenhorn *et al.* 2006; see Chapter 6). Numerous hypotheses have been proposed to account for variation in dimorphism. The most common of these is that sexual selection varies among populations (e.g. Blanckenhorn *et al.* 1995; reviewed in Fairbairn 2005). Alternatively, abiotic and other biotic factors may have different effects on males compared with females, either because the fitness consequences of body size differ between males and females 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; Stillwell and Fox, in press; see Chapter 6). For example, in *S. limbatus*, body size and sexual size dimorphism vary with latitude—beetles are smaller but more dimorphic at lower latitudes (Figure 8.1). This cline in dimorphism reflects genetic variation in body size among populations (Amarillo-Suárez and Fox 2006) and occurs because females exhibit a steeper latitudinal cline in body size than do males (R.C. Stillwell, G.E. Morse, and C.W. Fox, unpublished work), suggesting that males and females are responding differently to selection imposed by abiotic and biotic factors that covary with latitude.

We explored the potential causes of systematic geographic variation in *S. limbatus* body size and sexual size dimorphism by testing whether climatic variables (based on weather-station data) and seed size can explain the observed latitudinal clines (R.C. Stillwell, G.E. Morse, and C.W. Fox, unpublished work). In contrast to many other studies examining latitudinal clines in body size, the latitudinal cline in *S. limbatus* body size is not correlated with a gradient in mean annual temperature but instead with host-plant seed size
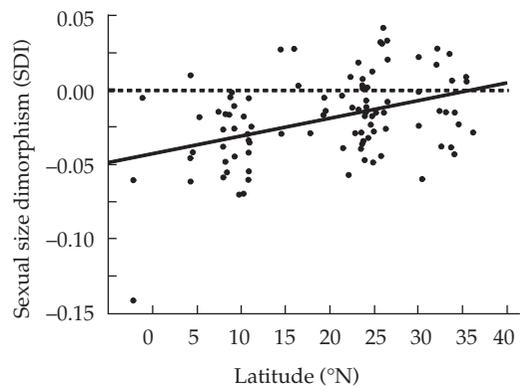
Figure 8.1   The latitudinal cline in sexual size dimorphism (pronotum width), estimated as (mean size of the larger sex/mean size of the smaller sex) − 1, made positive when females are the larger sex and negative when males are the larger sex (the SDI statistic of Lovich and Gibbons 1992), in the seed beetle *S. limbatus*. The dashed line indicates the point where populations are monomorphic (no dimorphism). Latitudes to the left of zero are located south of the equator (°S) while latitudes to the right of zero are located north of the equator (°N). Beetles are larger, but also less sexually dimorphic (the regression line approaches the dashed line), at higher latitudes. Data are based on field collections from 95 localities throughout the New World (R. C. Stillwell, G. E. Morse, and C. W. Fox, unpublished data).

(beetles are larger when adapted to large-seeded hosts), moisture/humidity (beetles are smaller in more moist/humid locations), and seasonality (beetles are larger in locations where seasonality is most pronounced). Only humidity covaries (positively) with geographic variation in sexual size dimorphism, but the cline in dimorphism persists even after removing the humidity effect, suggesting that other environmental variables are responsible for producing this dimorphism cline.

### 8.3.1 Variation in selection on male and female size

Our latitudinal cline study suggests a variety of ecological variables that may have effects on the fitness consequences of male compared with female body size, including host-plant characteristics (e.g. seed size and possibly seed quality), seasonality (including seasonal variation in temperature), and humidity. Below we explore how these variables affect selection on body size in *S. limbatus* and *C. maculatus* and, most importantly, examine whether these variables have different effects on the fitness consequences of male and female size.

Host plant affects selection on male and
female body size
Both *C. maculatus* and *S. limbatus* are generalist feeders. *S. limbatus* uses more than 70 legume species as hosts. The natural diet of *C. maculatus* is less broad; their natural hosts are all in the genus *Vigna*, but beetles have colonized a wide variety of agricultural crops to which they rapidly adapt. These various hosts of *S. limbatus* and *C. maculatus* vary substantially in seed size and quality. Beetles develop from egg to adult completely inside a single seed so the resources available for development depend greatly on seed size and the density of larvae inside the seed. Beetle populations have evolved considerably in growth, life history, and behavior in response to their local hosts. For example, we commonly study a *C. maculatus* population from Burkina Faso (BF) adapted to the large-seeded cowpea (*Vigna unguiculata*) and one from South India (SI) adapted to the small-seeded mung bean (*Vigna radiata*). Although females are larger than males in both populations, the SI

population is more sexually dimorphic than the BF population (Stillwell and Fox in press). In a recent experimental evolution study, replicate SI populations were allowed to adapt to cowpea (the host of the BF beetles). These new cowpea-adapted beetles evolved to be smaller and less sexually dimorphic than the ancestral populations maintained on their native host (mung), consistent with the difference between the SI and BF populations (Messina 2004). Apparently the switch in rearing host changed the relative magnitude of selection on male and female body size, driving the evolution of sexual dimorphism. Exactly how selection changed is unknown but female size evolved faster than male size, suggesting greater sensitivity of female body size-mediated effects on fitness to larval competition and resource availability (Messina 2004).

Body size and sexual dimorphism also vary among host plants for *S. limbatus*. Two of the most common seeds used in the Sonoran desert of the southwestern USA are cat-claw acacia (*Acacia greggii*) and blue paloverde (*Parkinsonia florida*). Using path analysis, Fox and Czesak (2006) showed that this difference in selection on egg size indirectly affects the relative magnitude of selection on male versus female body size (Figure 8.2). When females lay their eggs on seeds of *A. greggii*, larval survival is very high and not affected by egg size. Because fecundity selection is of similar magnitude on male and female body sizes, total selection on male and female body sizes are nearly identical when eggs are laid on seeds of *A. greggii*. In contrast, when offspring are reared on seeds of *P. florida*, egg size affects offspring survival (larvae from small eggs die while trying to penetrate the seed; Fox and Mousseau 1996; Fox *et al.* 2001) and, consequently, directly affects parental fitness. Because egg size is affected by female size, there is selection on female body size through both the fecundity (body size → fecundity → fitness) and egg size (body size → egg size → fitness) paths. However, egg size is not correlated with male body size such that selection on egg size does not translate into indirect selection on male size. Thus, because of the difference in seed suitability for larval development, (1) total selection on male body size is much lower when eggs are laid on
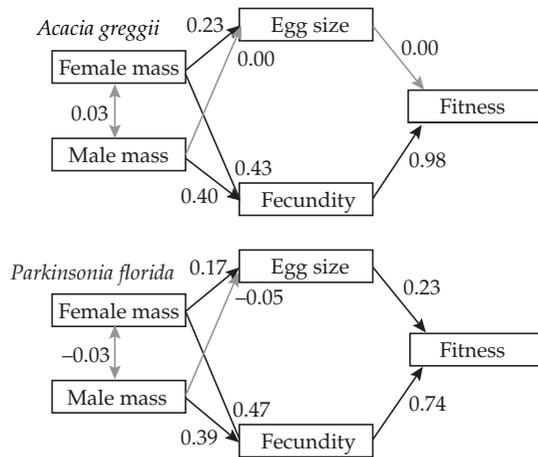
Figure 8.2 Path analysis showing how oviposition host affects the magnitude of selection on body size in the seed beetle *S. limbatus*. Black paths are statistically significant and gray paths are non-significant. Fitness is defined as the number of larvae produced that successfully survive until completely inside their host seed. All standard errors are less than 0.035. From Fox and Czesak (2006).

seeds of *P. florida* and (2) the host upon which females lay their eggs causes a large change in the relative magnitude of selection on male compared with female size by an amount similar in magnitude to the median total amount of directional selection observed in nature in studies of morphological traits (Kingsolver *et al.* 2001). This shift in relative selection on males and females is a consequence of where females lay their eggs, independent of any changes in male or female investment into reproduction, variation in sexual selection, or any other direct effects on adult beetles. It is caused by variation among hosts in offspring survival and not caused by differential mortality of males and females, large or small beetles, or any direct effect of male size on fitness. We suspect that variation among hosts in such indirect selection on body size is a major source of variation in selection on *S. limbatus* in nature.

Temperature affects selection on male body size
Although male seed beetles appear to experience very little direct contest competition for females, they are under intense (scramble) competition to find mates. Laboratory experiments with *S. limbatus* have demonstrated that selection favors small males because these males can reach potential

mates more quickly than can large males. The advantage of being small is especially great at low temperature (20 compared with 30°C; J. Moya-Laraño, M. El Tigani El-Sayyid, and C.W. Fox, unpublished work). This strong selection against large males at low temperature is probably due to their decreased ability to initiate flight: at low temperature large males take off much more slowly than do small males, whereas there is no difference at high temperature. Because temperature and diel variation in temperature vary among *S. limbatus* populations, we interpret these scramble competition results as evidence that variation in temperature can alter the fitness consequences of male body size. Although females also fly to search for host seed pods, plants are sedentary, such that the selection for rapid take-off is likely to be less. The mechanism for the temperature effect on male flight is not yet known. However, if beetles generate metabolic heat to warm up flight muscles, smaller beetles may more quickly reach the minimum muscle temperature required to take off, a relationship observed for other insects (Harrison and Roberts 2000).

8.3.2 Sex differences in phenotypic plasticity in body size
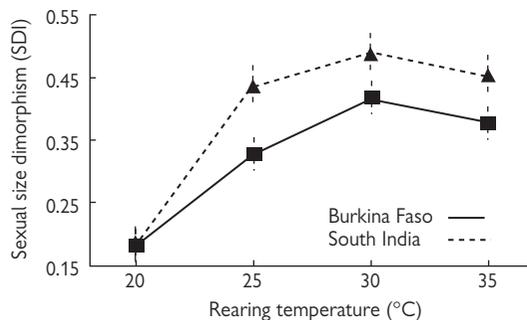
Body size can be highly plastic in response to rearing conditions. Two of the most important environmental factors affecting plasticity in body size of ectothermic animals are diet and temperature (Nylin and Gotthard 1998; Angilletta and Dunham 2003). Variation among populations in sexual size dimorphism can be produced when environmental conditions vary among populations and males and females exhibit different responses to these environmental variables (differential-plasticity hypothesis; Fairbairn 2005).

Effect of temperature on sexual size dimorphism
In most ecotherms, body size increases with decreasing rearing temperature (Angilletta and Dunham 2003). Females and males generally exhibit plastic responses that are in the same direction but the sexes can differ in their sensitivity to rearing temperature, generating temperature-induced variation in dimorphism. In *C. maculatus*,

males reared at 20°C were on average 63% larger than males reared at 35°C, whereas females were only 38% larger (Stillwell and Fox, in press). This creates substantial variation in sexual dimorphism across rearing temperatures (Figure 8.3). This plasticity is caused primarily by sex differences in growth rate: growth rate increased with rearing temperature but females grew approximately 25% faster than males when reared at 30°C and only approximately 9% faster when reared at 20°C (Stillwell and Fox, in press), a pattern observed for other arthropods (Blanckenhorn et al. 2007).

The effect of temperature on growth rate and body size typically differs between male and female insects (Chapter 20) but the causes of this difference are unknown. In beetles, temperature may have non-random effects on larval mortality of large and small phenotypes. The proportion of males to females emerging successfully declines with decreasing temperature and becomes significantly female-biased at 20°C. If smaller males are experiencing greater mortality at low temperature, then temperature-mediated non-random mortality could generate the observed temperature effect on dimorphism (Stillwell and Fox, in press). Size dimorphism likewise changes with temperature in dung flies, concurrent with a change in sex ratio of emerging flies, suggesting that temperature may likewise shift the relative magnitude of larval mortality of large and small flies (Blanckenhorn 1997a).
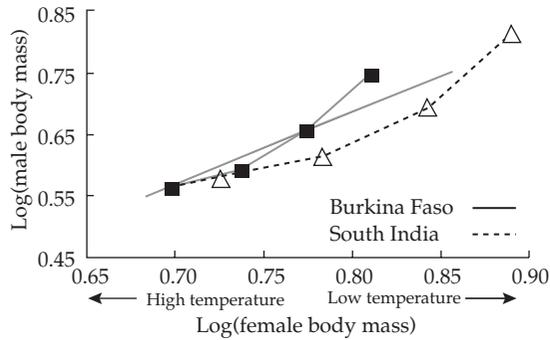
Alternatively, temperature-induced variation in dimorphism could reflect greater canalization of female body size against environmental perturbation, which may be adaptive because of the large effect female body size on fecundity (Fairbairn 2005). Recent work on butterflies supports this hypothesis (Fischer and Fiedler 2000, 2001). Because male size has little effect on male fitness in C. maculatus (Savalli and Fox 1999b) male size might be less canalized and thus more susceptible to environmental conditions, as observed in our study. Interestingly, sexual size dimorphism does not appear to vary with temperature in S. limbatus (Stillwell and Fox 2005), the species for which body size has large effects on fitness of both males and females, consistent with the prediction of the adaptive canalization hypothesis.

Implications of phenotypic plasticity in body size for Rensch's rule

A common phenomenon observed in almost all animals is that male body size varies more than female size among species, or among populations within species, a pattern known as Rensch's rule (Fairbairn 1997; see Chapter 6). This pattern is generally assumed to be due to differences in selection on males and females but, when applied to variation within species, could also be generated by sex differences in plasticity of body size (Fairbairn 2005). To illustrate this point, Figure 8.4 depicts a plot of male size against female size for two populations of C. maculatus reared at a variety of temperatures (Stillwell and Fox, in press). Suppose that each rearing temperature represents a different field population and that these populations do not differ genetically in size but do vary in the temperatures that larvae experience during development. If our field populations varied in temperature only between 30 and 35°C we would conclude that female body size varies more among populations than does male body size, as the slope of the regression of male size against female size would be <1, opposite to Rensch's rule. In contrast, if our range of temperatures experienced in nature was <25°C we would conclude that male body size varies

Figure 8.3 The effect of temperature on sexual size dimorphism of two populations of C. maculatus, estimated as (mean female size/mean male size) − 1. Dimorphism was calculated separately for each family, then averaged across families. The figure pools data from three different rearing hosts; rearing host did not affect dimorphism in this study (R.C. Stillwell and C.W. Fox, unpublished work).

Figure 8.4 Reduced major-axis regression of log(male body size) on log(female body size) for two populations of *C. maculatus* reared at four different temperatures. Lines connect the four temperature treatments for each population. Small beetles are those reared at high temperature and large beetles are those reared at low temperature. The gray line denotes the linear reduced major-axis regression slope of 1.0 through all points. Note that the slope of the relationship changes non-linearly from <1 to >1 depending on which pair of temperatures we compare (R.C. Stillwell and C.W. Fox, unpublished work).

more among populations than does female body size, as the slope of the regression would be >1, following Rensch's rule. However, both conclusions would be wrong: our populations do not differ genetically in body size, only in the temperatures experienced by larvae during development. Hence, sex differences in plasticity can severely impact evaluations of Rensch's rule (Fairbairn 2005).

8.4 Evolutionary genetics of sexual size dimorphism

Adaptive hypotheses for the evolution of sexual size dimorphism assume that organisms can evolve quickly in response to changing patterns of selection. Indeed, when genetic and phenotypic variances are the same for the sexes, the rate of evolution of dimorphism will be a function of the difference in selection on male and female body size (Reeve and Fairbairn 2001; Badyaev 2002). However, some researchers have argued that patterns of dimorphism may be better explained by genetic constraints, such as phylogentic inertia, allometry, and genetic correlations between the two sexes (Cheverud *et al.* 1985; Cowley *et al.* 1986; Fairbairn 1997).

The degree to which body size of males and females can evolve independently can be quantified as a cross-sex genetic correlation, r_G. When r_G is non-zero selection on one sex will necessarily affect evolution of the opposite sex (Lande 1980a) and if r_G is high then sexual size dimorphism will evolve very slowly. When r_G is 1.0 then sexual dimorphism can evolve only if the genetic and/or phenotypic variance for body size differs between males and females (see below; Reeve and Fairbairn 2001; Badyaev 2002). Experimental studies have consistently demonstrated that between-sex genetic correlations (r_G) for body size are quite high (generally >0.80) but that they vary substantially among taxa (Roff 1997) and even within studies depending on the trait used to estimate body size (Cowley *et al.* 1986; del Castillo 2005; Chapter 9). For *C. maculatus* we estimated r_G for body mass using data from a variety of full-sib and half-sib experiments conducted by Fox and colleagues over the last 16 years. All estimates were >0.80 and only one estimate differed significantly from 1.0 (Fox 1994). Likewise, for *S. limbatus*, estimates of r_G were all >0.95 and not significantly less than 1.0, with one exception (Fox 1998). Also, r_G does not vary with temperature or host species (R.C. Stillwell and C.W. Fox, unpublished work); the between-sex r_G is approximately 1.0 at all temperatures and on all hosts upon which beetles were reared, suggesting that environmental effects on r_G are unlikely to be a major influence on the rate and trajectory of dimorphism evolution.

But how much do high genetic correlations constrain the evolution of sexual size dimorphism? High genetic correlations do not constrain males and females from ultimately attaining their 'optimal' body size unless $r_G = 1.0$ (Lande 1980a; Reeve and Fairbairn 2001), but r_G does affect the rate and trajectory of body size and dimorphism evolution (Fry 1996). Yet we know that dimorphism can evolve very quickly in *C. maculatus*, despite very high values of r_G: Messina (2004) demonstrated substantial evolution of dimorphism after just 40 generations of natural selection following a host shift. Why? First, r_G is only one of the important genetic parameters for the evolution of dimorphism. Despite high genetic correlations between the sexes, sexual size dimorphism can evolve when

the heritability (h^2) or phenotypic variance (V_P) for body size differ between the sexes (Reeve and Fairbairn 1996, 2001; Badyaev 2002). It is common to find that genes have sex-specific effects in *Drosophila*, and several studies (including seed beetles) have shown that genetic architecture changes with rearing conditions (Kawecki 1995; Guntrip *et al.* 1997), but the heritability of body size in *C. maculatus* and *S. limbatus* rarely differs between males and females (Fox 1994, 1998; Fox *et al.* 2004; R.C. Stillwell and C.W. Fox, unpublished work). Studies on other seed beetles likewise suggest that h^2 for body size and genetic covariances between body size and other traits (such as development time) are similar for both sexes (Tucić *et al.* 1998; Šešlija and Tucić 2003). Thus, neither sex differences in h^2 or V_P for body mass, nor changes in h^2 or V_P in males relative to females associated with a change in diet, are likely explanations for the rapid evolution of dimorphism in Messina's study (2004).

A more likely explanation for why the high genetic correlation between males and females is not a major constraint on the evolution of sexual size dimorphism is that genetic correlations are not good predictors of correlated responses to selection when few loci contribute to differences between the sexes. Most quantitative genetic modeling is based on the Gaussian infinitesimal model, in which r_G is a very good predictor of correlated responses to selection regardless of the direction of selection and the trait on which selection acts. However, real-world traits are affected by a finite number of genes that often have asymmetric effects on the two sexes. When the number of loci affecting two traits is finite and the pleiotropic effects of alleles at those loci are asymmetrical (i.e. some loci have large effects on only one sex) then r_G poorly predicts correlated responses to selection (Czesak *et al.* 2006); even when r_G is 1.0 dimorphism can evolve rapidly, or fail to evolve, depending on the genetic architecture underlying the genetic correlation.

8.5   Future directions and summary

Studies with seed beetles have shown that variation in sexual size dimorphism observed within and among species of seed beetles is due to both differences in the sources of selection on males and females and differential phenotypic plasticity of the sexes. However, our studies also raise a variety of exciting unanswered questions, as follows.

• Male ejaculate size clearly affects male fitness in *S. limbatus*, via both fecundity and sexual selection, imposing selection on male size. In contrast, neither of these sources of selection appears to be significant in *C. maculatus*. This difference in selection can contribute to explaining the difference in size dimorphism between species but leaves us wondering why male *C. maculatus* produce such large ejaculates.

• Female *S. limbatus* lay more eggs when mating with large males. Does this reflect direct nutritional benefits obtained from male ejaculates or increased allocation of resources by females following mating with large males?

• Variation in body size among populations probably reflects genetically based differentiation in most species. However, plasticity in body size is the norm rather than the exception, and the degree of plasticity frequently differs between the sexes, at least for some environmental variables. Why does plasticity in body size frequently differ between the sexes, and how much does this sex difference in plasticity influence patterns of dimorphism observed in nature (see Fairbairn 2005)?

• A substantial literature is developing on how genetic and phenotypic covariance matrices (i.e. V_G, h^2, and r_G) vary among species and among populations within species. However, few studies have examined how genetic covariance matrices, and sex differences in genetic covariance matrices, vary with environmental conditions. Yet environmental effects on these genetic parameters can have substantial influence on the evolutionary dynamics of sexual dimorphism and may provide an explanation for evolutionary dynamics observed in nature.

8.6   Acknowledgments

8.7 Suggested reading

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Fairbairn, D.J. (2005) Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider *Aquarius remigis*. *American Naturalist* **166**, S69–S84.

Teder, T. and Tammaru, T. (2005) Sexual size dimorphism within species increases with body size in insects. *Oikos* **108**, 321–334.