

# SEXUAL DIMORPHISM IS ASSOCIATED WITH POPULATION FITNESS IN THE SEED BEETLE *CALLOSOBRUCHUS MACULATUS*

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The population consequences of sexual selection remain empirically unexplored. Comparative studies, involving extinction risk, have yielded different results as to the effect of sexual selection on population densities make contrasting predictions. Here, we investigate the relationship between sexual dimorphism (SD) and population productivity in the seed beetle *Callosobruchus maculatus*, using 13 populations that have evolved in isolation. Geometric morphometric methods and image analysis are employed to form integrative measures of sexual dimorphism, composed of variation in weight, size, body shape, and pigmentation. We found a positive relationship between SD and adult fitness (net adult offspring production) across our study populations, but failed to find any association between SD and juvenile fitness (egg-to-adult survival). Several mechanisms may have contributed to the pattern found, and variance in sexual selection regimes across populations, either in female choice for “good genes” or in the magnitude of direct benefits provided by their mates, would tend to produce the pattern seen. However, our results suggest that evolutionary constraints in the form of intralocus sexual conflict may have been the major generator of the relationship seen between SD and population fitness.

**KEY WORDS:** Bruchidae, intralocus conflict, larval fitness, mating system, population density.

Theories of sexual selection assume direct and indirect costs and benefits to the individuals involved (Promislow 1992; Promislow et al. 1992; Andersson 1994; Høglund and Sheldon 1998; Brooks 2000; Gavrillets et al. 2001; Arnqvist and Rowe 2005). Any cost or benefit that affects the fecundity and survival at the level of the individual is likely to have important effects at the level of the population. Theory suggests that the rate of fixation of beneficial alleles may increase under sexual selection (Whitlock 2000; Lorch et al. 2003) and that deleterious alleles may be purged more rapidly (Agrawal 2001; Siller 2001). These effects would both tend to ele-

vate population fitness. In contrast, several other models show that sexual selection can instead impose a net reproductive load on populations (Lande 1980; Kirkpatrick 1982; Tanaka 1996; Gavrillets et al. 2001; Houle and Kondrashov 2001), and thus depress population fitness (Arnqvist and Rowe 2005). Yet, the population consequences of costs involved in sexual selection still remain relatively unexplored empirically (Kokko and Brooks 2003).

Male harassment, where males act aggressively toward females to gain access to matings, is very likely to have a negative impact on female fitness and population density (see Arnqvist and Rowe 2005; Rankin and Kokko 2007). These costs may come in the form of direct female mortality by male harassment (e.g., Réale et al. 1996; Le Galliard et al. 2005; Rankin and Kokko 2006), toxic seminal fluid (e.g., Chapman et al. 1995; Rice 1996), or harmful

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morphologies (e.g., Crudginton and Siva-Jothy 2000). As the costs of male harm will affect female survival and fecundity, females are expected to evolve resistance (Arnqvist and Rowe 2002; Wigby and Chapman 2004), which is likely to lessen the detrimental effects of sexually antagonistic adaptations at the level of the population (Rönn et al. 2007).

If male reproductive success is negatively correlated with offspring survival, we expect negative fitness effects of mating with attractive males (Brooks 2000). A dramatic illustration of this is the Japanese medaka fish *Oryzias latipes*, where transgenic males are preferred by females despite the fact that the fitness of offspring between transgenic males and wild-type females is very low (Howard et al. 2004). If this preference is maintained over a number of generations, then the end result could be an overall reduction in population fitness, possibly leading to extinction (Muir and Howard 1999; Howard et al. 2004).

If male reproductive success is positively correlated with offspring survival, theory suggests that indirect benefits from female choice may elevate population fitness (see references above). However, direct benefits provided by males may also have a positive impact on both female fitness and population fitness. For example, nuptial gifts provide direct benefits in terms of extra nutrition, which may enhance female survival (e.g., Arnqvist and Nilsson 2000; Møller and Jennions 2001), whereas male parental investment can provide a direct benefit to offspring survival (Houston et al. 2005). Such effects should increase productivity and lead to higher population fitness.

Despite the potential for sexual selection to have a multitude of effects on population processes, there is almost a complete lack of empirical studies testing for such relationships. There have been a few interesting comparative studies of the risk of extinction, but the results of these studies are not entirely consistent. Although some studies have suggested an influence of sexual selection in extinction risk (Doherty et al. 2003; Morrow and Pitcher 2003), others have failed to find such a relationship (Prinzing et al. 2002; Morrow and Fricke 2004). The variation in these results is likely to be due to the variety of possible mechanisms by which sexual selection may operate, each one having a distinct impact at the population level. Additionally, sexual selection may have fairly subtle influences on population fitness, and this signal may not necessarily be picked up by relatively crude data on extinction risks. Therefore, experiments that explicitly look at the influence of sexual selection on demography are preferable.

There are two ways to quantify sexual selection in comparative studies. The first is to secure direct estimates of sexual selection by looking at selection gradients in extant populations. This has the obvious benefit of providing direct measures of sexual selection. However, it is also problematic because estimates of sexual selection gradients depend on a range of parameters, such as environmental conditions and the traits measured, and

because sexual selection gradients are known to vary both temporally and spatially (Kingsolver et al. 2001). The second, and most commonly used measure involves taking the degree of sexual dimorphism (SD) as a proxy for overall intensity of sexual selection (for a few examples see Darwin 1871; Promislow 1992; Badyaev 1997; Gage et al. 2002; Morrow and Pitcher 2003; Morrow et al. 2003; Morrow and Fricke 2004). The major benefit of this approach is that it provides a more integrative measure that should be correlated with the overall strength of sexual selection in the past (e.g., Székely et al. 2000). The main limitation is that it is indirect, and that SD may in part reflect other forms of sex-specific selection (such as sex-specific natural selection) or sex-specific evolutionary constraints.

Here, we follow the second line of inquiry and compare different distinct populations of the seed beetle *Callosobruchus maculatus*. We use a variety of morphological measures of sexual dimorphism, as putative indicators of the strength of sexual selection. We then use two measures of population fitness, juvenile and adult fitness, to relate how SD is associated with population level traits.

Our rationale partly relies on differences in sexual selection regimes across populations in this species. Previous research has provided ample support for this assumption. In particular, many key mating system parameters have been shown to vary considerably across different seed beetle populations (e.g., female mating propensity: [Fricke and Arnqvist 2004]; the degree of female polyandry: [Fricke and Arnqvist 2004; Harano and Miyatake 2005, 2007]; the cost of mating to females [Rönn et al. 2006]; male ejaculate allocation [Savalli et al. 2000; Yamane and Miyatake 2005]; the degree of last male sperm precedence: [Brown and Eady 2001]) and these should be associated with differences in sexual selection regimes. Further, the seed beetle *C. maculatus* exhibits striking sexual dimorphism, not only in body size and shape but also in the pattern of pigmentation and antennal morphology as well as in the pattern of ageing (Southgate et al. 1957; Rup 1988; Bandara and Saxena 1995; Mbata et al. 1997; Savalli and Fox 1999; Fox et al. 2003; Colgoni and Vamosi 2006). It has also been shown that genetic correlations in life-history characters between the sexes differ between populations (Fox et al. 2004), and several studies of seed beetles have also documented sexual selection on size-related traits in males (e.g., Savalli and Fox 1998, 1999; Savalli et al. 2000; Czesak and Fox 2003; Moya-Laraño and Fox 2006).

## Methods

### POPULATION FITNESS

We used the following 13 populations of *C. maculatus*: Benin, Brazil/USA, California, Mali, Nigeria/Lossa, Nigeria/OYO, Nigeria/Zaire, Oman, Uganda, Upper Volta, IITA, South India, and Yemen. Each of these populations represents a different wild-type

stock brought into the laboratory at various times. All populations had, however, been reared in our laboratory for at least 4 years prior to starting our experiments, and so should be well adapted to the laboratory conditions used: all beetles used were kept on, and adapted to, black-eyed beans (*Vigna unguiculata*) and were held in incubators under constant conditions at  $30 \pm 0.5^\circ\text{C}$  and  $60 \pm 10\%$  RH with a 12:12 h L:D cycle. Further, the populations used are known to be genetically distinct. For example, sequencing of 553 bp of CO II (mtDNA) of nine of these populations revealed a very high proportion of variable sites (approximately 15%) (G. Arnqvist, unpubl. data).

Beetles used in these fitness assays were collected as virgin adults from parental populations standardized to 250 parental individuals reared on 120 g of medium (black-eyed beans) to reduce any impact that population-specific maternal effects might have, due to differing amount of resources per individual. We set up six replicates per population, each replicate consisting of a group of 10 virgin males and 10 virgin females all of whom were collected immediately after hatching. Each group was placed in a 15 cm  $\varnothing$  petri dish provided with 100 mL of black-eyed beans, which is equivalent to approximately 60 beans per female. Because females lay on average 60–80 eggs each, our design minimizes effects of larval competition within beans on offspring production: there was just over one individual larvae per bean on average (Toquenaga and Fuji 1990). All adults from each replicate were counted after 37 days, after excluding the 10 males and 10 females introduced from the original adult population but including those hatched from the juvenile fitness assay (see below), and the average offspring production per replicate was used as our measure of population fitness. We note that our design minimizes any impact that variation in within-bean density-dependent larval competition behavior across populations might have on population fitness (Toquenaga and Fuji 1990), because (1) all populations were similarly well adapted to black-eyed beans, a large food item for these insects, prior to our assays and (2) density was low enough to avoid larval competition.

#### JUVENILE FITNESS

We used the following method to derive an estimate of egg-to-adult survival for each population. After the parental adults in the population fitness assay described above had laid their eggs and died (at day 15), 25 beans, with more than one egg per bean, were collected from each replicate and population and placed into separate, isolated chambers, in a subdivided petri dish. The number of eggs laid on each bean and the number of adults subsequently emerging from each bean were counted. We then divided the number of adults emerged by the number of eggs laid per replicate (i.e., egg-to-adult survival) and the average of this ratio per population was used as a measure of juvenile fitness. The number of hatching adults was log transformed, and egg-to-adult survival was arcsine

transformed, prior to statistical inference to stabilize variances and meet the assumptions of the inferential models used.

#### SEXUAL DIMORPHISM

We quantified four distinct types of sexual dimorphism. (1) For each population, we weighed 15 beetles of each sex, using the animal weighing function on a Sartorius Genius microbalance (Sartorius AG, Goettingen, Germany). The individuals were collected and frozen as soon as they emerged, and were dried prior to weighing. The average weight across all individuals was taken as the population-specific individual weight and the average weight of males divided by the sum of average weights of males and females as the degree of SD in weight.

For each population, we also captured digital images of the same 15 beetles used for weighing, of each sex in dorsal view under standardized illumination and positioning, using a Leica MZ8 digital camera (Leica Microsystems GmbH, Wetzlar, Germany) mounted on a dissecting microscope. These measures were taken prior to drying the beetles, and we used the same beetles to gain a more accurate picture of how the different indicators of dimorphism varied across populations. We then traced the two-dimensional outline of the elytra of each beetle using TpsDig (<http://life.bio.sunysb.edu/morph/>). (2) We measured the enclosed area of the elytra, and the average area across all individuals were taken as the population-specific elytral size and the average elytral size of males divided by the sum of average elytral sizes of males and females as the degree of SD in size of elytra. (3) The outlines of all individuals were then subjected to one common elliptic Fourier analysis (see Rohlf 1992 for details), using 20 harmonics, implementing the software package EFAWin (<http://life.bio.sunysb.edu/morph/>). The dimensionality of the resulting matrix of Fourier coefficients was subsequently reduced by means of a factor analysis, based on the covariance matrix in which the first five principal components (collectively explaining >96% of the variance in Fourier coefficients) were retained for further analysis. These five principal components form a multi-dimensional space collectively describing the existing variation in elytral shape. For each population and sex, we then calculated the average score on each principal component. Males and females from all populations were then ordinated in the multidimensional space described by the five principal components, and the Euclidean distance between males and females were taken as our measure of SD in shape of elytra (see Arnqvist 1998 for an analogous analytical strategy).

Finally, (4) we recorded the pigmentation of the elytra of all beetles, by recording grayscale histogram data in the image analysis package Image J (<http://rsb.info.nih.gov/ij/>). The dimensionality of the resulting data on pigmentation was again reduced by means of a factor analysis, based on the covariance matrix in which we retained the first five principal components

(collectively explaining >94% of the variance in pigmentation). For each population and sex, we then calculated the average score on each of these principal components. Males and females from all populations were then ordinated in the multidimensional space of variation in pigmentation described by these five principal components, and the Euclidean distance between males and females was taken as our measure of SD in pigmentation of elytra.

## Results

Multivariate analysis of variance (MANOVA), using the five shape factors as response variables, confirmed that there was extensive variation across populations (population: Wilks'  $\lambda = 0.440$ ,  $F_{60,1591} = 5.09$ ,  $P < 0.001$ ) and between the sexes (sex: Wilks'  $\lambda = 0.519$ ,  $F_{5,339} = 62.80$ ,  $P < 0.001$ ) in the shape of elytra. Moreover, SD in the shape of elytra differed across populations (population  $\times$  sex: Wilks'  $\lambda = 0.758$ ,  $F_{60,1591} = 1.616$ ,  $P = 0.002$ ). Similarly, MANOVA of the five pigmentation factors showed that both populations (population: Wilks'  $\lambda = 0.117$ ,  $F_{60,1619} = 15.66$ ,  $P < 0.001$ ) and sexes (sex: Wilks'  $\lambda = 0.323$ ,  $F_{5,345} = 144.71$ ,  $P < 0.001$ ) differed in pigmentation of elytra and that the degree of SD in pigmentation differed across populations (population  $\times$  sex: Wilks'  $\lambda = 0.247$ ,  $F_{60,1619} = 9.393$ ,  $P < 0.001$ ). Using the area of the elytra and the weight of the beetle as response variables in a MANOVA confirmed that there was variation across populations (population: Wilks'  $\lambda = 0.7116$ ,  $F_{12,359} = 5.53$ ,  $P < 0.001$ ) and between the sexes (sex: Wilks'  $\lambda = 0.583$ ,  $F_{1,370} = 132$ ,  $P < 0.001$ ) but SD did not differ significantly across populations for these two traits collectively (population  $\times$  sex: Wilks'  $\lambda = 0.941$ ,  $F_{12,1591} = 0.893$ ,  $P = 0.613$ ). Univariate analyses of variance did, however, reveal significant differences in SD in weight (population  $\times$  sex:  $F_{12,360} = 1.84$ ,  $P = 0.041$ ) but not in the area of the elytra (population  $\times$  sex:  $F_{12,343} = 0.79$ ,  $P = 0.656$ ) across populations. Finally, univariate analyses of variance showed that both juvenile fitness ( $F_{12,1805} = 2.61$ ,  $P = 0.002$ ) and population fitness ( $F_{12,65} = 6.21$ ,  $P < 0.001$ ) differed significantly across populations.

To avoid problems due to multicollinearity when analyzing the effects of SD on fitness across populations, we first reduced the

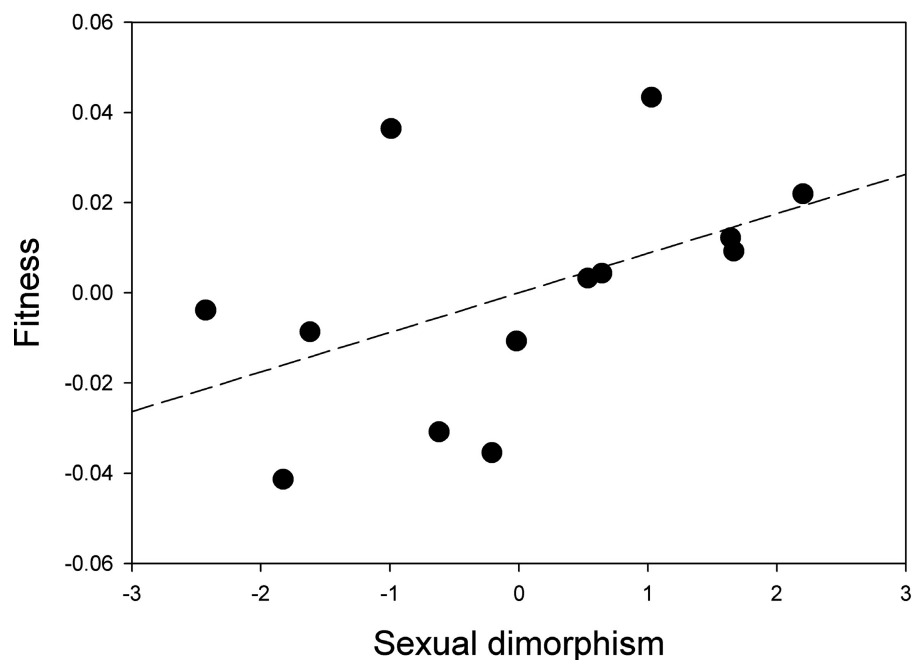
number of SD variables from four to two in a principal component analysis based on the correlation matrix. The first principal component accounted for 52.8% of total variance in SD and primarily captured variation in SD in overall dimensionality (component loadings; SD in weight: 0.98, SD in size of elytra: 0.90, SD in shape: 0.32, SD in pigmentation:  $-0.48$ ), and will be referred to here as SD in size. The second principal component accounted for 26.5% of total variance in SD and correlated primarily with variation in SD in shape (component loadings; SD in weight: 0.01, SD in size of elytra: 0.05, SD in shape: 0.81, SD in pigmentation: 0.64), and will be referred to here as SD in shape.

Population fitness was only weakly, and not significantly, correlated with juvenile fitness across populations ( $r = 0.356$ ,  $N = 13$ ,  $P = 0.233$ ). We analyzed the independent effects of overall morphology and SD on fitness using conventional multiple regression models. To assess associations between SD and different components of fitness, we first partitioned population fitness (total offspring production) into juvenile fitness, represented by the probability of eggs surviving to become adults, and adult fitness, represented by the number of offspring produced while statistically controlling for egg-to-adult survival. Our inferential models are presented in Table 1. The number of years since a population was brought into the laboratory did not significantly improve the fit of either of these two models (partial  $F$ -tests;  $P > 0.4$  in both cases).

Although juvenile fitness differed significantly across populations (see above), this variation was not significantly related to any morphological metric. In contrast, variation in adult fitness across populations was well explained by variation in morphology (see Table 1). Both overall weight and size of elytra had substantial and independent effects on adult fitness, such that populations characterized by adult beetles that were larger (i.e., had a larger elytra) relative to their weight had a higher offspring production. More importantly, SD in size was significantly and positively related to adult fitness. Populations with a higher degree of SD in size exhibited higher adult fitness (see Figure 1). In theory, this could be due to correlated evolution between adult fitness and (1) male morphology, (2) female morphology or (3) both male

**Table 1.** Multiple regression models of the effects of weight, size and sexual dimorphism on juvenile and adult fitness (overall  $F$ -tests of entire models at the bottom).

	Juvenile fitness				Adult fitness			
	$\beta$	$SE_{\beta}$	$T$	$P$	$\beta$	$SE_{\beta}$	$t$	$P$
Weight	0.148	0.199	0.743	0.479	-0.233	0.059	3.915	0.006
Size of elytra	-0.003	0.007	0.424	0.682	0.008	0.002	3.917	0.006
SD in size	-0.018	0.018	0.977	0.357	0.014	0.006	2.557	0.038
SD in shape	-0.000	0.028	0.006	0.995	0.014	0.008	1.735	0.126
Egg-to-adult survival	-	-	-	-	0.293	0.102	2.867	0.024
	$(F_{4,8} = 0.344, P = 0.841, R^2 = 0.147)$				$(F_{5,7} = 4.409, P = 0.039, R^2 = 0.759)$			



**Figure 1.** Visualization of the relationship between adult fitness and the degree of sexual dimorphism in size (i.e., PC1) across all 13 populations. Hatched line represents an ordinary least-squares regression. Here, adult fitness represents residuals from a multiple regression of population fitness, including average weight, size of elytra and egg-to-adult survival as independent variables (see Table 1 for statistical evaluation).

and female morphology. We estimated the independent effects of male and female morphology on fitness in a multiple regression model of population fitness, including egg-to-adult survival, male weight and size of elytra and female weight and size of elytra as independent variables ( $F_{5,7} = 3.672$ ,  $P = 0.058$ ,  $R^2 = 0.723$ ). In this model, the two standardized regression coefficients for male morphology ( $\beta$ 's for weight and size:  $-0.21$  and  $0.94$ , respectively) were similar in magnitude to those for female morphology ( $\beta$ 's for weight and size:  $-0.97$  and  $0.11$ , respectively). Further, the reduction in fit to data when excluding male weight and size from this full model ( $F_{2,7} = 2.24$ ) was similar in magnitude to when female weight and size were instead excluded ( $F_{2,7} = 3.48$ ). This exercise thus strongly suggests that our main result is due to independent effects of comparable magnitude in both sexes.

## Discussion

In our study species, SD is apparently positively associated with adult fitness across populations. This finding apparently contrasts with the predictions of several models of sexual selection (Kokko and Brooks 2003) and our study is to our knowledge the first demonstration of a positive relationship between SD and population fitness under standardized experimental conditions. We note that our study is built upon data on lifetime productivity of females, which integrates reproductive life span and the rate of egg production. Our analyses also exclude the possibility that our results

are simply an effect of females being larger and more productive in more dimorphic populations. Our results instead suggest that the evolutionary processes responsible for variance in SD across our populations also have important implications for adult fitness. Below, we discuss the processes most likely to have caused the pattern seen here.

## INDIRECT BENEFITS

Because higher SD is assumed to indicate a higher level of sexual selection (Darwin 1871; Andersson 1994), our results are seemingly consistent with a scenario in which females choose males for the indirect benefits that males provide. Positive effects of female choice have been found in a variety of systems (e.g., Reynolds and Gross 1992; Moore 1994; Petrie 1994; Promislow et al. 1998; Welch et al. 1998; Konior et al. 2001) and a meta-analysis by Møller and Alatalo (1999) suggested that good genes effects are common but relatively minor in magnitude. We note that females may, in general, also obtain indirect benefits from choosing mates that are genetically more compatible (Tregenza and Wedell 1998, 2002; Mays and Hill 2004), but it is unclear whether and how such processes would affect the evolution of population fitness.

In *C. maculatus*, females resist matings vigorously by kicking and trying to evade males and this is expected to result in female choice for more persistent males (Arnqvist and Rowe 2005). More intense female choice (in its widest sense) in some populations may thus have led to both higher degrees of SD and to



higher rates of adaptation and thus a higher overall population fitness (see Whitlock 2000; Lorch et al. 2003). Indeed, Fricke and Arnqvist (2004) recently showed that the rate of adaptation to a novel food resource in *C. maculatus* is decelerated when sexual selection is removed. This finding is seemingly consistent with our results, again provided that SD indeed reflects differences in sexual selection regimes across populations.

There are, however, general reasons to believe that indirect benefits to females are often outweighed by direct costs to choosy females (e.g., Kirkpatrick and Barton 1997; Arnqvist and Kirkpatrick 2005). Although indirect benefits seem capable of outweighing direct costs in some systems (Head et al. 2005), female *C. maculatus* do bear costs of mating (e.g., Crudginton and Siva-Jothy 2000; Rönn et al. 2006) which may result in a decrease in female fecundity and population fitness with an increase in the intensity of sexual selection (Arnqvist et al. 2005). Even if there is a positive genetic correlation between male persistence and male quality, such that more harmful males provided indirect benefits to resistant females, negative population effects of more persistent males may outweigh the positive indirect effects (Arnqvist and Rowe 2005). This line of reasoning suggests that the evolution of more persistent males, and thus higher degrees of sexual dimorphism, may be negatively associated with evolution of net population fitness. However, the evolution of female resistance may in theory obscure such effects (Arnqvist and Rowe 2002), a proposition supported by a recent comparative study of *Callosobruchus* seed beetles (Rönn et al. 2007).

#### DIRECT BENEFITS

An alternative explanation for our results is the possibility that males provide females with direct benefits (Møller and Jennions 2001). In our study system, *C. maculatus* males are known to transfer a large ejaculate to females during mating (Savalli and Fox 1998) and this ejaculate may provide direct benefits to the females, such as hydration (Labeyrie 1981; Edvardsson 2007) or other substances contained in the ejaculate (Vahed 1998). A study investigating multiple mating, another indicator of the intensity of sexual selection, found that female *C. maculatus* produced more offspring at a higher mating rate than at an intermediate mating rate, suggesting that direct benefits may elevate female life-time offspring production by outweighing the direct costs of mating (Arnqvist et al. 2005). If more intense sexual selection, as indicated by a higher degree of sexual dimorphism, has been associated with more beneficial or larger ejaculates, this could also certainly contribute to the pattern we see across populations.

#### INTRALOCUS SEXUAL CONFLICT

Sex-specific evolutionary constraints may also contribute to covariation between population fitness and the evolution of SD (Lande 1980). In particular, recent research has highlighted the

potential importance of intralocus sexual conflict, i.e., a genetic conflict between alleles expressed in males and females (e.g., Chippindale et al. 2001). If a trait is partly encoded by alleles at the same locus in both sexes and males and females have different fitness optima for this trait, intralocus sexual conflict will arise (Rice and Chippindale 2001; Arnqvist and Rowe 2005). In the case of our study, such a conflict would occur if it was advantageous for males to be of one particular size and/or shape but advantageous for females to be of a different size and/or shape, given a genetic correlation between the sexes for such traits. In such cases, selection will act in opposite directions in the two sexes and adaptive evolution in one sex will be constrained by selection in the other. The evolution of sex-limited gene expression, and hence sexual dimorphism, is one way out of this bind (Rice 1984) but theory suggests that the evolution of sex-limited expression of sexually antagonistic genes may be quite slow (Lande 1980, 1987). There is some evidence for sexually antagonistic selection on morphological traits (Price and Burley 1994; Björklund and Senar 2001) and experimental studies on *Drosophila melanogaster* have revealed quite intense intralocus sexual conflict (Chippindale et al. 2001; Gibson et al. 2002). In addition to this, it has recently been shown that intralocus sexual conflict can actually reduce the genetic benefits of sexual selection, because under sexual selection, intralocus sexual conflict means that high-fitness males/females produce low-fitness daughters/sons, respectively (Pichedda and Chippindale 2006). This would add to the potential negative effects of dimorphism observed in our study.

Results such as ours are consistent with variation in intralocus sexual conflict, simply because less-dimorphic populations may be more constrained from evolving adaptively under such genetic conflicts compared to more dimorphic ones. Intralocus conflicts can be partly resolved through evolution of the genetic architecture (Bonduriansky and Rowe 2005). When an intralocus conflict is thus resolved, females and males are both allowed to reach their fitness optima, which will result both in higher degrees of SD and in elevated population fitness. Thus, variation in the degree to which different populations of *C. maculatus* suffer from intralocus sexual conflict would contribute to the results seen here.

As is clear from above, our results can in theory be accommodated by at least three different processes, although it is very difficult to disentangle these given our data. We suggest that intralocus sexual conflict may be the most important contributor to our result for the following three reasons. First, indirect effects of viability genes are generally manifested during the juvenile stages (see Møller and Alatalo 1999). Because we found no effects of dimorphism on egg-to-adult survival, but only on adult fitness, this makes good genes processes a less likely explanation. Second, we found effects of SD on adult fitness when statistically controlling for average size of males and females (see Table 1). Because females are the larger sex in *C. maculatus*, this means

that adult fitness tended to increase when males evolved a reduced weight relative to females. Given that the magnitude of any direct benefits in the form of an ejaculate should scale with male weight (Edvardsson and Tregenza 2005), increased, and not reduced, male weight should be associated with elevated adult fitness if direct benefits were a major contributor to our results. Third, as pointed out by Chippindale et al. (2001), intralocus sexual conflict should be manifesting more during the adult than the juvenile stage, simply because fitness optima of males and females will generally be similar early in life but will diverge as individuals reach adulthood and engage in reproductive activities. The fact that our index of sexual selection was apparently related to adult, but not juvenile, fitness is at least consistent with this feature of intralocus sexual conflict.

One way to help disentangle these processes would be to assess genetic correlations across sexes, for populations with differing degrees of sexual dimorphism. If intralocus conflict is currently constraining adaptation in less-dimorphic populations, we would expect a tighter genetic correlation between the sexes for the same trait in such populations (Lande 1980). In contrast, if sexual selection is responsible for the pattern seen, more dimorphic populations may show a tighter genetic correlation between female reproductive behavior and male traits, due to assortative mating and male–female coevolution.

## Conclusions

To our knowledge, we have described the first controlled study showing that SD is positively related to population fitness. We point to the fact that this can be due to either of several processes, and that the predictions of models of sexual selection and those of intralocus ontogenetic conflict are very similar. Sexual selection by female choice based on indirect or direct benefits could generate patterns such as those documented here, as would variation in the degree to which populations are free to respond to sex-specific natural selection. Thus, correlations between dimorphism and fitness can be generated by either selection or genetic constraints, and we suggest that detailed data on the genetic architecture of populations can help distinguishing between these alternatives. However, irrespective of which process is responsible for the pattern we document, our study does provide comparative evidence to the suggestion that population fitness can be affected by sex-specific selection.

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