

Selection on body size and sexual size dimorphism differs between host species in a seed-feeding beetle

C. W. FOX* & M. E. CZESAK†

*Department of Entomology, University of Kentucky, Lexington, KY, USA

†Department of Biology, Vassar College, Poughkeepsie, NY, USA

Keywords:

egg size;
fecundity selection;
natural selection;
path analysis.

Abstract

Sexual size dimorphism varies substantially among populations and species but we have little understanding of the sources of selection generating this variation. We used path analysis to study how oviposition host affects selection on body size in a seed-feeding beetle (*Stator limbatus*) in which males contribute large ejaculates (nuptial gifts) to females. Females use nutrients in these ejaculates for egg production. Male body size, which affects ejaculate size, affects female fecundity and is thus under fecundity selection similar in magnitude to the fecundity selection on female body size. We show that when eggs are laid on a host on which larval mortality is low (seeds of *Acacia greggii*) fecundity predicts fitness very well and fecundity selection is the major source of selection on both male and female adult size. In contrast, when eggs are laid on a host on which larval mortality is high (seeds of *Parkinsonia florida*) fecundity poorly predicts fitness such that fecundity selection is relaxed on both male and female size. However, because egg size affects larval mortality on this poor host (*P. florida*) there is selection on female size via the female size → egg size → fitness path; this selection via egg size offsets the reduction in fecundity selection on female, but not male, body size. Thus, differences in host suitability (due to differences in larval mortality) affect the relative importance of two sources of selection on adult body size; fecundity selection on both male and female body size is lower on the poor quality host (*P. florida*) relative to the high quality host (*A. greggii*) whereas selection on female body size via effects of egg size on offspring survival (body size → egg size → fitness) is greater on the poor quality host relative to the high quality host. Because selection via the egg size path affects only females the difference in larval survival between hosts shifts the relative magnitude of selection on female vs. male size. Researchers working on other study systems should be alerted to the possible importance of subtle, but consequential, indirect selection on their study organisms.

Introduction

Sexual size dimorphism is prevalent in most taxa of animals (Fairbairn, 1997, 2005). However, sexual size dimorphism varies substantially among species (e.g.

Meiri *et al.*, 2005) and even among populations within species (e.g. Fairbairn & Preziosi, 1994; Pearson *et al.*, 2002; Jannot & Kerans, 2003; Krause *et al.*, 2003; Manier, 2004; Fairbairn, 2005; and references cited therein). Numerous hypotheses have been proposed to account for this variation, including that sexual selection varies among populations/species (e.g. Blanckenhorn *et al.*, 1995; Pearson *et al.*, 2002; review in Fairbairn, 2005), that direct effects of climate or other environmental variables on the fitness consequences of large vs.

Correspondence: Charles W. Fox, Department of Entomology, University of Kentucky, Lexington, KY 40546-0091, USA.
Tel.: 859 257 7474; fax: 859 323 1120;
e-mail: fox@uky.edu

small size differ between males and females (e.g. Slatkin, 1984), or that variation in sexual dimorphism is a consequence of sex-specific differences in developmental canalization/plasticity (Fairbairn, 2005). Though many studies have shown how ecological variation can drive the evolution of body size (e.g. the classic study of Grant & Grant, 1995) few have demonstrated how environmental factors can differentially affect males and females (other than via changing sexual selection) and thus drive the evolution of geographic variation in sexual size dimorphism (but see Badyaev *et al.*, 2000, 2001; Blondel *et al.*, 2002; Gonzalez-Solis, 2004).

In the seed beetle, *Stator limbatus*, males are larger than females, opposite the pattern common in most insects. Large male body size is favoured in *S. limbatus* by both fecundity selection and sexual selection. Fecundity selection occurs because large males have direct effects on the fecundity of their mates (Savalli & Fox, 1998; Czesak & Fox, 2003a) mediated at least in part through the size of their ejaculate (J. Moya-Laraño & C.W. Fox, unpublished data). Simultaneously, although females exhibit no detectable behavioural differences towards large vs. small males, they do remate sooner after mating to a small male (Savalli & Fox, 1998) creating sperm competition and sexual selection for large male size. Sexual dimorphism in *S. limbatus* varies geographically, both with latitude (less dimorphic at higher latitudes) and among host species (R. C. Stillwell, G. Morse & C. W. Fox, unpublished data). However, the mechanisms generating this variation in sexual size dimorphism are unknown. Here we examine how the host plant upon which *S. limbatus* females lay their eggs can affect the relative importance of fecundity selection on male vs. female body size, and thus drive the evolution of geographic variation in sexual size dimorphism.

Numerous techniques are available for measuring the magnitude of selection on traits (e.g. Brodie *et al.*, 1995; Mauricio & Mojonner, 1997). Path analysis is unique among these methods in allowing us to consider known causal relationships between traits in our selection model. This is particularly useful for distinguishing direct selection (direct effects of traits on fitness) from indirect selection due to selection on correlated traits (Crespi, 1990; Kingsolver & Schemske, 1991; Scheiner *et al.*, 2000; Geber & Griffen, 2003). Because the path model considers *a priori* causal relationships, path analysis allows us to test how environmental conditions influence the mechanism via which selection is imposed on traits of interest. We use path analysis to examine how the host upon which females lay their eggs affects the relative importance of fecundity selection on body size vs. selection on body size via egg size effects on larval survival. We find that the relative importance of two sources of selection on body size differs between hosts and thus that oviposition host affects the relative magnitude of selection on maternal vs. paternal body size.

Methods

Stator limbatus (Coleoptera; Chrysomelidae; Bruchinae) is a beetle whose life cycle revolves around seeds. Following mating, females glue their eggs to the seeds of their host plant. When eggs hatch, larvae burrow under the egg into the seed, where they complete development; they do not emerge from the seed until they are adults. Throughout its large geographical range (from northern South America to the south-western United States) *S. limbatus* uses many species as hosts, including *c.* 50 native plant species (most of which are mimosoid or caesalpinoid legumes; Morse & Farrell, 2005a,b) and >20 non-native species. In central Arizona and southern California *S. limbatus* primarily uses seeds of three native species as hosts: *Acacia greggii* (cat-claw acacia), *Parkinsonia florida* (blue paloverde; formerly *Cercidium floridum*) and *P. microphylla* (small-leaf paloverde; formerly *C. microphyllum*).

In this study we focus on beetle oviposition on seeds of *A. greggii* and *P. florida* because previous studies have demonstrated that selection on egg size differs substantially between these two host species (Fox & Mousseau, 1996; Fox *et al.*, 2001). Specifically, larval mortality is very high and positively correlated with egg size when eggs are laid on seeds of *P. florida* due in large part to defences on the seed coat (larvae die while trying to penetrate the seed) (Fox & Mousseau, 1996; Fox *et al.*, 2001). In contrast, larval mortality is low and unrelated to egg size when larvae develop on seeds of *A. greggii*.

Experimental populations

Beetles were collected in August 1998 along Mountain-view Road in Apache Junction, Pinal County, Arizona, near the base of the Superstition Mountains (in central Arizona; 33°48'N, 111°47'W). *Acacia greggii*, *P. florida* and *P. microphylla* trees are all present at this location. Beetles were collected as larvae inside *A. greggii* seeds. The laboratory colony was initiated with >300 individuals collected from more than 20 trees.

Seeds were collected from both *A. greggii* and *P. florida* trees. Undamaged fruits were shipped to the laboratory where seeds were frozen until used in experiments. Within a species, seeds from all trees were thoroughly mixed to control for variation among trees in effects on beetle survival and life history (Fox *et al.*, 2001). Beetles were raised in the lab for two generations before starting this experiment.

Experimental design

Males and females were raised to adult on seeds of *A. greggii* at a density of one beetle per seed (to eliminate larval competition within seeds) and one seed per 35 mm Petri dish, in a reach-in growth chamber at 30 °C and 16 : 8 Light : Dark. We use *A. greggii* seeds for rearing

these beetles because larval survival is very high on this host (generally >97% in the lab). Emerging adult beetles were always virgin because they emerged alone into their dish. Females usually take 24–48 h before they mate and begin ovipositing. Thus, upon emergence from their host seed each female was weighed and then placed in a 35 mm Petri dish containing three seeds of either *A. greggii* or *P. florida* and aged for 24 h. Females were then paired with a random nonsibling male of the same age (24 h post-emergence; also weighed within 12 h of emergence) and confined in a 35 mm petri dish containing eight seeds of either *A. greggii* or *P. florida*. Dishes were checked every 12 h until females laid at least three eggs, after which the pairs were transferred to a new dish containing 30 seeds of the same host. They were left in these dishes until the female died. In total, 1291 pairs laid eggs on *A. greggii* and 1292 pairs laid eggs on *P. florida*.

The size of eggs laid by females was estimated by measuring the length and width of three eggs laid during the first 12 h of female oviposition. Eggs cannot be weighed because they are glued to the host seed. Instead, we estimated egg volume as $0.5 \times \text{Egg Length} \times \text{Egg Width}^2$ (the 0.5 is included because eggs glued to seeds with one side flat; because we examine standardized path coefficients, the constants in the equation have no effect on the estimated path coefficients). All analyses presented here are consistent whether we present egg length, egg width, or other estimates of egg size (e.g. estimated egg mass).

Previous studies have demonstrated that the majority of larval mortality occurs while larvae are first instars (Fox & Mousseau, 1996; Fox *et al.*, 2001). We thus defined *fitness* of a mated pair as the *number* of offspring that successfully survived until they were completely inside their host seed (i.e. survived past the period of high larval mortality). Within a pair males and females have exactly the same fitness because all matings are monogamous within the experiment.

Analyses

To test hypotheses about how oviposition host affects selection on male vs. female size, we first need to define the appropriate path model. Fortunately, many of the relationships in our path model have been examined in separate experiments with *S. limbatus*. Considering these known relationships we constructed our path model as in Fig. 1. This model included effects of both male and female body size on both egg size and fecundity (paths A–D). Of these four possible relationships, three are consistently demonstrated in previous experiments [effects of female size on egg size (path A) and fecundity (path C), and the effect of male size on the fecundity of his mate (path D); Fox *et al.*, 1995, 1997; Savalli & Fox, 1998; Czesak & Fox, 2003a]. An effect of male body size on egg size (path B) has been demonstrated in one previous study (Fox *et al.*, 1995) but has not been

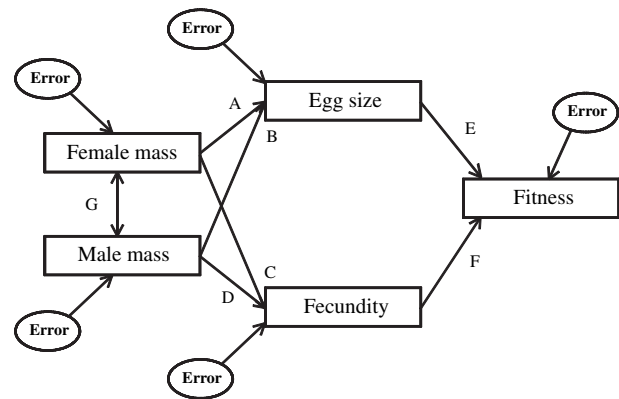


Fig. 1 The path model used for analysis of the effects of host species on selection on male and female body size. Letters designate the estimated path coefficients as discussed in the *Analyses* section of the *Methods*.

observed in subsequent studies (Savalli & Fox, 1998; Czesak & Fox, 2003a). Egg size is known to have a positive and causal effect on egg hatching and larval first instar survival (Fox & Mousseau, 1996) and thus can directly affect the fitness of parents (path E). Fecundity also has a direct affect on fitness (path F). Path G is the within pair correlation between male and female size. In this model male and female body size can affect their fitness only indirectly through effects on fecundity and egg size, both of which can have direct effects on fitness.

It is important to consider that our path coefficients, and thus our estimates of selection, are dependent on the paths included in the model (Petraitis *et al.*, 1996). Thus, in addition to the model in Fig. 1 we considered two additional path models. In one model we included a path in which egg size directly affects fecundity (to account for an egg size/number trade-off, as has been demonstrated in *S. limbatus*; Fox *et al.*, 1999; Czesak & Fox, 2003b). In all cases this egg size → fecundity path was negative and significant and inclusion of this path reduced the model Akaike's Information Criterion (Burnham & Anderson, 1998). However, including this path changed the estimated path coefficients only slightly and had very little effect on the estimates of total selection on male vs. female size (Table 1; the 'plus trade-off model'). The other path model we considered was one with direct effects between body size and fitness (male body size → fitness and female body size → fitness). These paths were significant in only the *P. florida* treatment; for the *A. greggii* treatment the estimated standardized path coefficients were between -0.01 and 0.01 (with standard errors *c.* 0.04) (Table 1, the 'full model'). Below we focus on the results of our simplest model but emphasize that the total selection on male and female size and the effect of oviposition host on the relative amount of selection on male vs. female size differ little regardless of which model we present (see Table 1).

Table 1 Estimates of total selection (\pm SE) on body mass (total effect of adult body mass on the number of surviving offspring) in *Stator limbatus* when their eggs are laid and their larvae are reared on seeds of *Acacia greggii* vs. *Parkinsonia florida*. These estimates are in SD; e.g. an estimate of 0.4 indicates that a change in mass by 1 SD changes fitness by 0.4 SD. The 'simplest model' is shown in Fig. 2. The 'Plus trade-off model' includes the egg size \rightarrow fecundity path. The 'Full model' includes the egg size/number trade-off and the direct effects of body size on fitness (male body size \rightarrow fitness and female body size \rightarrow fitness paths) which are significant only on *P. florida*. $i_{\text{female}}/i_{\text{male}}$ is the ratio of selection on female size to selection on male size. Note that selection on body size does not differ ($P > 0.47$) between the sexes when eggs are laid on *A. greggii* but differs substantially ($P < 0.001$) when eggs are laid on *P. florida*.

	<i>Acacia greggii</i>	<i>Parkinsonia florida</i>
Number of pairs	1291	1292
Simplest model		
Female mass	0.40 \pm 0.02	0.38 \pm 0.02
Male mass	0.39 \pm 0.02	0.28 \pm 0.02
$i_{\text{female}}/i_{\text{male}}$	1.03 <i>ns</i>	1.36*
Plus trade-off model		
Female mass	0.42 \pm 0.02	0.41 \pm 0.02
Male mass	0.40 \pm 0.02	0.30 \pm 0.02
$i_{\text{female}}/i_{\text{male}}$	1.07 <i>ns</i>	1.38*
Full model		
Female mass	0.42 \pm 0.02	0.46 \pm 0.02
Male mass	0.40 \pm 0.02	0.31 \pm 0.02
$i_{\text{female}}/i_{\text{male}}$	1.06 <i>ns</i>	1.46*

ns, selection not significantly different between the sexes, Wald χ^2 test, $P > 0.47$.

*Selection significantly different between the sexes, Wald χ^2 test, $P < 0.001$.

All analyses were performed using AMOS 5.0 (Arbuckle & Wothke, 1999; Arbuckle, 2003). All standard errors were estimated by bootstrapping the path model parameter estimates in AMOS 5.0. We compared selection between the sexes using a Wald χ^2 test (Allison, 1995).

Results

Figure 2 presents the path model for the magnitude of selection (standardized path coefficients) on female and male body size mediated via egg size and fecundity effects on fitness. All path coefficients are standardized; i.e. they are presented in SD. Thus, a coefficient of r for the path $X \rightarrow Y$ indicates that a change in X of 1 SD will produce a change in Y of r SD. Body sizes of females and males in this experiment (\pm SD) were 3.24 ± 0.39 mg and 3.45 ± 0.44 mg, respectively. Males were significantly larger than females (6.5% larger; $t_{5164} = 18.3$, $P < 0.001$) as observed in other experiments.

Regardless of oviposition host, male body size had a large and highly significant effect on fecundity of the mated pair, similar in magnitude to the effect of female body size on her fecundity (Fig. 2). This is consistent with

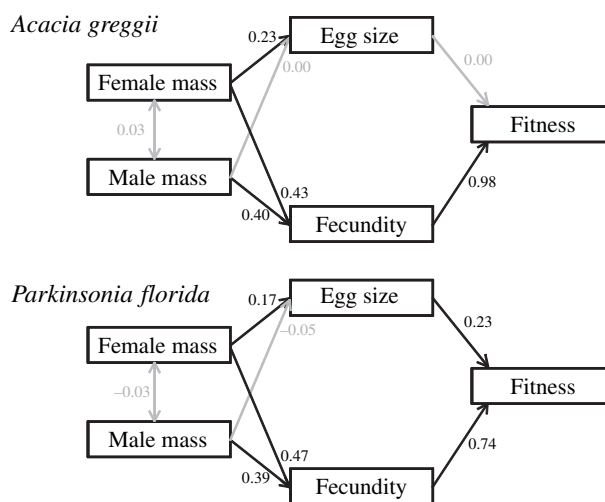


Fig. 2 Path analysis for the effects of oviposition host on the magnitude of selection on body size. Path coefficients are standardized coefficients (i.e. in SD). Grey paths are not significantly different from 0; all others are significant ($P < 0.05$). Note that body size affects fitness through both the egg size and fecundity paths when eggs are laid on seeds of *Parkinsonia florida*, but only through the fecundity path when eggs are laid on seeds of *Acacia greggii*. Fitness is the number of larvae produced that successfully survive until completely inside their host seed (i.e. survive beyond the period of highest mortality). All standard errors are < 0.035 and most are < 0.020 .

previous studies showing that male body size is under strong fecundity selection (Fox *et al.*, 1995; Savalli & Fox, 1998; Czesak & Fox, 2003a) mediated at least in part via nutrients in his ejaculate (J. Moya-Laraño and C.W. Fox, unpublished data). Also consistent with most previous results (e.g. Savalli & Fox, 1998), female body size affected the size of eggs that she laid but male body size did not influence the size of eggs laid by his mate, regardless of seed species (Fig. 2).

When females laid their eggs on seeds of *A. greggii*, and thus their larvae were reared on seeds of *A. greggii*, larval survival was very high ($>99\%$). Because offspring survival was so high on *A. greggii*, fecundity was highly correlated with the number of offspring that survived ($r = 0.98$). Egg size did not affect the survival of offspring on *A. greggii* and thus egg size had no effect on fitness (Fig. 2). Thus, all selection on male and female body size was through the fecundity path (body size \rightarrow fecundity \rightarrow fitness) and not the egg size path (body size \rightarrow egg size \rightarrow fitness) (Fig. 2). Also, because male size and female size effects on fecundity are of similar magnitude, when offspring were reared on seeds of *A. greggii* total selection on male and female body sizes were nearly identical (ratio of selection on female size to selection on male size of 1.03–1.07 depending on the details of the path model; Table 1; Wald $\chi^2 < 0.5$, $P > 0.47$ for all three models).

In contrast, when offspring were reared on seeds of *P. florida* selection on body size was through both the fecundity and egg size paths (Fig. 2). Offspring survivorship was much lower on *P. florida* than on *A. greggii* ($83 \pm 0.4\%$ vs. $>99\%$). Because egg size was positively correlated with offspring survival when offspring were reared on *P. florida*, egg size directly affected the number of offspring surviving and thus affected parental fitness (egg size \rightarrow fitness paths in Fig. 2). This effect of egg size on fitness reduced the relative effect of fecundity on fitness by about one-quarter (Fig. 2). Because egg size was correlated to female body mass, selection on egg size translated into indirect selection on female body size. However, egg size was not correlated with male body size; thus, selection on egg size did not translate into indirect selection on male size. The result was that (a) total selection on male body size was much lower when eggs were laid on seeds of *P. florida* (relative to *A. greggii*) (Wald $\chi^2 > 10.1$, $P < 0.01$ for all three models) and (b) the relative magnitude of selection on female vs. male body size was much higher when eggs were laid on *P. florida* (ratio of selection on female body size to selection on male body size was between 1.36 and 1.46 depending on the details of the path model; Wald $\chi^2 > 12.5$, $P < 0.001$ for all three models).

Discussion

Our path analysis revealed two results that were not observed in previous studies. First, despite the observation that the partial correlations between body size and fecundity were similar whether eggs were laid on *P. florida* or *A. greggii*, the magnitude of fecundity selection on both male and female body size (selection through the body size \rightarrow fecundity \rightarrow fitness path) was much lower when eggs were laid on *P. florida* than when they were laid on *A. greggii*. This was because egg size influenced larval survival on seeds of *P. florida* but not on seeds of *A. greggii*. This effect of egg size on larval survival reduced the influence of fecundity on total fitness when offspring were raised on *P. florida*, reducing the magnitude of fecundity selection on both male and female body size.

Secondly, although the partial correlations between fecundity and body size (body size \rightarrow fecundity path) were of similar magnitude for both sexes regardless of the host upon which eggs were laid (i.e. the effect of female size on her fecundity was similar in magnitude to the effect of male size on the fecundity of his mate), the relative amount of selection on female vs. male size differed between the two hosts. This is not because oviposition on *P. florida* increases total selection on female size. Instead, oviposition on *P. florida* reduces fecundity selection on both sexes but the reduction in fecundity selection on female body size is partially offset by an increase in selection on female body size via the egg size path (female body size \rightarrow egg size \rightarrow fitness)

– when eggs are laid on *P. florida* the increase in larval mortality imposes selection on egg size and thus, indirectly, female body size. The reduction in fecundity selection on male body size is not offset by selection through the egg size path, such that the relative magnitude of selection on male vs. female size differs between host species.

These results are very intriguing because they indicate that the relative magnitude of selection on male vs. female body size can change substantially depending on 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. The difference in relative selection on male vs. female size is entirely indirect due to variation among hosts in offspring survival. Most importantly, this effect of larval mortality on the magnitude of selection is not caused by differential mortality of males vs. females, large vs. small beetles, or any direct effect of male size on fitness. Instead, the difference in selection between hosts is entirely indirect, mediated through a change in the relationship between egg size and offspring survival, which changes the relative importance of fecundity selection on male and female size.

The path coefficients estimated in this study reflect phenotypic selection coefficients. For these selection coefficients to have any influence on the evolution of body size in *S. limbatus* the variables in the path model need to be heritable. Indeed, numerous studies have shown all these parameters to exhibit heritable variation in *S. limbatus* (Fox 1998, Fox *et al.*, 1999; Czesak & Fox, 2003a,b) such that the selection observed here is relevant to the evolution of body size.

Our study was performed entirely in the laboratory. The advantage of our laboratory study is that we can control environmental variation that biases estimates of selection (Scheiner *et al.*, 2002). But how relevant are these results to selection in nature? In nature, beetle body size is likely under many sources of selection, some of which most certainly affect male body size differently than female body size, as shown in other studies (e.g. Preziosi & Fairbairn, 1997, 2000). We do not propose that the selection coefficients measured here reflect total selection on body size that beetles will experience in nature. However, we do argue that, all other sources of selection being equal, the host upon which females lay their eggs causes a large change in the relative magnitude of selection on male vs. female size from equal selection on the sexes when eggs are laid on *A. greggii* to a difference in selection intensity, i , between the sexes of $c. 0.10$ – 0.15 when eggs are laid on *P. florida* (Table 1). A selection intensity of between 0.10 and 0.15 is near the median total amount of directional selection observed in nature in studies of morphological traits, and larger than the median total amount of directional selection observed in studies of life history traits (Endler,

1986; Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001). Thus, the magnitude of the host plant effect on the difference in selection between male and female *S. limbatus* is quite large relative to typical estimates observed in nature. However, we suspect that the effect of host species on selection in nature may even be larger than that observed here. Larval survival on seeds of *P. florida* was much higher in this lab experiment (83%) than typically observed in nature or our previous lab experiments (survival is frequently <50% on *P. florida*) and the egg size effect on larval survival is usually greater than that observed here (e.g. Fox & Mousseau, 1996; Fox, 2000; Fox *et al.*, 2001). Lower larval survival and a larger effect of egg size on total fitness would both reduce the effect of fecundity on fitness, further reducing the importance of fecundity selection on body size, and increase the importance of the body size → egg size path, further shifting the relative magnitude of selection on maternal vs. paternal body size.

Our measure of individual fitness is the number of offspring produced by females that survived until they completely entered the host seed (i.e. past the period of highest larval mortality). This measure of fitness crosses generations by including both maternal reproduction and offspring survival. There has been extensive discussion of the consequences of crossing generational boundaries when measuring fitness (e.g. Arnold, 1983; Lande & Arnold, 1983; Cheverud, 1984; Grafen, 1988; Wolf & Wade, 2001) and some authors have argued that estimates of fitness should never cross generational boundaries (Prout, 1969; Cheverud & Moore, 1994). However, for some traits the fitness consequences of the parental phenotype are not expressed until the offspring generation (due to 'maternal' or 'parental' effects; Mousseau & Fox, 1998 and references therein). For this reason models of the evolution of egg size and other traits with delayed fitness consequences (e.g. parental care) often consider fitness across generations, such as the number of surviving offspring (Shine, 1978; analogous to our usage here) or even the number of grand-offspring (e.g. Smith & Fretwell, 1974). Likewise, empirical studies in behavioural ecology involving parental care routinely consider early offspring performance (especially survival) as a component of parental fitness (e.g. Clutton-Brock, 1988). This allows detection of the component of selection on parental traits that is due to kin selection and would otherwise be undetectable but may produce incorrect estimates of both direct and indirect selection and can even lead to incorrect conclusions about the direction of selection (though the latter occurs under fairly restrictive conditions; see discussion in Wolf & Wade, 2001). However, when there are biological reasons to assume that offspring fitness is largely or entirely controlled by the mother (e.g. the major source of variation in early larval survival is egg size rather than offspring genotype) then it is beneficial to assign these components to the mother (Wolf & Wade, 2001). We

have opted to consider larval survival in our parental fitness estimate because if we quantify fitness as the number of fertilized eggs (zygotes) produced by a male or female we would miss the selection on parental body size that occurs due to the effects of egg size on offspring survival. We would thus incorrectly conclude that (a) selection on body size was similar for males and females regardless of the host upon which eggs were laid and (b) the most fecund females always have the greatest fitness.

Our ultimate objective in dissecting selection on male vs. female size is to understand geographical variation in sexual size dimorphism. Our previous studies have demonstrated that male body size is under substantial fecundity selection because females use nutrients in the male ejaculate to make eggs. Here we extend those results by demonstrating that the magnitude of fecundity selection on body size, and the relative magnitude of selection on male vs. female size, differs between two common hosts of this seed beetle. However, these are only two of the large number (>70) species of hosts that *S. limbatus* uses. We have studied fecundity selection and effects of egg size on larval mortality in only a few of these hosts, and consider only two hosts here. However, it is evident from our previous studies that larval mortality and its relationship to egg size varies substantially among host species (Fox & Mousseau, 1996; Fox, 2000; Fox & Savalli, 2000; A. R. Amarillo-Suárez & C.W. Fox, unpublished data) and even among populations of the same host species (e.g. due to variation in seed-coat resistance; Fox *et al.*, 2001). We thus believe that variation among hosts in this indirect selection on body size, via host effects on the importance of the body size → egg size → fitness path relative to the body size → fecundity → fitness path, will be a major source of variation in selection in nature. However, the degree to which host-plant mediated variation in indirect selection on body size can explain geographical variation in body size and sexual size dimorphism has yet to be tested. To more thoroughly understand the ecology of body size evolution of the sexes, researchers working in other study systems should likewise be alerted to the possible importance of subtle, but consequential, indirect selection on their study organisms.

Acknowledgments

We thank B. Byrnes and U. Savalli for help with this experiment, W. Blanckenhorn, S. P. Carroll, D. J. Fairbairn, J. Moya-Laraño, J. J. Sloggett and R. C. Stillwell for comments, J. Moya-Laraño for statistical advice, A. J. Moore for comments about our path analysis, and J. B. Wolf for discussions on the assignment of fitness to parents vs. offspring. This work was funded in part by grants NSF DEB-98-07315 and DEB-02-71929 to CWF. This paper is publication 06-08-024 for the Kentucky Agricultural Experiment Station.

References

- Allison, P.D. 1995. *Survival Analysis Using the SAS system: A Practical Guide*. SAS Institute Inc., Cary, NC.
- Arbuckle, J.L. 2003. *Amos 5.0 Update to the Amos User's Guide*. Smallwaters Corporation, Chicago, IL.
- Arbuckle, J.L. & Wothke, W. 1999. *Amos 4.0 User's Guide*. Smallwaters Corporation, Chicago, IL.
- Arnold, S.J. 1983. Sexual selection: the interface of theory and empiricism. In: *Mate Choice* (P. Bateson, ed.), pp. 67–107. Cambridge University Press, Cambridge, UK.
- Badyaev, A.V., Hill, G.E., Stoehr, A.M., Nolan, P.M. & McGraw, K.J. 2000. The evolution of sexual size dimorphism in the house finch. II. Population divergence in relation to local selection. *Evolution* **54**: 2134–2144.
- Badyaev, A.V., Hill, G.E. & Whittingham, L.A. 2001. The evolution of sexual size dimorphism in the house finch. IV. Population divergence in ontogeny. *Evolution* **55**: 2534–2549.
- Blanckenhorn, W.U., Preziosi, R.F. & Fairbairn, D.J. 1995. Time and energy constraints and the evolution of sexual size dimorphism – to eat or to mate. *Evol. Ecol.* **9**: 369–381.
- Blondel, J., Perret, P., Anstett, M.C. & Thebaud, C. 2002. Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. *J. Evol. Biol.* **15**: 440–450.
- Brodie, E.D. III, Moore, A.J. & Janzen, F.J. 1995. Visualizing and quantifying natural selection. *Trends Ecol. Evol.* **10**: 313–318.
- Burnham, K.P. & Anderson, D.A. 1998. *Model Selection and Inference*. Springer Mathematics, New York, NY, USA.
- Cheverud, J.M. 1984. Evolution by kin selection: a quantitative genetic model illustrated by maternal performance in mice. *Evolution* **38**: 766–777.
- Cheverud, J.M. & Moore, A.J. 1994. Quantitative genetics and the role of the environment provided by relatives in the evolution of behavior. In: *Quantitative Genetic Studies of Behavioral Evolution* (C.R.B. Boake, ed.), pp. 67–100. University of Chicago Press, Chicago.
- Clutton-Brock, T.H. 1988. *Reproductive Success*. University of Chicago Press, Chicago.
- Crespi, B.J. 1990. Measuring the effect of natural selection on phenotypic interaction systems. *Am. Nat.* **135**: 32–47.
- Czesak, M.E. & Fox, C.W. 2003a. Genetic variation in male effects on female reproduction and the genetic covariance between the sexes. *Evolution* **57**: 1359–1366.
- Czesak, M.E. & Fox, C.W. 2003b. Evolutionary ecology of size and number in a seed beetle: genetic trade-offs differ between environments. *Evolution* **57**: 1121–1132.
- Endler, J.A. 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ.
- Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annu. Rev. Ecol. Syst.* **28**: 659–687.
- Fairbairn, D.J. 2005. Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider *Aquarius remigis*. *Am. Nat.* **166**: S69–S84.
- Fairbairn, D.J. & Preziosi, R.F. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider, *Aquarius remigis*. *Am. Nat.* **144**: 101–118.
- Fox, C.W. 1998. Genetic and maternal influences on body size and development time in the seed beetle, *Stator limbatus* (Coleoptera: Bruchidae). *Ann. Entomol. Soc. Am.* **91**, 128–134.
- Fox, C.W. 2000. Natural selection on seed beetle egg size in the field and the lab: variation among environments. *Ecology* **81**, 3029–3035.
- Fox, C.W. & Mousseau, T.A. 1996. Larval host plant affects the fitness consequences of egg size in the seed beetle *Stator limbatus*. *Oecologia* **107**: 541–548.
- Fox, C.W. & Savalli, U.M. 2000. Maternal effects mediate host expansion in a seed-feeding beetle. *Ecology* **81**: 3–7.
- Fox, C.W., McLennan, L.A. & Mousseau, T.A. 1995. Male body size affects female lifetime reproductive success in a seed beetle. *Anim. Behav.* **50**: 281–284.
- Fox, C.W., Thakar, M.S. & Mousseau, T.A. 1997. Egg size plasticity in a seed beetle: an adaptive maternal effect. *Am. Nat.* **149**: 149–163.
- Fox, C.W., Czesak, M.E., Mousseau, T.A. & Roff, D.A. 1999. The evolutionary genetics of an adaptive maternal effect: Egg size plasticity in a seed beetle. *Evolution* **53**: 552–560.
- Fox, C.W., Czesak, M.E. & Fox, R.W. 2001. Consequences of plant resistance for herbivore survivorship, growth, and selection on egg size. *Ecology* **82**: 2790–2804.
- Geber, M.A. & Griffen, L.R. 2003. Inheritance and natural selection on functional traits. *Int. J. Plant Sci.* **164**: S21–S24.
- Gonzalez-Solis, J. 2004. Sexual size dimorphism in northern giant petrels: ecological correlates and scaling. *Oikos* **105**: 247–254.
- Grafen, A. 1988. On the uses of data on lifetime reproductive success. In: *Reproductive Success* (T.H. Clutton-Brock, ed.), pp. 454–471. University of Chicago Press, Chicago.
- Grant, P.R. & Grant, B.R. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* **49**: 241–251.
- Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hill, C.E., Beerli, P. & Kingsolver, J.G. 2001. Strength and tempo of natural selection in the wild. *PNAS* **98**: 9157–9160.
- Jannot, J.E. & Kerans, B.L. 2003. Body size, sexual size dimorphism, and Rensch's rule in adult hydroptychid caddisflies (Trichoptera : Hydroptychidae). *Can. J. Zool.* **81**: 1956–1964.
- Kingsolver, J.G. & Schemske, D.W. 1991. Path analysis of selection. *Tr. Ecol. Evol.* **6**: 276–280.
- Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.H., Hoang, A., Gibert, P. & Beerli, P. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* **157**: 245–261.
- Krause, M.A., Burghardt, G.M. & Gillingham, J.C. 2003. Body size plasticity and local variation of relative head and body size sexual dimorphism in garter snakes (*Thamnophis sirtalis*). *J. Zoology* **261**: 399–407.
- Lande, R. & Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.
- Manier, M.K. 2004. Geographic variation in the long-nosed snake, *Rhinocheilus lecontei* (Colubridae): beyond the subspecies debate. *Biol. J. Linnean Soc.* **83**: 65–85.
- Mauricio, R. & Mojonier, L.E. 1997. Reducing bias in the measurement of selection. *Tr. Ecol. Evol.* **12**: 433–436.
- Meiri, S., Dayan, T. & Simberloff, D. 2005. Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology* **86**: 1432–1440.
- Morse, G.E. & Farrell, B.D. 2005a. Ecological and evolutionary diversification of the seed beetle genus *Stator* (Coleoptera: Chrysomelidae: Bruchinae). *Evolution* **59**: 1315–1333.

- Morse, G.E. & Farrell, B.D. 2005b. Interspecific phylogeography of the *Stator limbatus* species complex: the geographic context of speciation and specialization. *Mol. Phyl. Evol.* **36**: 201–213.
- Mousseau, T.A. & Fox C.W. 1998. *Maternal Effects as Adaptations*. Oxford Univ. Press, NY, NY.
- Pearson, D., Shine, R. & Williams, A. 2002. Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* **131**: 418–426.
- Petraitis, P.S., Dunham, A.E. & Niewiarowski, P.H. 1996. Inferring multiple causality: the limitations of path analysis. *Funct. Ecol.* **10**: 421–431.
- Preziosi, R.F. & Fairbairn, D.J. 1997. Sexual size dimorphism and selection in the wild in the waterstrider *Aquarius remigis*: lifetime fecundity selection on female length and its components. *Evolution* **51**: 467–474.
- Preziosi, R.F. & Fairbairn, D.J. 2000. Lifetime selection on adult body size and components of body size in a waterstrider: opposing selection and maintenance of sexual size dimorphism. *Evolution* **54**: 558–566.
- Prout, T. 1969. Estimation of fitnesses from population data. *Genetics* **63**: 949–967.
- Savalli, U.M. & Fox, C.W. 1998. Sexual selection and the fitness consequences of male body size in the seed beetle, *Stator limbatus*. *Anim. Behav.* **55**: 473–483.
- Scheiner, S.M., Mitchell, R.J. & Callahan, H.S. 2000. Using path analysis to measure natural selection. *J. Evol. Biol.* **13**: 423–433.
- Scheiner, S.M., Donohue, K., Dorn, L.A., Mazer, S.J. & Wolfe, L.M. 2002. Reducing environmental bias when measuring natural selection. *Evolution* **56**: 2156–2167.
- Shine, R. 1978. Propagule size and parental care: the 'safe harbor' hypothesis. *J. Theor. Biol.* **75**: 417–424.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* **38**: 622–630.
- Smith, C.C. & Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Amer. Nat.* **108**: 499–506.
- Wolf, J.B. & Wade, M.J. 2001. On the assignment of fitness to parents and offspring: whose fitness is it and does it matter? *J. Evol. Biol.* **14**: 347–356.

Received 20 October 2005; revised 16 December 2005; accepted 22 December 2005