

SHORT COMMUNICATION

Male body size affects female lifetime reproductive success in a seed beetle

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Males of many animal taxa allocate resources largely to mate acquisition and defence, contributing little more than gametes to embryo production. In many insects, however, males transfer large spermatophores or ejaculates to females during mating, and extragametic substances derived from these packages are used for somatic maintenance and egg production by the recipient females (e.g. Boggs 1981). Females receiving multiple male contributions lay more (Ridley 1988) and often larger eggs (Fox 1993a) than do once-mated females, indicating large effects of male-derived nutrients on female reproduction. Furthermore, large males produce larger ejaculates or spermatophores than small males (Fox et al. 1995), and females of some insects preferentially mate with large males (Thornhill & Alcock 1983). To date, however, there has been no clear demonstration in any insect of a direct fitness advantage to mating with large males (e.g. Pitnick 1991; but see Gwynne 1988). Here, we provide evidence that variation among males in body size has a direct effect on female reproductive success (lifetime fecundity and egg size) in a seed beetle, *Stator limbatus*, and suggest that this is likely to be caused by extragametic nutrients being transferred in male ejaculates during mating.

In seed beetles (Coleoptera: Bruchidae), radio-labelled nutrients in male ejaculates are incorporated into both somatic and reproductive tissues of females (Huignard 1983; Boucher & Huignard 1987). Females that receive multiple ejaculates live longer, lay more eggs, and lay larger eggs than once-mated females (Fox 1993a, b). As in other seed beetles, male *S. limbatus* produce large ejaculates, averaging (\pm SE) 0.14 ± 0.01 mg ($4.8 \pm 0.1\%$ of their body weight) during mating. In addition, ejaculate size of *S. limbatus* varies substantially between individual males, and is positively correlated with male body size ($r^2=0.22$, $N=30$, $P=0.009$).

Stator limbatus for this experiment were collected from *Cercidium floridum* in Scottsdale, Arizona, and from *Acacia greggii* in Black Canyon City, Arizona (approximately 50 km apart). Both laboratory populations were initiated with 500–1000 field collected individuals. All beetles were reared in the laboratory for one generation on seeds of their natural host plant before this experiment.

To quantify the effects of male body size on female reproductive success in *S. limbatus*, we collected virgin males and females from isolated seeds of their natural host (*A. greggii* or *C. floridum*) within 24 h of adult emergence. We weighed each beetle and then randomly paired it with a virgin beetle of the opposite sex in a 60-mm petri dish containing 12–13 seeds of the same species they were reared from. At 12-h intervals we checked all dishes for eggs; beetles were briefly removed from each dish, and each seed was individually examined for eggs. Females oviposit directly onto seeds, so seeds containing eggs were removed and replaced with clean seeds. We recorded lifetime fecundity for half of the pairs in each population (the remaining pairs were used in another experiment), and we recorded the length and width of all eggs laid within the first 12 h after egg laying was initiated for all pairs from the Black Canyon City population.

Stator limbatus females mated to large males laid more eggs than females mated to small males; lifetime fecundity was positively correlated with male body size in both replicates (Fig. 1). In addition, the mean width and volume (calculated as $0.25 \times \text{length} \times \text{width}^2$, modified from Hoyt 1979) of a female's eggs were positively correlated with her mate's size (Fig. 2). Neither result was due to an inadvertent correlation between male and female body sizes; there was no significant relationship between the body size of mothers and

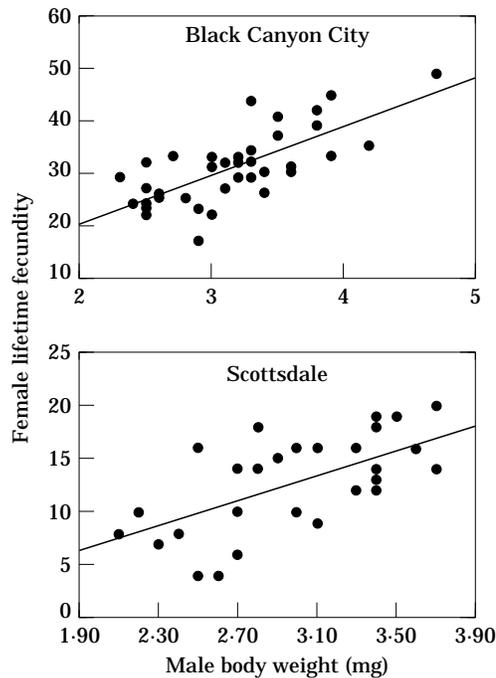


Figure 1. The effect of male size on the lifetime fecundity of his mate in two populations of *S. limbatus* (Black Canyon City: $r^2=0.25$, $N=38$, $P<0.001$; Scottsdale: $r^2=0.40$, $N=30$, $P<0.001$). The differences in mean number of eggs laid in the two experiments are due to large population and host plant effects on egg size; Scottsdale beetles lay fewer large eggs, and Black Canyon City beetles lay more small eggs.

fathers in either population (Black Canyon City: $r^2=0.02$, $N=73$, $P>0.05$; Scottsdale: $r^2=0.08$, $N=30$, $P>0.05$). Also, in a multiple regression analysis the simultaneous effects of both male and female body sizes on lifetime fecundity and egg size were large (Table I). Partial correlations between body weight and fecundity, and between body weight and egg size, are of approximately the same magnitude for both sexes (Table I), indicating that male body size correlations with female fecundity and egg size are nearly identical to female correlations with these characters.

These experiments demonstrate that a female's lifetime fecundity and egg size are affected by her mate's body size, or some character correlated with her mate's body size. It is often observed that females preferentially mate with large males when given a choice between males of varying size, re-mate sooner with a large male than a small

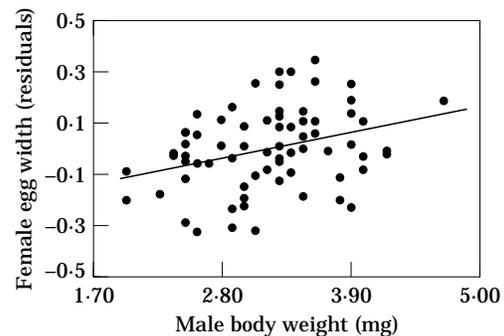


Figure 2. The effect of male size on the size of eggs produced by his mate (statistics in Table I). Plotted is the relationship between male body size and the deviation from the expected egg width due to female weight (i.e. the residuals following the regression of egg width on female weight). These data were collected for the Black Canyon City population only. Egg length and width were estimated for three randomly chosen eggs laid less than 12 h after a female initiated oviposition. Thus, maternal age effects do not contribute to the observed variation. The relationship between male body size and egg width was significant (see Table I), but there was no relationship between body size and egg length ($r^2=0.00$, $N=73$, $P=0.90$). Egg volume was also significantly correlated with male body size ($r^2=0.06$, $P=0.02$).

male if presented with potential mates individually (Simmons 1988; Pitnick 1991), or oviposit only after mating with a preferred male (Waage 1984). It is unclear, however, why females should prefer to mate with large males. One possible explanation is that, because body size is generally highly heritable (Mousseau & Roff 1987), large fathers will produce large offspring that generally have higher fitness than small offspring (e.g. they have higher fecundity and lay larger eggs). In *S. limbatus*, body size is heritable (C. W. Fox, unpublished data), such that females mated to large males produce larger offspring, on average, than females mated to small males, and these larger offspring subsequently lay more and larger eggs (Table I).

Alternatively, females may obtain a direct fitness advantage from mating with large males. However, attempts to measure direct fitness advantages have been unsuccessful (e.g. Pitnick 1991). Our manipulative experiment provides the first conclusive evidence that male body size is positively correlated with female lifetime reproductive success. In addition, we show that these male effects are nearly identical in magnitude to

Table I. The simultaneous effects of male and female body weight of lifetime fecundity and egg size (estimated as egg width) of females

Variable	Squared partial correlation	<i>P</i>
Lifetime fecundity		
Replicate 1		
Mother's weight	0.22	<0.001
Father's weight	0.42	<0.001
		$r^2=0.55$
Replicate 2		
Mother's weight	0.48	<0.001
Father's weight	0.29	<0.001
		$r^2=0.63$
Egg size (width)*		
Mother's weight	0.07	0.008
Father's weight	0.10	0.006
		$r^2=0.16$

*Egg size data were collected for Black Canyon City population only.

female size effects on these characters (Table I), setting the stage for the evolution of mate discrimination by males, and female-female competition for large ejaculates (Gwynne 1988).

Because a male's ejaculate size is positively correlated with his body size, we suggest that male effects on egg size and fecundity are mediated through the size of their ejaculate (and possibly ejaculate quality). However, three alternative hypotheses may account for this relationship. (1) Large males may mate more frequently with females, because of either female choice, male aggressiveness, or male life span (e.g. large males live longer, and thus may mate more often). To test this hypothesis, virgin beetles (Scottsdale population) were paired within 24 h of adult emergence and confined in 60-mm petri dishes with 35 seeds ($N=22$). These pairs were videotaped continuously for 5 days (longer than the reproductive life span of a female). All matings were recorded. We found no relationship between the number of times a pair copulated and the size of the male ($r^2=0.01$, $P>0.05$), nor between the number of copulations and female fecundity ($r^2=0.00$, $P>0.05$). However, male size was positively correlated with female fecundity ($r^2=0.332$, $P<0.01$). Thus, we reject the hypothesis that male size affects female fecundity through changes in mating frequency. (2) Females may exhibit cryptic mate choice, in which they increase their reproductive output after mating with a large male (Thornhill

1983). (3) Male size may correlate with the introduction of hormonal stimulants or other accessory fluids that stimulate egg laying, and potentially influence egg size, but are not incorporated into eggs (Stanley-Samuelson & Loher 1986). At this time, we cannot reject these last two hypotheses.

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