

# Female crickets trade offspring viability for fecundity

L. W. SIMMONS & F. GARCÍA-GONZÁLEZ

*Centre for Evolutionary Biology, School of Animal Biology (M092), The University of Western Australia, Crawley, WA, Australia*

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## Abstract

A growing number of studies are suggesting that females can improve the viability of their embryos by mating with multiple males. However, the reason why females should have low rates of embryo viability is puzzling. Here we conduct a quantitative genetic study of maternal effects on embryo viability in the field cricket *Teleogryllus oceanicus*. After controlling for female body size, we find significant additive genetic variance for ovary weight, a measure of fecundity, and egg hatching success, a measure of embryo viability. Moreover, we show a genetic trade-off between these traits that is predicted from life-history theory. High rates of embryo mortality in this highly fecund species might therefore be explained by selection favouring an optimum balance between fecundity and embryo viability that maximizes maternal fitness. Paternal effects on female fecundity and embryo viability are often seen as benefits driving the evolution of polyandrous behaviour. However, we raise the alternative possibility that paternal effects might shift females from their naturally selected optimum, and present some support for the notion that sexual conflict over a female's optimal fecundity and embryo viability might generate antagonistic coevolution between the sexes.

## Introduction

A fundamental assumption underlying life-history theory is the existence of a trade-off between offspring size and number. Although maternal fitness should increase with the number of offspring produced, females do not have limitless resources to invest in reproduction so that any increase in the number of offspring produced should result in a reduction in the amount of resources allocated to each offspring. Where offspring fitness depends on maternal provisioning, selection is expected to favour a level of provisioning that maximizes female fitness, even though this might conflict with the interests of offspring (Smith & Fretwell, 1974; Parker & Begon, 1986). Much evidence has accumulated from phenotypic studies of both plants and animals that supports the assumption of a negative relationship between offspring size and number (e.g. Sinervo *et al.*, 1992; Einum & Fleming, 2000; reviewed in Roff, 2002), and a positive relationship

between offspring size and offspring fitness (e.g. Fox & Czesak, 2000; Dziminski & Roberts, 2006). However, the evolutionary significance of such phenotypic correlations depends upon the genetic architecture of life-history traits (Reznick, 1992; Roff, 2002).

Comparative studies across fish (Elgar, 1990; Kolm *et al.*, 2006), frogs (Byrne *et al.*, 2003) and copepods (Poulin, 1995) suggest that evolutionary increases in egg size are associated with evolutionary decreases in egg number. Although these patterns are consistent with an evolutionary trade-off between offspring size and number, there remains a paucity of data on the quantitative genetic basis of this life-history trade-off. Evidence of the negative genetic correlation required for an evolutionary trade-off between offspring size and number has only recently begun to accumulate. Thus far, the evidence for a genetic trade-off is mixed. Correlated reductions in fecundity with selection for increased egg size have been reported (Fischer *et al.*, 2006), and quantitative genetic analyses have yielded negative genetic correlations between offspring size and number (Snyder, 1991; Gall & Neira, 2004; Mappes & Koskela, 2004; Shikano & Taniguchi, 2005). However, positive (Lessells *et al.*, 1989; Su *et al.*, 1997) and zero correlations (Yanagi *et al.*, 2006)

*Correspondence:* L. W. Simmons, Centre for Evolutionary Biology, School of Animal Biology (M092), The University of Western Australia, Crawley, WA 6009, Australia.  
Tel.: +61 8 6488 2221; fax: +61 8 6488 1029; e-mail: lsimmons@cyllene.uwa.edu.au

have also been reported. These conflicting results may be explained in part because the strength of trade-offs can depend on environmental conditions experienced by populations (Czesak & Fox, 2003; Blanckenhorn & Heyland, 2004), and can be masked by favourable conditions (Hoffmann & Merilä, 1999). Clearly, more quantitative genetic studies of this important life-history trade-off are required.

Crickets (Orthoptera: Gryllidae) have become increasingly utilized as a model system for examining the costs and benefits of female multiple mating (polyandry). In a variety of species, females have been shown to accrue reproductive benefits from polyandry in the form of increased embryo viability, manifest as an increased egg hatching success (reviewed in Simmons, 2005). Across these studies, average rates of embryo survival as low as 30% have been reported. These data beg the question of why female crickets should have such low rates of embryo viability.

Crickets are highly fecund insects; depending upon nutrient availability, they are capable of producing several hundreds of eggs each day (e.g. Simmons, 1988). In their study of three species of *Gryllus*, Carrière & Roff (1995) documented a phenotypic trade-off between egg size and number. Typical for crickets, they reported embryo viability rates ranging from 9% to 28% for eggs held under field (*Gryllus pennsylvanicus*), and laboratory (*Gryllus veletus* and *Gryllus firmis*) conditions. Although hatching success was in part dependent upon environmental factors, such as soil moisture and depth, egg size played a critical role in embryo viability (Carrière & Roff, 1995). These data suggest that female crickets may trade embryo viability for fecundity.

The Australian field cricket *Teleogryllus oceanicus* is typical of cricket species in having a low embryo viability that can be elevated through polyandrous mating behaviour (Simmons, 2001). Female fecundity shows moderate heritable variation (Simmons, 2003), as does a male's ability to elevate embryo viability (García-González & Simmons, 2005). However, as with other species, the reasons why females should produce eggs with low viability are unclear, and there are no data for any cricket that examines the genetic trade-off between offspring viability and number. Here, we present data from a quantitative genetic analysis of female investment into fecundity and embryo viability, and provide evidence that females must sacrifice embryo viability to increase fecundity. We discuss the possibility that paternal effects might shift females from their naturally selected optima for this important life-history trade-off, and thereby generate sexual conflict over the allocation of maternal resources to offspring number and quality.

## Methods

Crickets were obtained from an outbred stock that was the fourth generation derived from 120 adult females

collected from a banana plantation in Carnarvon, Western Australia. Crickets were bred in plastic containers, fed with cat chow and supplied with water through vials upturned onto pads of cotton wool. Females also utilized the moist cotton wool pads as an oviposition substrate.

We randomly sampled 30 males and 120 females from the stock population as the parents for our quantitative genetic design. Each male was provided with four females and housed in a 1-L container for 7 days for mating. Females were then housed individually and allowed to oviposit for 21 days. Resultant nymphs were raised in 5-L containers and the sexes were separated during their final nymphal instar. Of the 120 dam families originally established, we obtained data for our analyses from 378 adult female offspring, from 84 dam families distributed across 27 sires (mean  $\pm$  SE number of offspring per family  $4.5 \pm 0.2$ , range 1–9; number of dams per sire  $3.1 \pm 0.14$ , range 2–4).

When females were 2 weeks of adult age, they were mated twice to a single unrelated male. Matings were conducted in small plastic boxes (7 cm  $\times$  7 cm  $\times$  5 cm). After mating, the males were left to guard the females for 40 min thereby preventing removal of the spermatophore before insemination was complete (Simmons *et al.*, 2003). To standardize the amount of ejaculate received across all females, spermatophores were removed with forceps after 40 min and the pair left until they had mated a second time. The second spermatophore was also removed after 40 min. After mating, females were provided with a Petri dish containing damp sand and allowed to oviposit for 10 days before being frozen.

Eggs were rinsed from the sand, and a random sample placed onto moist filter paper and incubated at 25 °C. Hatching was checked daily until 2 weeks after the last nymph had emerged. Fertilization rates exceed 90% in this species, and hatching failure reflects death of embryos during development (see Simmons, 2001). Hatching success thereby provides a measure of embryo viability.

Frozen females were thawed, weighed to the nearest 0.01 mg, and their pronotum widths measured to 0.01 mm using digital callipers. We dissected females and removed and weighed the ovaries. The relationship between ovary weight and the number of eggs currently available for oviposition is strong and significant ( $r^2 = 0.80$ ,  $F_{1,23} = 93.67$ ;  $P < 0.001$ ) (see Simmons, 2003). We also counted the total number of eggs laid by a subset of females during the 10 days of oviposition. The strength of the relationship between ovary weight and eggs laid was weaker, but nonetheless highly significant ( $r^2 = 0.12$ ,  $F_{1,64} = 8.95$ ,  $P = 0.004$ ). Ovary weight is thus a reliable measure of past and future female fecundity. Soma weight was calculated as female body weight minus the weight of the ovaries. Finally, we removed the spermatheca of any female with zero hatching success, and examined it for the presence of sperm. Females that had not been inseminated were removed from our analyses.

Mixed model nested analyses of variance, with dams nested within sires, were used to test the statistical significance of sire and dam effects, using Satterthwaite's approximation of the error term to account for unequal sample sizes of offspring, as recommended by Lynch & Walsh (1998). Analyses of genetic variation were conducted using sire and dam variance components estimated from restricted maximum likelihood (REML) procedures in S-Plus (Roff, 2006). Narrow sense and broad sense heritabilities were calculated from the sire and dam variance components following Becker (1984). Coefficients of phenotypic, additive genetic and residual variation were calculated following Houle (1992). Covariances between traits that were due to sires and dams were also estimated using procedures in S-Plus outlined by Roff (2006). Standard errors for heritabilities and genetic correlations were estimated by jackknifing across paternal half-sib families (Roff, 2006). All mean values are presented  $\pm 1$  SE.

## Results

The magnitude of sire effects on female pronotum width, soma weight and ovary weight were similar, but statistically significant only for pronotum width (Table 1). The sire effect on egg viability was 10% lower than its effect on body size and ovary weight, and not statistically significant. In all cases dam effects were twice the size of

sire effects as expected, as in addition to additive genetic effects, dam effects include maternal and dominance effects. Coefficients of additive genetic variation were low for body size, but those for ovary weight and egg viability were moderately high (Table 2). High coefficients of residual variation rendered the narrow sense heritabilities statistically nonsignificant (but see below). The magnitude of these genetic statistics are similar to those reported in a previous quantitative genetic study of this species (Simmons, 2003).

The genetic variance-covariance (**G**) matrix revealed strong and significant correlations between measures of female body size, and our measures of reproductive fitness, ovary weight and egg viability. Genetic correlations based on sire family means are shown above the diagonal in Table 3. Although sire family mean correlations tend to underestimate the true magnitude of genetic correlations, they are adequate for establishing their sign and significance (Astles *et al.*, 2006). There was a significant negative genetic covariance between ovary weight and egg viability (Fig. 1). This analysis was robust to the removal of the sire family to the bottom right of Fig. 1 (sire family mean  $r = 0.416$ ,  $n = 26$ ,  $P = 0.034$ ). Thus, our data provide evidence of a genetic trade-off between female fecundity and offspring viability. Because of the significant correlations between pronotum width and ovary weight, and between soma weight and egg viability, this apparent trade-off might be due to

**Table 1** Nested analysis of variance for size and reproductive traits of female *Teleogryllus oceanicus*.

Trait	Source	SS	d.f.	MS	<i>F</i>	<i>P</i>	<i>d</i>
Pronotum (mm)	Sire	13.49	26	0.52	2.37	0.002	0.36
	Dam	12.77	57	0.22	1.19	0.180	0.44
	Error	50.15	267	0.19			
Soma (mg)	Sire	632 672.00	26	24 333.50	1.62	0.059	0.39
	Dam	920 129.00	56	16 430.90	2.32	< 0.001	0.61
	Error	1 867 549.80	264	7074.10			
Ovaries (mg)	Sire	158 220.00	26	6085.39	1.46	0.110	0.37
	Dam	255 387.00	56	4560.49	2.32	< 0.001	0.61
	Error	518 714.07	264	1964.83			
Embryo viability (%)	Sire	18 962.50	26	729.33	1.34	0.166	0.27
	Dam	32 203.70	57	564.98	1.33	0.071	0.45
	Error	125 123.36	294	425.59			

SS, sums of squares; df, degree of freedom; MS, mean squares; *F*, variance ratio; *P*, probability; *d*, Cohen's standardized effect size.

**Table 2** Descriptive phenotypic and genetic statistics for body size and reproductive variables of female *Teleogryllus oceanicus*.

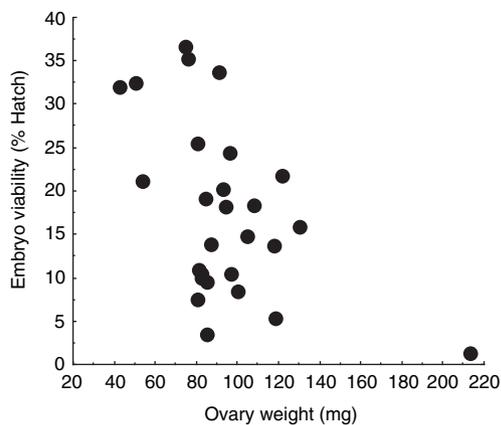
Trait	Mean	$V_P$	$V_A$	$h^2$ (SE)	$H^2$	$CV_P$	$CV_A$	$CV_R$
Pronotum (mm)	5.69	0.228	0.027	0.48 (0.12)	0.35	8.39	2.89	7.62
Soma (mg)	553.61	10 271.58	770.37	0.30 (0.11)	0.61	18.31	5.01	15.25
Ovaries (mg)	91.11	2960.84	221.58	0.30 (0.17)	0.68	59.72	16.35	48.60
Embryo viability (%)	17.07	495.78	27.19	0.22 (0.04)	0.30	130.44	30.55	120.26

$V$ , variance component;  $h^2$ , narrow sense heritability;  $H^2$ , broad sense heritability;  $CV$ , coefficient of variance;  $P$ , phenotypic;  $A$ , additive genetic;  $R$ , residual.

**Table 3** The genetic covariance (**G**) matrix based on sire family mean values of body size and reproductive variables of female *Teleogryllus oceanicus* (zero-order correlations are shown above the diagonal and correlations partialled with respect to all other variables are shown below the diagonal).

	Pronotum	Soma	Ovaries	Egg viability
Pronotum (mm)		0.746	0.460	-0.065
Soma (mg)	0.726		0.535	-0.384
Ovaries (mg)	0.285	0.075		-0.502
Egg viability (%)	0.436	-0.415	-0.452	

Critical zero-order  $r_{26,0.05} = 0.374$ ; critical partial  $r_{21,0.05} = 0.413$ .



**Fig. 1** Plot of sire family mean female fecundity estimated from the weight of ovaries, against embryo viability measured as the percentage of eggs that hatched. The data suggest a trade-off between the quantity and quality of offspring produced by female *Teleogryllus oceanicus*.

genetic covariation with female body size. The correlations partialled with respect to all other variables show that the genetic trade-off between fecundity and egg viability was not dependent on covariation with female body size (below the diagonal in Table 3). Genetic correlations and their standard errors estimated using REML and jackknife procedures are shown in Table 4, and confirm the findings in Table 3.

The correlations between measures of female size and ovary weight, and female size and embryo viability were of opposite sign (Table 3), a pattern which might obscure underlying additive genetic variance in embryo viability and ovary weight. There were also strong maternal effects on measures of female size (Table 1) that can augment, oppose or be uncorrelated with genetic effects on offspring (Qvarnström & Price, 2001). We therefore recalculated the quantitative genetic statistics for ovary weight and egg viability after controlling statistically for both pronotum width and soma weight by entering these body size variables as covariates into the nested analyses of variance shown in Table 1. These reanalyses revealed statistically significant sire effects on ovary weight (sire:

**Table 4** The genetic covariance (**G**) matrix calculated from restricted maximum likelihood variance component estimates of body size and reproductive variables of female *Teleogryllus oceanicus* (genetic correlations are shown above the diagonal and jackknifed standard errors are shown below the diagonal).

	Pronotum	Soma	Ovaries	Egg viability
Pronotum (mm)		0.704	0.485	-1.257
Soma (mg)	0.066		0.533	-0.222
Ovaries (mg)	0.286	0.209		-0.678
Egg viability (%)	11.429	0.151	0.075	

$F_{26,56} = 1.70$ ,  $P = 0.042$ ,  $d = 0.36$ ; dam:  $F_{56,262} = 1.82$ ,  $P = 0.001$ ,  $d = 0.54$ ) and egg viability (sire:  $F_{26,56} = 1.93$ ,  $P = 0.014$ ,  $d = 0.30$ ; dam:  $F_{56,262} = 0.98$ ,  $P = 0.525$ ,  $d = 0.40$ ), and correspondingly larger narrow sense heritabilities (ovaries:  $h^2 = 0.40$ ,  $CV_A = 16.89$ ; egg viability:  $h^2 = 0.52$ ,  $CV_A = 44.26$ ).

## Discussion

After controlling for covariation due to female body size, our data provide evidence for significant additive genetic variation in female fecundity and embryo viability. The heritability for ovary weight was close to the estimate obtained in a previous study of *T. oceanicus* ( $0.44 \pm 0.01$ : Simmons, 2003), and similar to values reported from field ( $0.25 \pm 0.12$ ) and laboratory ( $0.55 \pm 0.13$ ) studies of *G. pennsylvanicus* (Simmons & Roff, 1994). The coefficients of additive genetic and residual variation in ovary weight were broadly consistent with the median values reported from studies of fecundity in *Drosophila* ( $CV_A = 11.90$ ,  $CV_R = 39.02$ ), and similar in magnitude to those for life-history traits generally (Houle, 1992). The coefficient of additive genetic variation in embryo viability was twice that for fecundity, and the coefficient of residual variation an order of magnitude greater. Some of this residual variation undoubtedly stemmed from variation in paternal effects across females. Females were allocated a mate at random, and males are known to differ in their ability to influence the viability of embryos produced by their mates (García-González & Simmons, 2005). Overall, the levels of additive genetic variation in both fecundity and embryo viability are indicative of considerable evolutionary potential (Houle, 1992). Importantly, the data show substantial additive genetic covariation between fecundity and embryo viability, illustrating an evolutionary trade-off between these life-history variables. Thus, selection for increased embryo viability is expected to reduce female fecundity and vice versa. Our quantitative genetic data for *T. oceanicus* are consistent with the phenotypic trade-offs between egg number, size and viability seen in three species of *Gryllus* (Carrière & Roff, 1995), suggesting that trade-offs between the quantity and quality of offspring may well characterize crickets generally.

Einum & Fleming (2000) conducted an experimental field study of Atlantic salmon in which they manipulated the size of eggs in clutches and monitored the survival of juveniles. As with crickets (Carrière & Roff, 1995), they found that juveniles from large eggs survived better than those from small eggs. Moreover, they found that maternal fitness was maximized at an optimal egg size that provided relatively low offspring survival. Life-history trade-offs between offspring fitness and number, coupled with selection for maternal fitness maximization may thus explain the maintenance of low embryo viability found in highly fecund species such as crickets (Einum & Fleming, 2000). Future work with crickets that focuses on the lifetime fitness of females that produce relatively large viable vs. relatively small nonviable eggs, will allow us to determine whether the observed fecundity and embryo viability maximizes female fitness.

Studies of *T. oceanicus*, other cricket species and other insects have found that embryo viability can be improved by mating with multiple males (reviewed in Simmons, 2005). These studies have been taken as evidence that females benefit from multiple mating, assuming that increased embryo viability is in the female's interest. However, our data raise an interesting alternative view, that embryo viability might be the focus of sexual conflict. García-González & Simmons (2005) reported heritable additive genetic variation in the ability of male *T. oceanicus* to elevate the viability of embryos produced by their mates ( $h^2 = 0.46 \pm 0.29$ ,  $CV_A = 21.10$ ). They also reported a significant genetic correlation between the viability of embryos sired by a male and his investment into his accessory glands ( $r_g = 0.79 \pm 0.45$ ). These data implied male accessory gland products (Acps) as the mechanism by which embryo viability is enhanced. Indeed, a subsequent study revealed that males capable of inducing high embryo viability in their own offspring, also enhanced the embryo viability of offspring that were sired by their mate's other mating partners (García-González & Simmons, 2007). The data strongly suggest that male Acps, either directly or indirectly via their effects on maternal allocation, are involved in the increased embryo viability that results from polyandry. In *Teleogryllus commodus*, the male accessory glands secrete proteins into the ejaculate that, when transferred to the female's reproductive tract, are converted by prostaglandin synthetase derived from the testes, into prostaglandin which stimulates vitellogenesis and oviposition (Stanley-Samuels & Loher, 1983; Stanley-Samuels *et al.*, 1986; Stanley Samuelson *et al.*, 1987). Previously, we suggested that Acps might impact on the viability as well as quantity of eggs produced, thereby benefiting polyandrous female *T. oceanicus*. However, given the trade-off between fecundity and embryo viability documented in our current study, it is possible that males who induce females into greater investment into each egg, and thus elevate embryo viability, may displace females from their fitness maximizing optima,

leading to a sexual conflict over the quantity and quality of offspring produced.

Mills & Moore (2004) have modelled the evolutionary dynamics of male and female interests in resource allocation to offspring, within the context of the evolution of mammalian imprinted genes that affect foetal and placental growth. They showed that polyandry can drive the fixation of 'greedy' paternal alleles that increase offspring viability at the expense of maternal fecundity, and 'thrifty' maternal alleles of opposite effect. Although these models were developed specifically for biological systems in which embryos draw maternal nutrients during gestation, we see no reason why similar evolutionary dynamics could not apply to insects where both paternal and maternal effects influence the allocation of resources to eggs. Indeed, in their theoretical analyses of nuptial feeding in insects, Parker & Simmons (1989) show how there can be sexual conflict over the temporal pattern of allocation of male donations to future offspring.

The notion of antagonistic coevolution between maternal and paternal effects on fecundity and embryo viability generates a number of testable hypotheses. First, we would expect to see negative covariation between female investment into increased fecundity and male investment into enhanced embryo viability. Second, we would expect to see female adaptations to counter the effects of male Acps that influence a female's fecundity/embryo viability balance. Finally, we would expect sexual conflict to drive rapid evolutionary divergence in seminal Acps. There is some evidence to bring to bear on each of these predictions.

Some of the families used in this study were also used in García-González & Simmons' (2005) study of paternal effects on embryo viability. Thus there are 22 sire (64 dam) families for which data are available on female effects on embryo viability, and the paternal effects on embryo viability of their brothers. Across these sire family means, the correlation between a female's embryo viability and the embryo viability induced by their brothers was  $-0.304$  ( $n = 22$ ,  $P = 0.169$ ). The genetic correlation could not be calculated from variance component estimates because the data matrix contained too many missing values. Although not significant, the direction of the correlation suggests that genes in males that enhance embryo viability might be associated with genes in females that invest less in embryo viability, as predicted if these traits are coevolving antagonistically. Stronger evidence comes from a previous quantitative genetic study of *T. oceanicus* (Simmons, 2003). Here the genetic correlation between accessory gland weight in males (which is positively genetically correlated with paternal effects on embryo viability) and the weight of their sister's ovaries (which is negatively genetically correlated with embryo viability) was strong and significant (sire family mean estimate,  $0.724$ ; variance component estimate  $1.13 \pm 0.27$ ). Simmons (2003) suggested

that this genetic correlation may be indicative of a mechanism of indirect selection via cryptic female choice, with females investing more in egg production with males better able to stimulate oviposition. However, this genetic covariance is also consistent with coevolution driven by sexual conflict over fecundity and embryo viability.

There is also evidence to suggest that in some species females may possess mechanisms to counteract the effects of male Acps. In their study of *T. commodus*, Stanley-Samuelson & Loher (1985) found that 2 h following experimental injections of prostaglandin into the abdomen of females, there was a reduction in prostaglandin circulating in the haemolymph. A large proportion of the prostaglandins (50% in 1-day-old females, and 35% in 8-day-old females) was excreted by the female via the malpighian tubules and hindgut. These data suggest that female *T. commodus* may actively metabolize, rather than respond to male gonadotropic compounds. Interestingly, multiple mating by females has little effect on embryo viability in this species (Jennions *et al.*, 2007).

Finally, a recent evolutionary analysis of Acps across five species of *Gryllus* has revealed that genes encoding seminal proteins show rates of nonsynonymous substitutions that are three times higher than genes coding for proteins not involved in reproduction (Andrés *et al.*, 2006). These patterns strongly suggest that evolutionary divergence in seminal proteins in crickets has been accelerated by positive Darwinian selection, a process expected from all mechanisms of post-copulatory sexual selection, but highlighted in recent analyses of sexual conflict (Arnqvist & Rowe, 2005).

In conclusion, we have shown that female *T. oceanicus* are faced with a trade-off between the number of offspring they produce, and the viability of those offspring, so that selection is expected to favour an optimal investment that maximizes maternal fitness (Smith & Fretwell, 1974). Paternal effects on female fecundity and offspring viability have been widely reported in crickets, and are taken as evidence for benefits that may promote the evolution of polyandry (Simmons, 1988; Tregenza & Wedell, 1998; Wagner & Harper, 2003). This may be true for some cricket species where mating appears to increase rather than to decrease female lifetime offspring production (Simmons, 1988; Fedorka & Mousseau, 2002; Wagner & Harper, 2003). These studies imply that male Acps have synergistic effects on both fecundity and embryo viability. Nevertheless, we suggest that studies which measure lifetime maternal fitness in terms of the total numbers of surviving offspring are necessary to show unequivocally that paternal effects on fecundity or embryo viability are beneficial to females (e.g. Fedorka & Mousseau, 2002; Dunn *et al.*, 2005). A plausible alternative explanation for positive effects on short-term measures of female reproductive performance is that males shift females

from their naturally selected optima for these traits, leading to reduced maternal fitness and sexual conflict over the allocation of maternal resources to the number and viability of offspring. Future studies should thus attempt to distinguish between putative mechanisms of post-copulatory sexual selection acting on fecundity and embryo viability.

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