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Good genes, genetic compatibility and the evolution of polyandry: use of the diallel cross to address competing hypotheses

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Abstract

Genetic benefits can enhance the fitness of polyandrous females through the high intrinsic genetic quality of females' mates or through the interaction between female and male genes. I used a full diallel cross, a quantitative genetics design that involves all possible crosses among a set of genetically homogeneous lines, to determine the mechanism through which polyandrous female decorated crickets (*Gryllodes sigillatus*) obtain genetic benefits. I measured several traits related to fitness and partitioned the phenotypic variance into components representing the contribution of additive genetic variance ('good genes'), nonadditive genetic variance (genetic compatibility), as well as maternal and paternal effects. The results reveal a significant variance attributable to both nonadditive and additive sources in the measured traits, and their influence depended on which trait was considered. The lack of congruence in sources of phenotypic variance among these fitness-related traits suggests that the evolution and maintenance of polyandry are unlikely to have resulted from one selective influence, but rather are the result of the collective effects of a number of factors.

Introduction

In broad terms, mechanisms through which polyandrous females obtain genetic benefits can be separated into those that emphasize intrinsic male genetic quality and those that highlight the interaction between paternal and maternal genomes (Zeh & Zeh, 2003; Simmons, 2005). Hypotheses that focus on the intrinsic qualities of prospective mates include both those in which offspring viability is enhanced through paternally derived genes, and those in which the attractiveness of females' sons are enhanced through paternally derived genes (Kokko *et al.*, 2002). According to these hypotheses, females mating with many males enjoy higher fitness than females mating with fewer males because elevated levels of polyandry result in a greater likelihood that one or more males of high genetic quality will fertilize a female's eggs (Yasui, 1998; Fox & Rauter, 2003; Hosken *et al.*, 2003). Benefits derived through genetic interactions between males and females can arise in two ways. First, a female mating with many males might enhance her fitness by *decreasing* her chance of fertilizing eggs with the sperm of genetically incompatible males (Tregenza & Wedell, 2002). Genetic incompatibility between males and females can occur for many reasons including, but not limited to, inbreeding depression, selfish genetic elements, segregation distortion and immunological effects (Zeh & Zeh, 1996; Tregenza & Wedell, 2000). Regardless of the mechanism involved, the main consequence of genetic incompatibility is that gametes of certain males are more successful in producing viable offspring than those of other males when fertilizing a particular female's eggs (Jennions, 1997). Second, females mating polyandrously might benefit by *increasing* their chances of obtaining favourable genetic combinations, through dominance (nonadditive effects within loci) or epistatic interactions (nonadditive effects between loci; Lynch & Walsh, 1998). In particular, the effect of dominance, although often ignored when considering the benefit of genetic compatibility, should also be included when assessing the mechanisms through which polyandrous females gain genetic benefits, as it has been shown to significantly impact fitness-related traits (Crnokrak &

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Roff, 1995; DeRose & Roff, 1999; Merilä & Sheldon, 1999).

Although a growing number of studies have demonstrated the importance of genetic benefits to female fitness (reviewed in Jennions & Petrie, 2000), few studies have employed designs powerful enough to differentiate between mechanisms underlying such benefits (but see Wedekind *et al.*, 2001; Evans & Marshall, 2005; García-González & Simmons, 2005). A powerful and unambiguous way to disentangle the genetic benefits of female polyandry is to compare the contribution to fitness of additive genetic variance, which underlies intrinsic male genetic quality, to that of nonadditive genetic variance, which corresponds to genetic compatibility in its various forms (Neff & Pitcher, 2005; Puurtinen *et al.*, 2005). However, to date very few studies have estimated additive and nonadditive genetic variance in female fitness as a way to evaluate the selective benefits to polyandry.

The decorated cricket, *Gryllodes sigillatus*, occurs throughout the world in tropical and subtropical regions and is normally associated with human habitation (Smith & Thomas, 1988). During mating, male *G. sigillatus* transfer a spermatophore consisting of a small sperm-containing ampulla surrounded by a large gelatinous spermatophylax. Although the spermatophylax constitutes a nuptial food gift, it does not appear to provide female *G. sigillatus* with any detectable nutritional benefits (Will & Sakaluk, 1994; Kasuya & Sato, 1998). Females mate repeatedly throughout their lives and with many different males, copulating as frequently as one or more times nightly (Sakaluk *et al.*, 2002). Previous work on this species revealed that female decorated crickets enhance their fitness through polyandrous, but not monogamous, multiple mating, and the magnitude of fitness enhancement through multiple mating is contingent on the number of different males with whom a female mates rather than the number of times a female mates (Ivy & Sakaluk, 2005). Taken together, these results indicate that genetic benefits are important to female fitness in decorated crickets, whereas material benefits are much less so.

The aim of this study was to ascertain the relative importance of two mechanisms through which female *G. sigillatus* might secure genetic benefits for their offspring, intrinsic male quality and interactions between male and female genomes. To evaluate the impact of these processes, I employed a quantitative genetics design, the diallel cross, to estimate the contribution of additive and nonadditive genetic variation in traits related to fitness. This design is ideally suited to the study of genetic benefits because it finely partitions phenotypic variance into causal factors beyond those possible with more common quantitative genetics designs, such as parent–offspring analyses and nested-sib designs (Table 1). In particular, additive and dominance variance can be evaluated separately from maternal and paternal effects, which helps to avoid inflated parameter estimates (Lynch & Walsh, 1998). The diallel design involves crosses between homogeneous genetic lines in all possible combinations. In sexually reproducing animals with internal fertilization that cannot be artificially inseminated, inbred genetic lines serve as the genetic units to be crossed (Lynch & Walsh, 1998).

Table 1 Cockerham and Weir's statistical Model C (bio model), the six variance components estimated, and their biological interpretations with respect to the genetic benefits to polyandry: $Y_{ijk}=\mu + N_i + N_j + T_{ij} + P_i + M_j + K_{ij} + W_{k(ij)}$.

Parameter estimate	Biological interpretation
V_z	Total phenotypic variance
V_n	Additive effect of line nuclear genotype – *evidence for good genes*
V_t	Nonadditive interaction of maternal and paternal nuclear genes – *evidence for genetic compatibility*
V_m	Maternal extranuclear effects
V_p	Paternal extranuclear effects – *possible evidence for good genes*
V_k	Interactions involving extranuclear effects – *evidence for genetic compatibility*
V_e	Residual effect of environment

Adapted from Cockerham & Weir (1977) and Lynch and Walsh (1998).

Methods

Experimental protocol

Experimental *G. sigillatus* were the descendants of approximately 500 adults collected in Las Cruces, New Mexico, in May 2001. Unless otherwise specified, crickets were housed at 32 °C on a 16 h:8 h light:dark cycle and provisioned with Flukers® cricket chow *ad libitum*, water supplied in 40-mL plastic tissue culture flasks plugged with cotton dental rolls, egg carton to provide shelter and to increase surface area, and dishes of moistened peat moss to serve both as an oviposition substrate and as a source of additional water. Nine inbred lines were created by subjecting individuals, randomly selected from a large panmictic population (~5000 individuals), to four generations of full-sib mating of one male and one female (coefficient of inbreeding, $F = 0.55$).

To ameliorate the potentially confounding effects of common environment in quantitative genetics analyses, 10 containers were created for each line, each housing approximately 10 early- to mid-instar nymphs. These boxes were checked every other day for newly eclosed adults, which were separated by sex and housed individually in 0.47-l plastic containers.

At 5 days of adult age, I weighed both males and females to the nearest milligram. The following day, crickets were paired according to cross type in clear

plastic viewing chambers (10.5 × 7.5 × 3 cm) lined with paper towel and viewed under red-light illumination until mating occurred. In *G. sigillatus*, there is a positive linear relationship between the duration of ampulla attachment and the number of sperm transferred by males (Sakaluk, 1984). So, to ensure equal insemination across females, I removed females after mating occurred and placed them in small centrifuge tubes, restricting their movement and preventing them from removing sperm ampullae for a 50-min insemination period. To remove any influence of material benefits arising from consumption of the food gifts (Ivy *et al.*, 1999), females were not permitted to consume spermatophylaces after mating.

After the insemination period, I removed the attached spermatophore with forceps and placed females in 280-mL containers. Females were housed individually, provisioned with Flukers® cricket chow in a small weigh boat, water in a 13-mL polystyrene vial plugged with rolled cheesecloth, and peat moss in a 20-mL Fisherbrand® polystyrene beaker. Females were maintained in an incubator under the environmental conditions described previously. After 10 days, females were removed from the containers, and a random sample of 80 eggs was removed from the peat moss with forceps and placed in a 280-mL container lined on the bottom with moistened cheesecloth. Hatching containers were incubated under the same conditions as above, and their positions within the incubator were randomized daily to minimize position effects within the incubator.

The day of first hatch was recorded, and nymphs were counted each day thereafter. The first 30 nymphs to hatch were housed together in plastic shoeboxes (10.5 cm × 7.5 cm × 3 cm) and reared in an environmental chamber. Position within the incubator was randomized daily to minimize between-family environmental variations.

Because phenotypic differences among individuals are often only manifest under stressful conditions in insects (Hartl *et al.*, 1985; Ward, 1994; Hoffmann & Merila, 1999), offspring were reared under conditions of nutritional stress by providing a low-protein diet (13.5% crude protein), created by blending Flukers® cricket chow and flour in a 1.13 : 2 ratio. *G. sigillatus* nymphs from the same inbred lines maintained on a regular diet in the same environmental conditions take an average of 31 days to develop from nymph to adulthood, whereas nymphs on this stressful diet take around 47 days to develop into adults (T.M. Ivy, unpublished). The diet used here, therefore, does appear to present significant stress to developing crickets.

In addition to the proportion of eggs hatching, I measured three aspects of offspring quality for each family: (1) survival, calculated as the proportion of hatched offspring surviving to sexual maturity, (2) developmental time, with early development determined as the number of days from oviposition to hatch and late development as the average number of days from hatch until the first offspring had undergone adult eclosion, and (3) average adult mass upon the final molt. Because decorated crickets exhibit a sexual size dimorphism, with females being larger than males (Sakaluk *et al.*, 2002), I considered adult mass of offspring separately for the sexes. As mechanisms related to genetic incompatibility can affect sex ratios (Zeh & Zeh, 1996), I also calculated the proportion of female offspring produced by each family.

I attempted to replicate each of the 72 cross types twice to create 144 families. In three cases, because of repeated mechanical failures in mating (i.e. the male did not properly transfer the spermatophore); I could establish only one replicate for a particular cross type. In 23 of the remaining 69 cross types, a female in one of the two replicates failed to produce eggs or she laid eggs that did not hatch. In an effort to avoid missing data for measures of offspring performance, I attempted the crosses that failed one to three additional times. These compensatory efforts were successful in 12 cases and unsuccessful in 11 cases. In six cases, a cross type had three replicates rather than two. In total, I performed 175 crosses, with 136 of those producing offspring. Although 14 crosses were missing one replicate, no cross type was completely absent from the analysis.

For each fitness trait measured, I estimated the six causal components of variance described in the 'bio model' of Cockerham & Weir (1977, Box 1): (1) additive effects of nuclear genes, σ^2_n; (2) nuclear gene interaction effects, σ^2_t; (3) maternal effects, σ^2_m; (4) paternal effects, σ^2_p; (5) extranuclear interaction effects, σ^2_k, (includes both extranuclear–extranuclear interactions and extranuclear–nuclear interactions); and 6) residual variance attributed to within-family effects, σ^2_e. Parameter estimates of these variances components were obtained using restricted maximum likelihood (REML) by expressing the covariance between families as linear functions of the six causal components (Lynch & Walsh, 1998; Fry, 2004) using the type = lin(q) option of PROC MIXED in SAS v. 9.1 (SAS Institute, 2004). Lines were treated as random effects. To avoid negative estimates of variance, parameter estimates were constrained to be either greater than or equal to zero (Fry, 2004), and thus significance tests involving parameter estimates are one tailed. Response variables were transformed where necessary to meet the assumptions of REML. Variance parameters were tested for significance using χ^2-restricted likelihood-ratio tests, which evaluated significant differences in goodness-of-fit when comparing saturated models vs. models in which the parameter of interest was constrained to zero (Lynch & Walsh, 1998; Fry, 2004). Environmental variance (residual variance) was tested for a significant departure from zero using a one-tailed *z*-test, as the residual could not be held at zero. Coefficients of variation (CV) for each parameter estimate were calculated following Houle (1992), enabling comparisons

between the sources of phenotypic variation for a single fitness trait and also between sources of variation among different fitness traits.

Biological interpretation of variance components

The biological interpretations of the estimated variance components are summarized in Table 1. Significant variance associated with the nuclear genome (V_n) suggests that intrinsic male genetic quality contributes to offspring viability and/or performance, thereby supporting the 'good genes' hypothesis. Significant variance because of nuclear gene interaction (V_t) indicates that variance in fitness is determined by the combination of male and female genotypes in a nonadditive fashion (Lynch & Walsh, 1998). Nuclear interaction effects include dominance effects and epistatic interactions, both potential sources of genetic compatibility (Puurtinen *et al.*, 2005). Maternal and paternal effects (V_m and V_p) include genetic effects, such that of the mitochondrial genome (Alberts et al., 2002), nuclear genes that have sex-specific expression (see Barmina *et al.*, 2005), genomic imprinting (Reik & Walter, 2001), as well as environmental effects, such as the effect of maternal allocation of nutrients to eggs. Significant paternal effects may indicate intrinsic male quality, if they are the result of heritable variation and their effects enhance offspring viability or performance (for an example, see Manoli *et al.*, 2005). Extranuclear interactions (V_k) involve both interactions between extranuclear elements and interactions between nuclear and extranuclear elements. This category includes effects of cytoplasmic incompatibility (Hoffmann & Turelli, 1997) and certain types of transposable elements (Rio, 2002). Significant variance attributed to extranuclear interactions signifies the importance of genetic compatibility in determining female fitness.

Results

The means and standard errors of the fitness traits measured are presented in Table 2. Parameter estimates and coefficients of variation are presented in Table 3 and Fig. 1 and statistically significant parameter estimates are summarized here. Variance due to nuclear genes (V_n) contributed to the proportion of offspring surviving to adulthood (log-transformed). Dominance and/or epistatic interactions (V_t) influenced the number of days from hatching to adulthood (reciprocal squared-transformed). Paternal effects (V_p) were an important component of phenotypic variance in both proportion of eggs that hatched (arcsin-transformed) and the mass of male offspring (log-transformed). Interactions involving extranuclear elements (V_k) also contributed to male offspring

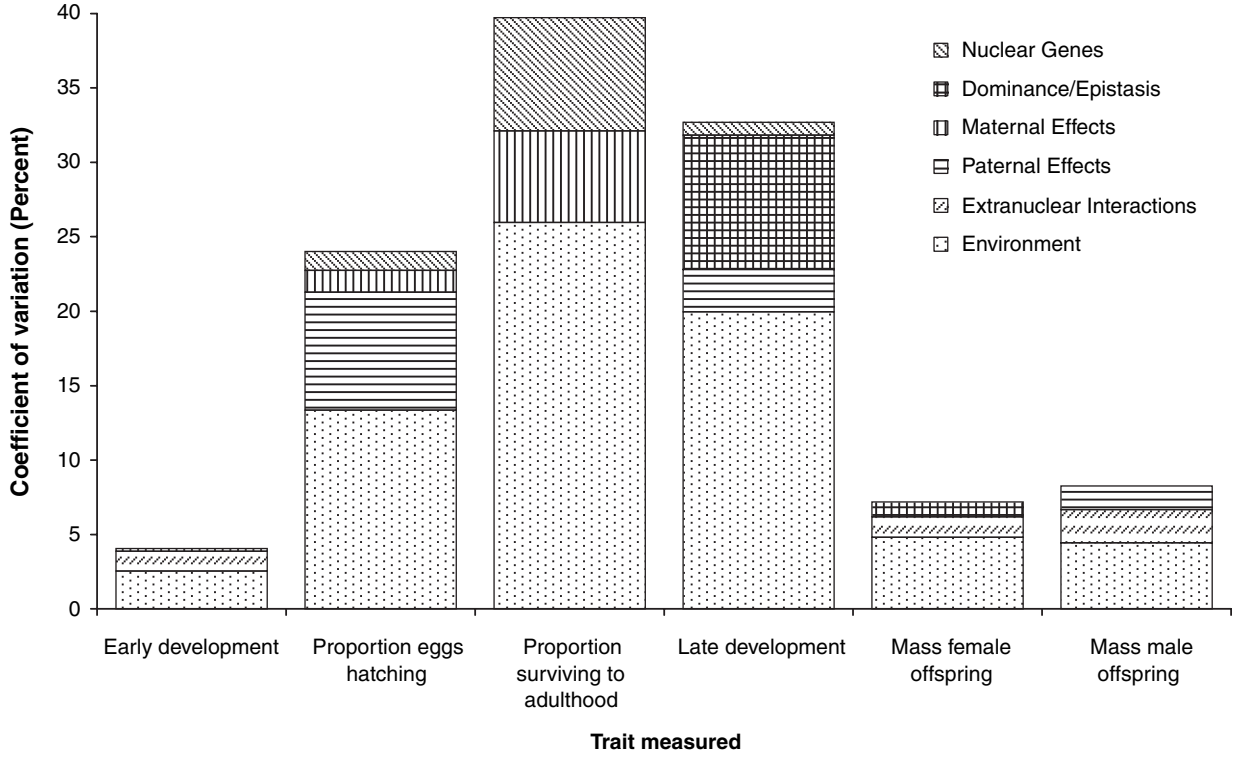

Fig. 1 Coefficients of variation (CV) and the relative proportion of variation explained by the six estimated components of phenotypic variance for each fitness-related trait measured.

Table 2 Sample sizes, means, and standard errors for each fitness trait measured

Trait measured	*n*	Mean	SE
Days to hatch	139	12.1	0.08
Proportion hatching (*without hatch failures*)	139	0.83	0.01
Proportion hatching (*with hatch failures*)	166	0.69	0.03
Proportion surviving	139	0.26	0.01
Days to adulthood	139	47.0	0.5
Female offspring mass (mg)	565	257.33	3.00
Male offspring mass (mg)	393	188.85	2.54

mass (log-transformed), as well as to female offspring mass (log-transformed) and days from egg to hatch (1/log-transformed), although the latter two effects were marginally statistically nonsignificant. The analysis revealed no statistically significant maternal effects (V_m).

As stated previously, 39 of 175 crosses failed to produce eggs that hatched, and it is unclear whether these cases represent unfertilized eggs or embryos that did not develop. With only 39 failures spread over nine lines and 72 cross types, it is difficult to assess statistically the cause of the failures. Males often had difficulty transferring spermatophores, and this problem seemed especially common in males from two of the nine lines. In addition, females from two lines different from those mentioned above appeared to have difficulty accepting spermatophores. Often, matings involving individuals from these four lines appeared to be successful, but the spermatophore would fall off almost immediately after the copulation occurred. It is possible that even when spermatophore transfer appeared to be successful (i.e. the spermatophore remained attached after copulation), males in these crosses failed to transfer sperm. Twenty-eight of the 72 cross types (39%) involved the two problematic male lines and the two problematic female lines in which I observed mechanical difficulties during mating, yet crosses involving these individuals represented 68% of the 39 cases where there was wholesale failure in hatching. Indeed, logistic regression indicated that crosses involving individuals belonging to one of the lines described above were far more likely to result in failure than crosses involving the other lines. (Wald $\chi^2 = 7.79$, $P < 0.01$). Further, when complete failures in hatching are disregarded, the lowest proportion of eggs hatching for any combination (including those that previously failed) was 0.425. Taken with the results of previous work on outbred *G. sigillatus*, in which there were no cases of reproductive failure (e.g. Ivy & Sakaluk, 2005), the strong influence that individuals from the four lines above had on the probability that a cross would fail, and the lack of continuous variation in hatching success, I believe that the hatching failures observed in this study are not part of the normal variation in hatching success, but rather failures in sperm transfer. I therefore excluded from the main analysis the 39 cases in which females failed to lay eggs or cases in which eggs failed to hatch. It is important to note, however, that the qualitative result of the analysis for proportion of eggs hatching did not change when the hatching failures were included.

Table 3 Parameter estimates of variance components and coefficient of variation for each fitness-related trait.

	Days from Egg to Hatch			Proportion of Eggs Hatching (without hatch failures)			Proportion of Offspring Surviving to Adulthood		
Source	Estimate	CV (%)	Proportion of variation	Estimate	CV (%)	Proportion of variation	Estimate	CV (%)	Proportion of variation
V_n	0	–	–	0.0002	1.27	0.05	0.012**	7.61	0.02
V_t	0	–	–	0	–	–	0	–	–
V_m	5.27×10^{-7}	0.19	0.05	0.0002	1.47	0.06	0.0078	6.16	0.16
V_p	0	–	–	0.0062***	7.92	0.33	0	–	–
V_k	$5.28 \times 10^{-5*}$	1.32	0.33	0	–	–	0	–	–
V_e	$1.4 \times 10^{-4****}$	2.55	0.63	0.0182****	13.36	0.56	0.1394****	25.96	0.65
	Days from hatch to adult			Mass of female offspring			Mass of male offspring		
V_n	1.64×10^{-7}	0.86	0.03	0	–	–	0	–	
V_t	$1.8 \times 10^{-5**}$	9.03	0.28	0.003	0.99	0.14	0	–	
V_m	0	–	–	0	–	–	0	–	
V_p	1.79×10^{-6}	2.85	0.09	0	–	–	0.0068**	1.58	0.19
V_k	0	–	–	0.0058*	1.38	0.19	0.0134****	2.22	0.27
V_e	$8.8 \times 10^{-5****}$	19.96	0.61	0.0704****	4.81	0.67	0.0534****	4.46	0.54

P-values are the result of restricted likelihood χ^2 tests, except for estimates of V_e, where they are the result of *z*-tests (see text). $^*P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$; $^{****}P < 0.0001$. Parameter estimate values represent the REML estimate of each variance component from analyses using transformed data to meet test assumptions when necessary (see text). Components estimated as zero include those estimated to be negative (see text).

The offspring sex ratio differed significantly from 1 : 1 (χ^2-test for equal proportions, $\chi^2 = 32.27$, $P < 0.0001$), with females comprising over 59% of all adult offspring. I used Monte Carlo randomization tests (1000 permutations) to test for effects of sire family, dam family, and their interaction on the proportion of female offspring, as I was unable to find a suitable transformation to meet the assumption of normality for ANOVA. The randomization ANOVA revealed no significant effects (sire family $P = 0.83$, dam family $P = 0.16$, interaction $P = 0.88$).

Discussion

The quantitative genetic analysis of traits related to fitness revealed support for both the 'good genes' hypothesis and the genetic compatibility hypothesis. Nonadditive sources of phenotypic variance (dominance, epistatic and extranuclear interactions) contributed to development times and masses of adult offspring in *G. sigillatus*. However, the phenotypic variance in offspring surviving to adulthood (arguably the most important component of fitness that I measured) was influenced primarily by the additive effects of nuclear genes. Strong paternal effects were detected in hatching success and the mass of male offspring. Thus, the type of genetic benefit afforded to *G. sigillatus* females depends upon which fitness-related trait one considers, underscoring the importance of examining more than one fitness parameter when evaluating which mechanism through which polyandrous females gain genetic benefits.

A common approach employed to disentangle the effects of genetic compatibility from those of intrinsic male quality in outbred populations has been to treat genetic compatibility as the null hypothesis tested against the alternative hypothesis of intrinsic male quality. In these studies, a lack of consistent results among different females that are mated to the same male is taken as evidence for genetic compatibility (see Tregenza & Wedell, 1998; Newcomer *et al.*, 1999; Engqvist, 2006). However, the power of these tests to detect a significant effect of intrinsic male quality is limited, especially when males are mated to a small number of females. A quantitative genetics approach that estimates the amount additive and nonadditive variation in fitness-related traits is preferred to the above approach because it is experimental, it does not regard intrinsic male quality and genetic compatibility as mutually exclusive hypotheses, and neither hypothesis is treated as the default explanation.

Likewise, studies evaluating potential genetic benefits to polyandry have sometimes attributed an increase in hatching success resulting from polyandry to a reduction in genetic incompatibility, whereas an increase in offspring viability and/or performance has often been attributed to genes obtained from superior sires (Zeh & Zeh, 1996, 2003). However, this distinction has been questioned on theoretical grounds (Colegrave *et al.*, 2002; García-González & Simmons, 2005; Ivy & Sakaluk, 2005), and the present results support the notion that this convention should be abandoned altogether. The analyses presented here failed to show a genetic compatibility effect of any kind on hatching success, although hatching was influenced by paternal effects, a potential indicator of intrinsic male quality. Likewise, the results of the present study demonstrate that measures of offspring performance (late development and offspring masses) can be strongly influenced by genetic compatibility in the form of dominance and/or epistatic interactions and interactions involving extranuclear elements.

One surprising result emerging from the present study was the significant variance attributed to paternal effects exhibited in the hatching success of eggs (33% of the total variation). Although further study will be needed to identify the mechanism(s) involved, it is clear that the effect is not the result of nutrition and/or other substances contained in the courtship food gift because females were not permitted to consume food gifts. Moreover, because females were equally inseminated, paternal effects are unlikely to be the result of females receiving differing amounts of sperm. Nonetheless, there are other possibilities that may account for the paternal effects on hatching success. Although females received equal amounts of seminal fluid, the paternal influence on hatching success may be a result of differences between lines in amounts and/or types of accessory gland products that are mediated by genes expressed in males, but not females (Chapman & Wolfner, 1988; García-González & Simmons, 2005). Genomic imprinting, in which the pattern of gene expression depends on whether a gene is maternally or paternally inherited, may also be responsible for paternal effects on hatching. Genomic imprinting has been documented in several insect species and can have wide-ranging effects on growth and development (Reik & Walter, 2001). Further, studies involving *Drosophila melanogaster* reveal that genes carried by the sperm and expressed after a sperm's entry into the egg are essential for early embryonic development (Yasuda *et al.*, 1995; Fitch *et al.*, 1998). Finally, rather than being a paternal effect *per se*, the paternal influence seen in this study may be a result of differential maternal investment in offspring, if females differentially invest in the offspring of males from particular lines, and the investment is independent of maternal nuclear genotype. However, this possibility seems extremely unlikely, given that females provision their eggs before fertilization takes place (Bonhag, 1958) and do not otherwise provide parental care. Regardless of the mechanism involved, the paternal effects on hatching success observed in this study represent a source of variation in hatching success that may have inflated previous estimates of additive genetic variation in hatching success, or has simply been overlooked in studies searching for benefits arising from polyandry.

Although many studies have investigated the effects of various types of paternal investment on offspring fitness (Zeh, 1985; Clutton-Brock, 1991), a vast majority of studies assume that nongenetic paternal effects are equal to zero in species that have no obvious parental care (for examples, see Grether *et al.*, 2001; Svensson *et al.*, 2001; Hunt & Simmons, 2002; but see Tallamy *et al.*, 2003). Indeed, the whole rationale behind using paternal half-sib families in quantitative genetics analysis is that nongenetic paternal effects are assumed to be negligible (Falconer & Mackay, 1996). The results of this study suggest that some caution is warranted before assuming that paternal effects are absent merely because there is no obvious paternal care.

Extranuclear interactions appeared to be an important source of phenotypic variation in early development and in the masses of offspring, although parameter estimates were statistically significant only in the case of male offspring mass. It should be noted, however, that the power for detecting extranuclear interactions is considerably lower than that of the other parameter estimates presented here because it compares each specific family combination to its reciprocal (i.e. $A_{♂}B_{♀}$ vs. $B_{♂}A_{♀}$). The potentially complex interactions involving extranuclear genes should be further clarified if only because of their tremendous potential to shape evolutionary dynamics. For example, the extranuclear interactions seen here may be examples of intragenomic conflict, in which different elements of an individual's genetic makeup interact antagonistically (reviewed in Zeh & Zeh, 1996; Rice & Holland, 1997). These conflicts may stem from interactions between the nuclear genome and components of the cytoplasm (Rand *et al.*, 2001) or transposable elements involving cytoplasm (Lozovskaya *et al.*, 1995), both potentially leading to Red Queen evolutionary dynamics between an individual's nuclear DNA and cytoplasm components.

The offspring sex ratio was significantly skewed toward females, although it is not clear whether the sex ratio was similarly skewed at the time of hatching or whether it reflects differential survival of males and females later in development. A skewed sex ratio at hatching may indicate the presence of selfish genetic elements that distort sex ratios, usually through the killing of male embryos (Werren, 1998). Similar effects occur through the action of parasitic endosymbionts, such as *Wolbachia*, a bacterium harboured by many insects (Werren *et al.*, 1995) that has been shown to influence hatching success in another cricket species, *Teleogryllus taiwanemma* (Kamoda *et al.*, 2000). Alternatively, the sex ratio may have been 1 : 1 at hatching, and became skewed later because developing male offspring suffered higher mortality than females. Should this be the case, it is interesting to note that the effects of extranuclear interactions influencing body mass were stronger in male offspring than in female offspring, although the difference is not statistically significant (offspring mass, $CV_{males} = 2.22$ and $CV_{females} = 1.38$; $F_{36,36} = 1.61$, $P > 0.05$). These results may be evidence that *G. sigillatus* males are 'maladapted' as a result of nucleocytoplasmic conflict between maternally inherited mitochondrial genes and their nuclear genome, as discussed by Zeh & Zeh (2005).

The purpose of this study was to ascertain the relative importance of sources of phenotypic variance, with the understanding that estimates of variance are sensitive to environmental variability (Hoffmann & Merila, 1999; Charmantier & Garant, 2005). However, the large variances attributed to the specific environment (residual variance, V_e) in this study indicate that environmental factors experienced by females probably play a critical role in the evolution of polyandry. Indeed, recent theoretical attention suggests that genotype-by-environment interactions (GEIs) are important, but often overlooked, in studies of sexual selection (Qvarnstrom & Price, 2001; Greenfield & Rodriguez, 2004; Hunt *et al.*, 2004). Future studies might examine the role that the environment plays in determining the benefits females receive through polyandrous mating (as in Sakaluk *et al.*, 2002; Tregenza *et al.*, 2003).

Although the good genes and genetic compatibility hypotheses are not mutually exclusive, theoretical treatments of the evolution of female mating strategies have generally treated them as such, perhaps because the two hypotheses make vastly different predictions regarding which males should be preferred by females (Colegrave *et al.*, 2002; Neff & Pitcher, 2005). Intrinsic-male-quality hypotheses predict that all females should favour the same males, whereas from a genetic compatibility perspective, there is no single male genotype that is optimal for all females. Yet, because phenotypic variance is not partitioned in the same way for different fitness-related traits, the conclusion one draws regarding the genetic benefits to polyandry in *G. sigillatus* depends heavily on which trait is examined. The results of this and other studies (e.g. Wedekind *et al.*, 2001) suggest that the dichotomy between good genes and genetic compatibility is overly simplistic, and the traditional approach that attempts to single out one mechanism through which females choose males or through which polyandrous females gain genetic benefits is unlikely to produce a complete picture of the selective forces that shape female mating strategies.

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