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Female mating bias results in conflicting sex-specific offspring fitness

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Indirect-benefit models of sexual selection assert that females gain heritable offspring advantages through a mating bias for males of superior genetic quality. This has generally been tested by associating a simple morphological quality indicator (for example, bird tail length) with offspring viability[1]. However, selection acts simultaneously on many characters, limiting the ability to detect significant associations, especially if the simple indicator is weakly correlated to male fitness[2,3]. Furthermore, recent conceptual developments suggest that the benefits gained from such mating biases may be sex-specific because of sexually antagonistic genes that differentially influence male and female reproductive ability[4]. A more suitable test of the indirect-benefit model would examine associations between an aggregate quality indicator[1,3] (such as male mating success) and gender-specific adult fitness components, under the expectation that these components may trade off[1]. Here, we show that a father's mating success in the cricket, *Allonemobius socius,* **is positively genetically correlated with his son's mating success but negatively with his daughter's reproductive success. This provides empirical evidence that a female mating bias can result in sexually antagonistic offspring fitness.**

With the exception of genetic monogamy, the sexes are expected to possess different optimal reproductive phenotypes[5,6]. Therefore, a conflict may arise because the sexes represent different environments in which homologous fitness-related traits are expressed[4]. Without the added evolution of sex-limited expression (that is, sexual dimorphism), sexual conflict of this nature may constrain the realization of fitness optima[6]. Unfortunately, evidence for this type of conflict is rare. However, recent empirical work in *Drosophila melanogaster* showed that adult relative fitness was negatively correlated between the sexes, even though there was a positive genetic correlation for fitness earlier in development[4]. The authors[4] further predicted that if these results were applicable outside *Drosophila*, a female mating bias for high-quality mates would produce at best only average-quality daughters.

We addressed this prediction in *A. socius* by examining the genetic correlation between a sire's field-determined mating success and his son's mating success and daughter's reproductive success. We chose these offspring variables on the assumption that they are accurate predictors of next-generation fitness. Previous work suggests that *A. socius* females mate with larger males to gain a larger haemolymph-based nuptial gift. This gift is obtained by chewing a specialized spur on the male hind tibia during copulation[7,8]. Therefore, the condition of the spur (chewed or unchewed) indicates a male's mating history (successful or unsuccessful): chewing behaviour is rarely uncoupled from sperm transfer. Spur condition also seems to be age-independent because spur categories persist throughout a breeding season that is characterized by little new male recruitment once a cohort emerges[8]. Use of an 'aggregate' indicator, such as mating success, is important because it represents the sum of interacting male traits[9], overcoming the implicit weakness of the traditional 'simple' indicator approach[1–3].

To estimate the sire–offspring correlations, we mated 47 wild-caught sires (25 successful and 22 unsuccessful) to 98 wild-caught females and reared their offspring. Sires were caught mid-breeding season and females were collected as late instar nymphs earlier in the season to ensure their virginity; on average there were two females per sire. Males that had mated in the field were larger than unmated males ($F_{1,45} = 7.25$, $P = 0.0099$) and there was no female size difference between sire groups ($F_{1,96} = 0.01$, $P = 0.9294$). From each female family, two or three sons ($n = 220$ total males) were separately placed into a mating arena with a randomly chosen, unrelated male and female taken from other sire families (see

Table 1 Genetic correlation between a sire's phenotype and offspring variables

Trait		Sire mating success		Sire size	
	n	r_G	P	r_G	P
Son mating success	4.7	**0.38**	**0.0076**	0.06	0.7679
Daughter reproductive	6.9	**− 0.36**	**0.0164**	−0.02	0.9280
Hatching*	545.9	0.01	0.9813	0.07	0.7549
Survivorship*	133.8	0.08	0.5708	0.03	0.8971
Son development*	21.2	−0.02	0.9134	0.01	0.9785
Daughter development*	23.8	0.03	0.8218	0.01	0.5381
Son size*	13.8	0.08	0.5924	0.17	0. 9670
Daughter size*	15.0	−0.16	0.2737	0.00	0.9990

*Juvenile viability variable.
Two sire phenotypes were examined, including sire mating success and sire size. *n* represents the average number of individuals per sire family. Bold values remain significant after a sequential Bonferroni. *P*-values corrected within each sire phenotype (mating success and size) and within each fitness stage (that is, adult fitness and juvenile viability).

Methods). The first male to pass a spermatophore was termed 'successful', while the unmated male was termed 'unsuccessful'. To obtain an estimate of male fitness variance, each male was tested on average five times against a different competitor, using a new virgin female for each trial. Thus, a son's mating success was estimated from the proportion of successful mating attempts and a daughter's reproductive success was estimated from her fecundity. In total, 1,067 mating trials were conducted, resulting in 327 inseminated females.

We conducted three additional tests to explore the data further. First, we estimated the genetic correlation between sire mating success and (1) offspring hatching success (ratio of hatchlings to eggs laid); (2) offspring survivorship (ratio of adults to hatchlings); (3) sex-specific offspring development time (days from hatching to adulthood); and (4) sex-specific offspring body size (femur length). This addressed the common indirect-benefit prediction that high-quality sires produce offspring of increased viability. Second, we estimated the genetic correlation between sire size (femur length) and offspring fitness as a contrast to our aggregate-indicator approach. Sire size represents a simple morphological quality indicator: previous work in *A. socius* suggests that females prefer larger males[8]. Third, we estimated the phenotypic correlation matrix between several male reproductive behaviours from the videotaped trials to examine potential mechanisms underlying male mating success. These included courtship duration (time elapsed from courtship onset to copulation); spur chewing duration (the time the female spent chewing the spur—longer chewing results in a larger gift[7]); and spermatophore attachment duration (the time the female kept the spermatophore attached, an estimate of sperm transfer) for each trial.

We found that a sire's field-determined mating success was positively genetically correlated to his son's mating success ($r_G = 0.38$, $P = 0.0076$; Table 1), and negatively genetically correlated to his daughter's reproductive success ($r_G = -0.36$, $P = 0.0164$; Table 1). Thus, successful sires produce successful sons, but unsuccessful daughters. When we calculated average relative offspring fitness, $\bar{w}$ (see statistical analysis) for each sire group, we found that the sons of successful sires were on average 1.7 times fitter than the sons of unsuccessful sires (Fig. 1). In contrast, successful sires produced daughters that were only 0.63 times as fit
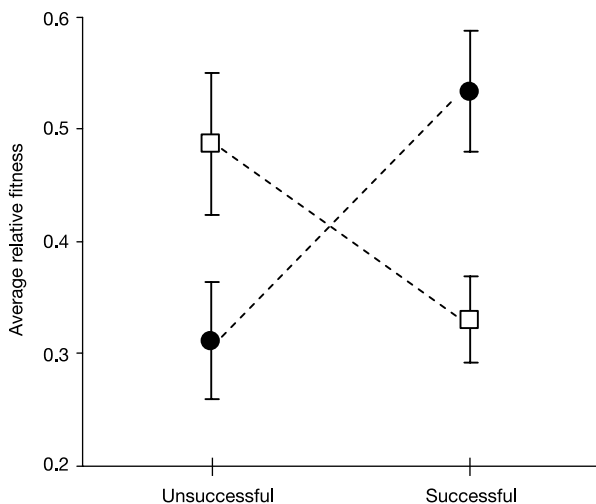
as their unsuccessful counterparts. This leads to a 17% greater relative offspring fitness for females mated to successful sires (($(1.7 + 0.63)/2 = 1.17$; after ref. 1). Our data also indicated that offspring sex ratio may vary among sire mating groups (two-tailed t-test: $t_{45} = 1.9$, $P = 0.064$). Accordingly, we recalculated $\bar{w}$ after correcting for sex ratio and found that offspring of successful sires were 24% more fit than offspring of unsuccessful sires. Assuming that these fitness estimates are accurate approximations of lifetime success, then female preference for high-quality males can still be maintained in the face of sexually antagonistic offspring fitness.

To determine whether the bias in daughter fecundity was due to a bias in mate quality, we examined the relative proportion of 'successful sons' (that is, sons of successful sires) mated to successful and unsuccessful daughters. We found that 60.6% (94/155) of the 'unsuccessful daughters' and 66.3% (114/172) of the 'successful daughters' were mated to successful sons. These groups were not significantly different ($x^2 = 1.12$, degrees of freedom, d.f. = 1, $n = 327$, $P = 0.2904$). This suggested that the difference in daughter fecundity between sire groups was not due to a bias in the quality of their mates.

Analysis of the mating trials indicated that the sons' reproductive phenotypes were significantly repeatable (Table 2; see Methods). Because these estimates are based on the intra-class correlation, they provide a far-upper-bound estimate of the underlying additive genetic variance. A son's femur length was positively correlated to his mating success ($r_P = 0.24$, $n = 220$, $P = 0.0003$) and gift size ($r_P = 0.33$, $n = 220$, $P < 0.0001$). Therefore, we examined the phenotypic correlation matrix between reproductive phenotypes using a partial correlation to adjust for the influence of body size. These results indicated that the more successful sons acquired mates more quickly (mating success and courtship duration correlation: $r_P = -0.27$, $n = 220$, $P = 0.0015$).

We found no significant genetic correlation between sire success and offspring hatching success, survivorship, son/daughter development time or body size (Table 1, all $P > 0.27$). This implies that the female mating bias for successful sires does not increase her offspring's viability. Furthermore, these data suggest that confounding non-genetic parental effects are minimal or non-existent, given that sire 'quality' had no effect on pre-adult components of fitness, which is where we would expect these effects to occur[10–13]. In addition, we found no significant genetic correlation between sire size (simple quality indicator) and any offspring fitness variable (Table 1), suggesting that an aggregate-indicator of male quality may be more revealing.

Our data support the hypothesis that mating biases for high-quality males can result in conflicting sex-specific offspring fitness returns. These data provide general support for the intersexual genetic conflict model of evolution[4,6], suggest an alternative approach in testing indirect-benefit models (for example, aggregate quality indicators coupled with sex-specific adult fitness estimates), and represent one of a few studies addressing the genetic relationship between father and son mating success.

The inequality of sex-specific fitness returns as presented here has several important consequences. First, owing to the transient nature of the sexual environment in which the underlying fitness loci are expressed, ample antagonistic fitness variation can be maintained through opposing gender-specific selection[4,6]. Second, opposing selection will cause the realization of gender-specific fitness optima

Figure 1 Female mating bias resulted in conflicting sex-specific offspring fitness. Successful sires produced sons with a higher mating success (circles), but daughters with a lower reproductive success (squares) when compared to unsuccessful sires (means ± s.e. are based on sire family means). The dashed line connects the same sex.

Table 2 Trait repeatability

Trait	d.f.	F	R	P<
Mating success	219, 1065	3.13	0.47	**0.0001**
Courtship	194, 568	1.51	0.15	**0.0004**
Gift size	144, 343	1.81	0.26	**0.0001**
Spermatophore	142, 326	1.28	0.11	0.0580

to be constrained[4]. Third, future sexual selection models should acknowledge that a mating bias for indirect-benefits or 'good genes' can result in conflicting sex-specific offspring fitness[4]. □

Methods

Organismal maintenance

Crickets were maintained in plastic cages ($10 \times 10 \times 8$ cm) containing ground cat food and a carrot slice (provided ad libitum), dampened cheesecloth (water source and oviposition material) and strips of brown paper towel for cover. The food, carrot and paper towel were replaced every two days. Cages were kept in a constant environment at 28 °C and a 12:12 light–dark photoperiod provided by a Percival incubator. The age of laboratory-reared experimental crickets was 10 ± 1 days post-eclosion (final adult moult).

Mating trials

Mating arenas were made from 100-mm Petri dishes lined with filter paper. Males from both successful and unsuccessful sires were randomly chosen for each mating trial to provide an equal sire-group representation. Females were also randomly chosen from either sire group. To help control for the potential influence of mating experience, males were tested against other males who had shared an equal number of previous trials (that is, 0, 1, 2, and so on). Each male was mated once per day. After mating, females were isolated to oviposit until their death. All trials were videotaped.

Statistical analysis

Repeatabilities (R) were estimated by calculating the intra-class correlation obtained from a one-way ANOVA (that is, $R = (MS_{among} - MS_{error})/[MS_{among} + (N - 1)MS_{error}]$, where MS is the mean square estimate and N is the number of repeated measures per individual)[14]. Genetic correlation coefficients were based on sire family means ($n = 47$). Because correlation estimates were cross-generational (that is, sire–offspring), estimates of trait (co)variance were based on different individuals within each sire family (as opposed to the same individuals), thereby providing a relatively unbiased estimator of the additive genetic correlation. Tests of significance were based on correlation-coefficient critical values derived from standard statistical tables[15].

For each sex, $\bar{w}$ among sire groups was calculated as:

$$\bar{w}_{jg} = \left(\sum_{1}^{n_{jg}} (w_{ji}/w_{j\max}) \right) / n_{jg} \qquad (1)$$

where w is the average offspring fitness of sex j for the ith sire; $w_{\max}$ represents the maximum observed fitness value; g represents the sire group (successful or unsuccessful); and n is the number of sires. Thus, four estimates of average relative fitness were calculated including the sons and daughters of successful sires, as well as the sons and daughters of unsuccessful sires. To correct for potential differences in sex ratio between sire groups, we recalculated $\bar{w}$ by first multiplying w_{ji} by a_{ji}, where a is the offspring abundance of sex j for the ith sire. Each new male and female estimate of $\bar{w}$ was then divided by their respective population sex ratios (male:female is 0.89 and female:male is 1.12), to adjust for the difference in the fisherian value between the sexes; that is, because fewer males existed, they possessed a higher breeding value. All analyses were performed using SAS v8.

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Naturalistic experience transforms sensory maps in the adult cortex of caged animals

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Much of what is known about the functional organization and plasticity of adult sensory cortex is derived from animals housed in standard laboratory cages[1,2]. Here we report that the transfer of adult rats reared in standard laboratory cages to a naturalistic habitat modifies the functional and morphological organization of the facial whisker representation in the somatosensory 'barrel' cortex. Cortical whisker representations, visualized with repeated intrinsic signal optical imaging in the same animals, contracted by 46% after four to six weeks of exposure to the naturalistic habitat. Acute, multi-site extracellular recordings demonstrated suppressed evoked neuronal responses and smaller, sharper constituent receptive fields in the upper cortical layers (II/III), but not in the thalamic recipient layer (IV), of rats with naturalistic experience. Morphological plasticity of the layer IV barrel field was observed, but on a substantially smaller scale than the functional plasticity. Thus, transferring animals to an environment that promotes the expression of natural, innate behaviours induces a large-scale functional refinement of cortical sensory maps.

In a previous study, we demonstrated that natural behaviours could have a powerful impact on the expression of plasticity in whisker-deprived adult rats, given a brief opportunity for natural whisker use outside the standard home cage[3]. We found that a few minutes of natural whisker use per week induces a profound contraction of the remaining (spared) whisker's cortical representation, and a decrease of its peak amplitude in contrast to the expansion and increase in peak amplitude of the remaining whisker representation that is commonly observed in rats that remain exclusively in their home cage[3–8]. In this study, we examined whether the effects of natural whisker use are limited to the cortex of whisker-deprived rats, or if similar plasticity can be observed in the barrel cortex of non-deprived adult rats, given greater opportunity for natural whisker use outside the home cage. Rather than simply elevate sensory activity through a traditional 'enriched environment' (typically, a larger cage filled with various toys, a running wheel and conspecifics), we used a new type of environment, the naturalistic habitat (NH), which promotes innate sensorimotor behaviours such as subterranean tunnelling, foraging and three-dimensional navigation, in addition to interactions with conspecifics (Supplementary Fig. S1).