

When are good genes good? Variable outcomes of female choice in wax moths

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SUMMARY

Female lesser wax moths (*Achroia grisella*) choose males based on characters of their ultrasonic advertisement signals. Because a female's opportunity to obtain increased somatic benefits by mating with a particular male is limited, we investigated whether females obtain genetic benefits for their offspring via mate choice. Controlled breeding experiments conducted under favourable food and temperature conditions showed that developmental characters are heritable, that sire attractiveness and offspring survivorship are unrelated, but that females mating with attractive signallers produce offspring who mature faster than the offspring of females mating with non-attractive signallers. However, under some unfavourable food or temperature conditions, it is the offspring of females mating with non-attractive males who mature faster; these offspring are heavier as well. Thus, the relationship between male attractiveness and offspring development is not environmentally robust, and support for a good genes model of mate choice in *A. grisella* is dependent on conditions. These findings suggest genotype-environment interactions and emphasize the necessity of testing sexual selection models under a range of natural environments.

1. INTRODUCTION

Male advertisement signals in most animal species are characterized by exaggeration and conspicuousness (Andersson 1994). Within a population, however, the level of exaggeration of a given signal character, e.g. intensity or duration, may vary considerably between and within males (Gerhardt 1991; Helversen & Helversen 1994). Where such variation occurs, females generally prefer males whose signal characters are more exaggerated than the mean level in the population (Ryan & Keddy-Hector 1992). Because producing signals whose characters are strongly exaggerated may demand more energy expenditure, overall 'vigour', and/or increased risk, the above generalization is consistent with the 'good genes' model of female choice: females choose certain males because their signals are reliable indicators of heritable survivorship, maturation rate, and/or size. Genetically inferior males might be unable to exaggerate the critical signal characters, and this constraint would selectively maintain the observed female preference (Kodric-Brown & Brown 1984; Pomiankowski 1988). This model is now supported by several studies showing positive phenotypic or genetic correlations between male (sire) attractiveness and offspring survivorship (e.g. Schantz 1989; Göransson *et al.* 1990; Norris 1993; Petrie 1994), maturation rate (Reynolds & Gross 1992; Moore 1994), or size (and potential fecundity) (Reynolds & Gross 1992). However, for the vast majority of species it remains entirely speculative (and see, for

example, Howard *et al.* (1994), Semlitsch (1994) and Nicoletto (1995) for negative evidence). Moreover, other equally cogent explanations for females preferring exaggerated signals exist (see Kirkpatrick & Ryan 1991).

Here, we present a study of the relationships between mate choice and offspring development in the lesser wax moth, *Achroia grisella* (Lepidoptera: Pyralidae). Our primary objective was to determine whether males that produced attractive signals sired offspring whose survivorship, maturation rate, and/or size exceeded that of offspring sired by non-attractive males and whether any such relationships were robust. Because *A. grisella* males neither invest in parental care nor large and possibly nutritious spermatophores, a female's opportunity to obtain somatic benefits for her offspring by virtue of mating with one male over another is restricted. Consequently, any consistent developmental differences between the offspring of attractive and non-attractive sires would likely reflect genetic factors, and female choice would thereby represent, at least in part, selection for good genes.

Unlike most Lepidoptera, pair formation in *A. grisella* entails ultrasonic (approximately 100 kHz) advertisement signals by stationary wing-fanning males that attract receptive females within a radius of several metres (Greenfield & Coffelt 1983; Spangler *et al.* 1984). Experiments using simulated signals showed that the ultrasonic pulses were as attractive as a live male (Spangler *et al.* 1984).

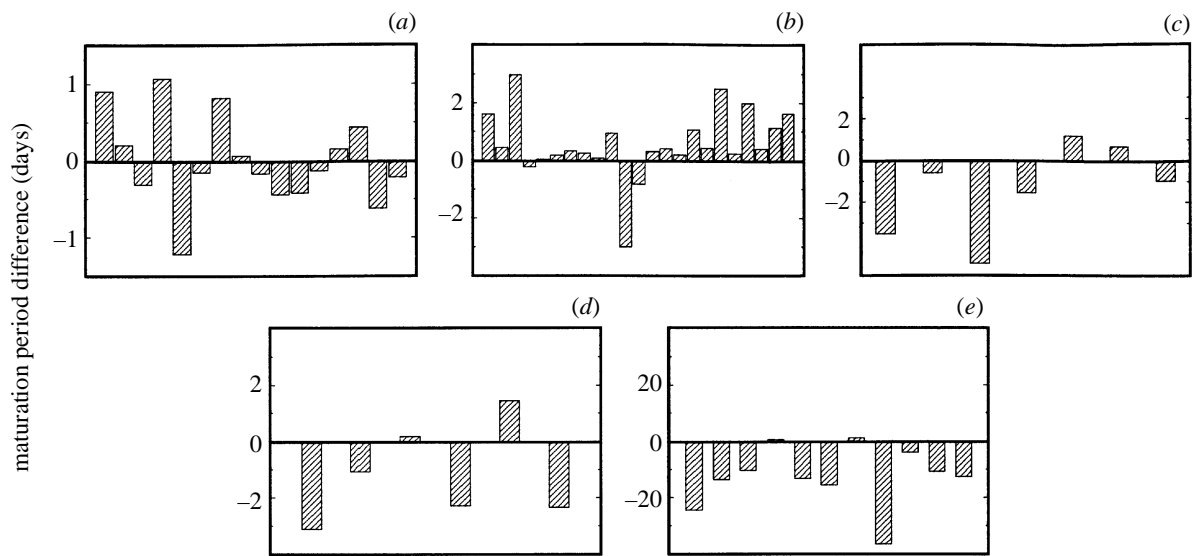


Figure 1. Difference between mean maturation period (days from oviposition to adult eclosion) of male offspring of a non-attractive and an attractive sire. Sires are paired as they were when evaluated for attractiveness by females (see text). Rearing conditions: (a) individual, adequate food, 25.5 °C; (b) collective, adequate food, 25.5 °C; (c) collective, reduced food quantity, 25.5 °C; (d) collective, reduced food quality, 25.5 °C; (e) collective, adequate food, 20 °C. (b) Mean maturation periods of offspring of attractive sires less than mean periods of offspring of non-attractive sires ($p < 0.05$; sign test, two-tailed). (e) Mean maturation periods of offspring of non-attractive sires less than mean periods of offspring of attractive sires.

Previous work on *A. grisella* populations revealed considerable variation in the signal characters that influence female choice, and that females prefer exaggerated characters (Jang & Greenfield 1996). These signal characters are all highly repeatable within individuals (Jang *et al.* 1997). Moreover, analyses of half-sib breeding experiments show that heritabilities of two critical signal characters, pulse rate and peak amplitude, are high ($h_s^2 > 0.50$; R. D. Collins, unpublished data). If developmental characters, too, are heritable and genetically correlated with signalling, a female could acquire genetic benefits for her offspring by exercising choice among available mates (see Moore 1994).

A. grisella are symbionts of honeybees (*Apis mellifera*), and consideration of their life history suggests specific ways in which variation among individuals may yield significant differences in fitness. The larvae feed on stored pollen and honey, wax and detritus in and near weakened honeybee colonies (Künike 1930). After eclosion, adults usually exit the colony immediately. The males signal for 6–10 h each night from stations near the colony entrance, occasionally jostling one another for access to particular stations. Females typically mate only once and then return to the colony and oviposit. Adults, who have an atrophied proboscis, neither feed nor drink, and they seldom live for more than 20 days (Greenfield & Coffelt 1983). When a honeybee colony declines sufficiently as a food resource, the eclosing adults—especially females—must disperse and seek other colonies, presumably relying on characteristic colony odours. These life history features suggest that individuals whose offspring exhibit rapid maturation, high fecundity and superior flight ability may

enjoy enhanced fitness, particularly when competition for limited (and declining) food resources and dispersal toward new resource patches are important.

2. MATERIALS AND METHODS

(a) Population studied

Approximately 150 *A. grisella* were collected from infested honeybee colonies near Auburn, Alabama, and cultured on a diet containing cereals, beeswax, brewer's yeast, honey, glycerol and water (see Dutky *et al.* 1962). We maintained the stock population at 25.5 °C and under a 12 h:12 h light:dark photoperiod. Each generation, males and females were paired according to a breeding protocol that avoided inbreeding and maintained an effective population size minimizing loss of genetic variance. To obtain virgin adults for our experiments, we selected larvae from the stock population and placed them individually in 28.4 ml containers supplied with adequate diet. These larvae pupated and eclosed to adults within the individual containers.

(b) Assessment of male attractiveness

We identified attractive and non-attractive males by first selecting four one-day old virgin adults and placing them individually in cylindrical screen cages (1 cm diameter; 1.5 cm height). The cages were arranged immediately outside the perimeter of a circular screen arena (80 cm diameter) mounted on a turntable. Azimuthal separations between adjacent cages were 90° relative to the arena centre. The arena was kept in a 3 m × 3.5 m × 2.5 m semi-anechoic room maintained at 25.5 °C and illuminated with a 25 W red incandescent bulb.

We assessed relative attractiveness of the four males by releasing twenty 1–2-day-old virgin females individually in the arena centre and tallying the number attracted

Table 1. Mean developmental characters of offspring (♣, ♠ and ♣+♠) of attractive (A) and non-attractive (NA) sires under various rearing conditions, where ♣ are males and ♠ are females

(Numerals in column 1 indicate rearing condition number in text: 1: Individual, adequate food, 25.5 °C; 2: collective, adequate food, 25.5 °C; 3: collective, reduced food quantity, 25.5 °C; 4: collective, reduced food quality, 25.5 °C; 5: collective, adequate food, 20 °C.)

rearing condition	maturation period (days)			adult weight (mg)		developmental rate (mg day ⁻¹)		
	♣	♠	♣+♠	♣	♠	♣	♠	♣+♠
1 (A)	36.8	38.3	37.5	33.3		0.87		
(NA)	36.8	38.3	37.6	33.2		0.87		
2 (A)	40.1	42.8	41.5	30.0		0.70		
(NA)	41.0	43.5	42.3	29.8		0.69		
3 (A)	41.3	44.1	42.6	23.5		0.53		
(NA)	40.4	43.1	41.8	25.6		0.59		
4 (A)	40.9	43.7	42.2	22.5		0.52		
(NA)	40.2	43.0	41.4	23.1		0.54		
5 (A)	131.9	122.9	127.4	15.6	30.4	0.125	0.27	0.19
(NA)	124.0	116.4	120.2	15.9	30.5	0.134	0.28	0.21

Table 2. Relationship between male attractiveness and offspring developmental characters (♣, ♠ and ♣+♠) under various rearing conditions

(*P*-values of the *F*-test for effect of sire attractiveness (attractive versus non-attractive) on offspring developmental characters (three-way ANOVA, general linear model for unbalanced data; see text) are shown. Numerals in column 1 indicate rearing condition number in text.)

rearing condition ^a	maturation period			adult weight		developmental rate		
	♣	♠	♣+♠	♣	♠	♣	♠	♣+♠
1	0.32	0.78	0.86		0.64		0.69	
2	0.0001 ^{bd}	0.009 ^{bd}	0.0001 ^{bd}		0.22		0.0006 ^{bd}	
3	0.06	0.006 ^{cd}	0.04 ^c		0.001 ^{cd}		0.0001 ^{cd}	
4	0.24	0.05 ^c	0.29		0.29		0.12	
5	0.0001 ^{cd}	0.0001 ^{cd}	0.0001 ^{cd}	0.06	0.73	0.0001 ^{cd}	0.0001 ^{cd}	0.0001 ^{cd}

^aSee table 1 and text for definitions of rearing conditions.

^bMaturation period of offspring of attractive sire less than period of offspring of non-attractive sire; developmental rate of offspring of attractive sire greater than rate of offspring of non-attractive sire.

^cMaturation period of offspring of non-attractive sire less than period of offspring of attractive sire; adult weight or developmental rate of offspring of non-attractive sire greater than weight or rate of offspring of attractive sire.

^d*P*-value significant ($\alpha = 0.05$) after correction for multiple tests via the Holm procedure (see Krauth 1988; Rice 1989).

toward each male. A female was judged to be attracted toward a male if she moved to within 5 cm of his cage and wing-fanned; attraction toward two or more males during a trial never occurred. Each female was tested once only. All tests were conducted during the initial half of scotophase, the period of maximum signalling and mating activity in *A. grisella* (Greenfield & Coffelt 1983).

We monitored the ultrasonic signals emitted by each male with an UltraSound Advice S-25 Bat Detector and only released a female when all four males were signalling. This requirement assured that males would be assessed based on the quality of their signalling rather than on whether or not they were undisturbed and remained signalling. Previous measurements showed that the screen of the cages and arena did not interfere with signal transmis-

sion (Jang *et al.* 1997). The arena turntable was rotated 90° after every five trials to minimize potential influences of position effects on attraction of females.

After testing of all 20 females, we identified the most attractive and least attractive males. If the most attractive male had attracted at least five more females than the least attractive male, the two males were each bred to determine the relationship between male attractiveness and offspring development. Because our assessment of male attractiveness was relative, we assessed four rather than two males at a time, to increase the probability that the individuals identified as attractive and non-attractive would bear these labels among the male population at large.

(c) Experimental pairings

For each male identified above as attractive or non-attractive, we randomly chose a set of three 1–2-day-old virgin females from the stock population as mates. A given male was paired with a different female on each of three successive days. Each designated pair was placed in a small screen cage (1 cm diameter; 1.5 cm height), and mating usually ensued regardless of the male's attractiveness. After mating, the male was removed, and deposited eggs were collected. By repeatedly mating each male, we improved the certainty with which we evaluated the relationship between male attractiveness and offspring development. The repeated matings also established a half-sib experimental design (Becker 1984; Falconer 1989) with which we determined the heritability of developmental characters.

(d) Rearing of offspring

Eggs collected from each of the pairings above were placed on 30 g of diet in a 17 cm × 12 cm × 6.5 cm plastic container kept in the chamber used for rearing the stock population. After the offspring attained the second larval instar, one of the following five rearing conditions was used.

(1) 30 larvae were randomly chosen from among the offspring of each mated female and placed individually in 28.4 ml containers with 0.7 g of diet. Offspring of 16 attractive and 16 non-attractive sires were tested.

(2) 30 larvae were chosen as in (1) and placed collectively on 30 g of diet in a 17 cm × 12 cm × 6.5 cm plastic container. The quantity of food supplied in (1) and (2) was much more than adequate, as judged by the large amount remaining after offspring eclosed to adults. Offspring of 23 attractive and 23 non-attractive sires were tested.

(3) 30 larvae were chosen and reared collectively as in (2), but only 7 g of diet were provided. This reduced quantity of diet was sufficient for development to the adult. Offspring of seven attractive and seven non-attractive sires were tested.

(4) 30 larvae were chosen and reared collectively as in (2), but the 30 g of diet provided lacked beeswax, and the amounts of brewer's yeast, honey and glycerol were reduced by 50%. Offspring of six attractive and six non-attractive sires were tested.

(5) 30 larvae were chosen and reared collectively as in (2), but they were maintained at 20 °C. Offspring of 11 attractive and 11 non-attractive sires were tested.

The various environmental conditions were used to determine whether any relationships between male attractiveness and offspring development were environmentally robust or varied according to competition ((1) versus (2)), food quantity ((2) versus (3)), food quality ((2) versus (4)) or temperature ((2) versus (5)). Offspring from each of the three dams paired with the sire were reared as three separate units and treated as full-sibships in data analysis.

(e) Measurement of offspring development

We measured the maturation period (from oviposition to adult eclosion), adult (female) weight (± 0.005 mg; determined at day of eclosion with a Mettler H51AR analytical balance), developmental rate (adult weight/maturation period), proportional survivorship (to the adult), and subsequent adult longevity of all individuals reared under the five conditions above. The life history

features of *A. grisella* suggest that these developmental characters may be relevant to an individual's fitness. From each dam whose offspring were reared under condition (2) above, we also randomly chose 40 deposited eggs and placed them collectively in a 28.4 ml container kept in the rearing room. After eight days, 2–3 days following expected hatching, we counted the numbers of hatched and unhatched eggs from a dam to determine her proportional hatchability.

(f) Data analysis

Relationships between sire attractiveness and offspring development characters (maturation period, adult weight, developmental rate) were determined by three-way ANOVA (SAS general linear model for unbalanced data; model factors were attractiveness of sire, individual sire (nested within attractiveness category), and individual dam (nested within individual sire)). Development character data were transformed to normal scores prior to ANOVA. This procedure was followed for both sons and daughters separately and combined. For the collective rearing conditions ((2)–(5)), we eliminated from analysis all full-sibships in which less than 75% of the larvae survived to adulthood. Thus, six full-sibships were eliminated from condition (2). This measure ensured that all larvae in a given rearing condition were exposed to comparable levels of competition. We also performed ANOVA on proportional hatchability, survivorship, and adult longevity; for hatchability and survivorship, full-sibships with low larval survivorship were not eliminated, and a two-way ANOVA (model factors were attractiveness of sire and individual sire (nested within attractiveness category)) was performed on the proportions calculated from each full sibship. Paternal heritabilities ($h_s^2 = 4\sigma_s^2/(\sigma_s^2 + \sigma_d^2 + \sigma_w^2)$) of developmental characters were calculated by the method of Becker (1984, p. 58).

3. RESULTS**(a) Sire attractiveness and offspring hatchability and survivorship**

Nearly all eggs hatched, and proportional hatchability of eggs fertilized by attractive and non-attractive sires did not differ (two-way ANOVA; $p > 0.05$, F -test). Similarly, over 80% of larvae survived to adulthood under all five rearing conditions, and in no case did the proportional survivorship of offspring of attractive sires differ from that of non-attractive sires (two-way ANOVA; $p > 0.05$, F -test). At 25.5 °C adult males survived approximately 16 days. As above, adult longevity of sons of attractive and non-attractive sires did not differ (three-way ANOVA; $p > 0.05$, F -test).

(b) Sire attractiveness and offspring developmental characters

We found that when reared collectively under a favourable environment (condition (2)), the offspring of attractive sires reached adulthood approximately one day sooner (maturation period of approximately 40 days) than the offspring of non-attractive sires (table 1; figure 1*b*). This difference was significant for both sons and daughters (table 2). Under a reduced quantity of diet (condition (3)) or lower tem-

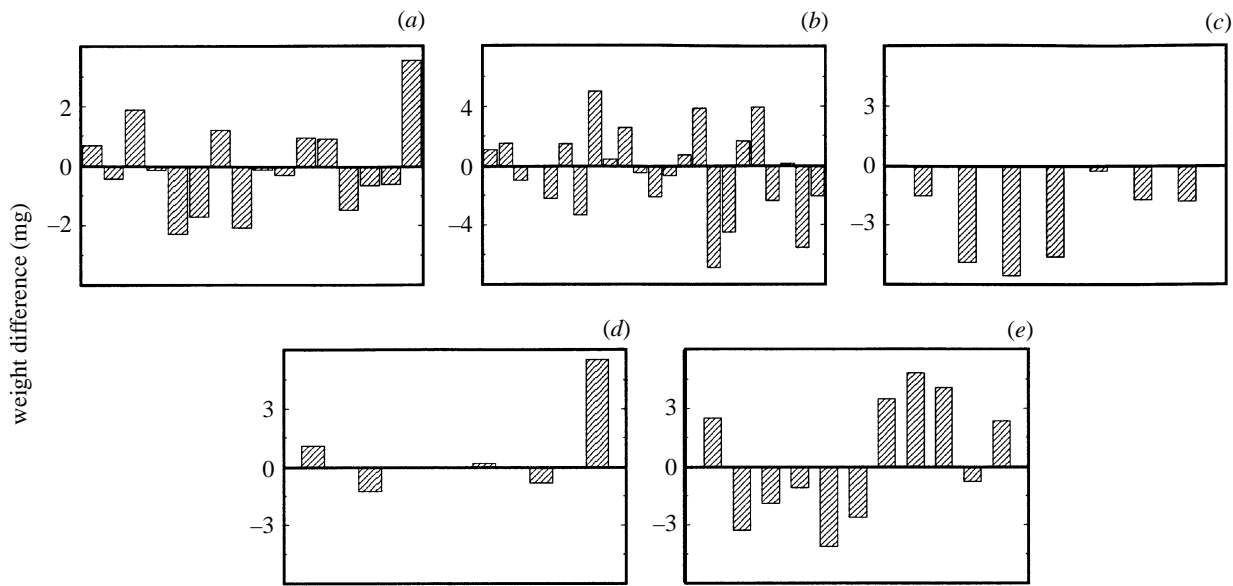


Figure 2. Difference between mean adult weight (measured on day of eclosion) of female offspring of an attractive and a non-attractive sire. Sire pairings and rearing conditions as in figure 1. (c) Mean weights of offspring of non-attractive sires greater than mean weights of offspring of attractive sires ($p < 0.05$; sign test, two-tailed).

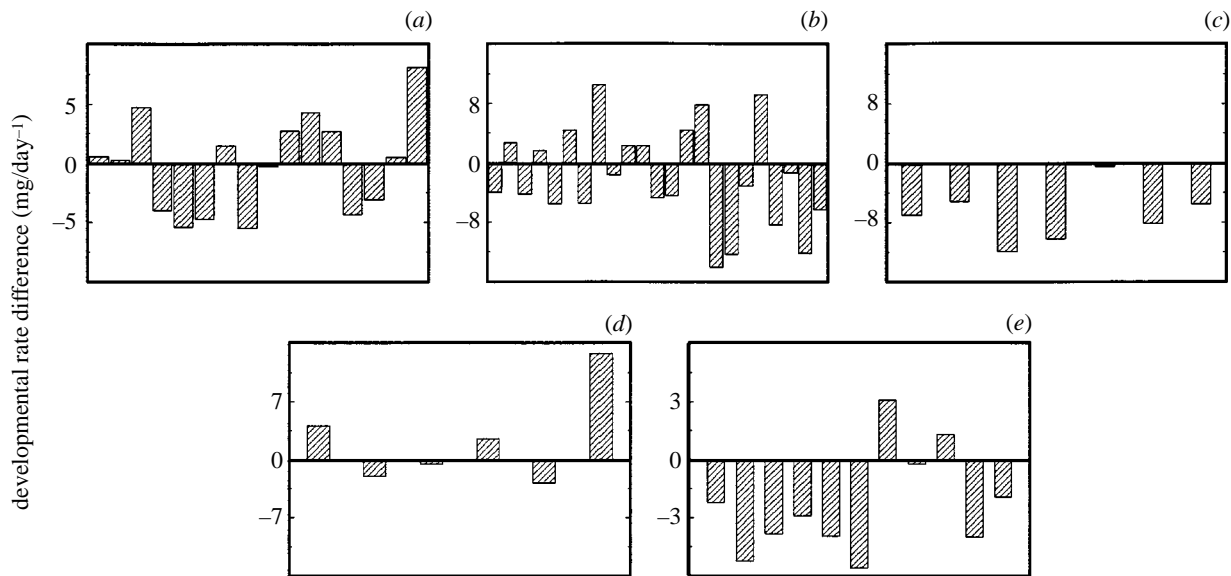


Figure 3. Difference between mean developmental rate (adult weight/maturation period) of female offspring of an attractive and a non-attractive sire. Sire pairings and rearing conditions as in figure 1. (c) Mean developmental rates of offspring of non-attractive sires greater than mean rates of offspring of attractive sires ($p < 0.05$; sign test, two-tailed).

perature (condition (5)), however, the offspring not only matured more slowly (maturation periods of approximately 42.2 and 124.4 days under conditions (3) and (5), respectively) but the difference was reversed: the offspring of non-attractive sires reached adulthood sooner (table 1; figure 1*c, e*). Neither positive nor negative relationships between sire attractiveness and offspring maturation period were found under other rearing conditions (table 2; figure 1*a, d*).

Relationships between sire attractiveness and offspring weight paralleled some of the above findings. We found that under a reduced quantity of diet the (female) offspring were approximately 10 mg lighter than under the favourable condition (2). Moreover,

the female offspring of non-attractive sires were approximately 2 mg heavier (adult female weight was approximately 25 mg) than the offspring of attractive sires (tables 1 and 2; figure 2). And when offspring weight was divided by maturation period to yield developmental rate, the offspring of non-attractive sires had significantly higher developmental rates; higher developmental rates among the offspring of non-attractive sires were also found under lower temperature. Neither positive nor negative relationships between sire attractiveness and offspring weight or developmental rate were found under other rearing conditions (table 2; figure 3). Thus, there were no indications of antagonistic pleiotropy constraining

Table 3. *Paternal heritability values ($h_s^2 \pm \text{s.e.}$), determined from half-sib analyses (see Becker 1984), for developmental characters (\clubsuit and \spadesuit) under various rearing conditions*

rearing condition ^a	maturation period		adult weight		developmental rate	
	\clubsuit	\spadesuit	\clubsuit	\spadesuit	\clubsuit	\spadesuit
1	0.43 ± 0.20^b	0.46 ± 0.21^b	—	0.76 ± 0.29^b	—	0.65 ± 0.27^b
2	0.60 ± 0.22^b	0.63 ± 0.22^b	—	0.39 ± 0.15^b	—	0.36 ± 0.15^b
3	0.31 ± 0.26	0.09 ± 0.19	—	1.23 ± 0.69^b	—	1.51 ± 0.81^b
4	0.52 ± 0.31	-0.04 ± 0.18	—	0.45 ± 0.36	—	0.22 ± 0.22
5	0.41 ± 0.22^b	0.39 ± 0.22^b	0.10 ± 0.10	0.06 ± 0.09	0.09 ± 0.25	0.19 ± 0.11

^aSee table 1 and text for definitions of rearing conditions.

^bLower confidence limit ($\alpha = 0.05$) for $h_s^2 > 0$.

the relationship between offspring maturation period and offspring weight, and under some conditions those offspring which matured faster were actually heavier.

(c) *Heritability of developmental characters*

We found relatively high amounts of additive genetic variance (V_A) for maturation period, adult weight, and developmental rate in *A. grisella*. All paternal heritability values (h_s^2) exceeded 0.36 for insects reared either individually (condition (1)) or collectively under adequate food and at 25.5 °C (condition (2); table 2); all values were significantly greater than zero ($p > 0.05$). Lower heritability values were obtained from insects reared under other conditions, particularly under 20 °C (condition (5); table 3). This decline possibly reflects higher environmental variance (V_E), yielding increased phenotypic variance (V_P), under unfavourable conditions.

4. DISCUSSION: DOES A GOOD GENES MODEL DESCRIBE MATE CHOICE IN *ACHROIA GRISELLA*?

Our initial findings under favourable food and temperature (condition (2)) led us to infer that the basic good genes model for intersexual selection operates in *A. grisella*. Subsequent work under other conditions, however, revealed unexpected reversals compelling us to modify this conclusion.

Under adequate food, 25.5 °C, and larval competition, a female who mates with an attractive male will produce sons that require approximately one day less to reach adult eclosion than sons of a female who does not exercise such choice (tables 1 and 2; figure 1b). This 2.5% decrease in offspring maturation period implies that females who mate with attractive males may accrue enhanced fitness over subsequent months. When food quality is reduced or larvae are reared individually, however, this relationship between a male's attractiveness and the maturation period of his offspring disappears. The latter finding suggests that the developmental factor in attractive males is only expressed under competition, which,

nonetheless, represents the natural circumstance for *A. grisella* larvae. And under reduced food quantity or lower temperature, it is the offspring of non-attractive males who fare better: they attain adulthood sooner (tables 1 and 2; figure 1c, e), and under the former condition are heavier as well (tables 1 and 2; figure 2c), which may afford advantages in dispersal and fecundity. These findings indicate that the relationship between male attractiveness and offspring development is not robust but rather varies with environmental conditions.

Our findings demonstrate that a female may obtain genetic benefits by mating with an attractive male, but that such benefits are not transferable to some unfavourable environments. The curious reversals of the relationship between male attractiveness and offspring development suggest the presence of genotype–environment interactions and mean that a good genes model may not fully describe mate choice in *A. grisella*. For example, any post-mating environmental change toward unfavourable food or temperature conditions would relegate the offspring of a choosy female to relatively longer maturation periods and lower weights. Thus, operation of a good genes mechanism alone appears unlikely in *A. grisella*—unless slow development and low weight are adaptive in unfavourable conditions, such conditions are rare, or female choice too reverses in such conditions—and the operation of additional sexual selection mechanisms remains probable, at least during certain times and locations.

Moreover, finding that the relationship between male attractiveness and offspring development is not robust presents a strong message regarding other studies purportedly upholding the good genes model. These studies seldom include comparable analyses across a range of environmental conditions, and it may be premature for them to claim full and unequivocal support for the good genes model without further investigation.

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