

# Quantitative genetics of female choice in an ultrasonic pyralid moth, *Achroia grisella*: variation and evolvability of preference along multiple dimensions of the male advertisement signal

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The mating system of *Achroia grisella* (Lepidoptera: Pyralidae) is characterized by male ultrasonic advertisement signalling to which females orientate. Although males provide no direct, somatic benefits to their mates, females prefer males whose signal characters are more exaggerated than the population means. Previous studies showed that the signal characters influencing mate attraction are highly repeatable and heritable. We measured the phenotypic and additive genetic variances (heritability) of female preference in *A. grisella*, as this additive genetic variance is one of the genetic assumptions of indirect models of sexual selection. We determined the preference index of female *A. grisella* by repeated phonotaxis trials in which a choice of simulated male signals was presented. These playback experiments showed that female preference indices varied but were repeatable within individuals. Specifically, females differ in the relative importance of the several signal characters during mate assessment. A subsequent half-sib breeding design revealed an amount of additive genetic variance for the female preference index ( $h_s^2 = 0.212$ ,  $SE = 0.1347$ ,  $P = 0.0611$ ;  $CV_A = 0.1826$ ). Our study highlights the importance of careful preparation of test signals and experimental design for quantifying individual variation in (female) preference along multiple signal dimensions.

**Keywords:** acoustic communication, female preference, indirect sexual selection.

## Introduction

The processes of sexual selection include competition within one sex, generally the male, for access to the other sex and intersexual selection in which one sex, generally the female, mates preferentially with certain members of the other sex based on various criteria. These criteria may be somatic, but in many species females discriminate among potential mates even when they accrue little or no direct, somatic benefit by virtue of mating with one male over another. In such cases it is proposed that females receive indirect, genetic benefits in the form of 'attractiveness alleles' (arbitrary, or Fisherian, model: Lande, 1981; Kirkpatrick, 1982) and 'viability alleles' (good-genes model: Pomiankowski, 1988) inherited by their offspring.

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Both the arbitrary and good-genes models of sexual selection are coevolutionary in that the male character and female preference coevolve in a reciprocally reinforcing manner. These models assume the existence of: (i) significant additive genetic variance (heritability) for both the male character and (ii) the female preference, as well as (iii) genetic correlation between these male and female traits (Kirkpatrick & Ryan, 1991). This genetic correlation may arise from the linkage disequilibrium established by assortative mating, and it may lead to extreme exaggeration of the male character and female preference. Confirmation of these three fundamental assumptions and determination that selection is occurring does not indicate which indirect model of sexual selection is operating, but failure to demonstrate the assumptions would suggest that neither model is responsible for the observed selection. Rather, a direct mechanism such as exploitation of sensory bias would be implicated.

Whereas various workers have reported evidence for heritability of male signal characters in diverse species, only a few have reported parallel findings for female preference. This disparity may reflect the relative difficulty of studying behavioural preference traits as opposed to morphological and signalling ones (Jang, 1997) or the lack of attention to and thorough analyses of preference in sexual selection studies (Rosenqvist & Berglund, 1992; Jennions & Petrie, 1997).

Several investigators have conducted genetic analyses of mate preference in species wherein different females exhibit markedly distinct choices (for review, see Bakker & Pomiankowski, 1995). Their studies have revealed genetic control of preferences by relatively few loci. But preferences in most species are continuous rather than discrete, indicating that they are polygenic and should be examined via quantitative genetic analyses of intra-population variation. A limited number of quantitative genetic studies have reported correlated responses of preference to artificial selection on male characters that suggested some genetic influence on female choice (for review, see Bakker & Pomiankowski, 1995; Jennions & Petrie, 1997). Whereas these correlated responses may suffice to confirm the fundamental genetic assumptions of indirect sexual selection models, they do not provide specific estimates of additive genetic variance, and heritability, of choice. Such estimates would be necessary to predict quantitatively a population's response to indirect sexual selection.

Here, we report a study examining phenotypic and additive genetic variation in female preference in the lesser wax moth *Achroia grisella* (Lepidoptera: Pyralidae). We exploited the relative ease with which female *A. grisella* can be tested and bred in the laboratory to calculate reliable preference indices for each individual and to determine the heritability of the index.

In the field *A. grisella* is a symbiont of honeybees (*Apis mellifera*). Unlike most Lepidoptera, pair formation in *A. grisella* entails ultrasonic advertisement signals by stationary, wing-fanning males that attract receptive females within a radius of several metres (Spangler *et al.*, 1984). Experiments using simulated signals showed that the ultrasound alone was as attractive as a live male. Acoustic signals in male *A. grisella* are produced by a pair of tymbals on the tegulae (see Spangler *et al.*, 1984). The tegulae are struck twice by the bases of the forewings during each complete cycle of wing movement (=1 period), once on the upstroke and once on the downstroke. A 100- $\mu$ s pulse of sound is emitted from the tymbal, which buckles in or out as the tegula is struck. Owing to slightly asynchronous wing movement, the insect's two tymbals produce a pair of pulses during each upstroke and downstroke that are usually separated by a brief (100–400  $\mu$ s) silent

gap. The sound pulses are loud [sound pressure level (SPL)=95 dB at 1 cm; 0 dB re 20  $\mu$ Pa] and include frequencies from 70 to 130 kHz. There exists no evidence that direct, somatic benefits of any kind, e.g. parental care or spermatophore nutrients, are provided by males and influence female preference (Greenfield & Coffelt, 1983).

Playback experiments and multivariate regression analyses revealed that the signal characters, pulse rate (PR), asynchrony interval (AI) and peak amplitude (PA), are the targets of female choice in *A. grisella* (Jang & Greenfield, 1996, 1998). Pulse rate is a measure of signal repetition rate and is defined as the inverse of the period between the beginning of a given pair of pulses to the beginning of the following pair of pulses. Asynchrony interval is the time interval from the beginning of the first pulse to the beginning of the second pulse in a pair of pulses produced by a given upstroke or downstroke. Peak amplitude is calculated as the greatest absolute value of the SPLs sampled during a pulse. On average, females prefer signals with PRs, AIs and PAs greater than mean values in the male population.

The three male signal characters influencing female preference vary considerably within populations but are repeatable within individuals (Jang *et al.*, 1997). Quantitative genetic experiments using a half-sib design determined that heritabilities ( $h_s^2$ ) of all three signal characters are significant among collectively reared moths, but only  $h_s^2$  of PA is significant in individually reared moths (Collins *et al.*, 1999). Estimates of phenotypic and genetic variance, including 'evolvability' (*sensu* Houle, 1992), of female preference would complement the above information and further our understanding of the potential for sexual selection to operate in *A. grisella*.

## Materials and methods

### Population studied

We studied a laboratory population of *A. grisella* derived from animals collected at infested honeybee colonies near Auburn, Alabama during September 1994. Throughout the 16 generations between founding and the study reported here, we maintained a random breeding protocol that minimized loss of genetic variation in the stock population. Larvae were reared on a diet containing a flour mixture, glycerine, Brewer's yeast, beeswax, honey and water (Dutky *et al.*, 1962) and kept under a 12:12 h light:dark photoperiod at 25.5°C. To ensure that the condition of tested adults was standardized, we used virgin and individually reared animals for all experiments. Virgin adults were obtained by individually placing second-instar larvae from the

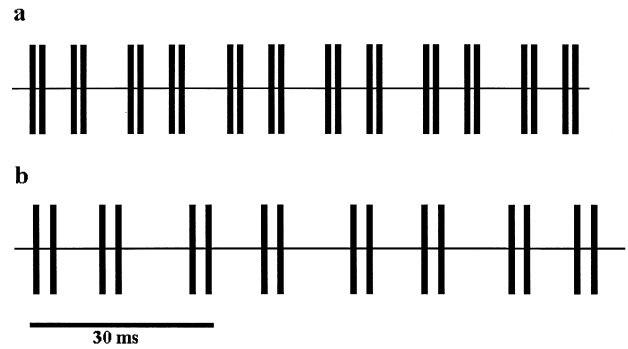
stock population in 30-mL containers supplied with diet *ad libitum* ( $\approx 1$  g). These larvae pupated and eclosed to adults within the individual containers.

### Measurement of female preference index

Because an acoustic signal of a male *A. grisella* is defined by several characters and male attractiveness is a function of these signal characters, female preference functions can be projected to multidimensional signal coordinates (Jang & Greenfield, 1998). However, such multidimensionality would render the characterization of preference functions of individual females over the entire range of signal coordinates rather complex. Therefore, we determined preference indices of individual females by using two-stimulus choice tests especially designed to reveal any fundamental differences in the relative importance of the various signal characters during mate assessment.

To measure the preference indices of individual females accurately, we repeatedly tested their phonotaxis toward loudspeaker playbacks of simulated male signals. We relied on a male attractiveness index ( $AT = 0.524 PA + 0.296 AI + 0.117 PR$ ) derived via the multivariate regression analysis (Lande & Arnold, 1983) of an earlier generation (fifth) of the stock population, to design the simulated signals used (multivariate regression model 1, see Jang & Greenfield, 1998). Two different signals, of which the expected attractiveness (AT) in the population at large was equal, but of which specific characters were quite different, were designed and constructed on a personal computer using a digital signal editing program. We constructed one signal with a high PR value ( $56.5\text{ s}^{-1}$ ), 2.53 SD above the population mean, and a commensurately short AI value ( $180\ \mu\text{s}$ ), 1.00 SD below the population mean (Fig. 1). The other signal bore reciprocal characters: low PR ( $36.5\text{ s}^{-1}$ ; 2.53 SD below the mean) but long AI ( $845\ \mu\text{s}$ ; 1.00 SD above the mean). We repeated the same standard pulse,  $108\ \mu\text{s}$  in length and 99 kHz in peak frequency, in both the high-PR and long-AI signals. This standard pulse had been recorded (see below for method) from a male in the stock population and approximated the population means in length and frequency.

All four PR and AI values of test signals fell within the ranges observed in the  $P_1$  generation. Moreover, the combinations of the test signals used in this study, and even more extreme combinations, were found in the  $P_1$  generation. Based on multivariate regression studies, there is no interaction effect between AI and PR on male attractiveness ( $\gamma_{PR, AI} = 0.052$ ,  $P = 0.208$ ; see Jang & Greenfield, 1998). Because our test signals are based on selection gradient studies on the male

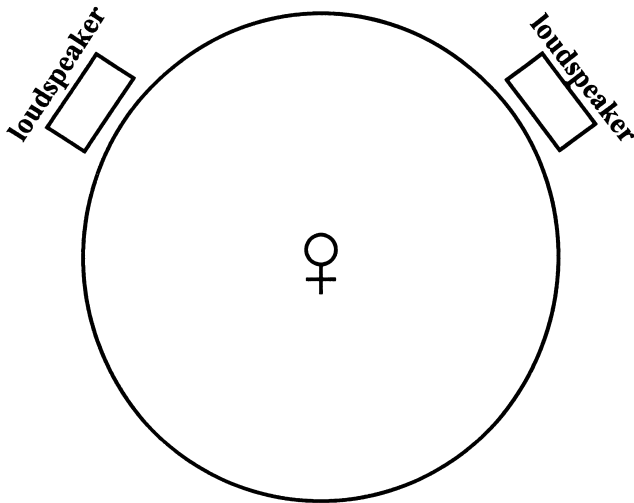


**Fig. 1** Male signals used in playback experiments determining female preference indices for *Achroia grisella*. (a) The high-pulse rate signal. This signal had a  $56.5\text{ s}^{-1}$  pulse rate (2.53 SD above the population mean) and a  $180\text{-}\mu\text{s}$  asynchrony interval (1.00 SD below the mean). (b) The long-asynchrony interval signal. This signal had a  $36.5\text{ s}^{-1}$  pulse rate (2.53 SD below the mean) and a  $845\text{-}\mu\text{s}$  asynchrony interval (1.00 SD above the mean). All pulses in both signals were identical in spectral and amplitude properties.

attractiveness index, the effects of different AI and PR values on female preference should be independent of each other.

The two playback signals were continuously and simultaneously played (looped) back using a custom computer program developed specifically for recording and playing back ultrasound. We used a sampling rate of 597 kHz during each trial. The signals were transformed into two analogue outputs in the soundcard (Supersound Engineering Version, SiliconSoft, San Jose, CA) of a personal computer (80486 processor; 66 MHz cpu). These outputs were amplified (UltraSound Advice model S55 amplifier; frequency response  $\pm 3$  dB from 18 to 300 000 Hz) and broadcast from ultrasonic loudspeakers (UltraSound Advice model S56; frequency response from 10 to 200 000 Hz). Before each testing session, we recorded the two signals played back by the two ultrasonic loudspeakers to ensure that the amplitude, frequency and temporal signal characters actually broadcast at the female release point were the intended ones. In all experiments, PA values, recorded as digitized voltages ordered on a linear scale, were adjusted (via amplifier gain controls) and re-measured until broadcasts from the two loudspeakers both equalled  $79 (\pm 0.3)$  dB SPL at the female release point.

The two loudspeakers were placed immediately outside the perimeter of a circular screen arena (80 cm diameter) and directed towards the arena centre (Fig. 2). Azimuthal separations between the loudspeakers were  $120^\circ$  relative to the centre. The arena was kept in a  $3.0 \times 3.5 \times 2.5\text{-m}$  semi-anechoic room whose photo-



**Fig. 2** A schematic diagram for the playback experimental setup. Female *Achroia grisella* were released from the centre of the circular screen arena (80 cm diameter) and were given a choice of two signals: high-pulse rate and long-asynchrony interval signals. Two ultrasonic loudspeakers were placed immediately outside the perimeter of the arena and were azimuthally separated by 120° relative to the arena centre.

period and temperature were maintained as for rearing of the stock population.

We determined female preference indices by releasing females individually and sequentially from a small cup placed at the arena centre. Releases were not made until each female had rested at the centre for at least 15 s. A female was judged to prefer a playback signal if she moved to within 5 cm of the loudspeaker broadcasting it. Females that did not respond within 2 min of release were not used in further analyses or breeding. All playback experiments were conducted during the initial half of scotophase, the period of peak mating activity in *A. grisella* (Greenfield & Coffelt, 1983).

Newly eclosed adult females, both parental ( $P_1$ ) and filial ( $F_1$ ) generations of experimental animals, were tested three times daily for two consecutive days beginning 6–12 h after eclosion. Thus, every female was tested a total of six times. For a given female, consecutive trials were separated by at least 30 min to avoid potential habituation to playback signals. The loudspeakers broadcasting the two playback signals, ‘high-PR’ and ‘long-AI’, were switched each time a given female was tested to eliminate any confounding directional influences on her preference. Our six-trial test yielded seven possible preference index values for each female, ranging from 0 (all responses to the long-AI signal) to 6 (all responses to the high-PR signal).

### Experimental pairings and breeding

We used a half-sib breeding design (see Becker, 1984; Falconer, 1989) to determine heritability of the female preference index. On each of two consecutive days, a given male was paired with a different female whose preference index had been determined. Each pair was placed in a small screen cage, and mating usually ensued regardless of the male’s attractiveness. After mating, the male was removed, and deposited eggs were collected. Twenty-six males were each mated to two females, five males were each mated to one female, and one male was mated to three females. Thus, the experimental pairings consisted of 60 full-sib families.

Eggs ( $F_1$ ) collected from each of the pairings were placed on 30 g of diet in a 17 × 12 × 6.5-cm plastic container kept in the chamber used for rearing the stock population. After hatching and attaining the second instar, 40 larvae were randomly chosen from among the offspring of each mated female ( $P_1$ ) and placed individually in 30-mL containers with 1 g diet. Following adult eclosion, females ( $F_1$ ) were tested for their preference indices. The same protocols used for measuring female preference indices in the  $P_1$  generation were used in the  $F_1$  generation.

### Statistical analyses

From the half-sib breeding design, we calculated the narrow-sense heritability ( $h_s^2$ ) (see Falconer, 1989) for the female preference index. Because distributions of female preference indices for both generations were normal (see Results), we used a nested analysis of variance (ANOVA, Model II) with unequal sample sizes (Sokal & Rohlf, 1981, pp. 294–299) to partition phenotypic variance for these indices into components resulting from fathers, mothers and offspring. Heritability was calculated as 4× the proportion of variance attributed to fathers (Falconer, 1989, p. 170, table 10.4). The standard error for the heritability of the female preference index followed Becker (1984, p. 59). To provide an additional estimate of evolvability, we also calculated the coefficient of additive genetic variance,  $CV_A = \sqrt{V_A}/\bar{x}$ , where  $\bar{x}$  is the mean value of the trait (preference index) (Houle, 1992).

### Results

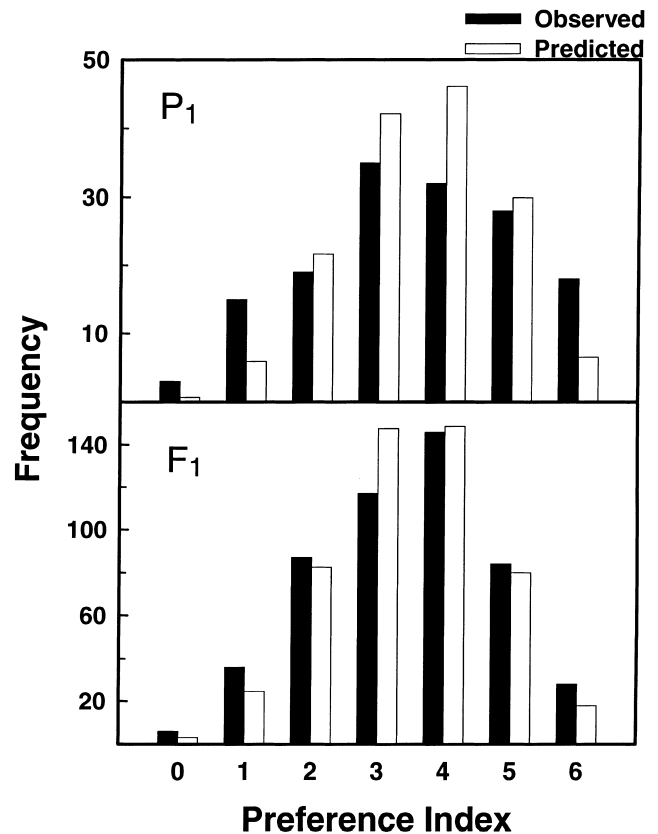
The distribution of preference indices in the  $F_1$  generation, averaged for each family, was normal (Anderson–Darling normality test,  $P=0.199$ ). A ln transformation served to normalize the distribution of preference indices in the  $P_1$  generation (Anderson–Darling normality test,  $P=0.721$ ). The means of mothers’ ( $3.43 \pm 1.57$  SD,

$N=60$ ) and daughters' ( $3.40 \pm 0.605$  SD,  $N=60$ ) preference indices did not differ significantly (Wilcoxon two-sample test,  $W=3688$ ,  $P=0.76$ ).

The means of preference indices for both generations deviated from 3.00, the expected value assuming equivalent attractiveness of the two simulated signals. Instead, the proportion of all 900 orientations ( $N=150$  females, six trials per female) towards the high-PR signal in the  $P_1$  generation was 0.593, and the proportion of all 3024 trials in the  $F_1$  generation ( $N=504$  females, six trials per female) toward the high-PR signal was 0.573. These observed proportions were significantly different ( $P < 0.0001$  for both generations; binomial test with normal approximation) from the expectation that equal numbers of responses should be directed towards each simulated signal. This discrepancy may reflect a change in female preference indices over the 11 generations elapsing between determination of the male attractiveness index and the study reported here. Estimation of heritability relies on consistent measurements over two successive generations ( $P_1$  and  $F_1$ ) rather than on values of the preference indices themselves. Because means of preference indices for both  $P_1$  and  $F_1$  generations were statistically similar, our method of quantification of female preference was consistent for both generations. Therefore, the observed departure from the initial expectation of equivalent orientation towards both test signals would not have affected our interpretation of the results.

We used the observed proportions of orientation towards the high-PR signal, 0.593 and 0.573, for the  $P_1$  and  $F_1$  generations, respectively, to calculate the expected binomial frequency distributions of female preference indices. In the six-trial tests, 31% of mothers and 23% of daughters preferred the high-PR signal five or six times, and 12% of mothers and 8% of daughters preferred the long-AI signal five or six times (Fig. 3). The observed frequency distributions of female preference indices were significantly different from the expected ones (binomial goodness-of-fit tests; for  $P_1$ :  $\chi^2_4=45.5$ ,  $P < 0.0001$ ; for  $F_1$ :  $\chi^2_4=20.1$ ,  $P=0.0002$ ), indicating that more females than expected by chance always chose the high-PR or the long-AI signal.

ANOVA of the female preference index among the  $F_1$  generation (daughters distributed among half-sib and full-sib families) revealed a significant added variance component attributable to fathers (Table 1). The heritability of the female preference index, estimated from ANOVA, was marginally significant ( $h^2_s=0.212$ ,  $SE=0.1347$ ,  $P=0.0611$ ). The  $CV_A$  of the female preference index was 0.1824. We also averaged the preference indices of daughters in each full-sib family and regressed these averages against the mother's index to obtain a second heritability estimate. The correlation of



**Fig. 3** Frequency histograms of mothers' ( $P_1$ ) and daughters' ( $F_1$ ) preference indices. Female *Achroia grisella* ( $P_1$ ,  $N=150$ ) were presented with a choice of a high-PR (pulse rate) signal and a long-AI (asynchrony interval) signal, which were played back from loudspeakers. The preference index is the number of times that a female chose the high-PR signal in six repeated trials. After testing, each of two females ( $P_1$ ) were mated with a male randomly chosen from a population. The preference indices of female offspring ( $F_1$ ,  $N=504$ ) were assessed according to the same methods as used for the mothers ( $P_1$ ). Predicted values are based on binomial frequency distributions calculated using mean proportions 0.593 and 0.573 for the  $P_1$  and  $F_1$  generations, respectively.

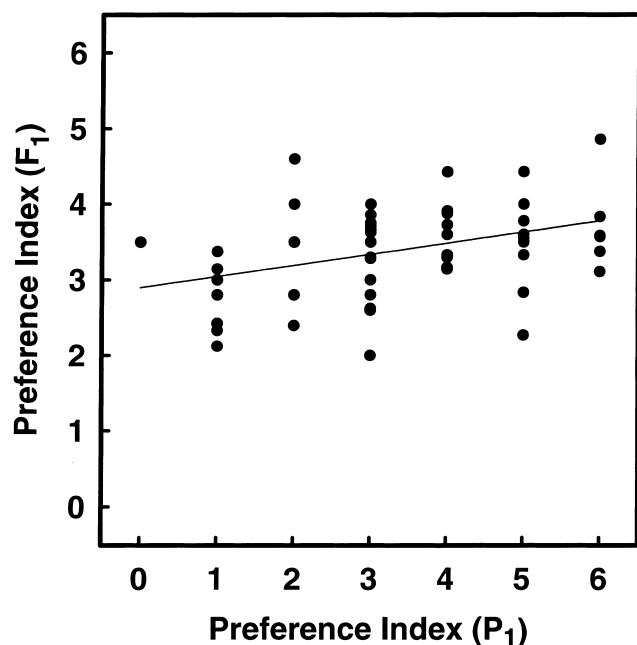
preference index between mothers and their daughters was positive and significant (least squares linear regression weighted by the number of daughters;  $b_{F_1, P_1}=0.119$ ,  $t=2.89$ ,  $P=0.005$ ; Fig. 4). Of course, this correlation may result, in part, from maternal effects (Falconer, 1989).

## Discussion

Assessment of phonotactic choices in playback experiments showed that female preference indices varied among individuals in *A. grisella*. Such phenotypic variance of female preference within a population is

**Table 1** Analysis of variance (ANOVA) table illustrating variation in female preference index in *Achroia grisella*. After recording signals, each male ( $P_1$ ) was usually mated with two females whose preference indices had been determined in six-trial choice experiments. Because of this half-sib design, the ‘mothers’ in the source column were nested within ‘fathers’ for analyses. From each full-sib family ( $F_1$ ), signals were recorded from a sample of 5–10 of the male offspring, and preference indices were assessed from a sample of 4–14 of the female offspring

Source	d.f.	SS	<i>F</i>	<i>P</i>
Fathers	31	99.38	2.01	<0.01
Mothers	28	44.75	0.93	>0.4
Offspring	441	760.73		



**Fig. 4** Regression of daughters' preference indices on their mother's preference index in *Achroia grisella*. The preference indices of female offspring of each full-sib family were averaged and regressed against their mother's preference index (weighted by the number of daughters).

documented in the sulphur butterfly (*Colias eurytheme*; Sappington & Taylor, 1990), the field cricket (*Gryllus integer*; Wagner *et al.*, 1995), the cricket frog (*Acris crepitans*; Ryan *et al.*, 1992), the barn swallow (*Hirundo rustica*; Møller, 1994) and the guppy (*Poecilia reticulata*; Godin & Dugatkin, 1995). Although phenotypic variance of female preference is a prerequisite for selection to operate on the preference, the phenotypic variance does not necessarily imply additive genetic variance (heritability) of female preference. Indirect models of

sexual selection assume additive genetic variances for both female preference and preferred male traits, and these variances are usually examined by quantitative genetic experiments.

The significant variation in preference indices included consistent responses towards high-PR or long-AI signals in some females (Fig. 3). Although three signal characters, including PR and AI, are the direct targets of female choice at a population level, our findings suggest that individual females differ in the relative importance of various signal characters during mate assessment. ANOVA of data from our half-sib breeding design indicates that additive genetic variation accounts for a substantial portion of this variation in female preference.

The heritability and evolvability estimates of the female preference index imply that this trait can respond to various selection pressures. Potential direct selection pressures include energetic costs and risks incurred while searching for mates. Alternatively, or additionally, selection may act indirectly on the female preference trait via male signal traits genetically correlated with female preference. Under such circumstances, a correlated response of female preference to selection on the male trait may result. Such correlated responses form the core of indirect sexual selection mechanisms, including arbitrary and good-genes selection (Kirkpatrick & Ryan, 1991). The existence of heritable variation in both male signal characters (Collins *et al.*, 1999) and female preference in *A. grisella* suggests that an indirect mechanism of sexual selection can operate (see Jia & Greenfield, 1997). An earlier attempt to detect any genetic correlation between the female preference index and male signal characters failed, and this absence of the genetic correlation probably reflects the lack of assortative mating during the many generations of laboratory breeding prior to quantitative genetic experiments (Jang, 1997; see also Bakker & Pomiankowski, 1995). Obviously, further work investigating genetic correlations between male signal and female preference traits in field populations and field studies of the mating pattern in natural population will be necessary to understand more fully the nature of sexual selection in *A. grisella*.

Our experimental design not only allowed us to estimate the evolvability of female preference but also revealed the manner in which this trait may vary within a population. Although female preference has been measured quantitatively in several taxa, these measurements entailed testing responses to a range of values from the one-dimensional distribution of a male trait [e.g. the three-spined sticklebacks (*Gasterosteus aculeatus*), Bakker, 1993]. Instead, we selected our test signals

from among the multidimensional coordinates of male signal characters such that their individual characters differed markedly but their expected attractiveness was equivalent. This careful design of test signals was implemented to maximize the chance of detecting individual variation in female preference for the multi-dimensional signal.

Female preference may be studied via bioassaying response to single-stimulus presentations or two-stimulus choice experiments. Although single-stimulus experiments provide information that may be used to construct readily a precise preference function (e.g. Ritchie, 1996; Wagner, 1998), multiple-stimulus designs may offer the opportunity to detect the relative attractiveness of the various stimuli, differences that may not be evident from single-stimulus presentations (Doherty, 1985). We chose to rely on the two-stimulus design to take advantage of this acute resolving power and because females in natural populations are generally confronted with a simultaneous choice of two or more signalling males. Studies of indirect sexual selection remain hindered by difficulties in quantifying the female preference trait. Our study shows that careful selection of test signals and an experimental design tailored for the behaviour of the experimental species will greatly enhance determination of individual variation of this critical yet elusive trait.

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