

ORIGINAL ARTICLE

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Variance in female quality, operational sex ratio and male mate choice in a bushcricket

Received: 5 January 1998 / Accepted after revision: 25 October 1998

Abstract Male bushcrickets, *Kawanaphila nartee*, exercise mate choice when nutrients are limited. Male mate choice is associated with a female-biased operational sex ratio (OSR) that arises from an increased relative paternal investment under nutrient limitation. However, increased male choosiness could be attributable to the fact that females vary more in fecundity, and consequently in mate quality, when nutrient limited. Our objective was to experimentally partition the influences of OSR (male or female bias) and variance in mate quality (high or low) and to assess their relative influence on the intensity of mate choice by male bushcrickets. Female quality was manipulated by controlled feeding regimes that directly affected female fecundity. We found that males and females engaged in sexual interactions sooner under a male-biased than a female-biased OSR. Males were more likely to reject females on their first encounter when variance in female quality was high. However, the effect of quality variance on the total number of rejections during a 4-h observation period was dependent on the perceived OSR. A male's prior experience of variance in female quality did not influence male choosiness. Our observed rates of mate rejection conformed well with those predicted from recent theoretical models of sexual differences in choosiness. In conclusion, our results show that the opportunity for selection via male mate choice is influenced by an interaction between OSR and the variance in mate quality that arises within nutrient-limited populations of females.

Key words *Kawanaphila nartee* · Mate choice · Mate quality · Operational sex ratio · Sexual selection · Tettigoniidae

Introduction

In many animal taxa, males compete for access to females while females often exercise mate choice. Sexual selection thus acts on males. In some sex-role-reversed taxa it is females that compete for access to choosy males. Although reversal of the sex roles can be associated with male parental care (Trivers 1972), male parental care does not necessarily result in sex role reversal (Gwynne 1991; Vincent et al. 1992). Recent theoretical and empirical investigations of animal mating systems have focused on the factors that control the direction and intensity of sexual selection (Clutton-Brock and Parker 1992; Arnold and Duvall 1994; Owens and Thompson 1994; Johnstone et al. 1996; Kvarnemo and Ahnesjö 1996; Parker and Simmons 1996).

Variation in sex roles has been explained mainly in terms of variation in operational sex ratios (OSRs), defined as the ratio of sexually active females to males at any given time and place (Emlen and Oring 1977). A biased OSR will affect sexual selection in a population because a shortage of one sex will increase competition for matings among members of the more abundant sex (reviewed in Kvarnemo and Ahnesjö 1996), while the sex in short supply will generally have greater opportunities for mate choice, as for example in pipefish (Berglund 1994), field crickets (Souroukis and Murray 1995), and bushcrickets (Gwynne and Simmons 1990).

A difference in potential reproductive rates between males and females is an important factor generating variation in OSR (Berglund et al. 1989; Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992; Vincent et al. 1992). The potential reproductive rate is the population average rate of reproduction each sex could achieve if not limited by the availability of sexual partners

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(Kvarnemo and Ahnesjö 1996) and is determined primarily by the time costs associated with parental expenditure (Parker and Simmons 1996). In most animals, males have the higher potential reproductive rate and are limited by the availability of sexually receptive females, resulting in conventional sex roles. However, the potential reproductive rate of each sex can be influenced by environmental factors, such as food, temperature or nest site availability (Gwynne 1990; Kvarnemo 1994; Ahnesjö 1995; Almada et al. 1995; Simmons 1995; Forsgren et al. 1996; Kvarnemo 1997), which thereby produce a shift in the OSR, intensifying competition among the potentially limited sex (Kvarnemo 1996) or reversing the bias in OSR so that sex roles become reversed (Gwynne and Simmons 1990; Gwynne 1993).

Choosiness has traditionally been considered to be the opposite "sex role" to competition, as it is often expressed by the non-competitive sex (Emlen and Oring 1977). However, mate choice is only expected to arise when there is variance in mate quality and the benefits of mate choice exceed the costs (Parker 1983; Owens and Thompson 1994; Johnstone et al. 1996). The degree of choosiness within a sex is predicted to be governed both by the relative potential reproductive rate of the sexes, and by the population variance in quality of the opposite sex (Owens and Thompson 1994; Johnstone et al. 1996). Johnstone et al.'s (1996) theoretical analysis predicts that the degree of choosiness exerted by each sex will be influenced by the cost:benefit ratio, with the cost of choice (inversely proportional to the potential reproductive rate) having the stronger influence. Naturally, variance in mate quality must play some role because it provides the potential benefit of choice, and thus contributes directly to the cost:benefit ratio. Thus, variance in mate quality can favour the evolution of mate choice by members of the non-competitive sex, as well as among members of the predominantly competitive sex (Summers 1992; Owens et al. 1994). At the same time, variation in mate quality can affect the direction and extent of sexual competition for high-quality mates (Clutton-Brock and Parker 1992). The relationship between OSR and choosiness is thus more complex than between OSR and mating competition.

Mate choice is expected to be of special importance in animals with paternal care or other male parental investments, because the potential reproductive rates of males and females will be more equal than in species with little or no paternal investment (e.g. Berglund et al. 1986; Simmons 1992; Simmons 1994). Indeed, the most dynamic sex roles are found within this category of species, changing both within populations, over time (sticklebacks: Kynard 1978; giant water bugs: Kraus 1989; bushcrickets: Gwynne and Simmons 1990; pipefish: Vincent et al. 1994) and between populations (bushcrickets: Gwynne 1984; red-winged blackbirds: Whittingham and Robertson 1994; a blennioid fish: Almada et al. 1995).

Male bushcrickets, *Kawanaphila nartee* (Tettigoniidae, Orthoptera), have been shown to be more choosy of their mates in a situation of food shortage (Gwynne

and Simmons 1990; Simmons and Bailey 1990). In previous work, this has been ascribed to the female-biased OSR that arises due to an increased relative paternal investment under nutrient limitation (Gwynne and Simmons 1990; Shelly and Bailey 1992). However, increased male choosiness may also be attributed to the fact that females vary more in fecundity, and consequently in mate quality, when food supplies are limited (Simmons and Bailey 1990). Our objective in this study was to experimentally partition the influences of OSR and variance in mate quality and to assess their relative influence on the intensity of mate choice by male bushcrickets. We then use the data on observed patterns of mate choosiness in our experiments, and those from field studies of *K. nartee*, to examine how well the mate choice model proposed by Johnstone et al. (1996) predicts patterns of choosiness in this species.

There are at least two ways in which variance in mate quality can influence the operation of sexual selection via mate choice. We assume that there is a threshold for mate acceptance and that males reject any female that falls below that threshold. Thresholds may be fixed or variable (Janetos 1980; Real 1990). In a population with high variance in female quality, a greater number of females within the population should fall below a male's critical threshold so that the incidence of male mate rejection should be higher, and the opportunity for intersexual selection correspondingly greater, than in a population with the same mean but lower variance in female quality. Variation in the opportunity for mate choice may thus arise without variation in male thresholds. However, the OSR is predicted to induce variance in male thresholds; males experiencing a male-biased OSR should have a lower critical threshold than those experiencing a female-biased OSR because of the increased costs of mate rejection (Johnstone et al. 1996). Thresholds might also vary, dependent on a male's prior experience with females of varying quality (Real 1990; Luttbeg 1996; Rosenqvist and Houde 1997). We performed two experiments in which each male was allocated a single female and recorded his decision to accept or reject that female. In the first experiment, we manipulated the perceived OSR and males were randomly allocated a female derived from a population with high or low variance in quality. Thus, we were able to determine (1) if the probability of mate rejection varied with the population variance in mate quality, and (2) if the perceived OSR influenced the probability of mate rejection. In our second experiment, we examined directly the influence of prior experience of variance in female quality on male acceptance thresholds.

Methods

Natural history

K. nartee is a member of the endemic Australian subfamily of Tettigoniidae, the Zaprochilinae, which feed exclusively on the

pollen and nectar of spring-flowering plants. Animals emerge in mid-winter and reproduce throughout the spring flowering period. Eggs over-summer below ground. Mating activity appears resource based, occurring on and around pollen-rich food plants during the first 3–4 h of darkness (Simmons and Bailey 1990). Females can also gain nutrients from a protein mass, the spermatophylax, that males transfer to the female at copulation (Simmons and Bailey 1990). Pollen availability shows considerable seasonal and spatial variation, and female fecundity and the importance of male-derived nutrients for egg production covary negatively with pollen availability (Simmons and Bailey 1990; Gwynne et al 1998). Thus, when pollen is scarce, females compete for access to a limited supply of nurturant males and males choose females on the basis of fecundity (Simmons and Bailey 1990; Gwynne and Simmons 1990; Gwynne et al. 1998).

We collected immature *K. nartee* females, as penultimate-instar nymphs, from Kings Park, Perth, Western Australia, during eight nights in mid-September 1996 (experiment 1) and 1997 (experiment 2). The females were brought to the laboratory and reared en masse in fly screen cages, supplied with water, spring flowers and pollen granules obtained from a health food store. The light cycle in the laboratory followed natural conditions (12L:12D).

Experiment 1

Manipulating variance in female quality

On the day of adult eclosion, females were placed individually into glass jars provided with a stick for perching. Females were supplied with water daily by misting and were randomly assigned to one of three feeding regimes; pollen was supplied ad libitum (high), every 2nd day (medium), or every 3rd day (low). The trays in the high feeding regime were cleaned and refilled once or twice a week as required. In the medium and low regimes, only a small amount of pollen (2.5–5.0 mg) was supplied on each feeding occasion, and the trays were removed from the jars the day after feeding. The females were kept on these feeding regimes for a period of 3 weeks (females require 10 days feeding before they become sexually active; Simmons and Gwynne 1991). Thirty-two females were selected at random from the medium feeding regime and assigned to the treatment in which there was to be a low variance in female quality. A further 32 females were assigned to the high-variance treatment, selected at random from each of the high ($n = 9$), medium ($n = 9$) and low ($n = 14$) feeding regimes.

We successfully manipulated the variances in female quality, measured as number of eggs in the ovaries in 50 of the 64 females (see below). Females in the high-variance treatment ($n = 22$) were significantly more variable in fecundity than females in the low-variance treatment ($n = 28$) (variance ratio test, $F_{21,27} = 2.48$, $P = 0.01$), while the mean fecundity was kept constant (t -test for unequal variances, $t = 0.863$, $df = 33.8$, $P = 0.39$). The mean \pm SE (s^2) number of eggs was 16.4 ± 1.8 (69.2) in the high-variance treatment (range 5–32), and 14.6 ± 1.0 (28.0) in the low-variance treatment (range 7–24).

Manipulating OSR

Calling males were collected on three nights in mid-October, which, for logistic reasons, were 1 week apart. The day after collection, the males were placed in vials in the laboratory, and randomly assigned to perceive one of two OSRs: males that were to experience a female bias were housed individually. During the first 3 h of the dark period, on each of the 3 days following collection, these males were provided with three randomly selected unreceptive (i.e. mature but previously mated) females. Each vial was separated by a sound-absorbing barrier (6-cm-thick blocks of compressed paper) to prevent them from hearing and responding to one another. Males to experience a male-biased OSR were housed in groups of three. For the first 3 h of the dark period, their vials were interspersed with vials each containing five sexually signalling males. The calling

behaviour was checked every half hour, using a bat detector. The males in the female-biased treatment consistently called at a slower rate than those in the male-biased treatment who were interacting acoustically; males increase their signalling rate when in audible distance of competitors (Simmons and Bailey 1993). Thus, our manipulations appeared to successfully mimic male- and female-biased OSRs.

Mating trials

On the 4th day, 30 min before the start of the dark period, each male was housed individually and provided with a female from either the high or the low variance in quality treatments. The pairs were monitored for the following 4 h, until reproductive activity ceased. Sexual interactions are initiated by the male who produces an acoustic signal to attract receptive females. Generally males encounter females singly although under conditions of role reversal, take-over attempts by additional females can occur (Gwynne and Simmons 1990; Simmons and Bailey 1990). Females mount and engage males in precopula by flexing their ovipositors through 180°, grasping the male's genitalia in the copulatory position. Precopulatory periods are variable in time, and depend on the outcome of the female's mating attempt. A successful mating attempt is terminated by the male transferring a spermatophore to the mounted female. Male rejection occurs when the male breaks free from the female without transferring a spermatophore (for a full description of behaviours see Simmons and Bailey 1990). For all interactions, the time at the beginning and end of precopula was noted, and whether or not they ended in rejection or acceptance. Data were available on the outcome (acceptance vs rejection) of initial mating attempts by 64 pairs of individuals, distributed between treatments as reported in Fig. 1. Fifty-one of these replicates eventually ended in acceptance; 10 high variance-male bias, 12 high variance-female bias, 15 low variance-male bias, and 14 low variance-female bias. Fifty of these pairs were measured for pronotum length and dissected for fecundity after the experiment (1 low variance-female bias pair was lost, and the other 13 pairs were saved for another experiment). We also counted the number of times each male rejected his female partner during the 4-h observation period, irrespective of whether the pair finally mated successfully.

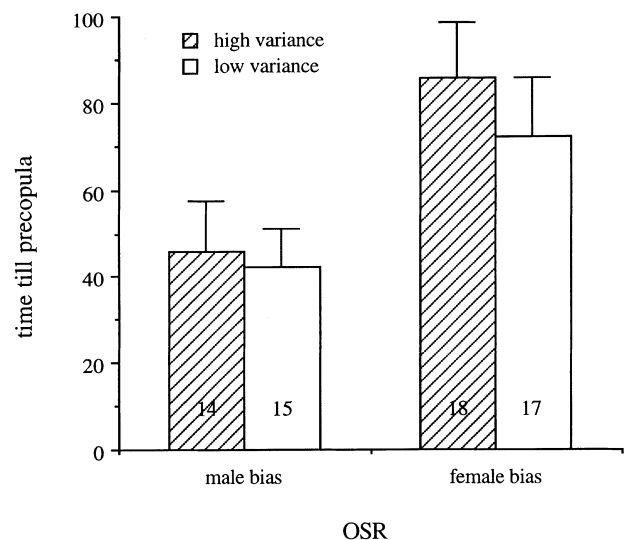


Fig. 1 Mean \pm SE time (min) passed before pairs entered precopula in the treatments with a male- or female-biased operational sex ratio (OSR) and with high or low variance in female quality. Sample sizes are given within each bar

Female pronotum length, which is a measure of body size, did not differ across the variance in quality treatments or the OSR treatments [mean \pm SE (s^2) 3.4 ± 0.02 mm (0.02); two-way ANOVA, qvar, $F_{1,46} = 0.2$, $P = 0.66$; osr, $F_{1,46} = 0.1$, $P = 0.79$; interaction, $F_{1,46} = 0.7$, $P = 0.42$] nor did male body size [3.1 ± 0.03 mm (0.04); qvar, $F_{1,46} = 0.1$, $P = 0.76$; osr, $F_{1,46} = 2.0$, $P = 0.16$; interaction, $F_{1,46} = 1.6$, $P = 0.22$]. Male body weight, which positively covaries with spermatophore weight and therefore estimates male quality, did not differ across treatments either [39.5 ± 0.9 mg (37.4); two-way ANOVA, qvar, $F_{1,46} = 0.9$, $P = 0.36$; osr, $F_{1,46} = 0.1$, $P = 0.77$; interaction, $F_{1,46} = 0.6$, $P = 0.43$].

Experiment 2

In this experiment we manipulated the mean and variance in fecundity among the pretreatment females, before providing males with a mate of low fecundity. Experimental methods followed those described for experiment 1, with the exception that all females were housed en masse (usually 60–80 females per cage), supplied with water, spring flowers, and in the case of pretreatment females, sexually receptive males. Pollen was provided on five “giant swabs” per cage every day (high), every 2nd day (medium) or every 3rd day (low feeding regime). The high-diet females were also provided with a dish containing excess pollen to allow feeding ad libitum.

Again we were successful in manipulating female quality. Among the pretreatment females, variance in female fecundity (number of eggs in the ovaries) was significantly greater in our high-variance compared with our low-variance treatment (variance ratio test, $F_{57,59} = 8.27$, $P < 0.001$). Mean fecundity also differed between the pretreatment groups (t -test for unequal variances, $t = 5.62$, $df = 70$, $P < 0.001$). The mean \pm SE (s^2) number of eggs was 9.5 ± 0.90 (46.7) for the high-variance treatment, and 4.2 ± 0.31 (5.7) for the low-variance treatment.

Calling males were collected on two nights in mid-October, 1 week apart. They were housed individually in vials. Two days after collection, they were mated to a virgin female, then kept isolated for 3 days, before being randomly assigned to either the high or the low variance in quality pretreatment group. Males were thus standardised with respect to their recent mating history. Males experiencing high female variance were provided with one low-, one medium- and one high-diet female, while those experiencing low female variance were provided with three low-diet females. The pretreatments ran for three nights, during the first 3 h of the dark period. Each night the males were given a new set of three females. On the fourth night (1 week after the first mating), each male was allocated a low-diet virgin female to mate with. The mating trials were identical to those of experiment 1. Forty males (20 of each treatment) went into precopula at least once, thus comprising our data set. Pronotum length of the females used in the final mating did not differ across the variance in quality treatments [mean \pm SE (s^2) 3.6 ± 0.02 mm (0.01); one-way ANOVA, $F_{1,38} = 1.8$, $P = 0.19$], nor did female fecundity [4.0 ± 0.5 eggs (9.5); one-way ANOVA, $F_{1,38} = 0.09$, $P = 0.76$], male pronotum length [3.3 ± 0.02 mm (0.02); $F_{1,38} = 0$, $P = 1.0$] or male body weight [51.5 ± 7.0 mg (48.4); one-way ANOVA, $F_{1,38} = 2.17$, $P = 0.15$].

Results

Experiment 1

Pairs entered precopula significantly earlier in the male-biased treatment than in the female-biased treatment, but this was unaffected by variance in female quality (two-way ANOVA; OSR, $F_{1,60} = 10.2$, $P = 0.002$; quality variance, $F_{1,60} = 0.3$, $P = 0.57$; interaction,

$F_{1,60} = 0.2$, $P = 0.67$; Fig. 1). Precopulas ending in rejection lasted for a clearly shorter time (mean \pm SE, 1.7 ± 0.6 min, $n = 13$) than those ending in acceptance (22.7 ± 1.3 min, $n = 51$) although the duration of precopula (square root transformed for normality) prior to successful mating was unaffected by OSR or variation in female quality treatments (two-way ANOVA; quality variance, $F_{1,47} = 0.4$, $P = 0.55$; OSR, $F_{1,47} = 2.4$, $P = 0.13$; interaction, $F_{1,47} = 0.1$, $P = 0.81$). We used a logistic regression to establish whether the time to first precopula influenced a male's mating decision. The probability of mate rejection was unrelated to the time to precopula (log-likelihood = -0.862 , $\chi^2 = 1.72$, $df = 1$, $P = 0.19$).

The probability that initial precopulas ended in mate rejection was analysed in a two-way design of a log-likelihood ratio test. However, in this analysis, more than one-fifth of fitted cells had a frequency less than five, which increases the risk of α (type 1) error. Given that there was no significant interaction term between variation in quality and OSR ($G = 1.37$, $df = 1$, $P = 0.24$), cells were collapsed to examine the influences of variation in quality and OSR using two separate one-way analyses: variance in mate quality significantly influenced the occurrence of mate rejection ($G = 6.61$, $df = 1$, $P = 0.010$) but OSR did not ($G = 0.83$, $df = 1$, $P = 0.361$; Fig. 2). The effect of variance in mate quality remained after sequential Bonferroni adjustment for two tests of the same data set (Rice 1989; critical Bonferroni $\alpha = 0.025$). Within the high-variance treatment, there was no significant difference in the frequency with which males accepted or rejected females from the three feeding regimes ($\chi^2 = 2.7$, $df = 2$,

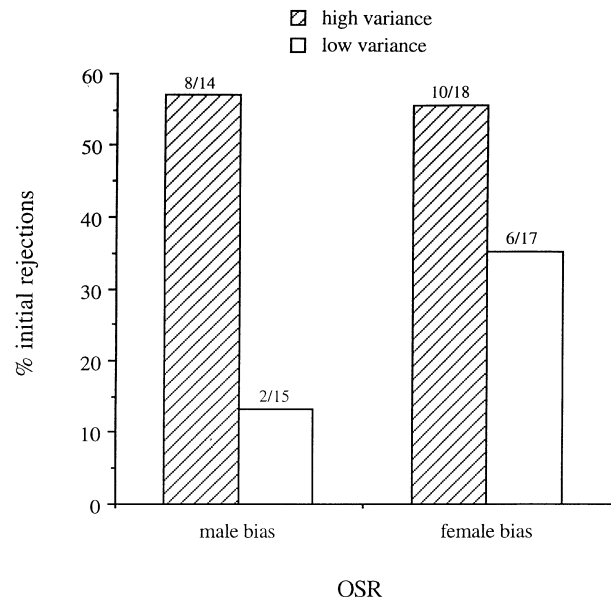


Fig. 2 The percentage of males entering precopula that rejected their female in treatments with male- or female-biased OSRs given access to females of high and low variance in quality. Actual values are given above each bar. Only the outcome of the first precopula in which a male engaged was included. Sample sizes as in Fig. 1

$P = 0.26$; Table 1), although the tendency was for medium-diet females to be accepted more often, a pattern consistent with the high acceptance rates of medium females in the low-variance treatment (binomial test, $n_1 = 8$, $n_2 = 24$, $P = 0.004$; Table 1).

Data on the total number of times each male rejected its mate could not be normalised by transformation. Given that two-way non-parametric ANOVAs are inadequate for the detection of interactions (Seaman et al. 1994; Zar 1996), we performed separate comparisons of treatment means using Mann-Whitney U -tests followed by sequential Bonferroni adjustment of probabilities. There was an obvious interaction between OSR and variance in female quality in determining the frequency with which males rejected their mates; under a male-biased OSR, the rejection frequency was lower when the variance in female quality was low (high vs low variance: $Z = 2.51$, $P = 0.0122$; which is less than the critical Bonferroni value of $\alpha = 0.0125$). However, under a female-biased OSR, variance in female quality had no influence on rejection frequencies (high vs low variance: $Z = 0.99$, $P = 0.32$). OSR per se had no direct influence on rejection frequencies (high female variance, male- vs female-biased OSR: $Z = 0$, $P = 1.0$; low female variance, male- vs female-biased OSR: $Z = 1.50$, $P = 0.13$) (Fig. 3).

Table 1 The observed frequency of accepted versus rejected females in the high variance in quality treatment, for each of the three feeding regimes high, medium and low, and in the low-variance treatment of medium-fed females. The data are pooled across the operational sex ratio treatments

	High variance				Low variance
	High	Medium	Low	Total	Medium
Reject	6	3	9	18	8
Accept	3	6	5	14	24
Totals	9	9	14	32	32

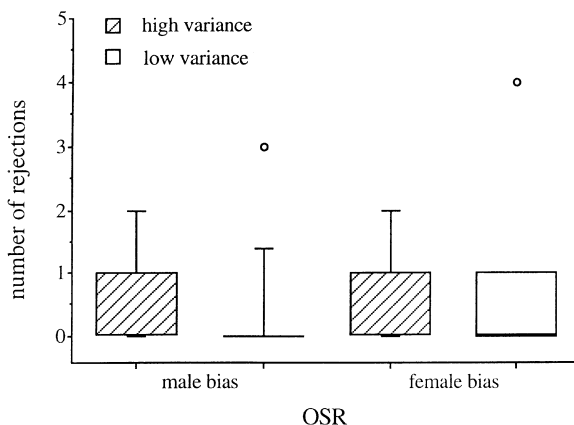


Fig. 3 Box plots giving the 10th, 25th, 50th, 75th and 90th percentiles for the total numbers of times a male rejected his female during the 4-h observation period, under male- and female-biased OSRs for each of the high and low variance in female quality treatments. All animals that went into precopula at least once were included, regardless of whether or not they finally mated. Sample sizes as in Fig. 1

Experiment 2

Experience of variance in female quality prior to encountering a low-quality female did not influence the likelihood that a male would reject its mate on initial precopula. Out of 20 males in each pretreatment, 8 males in the low-variance and 4 males in the high-variance pretreatments rejected their female ($\chi^2 = 1.1$, $df = 1$, $P = 0.30$). Time before first going into precopula did not differ between the treatments (log-transformed data for normality, one-way ANOVA, $F_{1,39} = 0.1$, $P = 0.75$), nor did time spent in the initial precopula (one-way ANOVA, $F_{1,39} = 0.1$, $P = 0.71$). Likewise, there was no significant difference between the treatments in total number of rejections (Mann-Whitney U -test, $Z = 1.5$, $P = 0.12$; mean \pm SE number of rejections for low-variance pretreatment, 0.8 ± 0.3 , range 0-5; high-variance pretreatment 0.2 ± 0.1 , range 0-1).

Discussion

We found that pairs engaged in precopula sooner in the treatment with a male-biased OSR than in that with a female-biased OSR, regardless of the variance in female quality within these treatments. After entering precopula the first time, the proportion of males that rejected their female was, however, higher in the treatment where the variance in female quality was high, compared to that where it was low. Although OSR did not influence the probability of rejection in these initial precopulas, the influence of variance in female quality on the males' total number of rejections was dependent on the OSR: males exposed to a male-biased OSR and paired with a female from the low-variance population were less likely to reject their female than were males in any other treatment.

It is not possible to distinguish between male and female control over the time to first precopula in our treatments. It may be that males had a greater sexual motivation when in competition with other males so that they were more likely to enter precopula on encountering a female. Alternatively, the increased calling activity associated with competing males (Simmons and Bailey 1993) may have represented a greater source of sexual stimulation for females so that they oriented to acoustically signalling males sooner. Whatever the causal explanation for the effect, mating speed had no influence on the probability of mate rejection in our study, and thus had no direct influence on the operation of intersexual selection via male mate choice. Delayed time to first precopula under a female-biased OSR could influence the potential for sexual selection operating via female-female competition, if it increased the probability of intrasexual interactions prior to precopula. The arrival of multiple females is common in natural populations where the OSR is female biased (Gwynne and Simmons 1990; Simmons and Bailey 1990; Gwynne et al. 1998).

It is clear from our study that although variance in mate quality had an influence on the opportunity for selection via male choice, the effect was dependent on the OSR. Johnstone et al.'s (1996) theoretical analysis predicts that the relative processing time (inversely proportional to potential reproductive rate and thus a direct correlate to OSR) should have the predominant influence on mate choosiness, since even a minor difference between the sexes in processing time can strongly affect the probability that an individual will reject a potential mating partner. Under a female-biased OSR, the costs of mate rejection would be low because of the high probability of encountering a second female. Consistent with expectation, mate rejection frequencies were found to be high in our female-biased OSR treatment. However, under a male-biased OSR, the costs of mate rejection should be greater. Again consistent with expectation, high frequencies of male mate rejection were maintained only in our treatment where variance in female quality, and thus the potential benefits of mate choice were high. Our results are further supported by those of Shelly and Bailey (1992). In their study of *K. nartee*, Shelly and Bailey manipulated the males' encounter rate with females and found that male mate rejection frequencies were reduced when encounter rates were low. Similarly, males collected from sites with male-biased sex ratios had lower rejection frequencies than those collected from sites with female-biased sex ratios, supporting the notion that the costs of mate rejection have a major impact on the opportunity for sexual selection via mate choice.

Unlike relative processing times, Johnstone et al.'s (1996) models predicted that relative variances in mate quality would influence choosiness only when the differences were large. In our study, the differences in OSR between our treatments were much greater than were the difference in variation in female quality: OSR treatments were 3:1 female bias or all males, while our variance in female quality treatments only differed by a factor of 2. Nevertheless, the differences in OSR are representative of those seen in natural populations (Simmons and Bailey 1990; Gwynne et al. 1998) while those of variance in female quality are greater (Simmons and Bailey 1990; see also below). Although even greater differences between our treatments might have strengthened the observed effect of variance in female quality, increasing the difference would have been both biologically unrealistic, and physically impossible to do.

Our separation of variance in mate quality and OSR is an unnatural one. Field data show that both the mean and variance in female fecundity are affected by pollen availability (mean fecundity declines and variance in fecundity increases with food scarcity; Simmons and Bailey 1990). Male quality is similarly influenced by pollen availability, as are potential reproductive rates and the OSR (Gwynne and Simmons 1990; Simmons and Bailey 1990; Simmons 1992, 1995). In reality, all of these parameters are inextricably linked. Our experimental manipulations, however, are of heuristic value

because they have allowed us to identify the precise parameters that influence the intensity of male mate choice. In natural populations, males are more choosy of their mates, rejecting females of low fecundity when resources are limited (Simmons and Bailey 1990). It is possible to use the data from field-collected male and female *K. nartee* to predict the intensities of male mate choice expected, based on changes in the relative variances in quality and processing times of males and females with changing resource availability. Variance in female fecundity (number of eggs) increased from 6.81 to 9.18 across nutrient-rich and -poor habitats, respectively (from data in Fig. 5 of Simmons and Bailey 1990). Corresponding variances in male quality, based on the weight (mg) of the spermatophore-producing gland, were 2.07 and 12.32 (Fig. 6 of Simmons and Bailey 1990). Processing times for high and low pollen availability can be estimated from the relationships between time out and nutrient intake described by Simmons (1995). For a high nutrient intake (80 J/day) female processing time will be about 28 days compared with only 1.25 days for males. For a low nutrient intake, processing times are about 5.7 days for females compared with 7.2 days for males. Using these parameters in Johnstone et al.'s (1996) model predicts that 75% of encounters should lead to rejection in nutrient-rich environments and 86% in nutrient poor. Of these, less than 1% of rejections should result from male mate choice in nutrient-rich environments compared with 75% in nutrient-poor environments (R.A. Johnstone, personal communication). The observed proportion of mate rejections resulting from male choice in rich and poor environments was 26% and 90%, respectively (Simmons and Bailey 1990). These values suggest that Johnstone et al.'s models make qualitatively accurate predictions of the operation of sexual selection via mate choice. The quantitative deviation between observed and predicted percentage rejections by males in nutrient-rich environments may arise from unrealistic assumptions in the model, inaccurate parameter estimation from field populations, or both. One assumption of the models is that there is no cost to mate assessment which, in the case of *K. nartee*, may be erroneous. For example, for females, the cost of mate rejection in nutrient-poor environments will be high; females need the nutrients provided by males to produce eggs and are unlikely to find alternative males capable of supplying these nutrients. In contrast, males are unlikely to suffer costs of mate rejection, given the high availability of hungry females (Gwynne et al. 1998). Ignoring assessment costs for females could have the affect of overestimating female rejection frequencies, and thus underestimating the proportion of rejections due to males.

While the first experiment reported here examined the influence of variation in female quality on the opportunity for selection at a population level, our second experiment examined what effect an experience of variation in mate quality had on individual mating decisions. We expected individuals that had experienced a

low mean and variance in female quality to be relatively indiscriminate at the time of mating, since their perceived chances of encountering a better female would be low. Conversely, individuals that experienced a high mean and variance in female quality were expected to reject a mate of low quality because they would have had prior experience of superior-quality females. However, our results do not support these predictions: experience of variance in mate quality had no influence on male mate choice. These results are best explained by a simple threshold model for mate choice (Janetos 1980; Real 1990), although the results of our first experiment suggest that any such threshold may vary with the costs of mate rejection.

In conclusion, the results of our manipulations show that while variation in selection arising from mating competition appears to be controlled predominantly through variation in the OSR in *K. nartee* (Gwynne and Simmons 1990), variation in the opportunity for selection via male mate choice is dependent on an interaction between OSR and changes in the variance in mate quality that arise in nutrient-limited populations.

Acknowledgements We thank Kylie Shai-Gaull and Leah Beesley for superb help in field and laboratory, and Rufus Johnstone for kindly predicting rejection frequencies from his theoretical models. Comments by John Alcock, Darryl Gwynne, John Reynolds and two anonymous referees greatly improved the manuscript. Funding was provided from the Swedish Natural Science Research Council (C.K.), the Foundation of Knut & Alice Wallenberg (C.K.) and the Australian Research Council (L.W.S.).

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Communicated by J.D. Reynolds