Evolutionary Ecology Research, 2001, **3**: 667–686

Inequality of opportunity: measuring the potential for sexual selection

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ABSTRACT

The opportunity for selection (I) is defined as the variance in relative fitness and sets the upper limit for the intensity of selection on any given trait. For Poisson or binomial fitness variables such as mating success or survival, I is mathematically dependent upon both mean fitness and sample size. Covariation with both mean mating success ($\bar{x}$) and the number of individuals competing for mates (n) is typical of most indices of inequality (i.e. indices of spatial dispersion, resource monopolization and reproductive skew) and confounds comparisons among populations. Several standardized indices of inequality have been developed that remove the confounding influence of $\bar{x}$ and n. We assessed the utility of these standardized indices as measures of the potential for sexual selection on male mealworm beetles. Specifically, we compared the opportunity for sexual selection (I_s) with the index of resource monopolization (Q), Morisita's index (I_δ) and the standardized Morisita index (I_p). We estimated male mating success from repeated scan samples in two separate experiments. Experiment 1 comprised nine treatments with all combinations of 10, 20 or 30 males and females, replicated three times for a total of 27 populations. Experiment 2 consisted of five populations with 10 males and 10, 20, 25, 30 or 35 females respectively. As expected, we found I_s to be negatively correlated with mean mating success and positively correlated with both number of males and sex ratio. In contrast, the indices of inequality increased as the sex ratio moved away from 1:1 in either direction, and reached maximum values at strongly female-biased sex ratios. We hypothesize that this concave relationship reflects a shift in the relative importance of female choice and male–male competition at female-biased versus male-biased sex ratios. We compare the properties of all four indices and recommend Morisita's index as the best estimator of the potential for sexual selection.

Keywords: mating success, Morisita's index of dispersion, opportunity for selection, relative fitness, resource monopolization, sexual selection, *Tenebrio molitor*.

INTRODUCTION

Natural selection can be defined most simply as a consistent relationship between phenotype and fitness (Futuyma, 1998; Fairbairn and Reeve, in press). Variance in fitness is,

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therefore, a prerequisite for adaptive evolution, a concept codified as Fisher's fundamental theorem of natural selection (Falconer, 1989; Hedrick, 2000). Because of its importance as a measure of the potential for adaptive evolution, the variance in relative fitness (I) is a standard parameter in evolutionary theory (Walsh and Lynch, in press). Although originally called the 'index of total selection' (Crow, 1958), it is now more generally known as the 'opportunity for selection' (Wade, 1979; Arnold and Wade, 1984; Bradbury and Andersson, 1987; Walsh and Lynch, in press). Formally, I sets the upper limit for the intensity of selection (i) on any given trait and $i = I$ if the trait is perfectly correlated with fitness.

The opportunity for sexual selection (I_s) is frequently used to quantify expected differences in the intensity of sexual selection between males and females or among males in different mating systems (Wade, 1979, 1995; Wade and Arnold, 1980; Bradbury and Andersson, 1987; Andersson, 1994; Arnold and Duvall, 1994; Webster *et al.*, 1995). However, such comparisons are problematic because the expected value of I_s depends upon both mean mating success ($\bar{x}$) and the number of individuals competing for mates (n) (Table 1). Dependence on $\bar{x}$ derives from the expected covariation between the mean and variance for Poisson or binomial variables (Downhower *et al.*, 1987; Ruzzante *et al.*, 1996; Walsh and Lynch, in press). For example, Downhower *et al.* (1987) showed that, if the number of mates per male follows a Poisson distribution, I_s reduces to $s^2/\bar{x}^2 = \bar{x}/\bar{x}^2 = \bar{x}^{-1}$, where s^2 is the variance of number of mates per male. Thus, I_s is inversely dependent on mean mating success. Walsh and Lynch (in press) provide a similar analysis for binomial variables (such as mating/not mating). In addition, the expected variance in mating success, $E(\sigma^2)$, is a positive function of both $\bar{x}$ and n, reaching a maximum of $n(\mu^2)$ when one male acquires all of the matings (Ruzzante *et al.*, 1996). Thus, the maximum value that I_s can attain equals n

Table 1. The influence of the distribution of mating success (i.e. number of mates per male), number of males competing for mates ($n = 10$ or 30) and mean mating success ($\bar{x} = 1$ or 3) on the opportunity for selection (I_s), the index of monopolization (Q), Morisita's index of dispersion (I_δ) and the standardized Morisita index (I_p)

		$n = 10$			$n = 30$		
$\bar{x}$	Parameter	Uniform	Poisson	Maximally contagious	Uniform	Poisson	Maximally contagious
1	s^2	0	1	10	0	1	30
	I_s	0	1	10	0	1	30
	Q	−0.11	0	1	−0.03	0	1
	I_δ	0	1	10	0	1	30
	I_p	−1	0	1	−1	0	1
3	s^2	0	3	90	0	3	270
	I_s	0	0.33	10	0	0.33	30
	Q	−0.03	0	1	−0.01	0	1
	I_δ	0.69	1	10	0.67	1	30
	I_p	−1	0	1	−1	0	1

Note: Minimum values are expected when all males have equal mating success (the uniform distribution). Maximum values are expected when one male monopolizes all the mates (the maximally contagious distribution). The Poisson distribution represents a random distribution of mates among competing males. The variance in mating success (s^2) is shown for comparison.

(Table 1; Ruzzante *et al.*, 1996; Kokko *et al.*, 1999). This property of covariation with both the mean and the sample size is typical of most indices of inequality (i.e. indices of spatial dispersion, resource monopolization and reproductive skew) and confounds comparisons among populations (Ruzzante *et al.*, 1996; Tsuji and Tsuji, 1998; Kokko *et al.*, 1999; Krebs, 1999).

In response to these problems, Ruzzante *et al.* (1996) derived an index of inequality called the 'index of resource monopolization':

$$Q = \frac{(s^2 - \bar{x})}{(n\bar{x}^2 - \bar{x})} \tag{1}$$

This index is also known as Green's F, having been independently derived by Green (1966) as a coefficient of spatial dispersion (Kokko *et al.*, 1999; Krebs, 1999). The advantage of Q is that the observed variance among competitors is expressed as a fraction of the maximum possible variance $[n(\mu^2)]$ and both are corrected by the variance expected if the resources are randomly distributed ($\sigma^2 = \mu^2$). Thus, $Q = 0$ when the resources are distributed randomly among competitors and $Q = 1$ when one competitor acquires all the resources (Table 1). Under these conditions, Q is independent of mean resource abundance and less dependent on the number of competitors than most other indices of inequality (Myers, 1978; Ruzzante *et al.*, 1996; Kokko *et al.*, 1999). However, when resources are underdispersed, Q becomes negative and less predictable (Table 1; Ruzzante *et al.*, 1996). Its lower limit when the distribution is uniform is $-1/(n\bar{x} - 1)$ and thus depends on both the mean resource abundance and the number of competitors. These problems are relatively minor in assessments of sexual selection because mating success is expected to be contagiously distributed (overdispersed). For example, Blanckenhorn *et al.* (1998) successfully used Q to measure monopolization of mates by male waterstriders competing in a resource queue.

Morisita's (1962) index of dispersion

$$I_\delta = n\left[\frac{\Sigma x^2 - \Sigma x}{(\Sigma x)^2 - \Sigma x}\right] \tag{2}$$

has much in common with Q and has been widely applied in studies of spatial dispersion (e.g. Smith-Gill, 1975; Myers, 1978; Krebs, 1999). Like Q, I_δ is standardized to the Poisson distribution [$E(I_\delta) = 1$ for a random distribution, < 1 for underdispersed distributions and >1 for overdispersed distributions] and is expected to be independent of $\bar{x}$ when resources are contagiously distributed (Morisita, 1962; Myers, 1978; Tsuji and Tsuji, 1998; Kokko *et al.*, 1999). When matings are uniformly distributed, I_δ, like Q, becomes dependent on both $\bar{x}$ and n, reaching a minimum of $1 - (n - 1)/((\Sigma x) - 1)$ (Table 1; Kokko *et al.*, 1999). However, unlike Q, I_δ does not express the degree of inequality relative to the maximum possible if one individual monopolizes all resources. When one male monopolizes all the matings, $I_\delta = n = I_s$ (Table 1; Tsuji and Tsuji, 1998; Kokko *et al.*, 1999). This latter property may produce notable differences in the patterns detected by Q and I_δ when the number of males differs among populations (Kokko *et al.*, 1999).

Although the expected value of I_δ is independent of $\bar{x}$ for $I_\delta > 1$, its confidence limits decline as $\bar{x}$ increases (Smith-Gill, 1975), a property it shares with Q (Ruzzante *et al.*, 1996). Smith-Gill (1975) derived a series of transformations to remove this effect and standardize the 95% confidence limits to ± 0.5 across all values of $\bar{x}$. The resulting values are transformed to a common scale ranging from +1 when one individual acquires all the resources to −1 when resources are uniformly distributed (Table 1). A Poisson distribution yields a value of 0. This 'standardized Morisita index', I_p, has been recommended by several authors for comparisons among populations differing in mean resource abundance (Smith-Gill, 1975; Myers, 1978; Krebs, 1999). However, Tsuji and Tsuji (1998) point out that such comparisons may be compromised because the standardization leads to a positive correlation between I_p and $\bar{x}$ when resources are contagiously distributed, a result confirmed by Kokko *et al.* (1999). We predict additional problems if comparisons are made among populations that differ in resource distribution, because the particular transformation applied depends upon the resource distribution (Smith-Gill, 1975; Tsuji and Tsuji, 1998; Krebs, 1999). For example, if resources are randomly distributed in one population and contagiously distributed in another, transformation of I_δ to I_p will involve a different algorithm in each population. Subsequent statistical comparisons of the two populations are therefore not valid, although both can be independently compared to an expected value of zero, using the 95% confidence limits. Given these problems, the standardized Morisita index would appear appropriate only for comparisons among populations with a similar degree of contagion and similar mean resource abundance. Nevertheless, Krebs (1999, pp. 216–217) calls it 'the best [index of dispersion] currently available', and recommends it specifically for use when $\bar{x}$ or n varies among the populations.

Following Kokko *et al.* (1999), we refer to Q, I_δ and I_p as indices of inequality. All share the property of expressing the degree of dispersion of mating success relative to the Poisson (random) distribution expected under the null model of equal mate acquisition propensities. In contrast, the null model for the opportunity for selection, I_s, is equality of realized mating success: the variance among males will be zero only when all males acquire the same number of mates. (Recall that, if mating *propensities* are equal, the expected distribution of realized mating success follows a Poisson distribution and the expected value of I_s is $\bar{x}^{-1}$.) Thus, correcting for the inherent statistical biases in I_s by using Q, I_δ and I_p alters the mathematical and biological interpretation of the resulting analyses. Furthermore, these 'corrected' indices have no precise, quantitative interpretation with respect to the expected intensity of sexual selection and so cannot be readily integrated with quantitative genetic theory. Because of this, I_s cannot simply be replaced with Q, I_δ, I_p, or any other index of inequality.

The aim of the present study was to explore these problems by comparing the performance of I_s, Q, I_δ and I_p when used as measures of the potential for sexual selection among male mealworm beetles, *Tenebrio molitor* (Coleoptera: Tenebrionidae). We manipulated the expected distribution of mating success and thus $E(I_s)$ by varying the operational sex ratio and the population density. Support for the hypothesis that I_s should covary with the operational sex ratio and density comes from theoretical considerations (e.g. Emlen and Oring, 1977; Ims, 1988; Clutton-Brock and Parker, 1992), comparative studies of the intensity of sexual selection on specific traits (e.g. Conner, 1989; Hoglund, 1989; Arnqvist, 1992; Krupa and Sih, 1993) and direct observations of changes in mating behaviour or I_s with density or operational sex ratio (e.g. Murray, 1987; Hoglund, 1989; Souroukis and Murray, 1995; Coltman *et al.*, 1999; Kvarnemo and Simmons, 1999). The strongest evidence for causative relationships (as opposed to correlations) comes from direct observations of changes in I_s, the variance in male mating success, or the intensity of sexual selection in response to manipulations of operational sex ratio, density or both (e.g. Thornhill and Alcock, 1983; Souroukis and Cade, 1993; Fleming and Gross, 1994; Grant *et al.*, 1995).

We report the results of two experiments in which we varied the numbers of males and females in laboratory populations of *T. molitor* to characterize the relationship between the opportunity for sexual selection on males (I_s) and (1) number of males, (2) operational sex ratio and (3) density. Comparisons of I_s among these populations are expected to be seriously confounded by differences in both $\bar{x}$ and n. We therefore assessed the degree of inequality in mating success using the three 'corrected' indices: Q, I_δ and I_p. Quantitative and qualitative differences in the patterns revealed by these four indices provide new insights into the relationship between the classic index of opportunity for selection and the true probability of a consistent relationship between phenotype and fitness (i.e. the potential for sexual selection).

METHODS

Estimating the indices

The opportunity for selection, defined as the variance in relative fitness (σ_w^2), is algebraically equivalent to the square of the coefficient of variation of absolute fitness:

$$I = \frac{\sigma_W^2}{\mu_W^2} = CV_W^2 \tag{3}$$

(Crow, 1958; Wade and Arnold, 1980; Arnold and Wade, 1984; Walsh and Lynch, in press). We therefore estimated the opportunity for sexual selection as

$$I_s = \frac{s^2}{\bar{x}^2} = CV^2 \tag{4}$$

where $\bar{x}$ and s^2 are the mean and variance of the number of observed matings per male within each experimental population.

We estimated Q and I_δ according to equations (1) and (2) respectively. The standardized Morisita index, I_p, was calculated using the transformations specified in Smith-Gill (1975) and Krebs (1999).

Study animal

Adult mealworm beetles are approximately 1.5 cm long and show little sexual dimorphism (Bousquet, 1990). The mating system is polygynandrous, both sexes mating many times during the 2–3 month adult stage. Female beetles release pheromones that elicit a sexual response from males (Happ and Wheeler, 1969) and males actively compete for matings. Copulation typically lasts only 1.5–2.5 min. Chitinous spines on the sheath of the male penis may serve as 'anchors' during copulation, as a defence against displacement by rival males (Siva-Jothy *et al.*, 1996). After insemination, males may guard females by remaining on or very close to them for up to 30 min (Gage and Baker, 1991; personal observations). Mating males also emit an inhibitory pheromone, rendering their mates less appealing to other males (Happ, 1969). In the presence of other males, *T. molitor* males initiate mating faster, produce more sperm per ejaculate and are more apt to exhibit post-copulatory guarding than when alone (Gage and Baker, 1991). Females also alter their mating behaviour in response to males. As in other polygynandrous species, female *T.*

molitor are less reluctant to mate and less discriminatory when the sex ratio is male-biased than when it is even (Gage and Baker, 1991). They also modulate their pheromone release in response to sex ratio and density, releasing more pheromones with increasing female density (Happ and Wheeler, 1969). These behaviours of *T. molitor* suggest that males are subject to sexual selection through both female choice and male–male competition, and that the intensity of this selection should be sensitive to both density and the operational sex ratio.

Experimental design

All observations were based on adult, post-teneral *T. molitor* sampled haphazardly from a laboratory colony of 1000–2000 individuals. The colony was maintained at room temperature under subdued natural lighting, in plastic cages containing bran to a depth of 2.5 cm with thin slices of potato on top of the bran. All animals were in at least their fourth day of adult life (i.e. ≥ 72 h post-eclosion) at the start of each experiment. Maximum ages (post-eclosion) were 6 days and 10 days for the first and second replicates of Experiment 1 respectively. We did not control for maximum age in replicate 3 or Experiment 2, but animals with detectable elytral wear were not used. [Strong similarities among replicates and between experiments (see below) indicated that controlling for age had no detectable influence on the assayed mating parameters.] All males used in the experiments were marked by painting numbers on their elytra using enamel paint.

Experiment 1 consisted of nine treatments representing all possible combinations of males and females at densities of 10, 20 or 30 for each sex. The operational sex ratio thus ranged from 0.33 to 3.0 and total densities ranged from 20 to 60 individuals. For each replicate, we sampled 180 adults of each sex and assigned each individual at random to one of the nine experimental treatments. We placed each of the resulting nine populations in a large opaque plastic box (37 × 48 × 20 cm). A thin layer of bran (about 2 mm) and slices of raw potato provided food, moisture, cover and oviposition sites within each box. The populations were kept under subdued natural lighting, at 24 ± 2°C, and left undisturbed for 17–22 h before initiation of scan sampling. To facilitate scan sampling, we removed the potato slices at the onset of the photophase and replaced them at the end of the final observation period.

We replicated the nine treatments in three randomized blocks between December 1998 and January 1999, with the treatments in each block synchronous in time. Within each block, the treatment positions were randomized to control for possible confounding effects of light and heat gradients within the room.

To record mating activity, we scanned the populations a minimum of five times per day for at least 3 days, resulting in a total of 23, 16 and 19 scans for replicates 1, 2 and 3 respectively. All scans were made at least 1 h after the onset of the photophase, and we allowed at least 45 min between scans to ensure independence of the observed matings. Each scan consisted of a 30 s observation of the population during which we recorded the identification numbers of all mating males. We defined all males mounted on the backs of females in the mating position as ‘mating’, even if the genitalia were not actually engaged at the time of sampling.

Experiment 2 was conducted in May 1999 to verify our observations of a strong effect of an extreme female-biased operational sex ratio in Experiment 1 (see Results). We maintained male density at 10 and set up five treatments (one population per treatment) with female densities of 10, 20, 25, 30 and 35. The operational sex ratio thus ranged from 1 to

0.29. Husbandry and observational methods were as in Experiment 1, with the exception that the populations were housed in a growth chamber with 14L:10D at 23°C.

Statistical analyses

All statistical tests were performed using SPSS 8.0. Of the four indices used, only Q is expected to be normally distributed (Smith-Gill, 1975; Ruzzante *et al.*, 1996; Kokko *et al.*, 1999). We therefore used caution in applying parametrical statistical methods. Unless otherwise indicated, the data did not deviate significantly from the assumptions of the parametric statistical analyses used. Nevertheless, we applied both parametric and non-parametric methods whenever possible. The two methods invariably yielded almost identical results; in such cases, we report only the parametric analyses. As an additional precaution, we tested hypotheses using the treatment means. By the Central Limit Theorem, mean values can be expected to be normally distributed even if the underlying variable is not (Sokal and Rohlf, 1995).

RESULTS

Experiment 1

The 27 experimental populations displayed a high degree of variation in mating success both within and among populations. The mean number of mates per male varied from 0.67 to 2.50 with a mean ± standard deviation of 1.4 ± 0.5, and the within-population variance varied from 0.48 to 3.39. Neither the among-population nor the within-population variances differed significantly among the three replicates (among-population: Levene statistic = 0.04, d.f. = 2, $P = 0.96$; within-population: Kruskal-Wallis ANOVA: $\chi^2 = 3.090$, d.f. = 2, $P = 0.213$). On average, 7.4 ± 2.5% of males were mating per scan, and the mean proportion mating per scan also did not differ significantly among the three replicates (Kruskal-Wallis ANOVA: $\chi^2 = 2.142$, d.f. = 2, $P = 0.343$). Because the three replicates were so similar (all $P > 0.2$), we analysed the treatment effects without including a blocking variable.

All four indices varied greatly among our 27 test populations ($I_s = 0.31$ to 2.13; $Q = -0.026$ to 0.099; $I_\delta = 0.52$ to 1.90; $I_p = -0.39$ to 0.52), although the observed ranges were considerably less than the theoretical maximum ranges illustrated in Table 1. The three indices of inequality had values both above and below the values expected for a random distribution of mating success, indicating that the populations varied in the degree of contagion, with some tending towards a more uniform distribution of matings and others towards a contagious distribution. However, 19 of the 27 populations had values above the expected for a random distribution, indicating a general tendency for mating success to be overdispersed (binomial test: $P_{\text{one-tailed}} = 0.05$). This is consistent with our expectation of sexual selection within these populations. Two of the populations (both from the 10 male: 30 female treatment) showed statistically significant contagion by the criterion of having the 95% confidence interval of I_p (± 0.5) not overlap 0.

As expected (Downhower *et al.*, 1987; Ruzzante *et al.*, 1996), the mean and variance in mating success were highly correlated among populations ($r_{25} = 0.71$, $P < 0.001$); I_s, therefore, was strongly negatively correlated with mean mating success (Table 2). Also as expected, I_s was strongly positively correlated with the number of males (Table 2). However, these patterns are not evident for the indices of inequality: Q, I_δ and I_p were not significantly correlated with mean mating success or number of males, and the direction of the relationships was opposite to those for I_s. We did not detect the expected dependence of I_δ on n, perhaps because our observed values were well below the theoretical maxima (Table 1). All three indices of inequality were highly positively correlated with the variance in mating success, while this correlation was weak and negative for I_s (Table 2). Thus, use of any of the indices of inequality removed the presumed biases caused by variation among populations in the number of competitors and mean mating success while retaining the pattern of variation among populations in the variance in mating success.

The three indices of inequality were highly correlated with each other, but only weakly correlated with I_s (Table 3). The correlations between I_s and the indices of inequality became significant when the effect of either number of males or mean mating success was held constant (Table 4), suggesting that the initial disparity was caused by the strong correlation of I_s with these variables.

The strong effects of $\bar{x}$ and n on I_s were also evident in the pattern of treatment effects (Fig. 1). Factorial analysis of variance (ANOVA) for I_s indicated a significant effect of number of males, but not of number of females or of the interaction between male and female numbers (Table 5). Mean mating success showed the same pattern of statistical

Table 2. Pearson product–moment correlation coefficients for correlations of indices of opportunity for sexual selection (I_s) and inequality (Q, I_δ and I_p) with the mean and variance in male mating success ($\bar{x}$, s^2), the number of males per population (n), the proportion males per population and the total density (N) for the 27 populations in Experiment 1

Index	$\bar{x}$	n	s^2	P(male)	N
I_s	–0.75***	0.54**	–0.37$^+$	0.51**	0.24
Q	0.21	–0.34$^+$	0.80***	–0.42*	–0.05
I_δ	0.12	–0.15	0.67***	–0.16	–0.06
I_p	0.12	–0.07	0.65***	–0.09	–0.02

Note: Statistical probabilities are indicated by superscripts as follows: $^+P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. All probabilities are two-tailed and not corrected for multiple comparisons.

Table 3. Pearson product–moment correlations among opportunity for sexual selection (I_s) and indices of inequality (Q, I_δ and I_p)

	I_s	Q	I_δ	I_p
I_s	–	0.12	0.35	0.37
Q	0.50*	–	0.88***	0.77***
I_δ	0.50*	1.00***	–	0.94***
I_p	0.37*	0.91***	0.91***	–

Note: Values above the diagonal are for the 27 populations in Experiment 1. Values below the diagonal are for the 14 populations with 10 males from Experiments 1 and 2 combined. The associated statistical probabilities are indicated by superscripts as follows: $^+P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. All probabilities are one-tailed and not corrected for multiple comparisons.

Table 4. Partial correlations between the opportunity for sexual selection (I_s) and the indices of inequality (Q, I_δ and I_p) with the effect of mean mating success ($\bar{x}$), number of males (n) or both held constant

	Partial correlation coefficient for I_s with:		
Variables held constant	Q	I_δ	I_p
$\bar{x}$	0.42*	0.67***	0.71***
n	0.38*	0.52**	0.48**
$\bar{x}$ and n	0.46**	0.68***	0.71***

Note: Data are for the 27 populations in Experiment 1. The associated statistical probabilities are indicated by superscripts as follows: $^{+}P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. All probabilities are one-tailed and not corrected for multiple comparisons.

Table 5. Results of factorial analyses of variance to detect the effects of number of males and number of females on mean mating success ($\bar{x}$), opportunity for sexual selection (I_s) and three indices of inequality (Q, I_δ and I_p) in Experiment 1

	Source of variance					
	Number of males		Number of females		Interaction	
Variable	$F_{2,18}$	P	$F_{2,18}$	P	$F_{4,18}$	P
$\bar{x}$	8.052	0.003	0.577	0.571	0.200	0.935
I_s	5.690	0.012	0.865	0.438	1.046	0.411
Q	3.512	0.576	1.951	0.171	4.545	0.010
I_δ	0.568	0.576	0.115	0.892	2.583	0.072
I_p	0.153	0.860	0.031	0.970	1.520	0.328

significance (Table 5), but was negatively rather than positively correlated with number of males ($r_{25} = -0.66$, $P < 0.001$). Thus, populations with relatively few males were characterized by high mean mating success and low opportunity for sexual selection, whereas populations with high numbers of males showed the opposite pattern.

As expected, given its relationship with number of males, I_s was positively correlated with proportion male (Table 2; $r_7 = 0.72$, $P = 0.03$ for treatment means). Regression analysis suggested a slight concavity in the relationship (Fig. 2), with I_s increasing slightly at the lowest proportion male (the 10:30 treatment). However, although the quadratic model described the data better than a strictly linear model ($I_s = 0.286 + 1.256x$; $F_{1,7} = 7.664$, $P = 0.028$, $R^2 = 0.52$), the improvement in the R^2 was not statistically significant ($F_{1,6} = 4.124$, $P = 0.089$). Thus, the evidence for non-linearity in the relationship is weak, and the dominant tendency was a general positive correlation.

To determine the relative influence of the operational sex ratio and absolute number of males on I_s, we performed a partial correlation analysis of I_s with number of males and proportion male. Although neither variable correlated significantly with I_s when controlling for the effect of the other (all $P \geq 0.14$), the partial correlation for number of males was

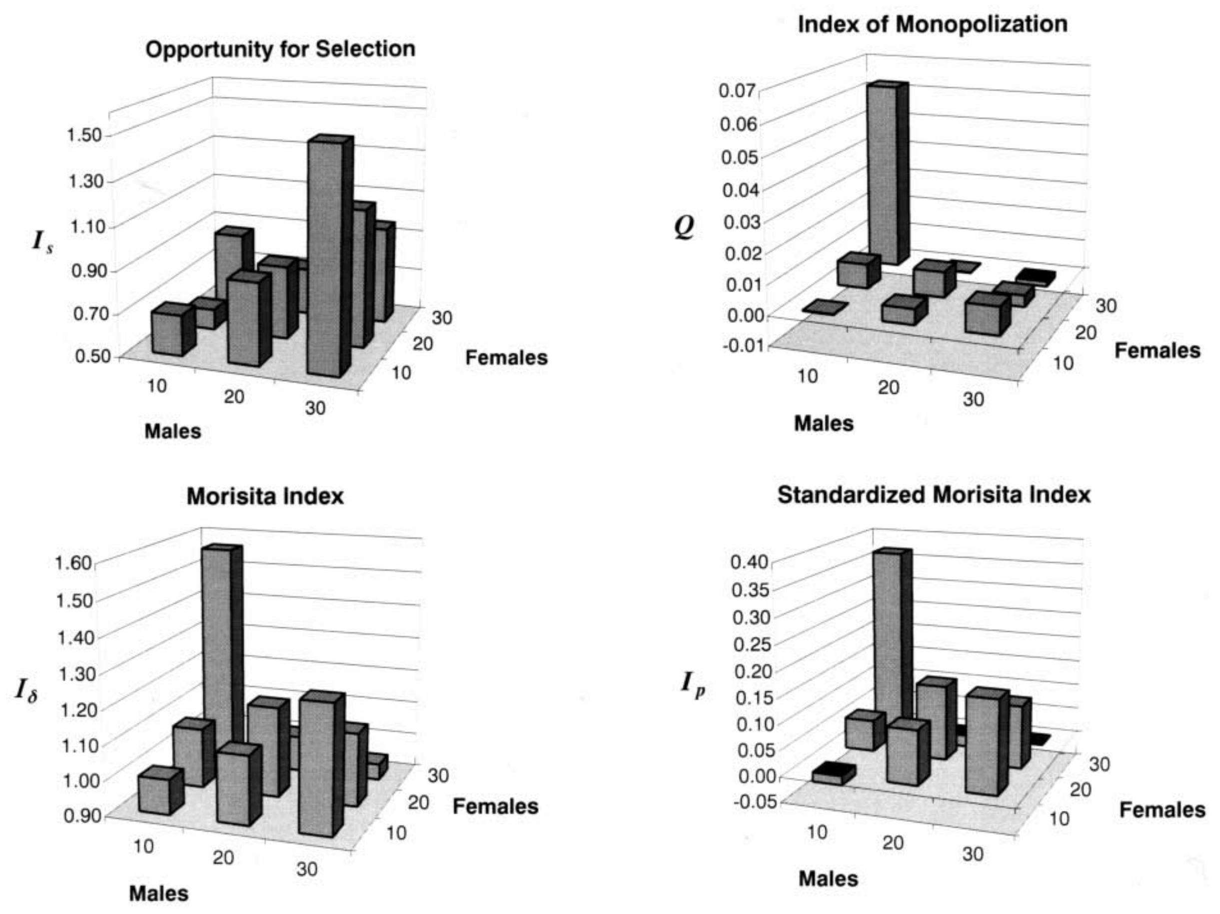

Fig. 1. Opportunity for selection (I_s), index of monopolization (Q), Morisita's index of dispersion (I_δ) and the standardized Morisita index (I_p) plotted against the numbers of males and females in each of the nine treatments in Experiment 1. Each bar represents the mean of three replicates. Note that the bar extends below the plane of the origin (i.e. the mean is negative) for Q in the 30:30 treatment and for I_p in the 10:10, 20:30 and 30:30 treatments.

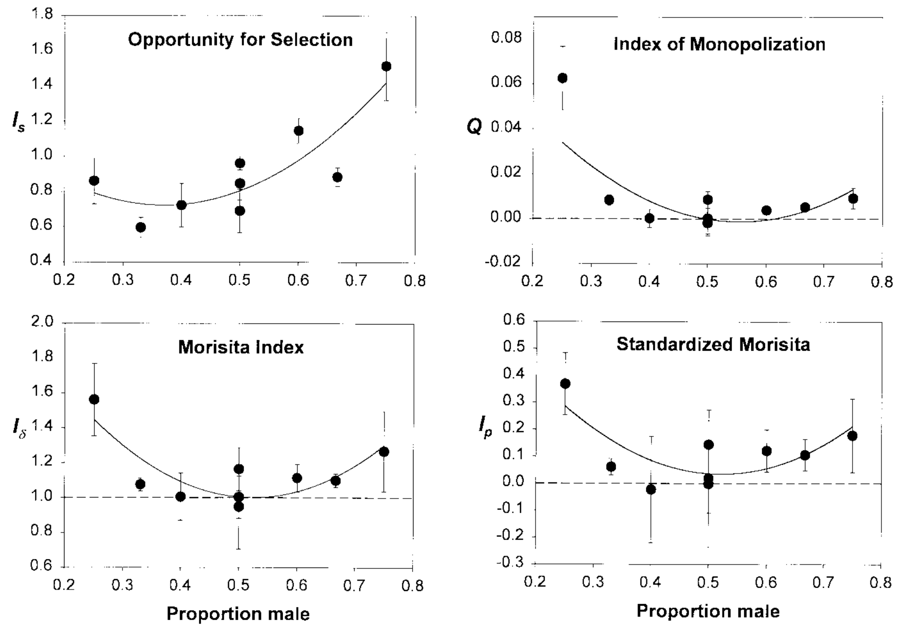

Fig. 2. Opportunity for selection (I_s), index of monopolization (Q), Morisita's index of dispersion (I_δ) and the standardized Morisita index (I_p) plotted against proportion male for the nine treatments in Experiment 1. Each point represents the mean of three replicate populations. The vertical bars represent ± 1 standard error. Quadratic regressions based on treatment means are drawn through each data set:

$$I_s = 1.383 - 3.568x + 4.824x^2;\ F_{2,6} = 7.604,\ P = 0.023,\ R^2 = 0.72$$
$$Q = 0.166 - 0.063x + 0.536x^2;\ F_{2,6} = 9.116,\ P = 0.015,\ R^2 = 0.75$$
$$I_\delta = 2.628 - 6.205x + 5.912x^2;\ F_{2,6} = 7.336,\ P = 0.025,\ R^2 = 0.71$$
$$I_p = 0.960 - 3.544x + 3.394x^2;\ F_{2,6} = 4.854,\ P = 0.056,\ R^2 = 0.62$$

slightly higher than that for proportion male, both overall (0.30 *vs* 0.22) and when comparisons were made among treatment means (0.53 *vs* 0.41). These results, combined with the absence of a significant interaction term in the ANOVA (Table 5), indicate that the number of males was the stronger determinant of opportunity for selection.

In contrast to I_s, Q was not significantly correlated with number of males (Tables 2 and 5), and the pattern of variation among treatments was dominated by very high values in the 10:30 treatment (Fig. 1). Among the remaining treatments, the effect of number of males clearly depended on the number of females. For example, as number of males increased (left to right in Fig. 1), Q increased when only 10 females were present (front row) but decreased when 30 females were present (back row). This complex relationship was detected statistically as a significant interaction between numbers of males and females in the absence of significant main effects (Table 5). [We found significant heteroscedasticity among treatments for Q (Levene's test: $F_{8,18} = 2.867$, $P = 0.03$). Removing a single outlier corrected this (Levene's test: $F_{8,18} = 2.125$, $P = 0.09$) and gave similar results: the main effects of male and female numbers remained non-significant ($P = 0.129$ and 0.433), while the interaction term remained significant ($F_{4,18} = 3.418$, $P = 0.030$).]

The significant interaction term in the absence of significant main effects suggests that Q was influenced primarily by the operational sex ratio rather than by the absolute density of either sex. Indeed, Q was negatively correlated with proportion male (Table 2). However, this negative relationship was caused by the very high values in the 10:30 treatment and disappeared when this treatment was removed ($r_{22} = 0.10$, $P = 0.66$). Quadratic regression suggests a concave relationship between Q and proportion male (Fig. 2; improvement over the linear model: $F_{1,6} = 11.314$, $P = 0.015$). Correcting for heteroscedasticity by removing the outlier, as above, resulted in a very similar regression model: $Q_s = 0.115 - 0.419x + 0.378x^2$ ($F_{2,6} = 9.725$, $P = 0.013$, $R^2 = 0.76$). Thus, the relationship between Q and the operational sex ratio was concave and characterized mainly by an unexpected and dramatic increase in Q when the sex ratio became strongly female-biased.

The overall patterns for Morisita's index and its standardized form were intermediate between the patterns for I_s and Q in that high values occurred in both the 10:30 and the 30:10 treatments (Fig. 1). The strong positive correlation with number of males that dominated the distribution of I_s was absent for I_δ and I_p (Tables 2 and 5). Inspection of Fig. 1 suggests the same pattern of interaction between numbers of males and females that occurred for Q, but this was not detected as a significant interaction in the ANOVA (Table 5). Nor did it produce a significant linear correlation with proportion male (Table 2; linear regression statistics for treatment means: $F_{1,7} = 0.470$, $P = 0.52$ for I_δ and $F_{1,7} = 0.323$, $P = 0.59$ for I_p). However, the quadratic regression of the treatment means on proportion male was statistically significant for I_δ and very close to being significant for I_p (Fig. 2). The lack of a linear trend in the presence of a significant quadratic relationship results from the apparent symmetry of the concave function around the central minimum (Fig. 2). The Morisita indices thus suggest that contagion in mating success increases as the sex ratio moves away from 1:1 in either direction.

In contrast to the effects of the operational sex ratio, total density had little effect on any of the indices. None were significantly correlated with total density over all 27 populations (Table 2) or when using only the nine treatment means ($r_7 = 0.34$, −0.6, 0.03 and −0.09 for I_s, Q, I_δ and I_p respectively; all $P > 0.36$). Removing the confounding effect of sex ratio by considering only the nine populations with an operational sex ratio = 1.0 did not improve these results ($r_7 = 0.44$, −0.06, 0.03 and −0.09 for I_s, Q, I_δ and I_p respectively; all $P > 0.23$). Similar results were obtained for partial correlations with the effect of sex ratio held constant ($r_{\text{indexdensity}.p(\text{male})} = 0.28$, −0.06, −0.06 and −0.01 for I_s, Q, I_δ and I_p respectively; all $P > 0.16$). Quadratic regression models were also not significant for any of the indices ($F_{2,24} = 1.310$, 1.916, 2.560 and 1.684 for I_s, Q, I_δ and I_p respectively; all $P > 0.10$). Correcting for heteroscedasticity by removing the outlier for Q did not change these conclusions. Thus, both the opportunity for selection and the degree of inequality in mating success were independent of total density.

Experiment 2

Comparisons among the five populations in Experiment 2 suggested a general decrease in all four indices as proportion male increased (Fig. 3). The contagion was statistically significant (indicated by $I_p > 0.5$) for the populations with 30 and 35 females (proportion male = 0.25 and 0.22). Covariance analysis revealed no difference between experiments in the relationship between index value and proportion male for populations with 10 males (all $P > 0.40$). We therefore combined the two data sets and looked for trends among all

14 populations (Fig. 3). Neither linear nor quadratic models were significant for I_s. However, both models were significant for Q and I_δ. The quadratic model gave a slightly better fit but the model improvement was not quite statistically significant ($F_{1,11} = 4.437$, $P = 0.059$ for Q; $F_{1,11} = 4.418$, $P = 0.059$ for I_δ). The overall trend, therefore, was negative and slightly concave. The standardized Morisitia index, I_p, showed a much weaker relationship (Fig. 3) and the quadratic model was not statistically significant ($R^2 = 0.38$, $F_{2,11} = 3.418$, $P = 0.070$).

These results confirm several trends suggested by the analysis of the full data set from Experiment 1. As in Experiment 1, all of the indices tended to increase as the operational sex ratio moved from unity to strongly female-biased, and the indices of inequality confirmed significant contagion in mating success when the proportion male was ≤ 0.25. The curvature in this relationship was also confirmed: the effect of the operational sex ratio

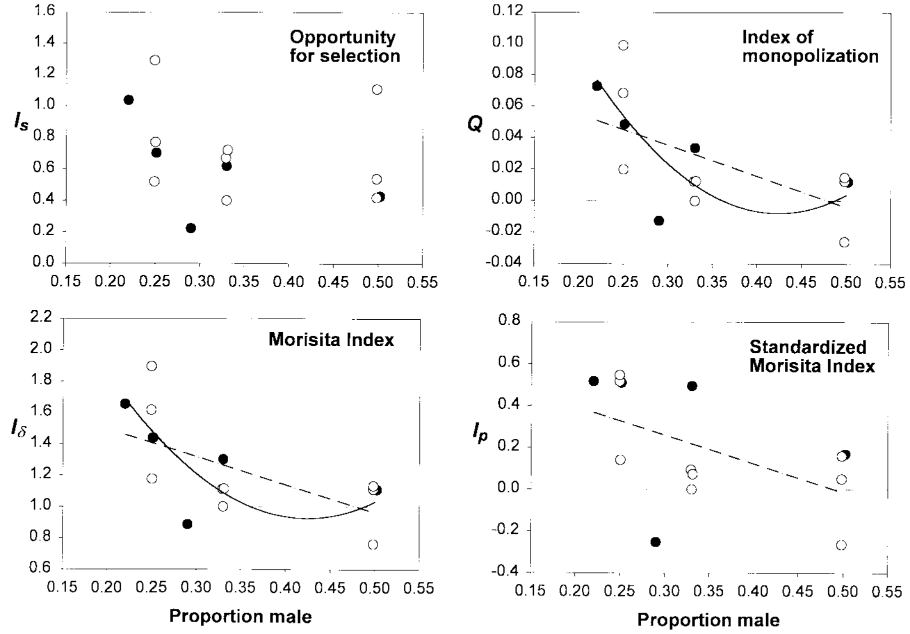

Fig. 3. Opportunity for selection (I_s), index of monopolization (Q), Morisita's index of dispersion (I_δ) and the standardized Morisita index (I_p) plotted against proportion male for the five populations in Experiment 2 (●) and the nine populations with 10 males in Experiment 1 (○). Neither linear nor quadratic regression models are significant for I_s ($P > 0.27$). For the other indices, linear and quadratic regression models are shown as dot-and-dashed and solid lines respectively. The linear regression solutions are:

$$Q = 0.094 - 0.197x;\ F_{1,12} = 7.192,\ P = 0.020,\ R^2 = 0.38$$
$$I_\delta = 1.851 - 1.778x;\ F_{1,12} = 7.181,\ P = 0.020,\ R^2 = 0.37$$
$$I_p = 0.671 - 1.372x;\ F_{1,12} = 4.651,\ P = 0.052,\ R^2 = 0.28$$

The significant quadratic models are:

$$Q = 0.357 - 1.721x + 2.029x^2;\ F_{2,11} = 6.845,\ P = 0.012,\ R^2 = 0.55$$
$$I_\delta = 4.215 - 15.507x + 18.282x^2;\ F_{2,11} = 6.823,\ P = 0.012,\ R^2 = 0.47$$

increased with increasing female-bias. Finally, as in Experiment 1, these patterns were not detected equally by the four indices. Both the effect of female-biased operational sex ratio and the curvature in the relationship were most evident for Q, followed closely by I_{δ}. Standardization of the Morisita index weakened this relationship, and the opportunity for selection was relatively insensitive to variation in female-biased operational sex ratio.

Despite these differences in sensitivity, correlations among the three indices of inequality were very high and statistically significant for the populations with 10 males (Table 3). The correlations between I_s and the three indices of inequality were also significant and somewhat stronger than in Experiment 1 (Table 3). This is consistent with the results of our previous partial correlation analysis, which indicated that I_s covaried with the other indices when the number of males was held constant. However, as in Experiment 1, the three indices of inequality were more highly correlated with each other than any was with opportunity for selection. Neither number of males nor mean mating success differed among the populations in Experiment 2 (Kruskal-Wallis ANOVA for mating success: $\chi^2 = 0.895$, d.f. = 4, $P = 0.925$), and thus the disparity between I_s and the indices of inequality cannot be attributed to these confounding variables. The pattern of variation detected as opportunity for selection appears to differ fundamentally from the pattern detected by the indices of inequality. In particular, I_s appears to be relatively insensitive to variation in degree of contagion in mating success when the sex ratio is female-biased.

DISCUSSION

We found significant variation among our populations in both the opportunity for sexual selection and the degree of inequality in mating success. The indices of inequality indicated that male mating success tended to be slightly overdispersed in most populations. Thus, some males achieved more matings than would be expected by chance if mating propensities were equal, while others obtained fewer than expected. The degree of contagion varied significantly among the treatments, but generally increased as the sex ratio deviated from 1:1. Our experimental design was thus effective in inducing variation in the potential for sexual selection in *T. molitor*.

As expected, the pattern of variation detected depended on which index we used to measure the potential for selection. Comparisons based on the standard measure, the opportunity for selection (I_s), indicated that the potential for sexual selection depended strongly and positively on the number of males competing for access to females. This effect was probably mediated through mean mating success, which varied inversely with both number of males and I_s (Downhower *et al.*, 1987; Ruzzante *et al.*, 1996). Neither number of females nor overall density had a significant effect on I_s. The overall pattern of variation in I_s was dominated by the high values in populations with 30 males, and particularly those with sex ratios of 3:1. This produced an overall positive relationship between I_s and the operational sex ratio that nearly obscured the slight increase seen in populations with strongly female-biased sex ratios. Thus, *T. molitor* males follow the expected pattern of increasing opportunity for sexual selection with increasing operational sex ratio, although the absolute number of males rather than the sex ratio *per se* seems to be the driving variable. The reverse relationship, a decline in opportunity for sexual selection with increasing operational sex ratio, would be expected if females show convenience polyandry, as has been postulated for other polygynandrous insect species (Arnqvist, 1992, 1997; Krupa and Sih, 1993; Weigensberg and Fairbairn, 1994; Fairbairn and Preziosi, 1996;

Reynolds, 1996). Such a reversal may occur in *T. molitor* when the sex ratio is female-biased, but it was evident in our data only when there were at least three females for every male.

In contrast to I_s, the indices of inequality were influenced more strongly by the operational sex ratio than by the absolute numbers of males, and all three indices reached their maximum values when the operational sex ratio was strongly female-biased. This trend dominated the pattern for the index of monopolization, Q, resulting in an overall negative relationship with the operational sex ratio. Even though this relationship was slightly concave, rising again as the sex ratio became strongly male-biased, the effect of female-biased sex ratios was clearly dominant. Thus, an analysis based only on Q would cause us to reject the general hypothesis of a positive correlation between the potential for sexual selection and the operational sex ratio and to postulate instead that female *T. molitor* show convenience polyandry.

Morisita's index of dispersion, I_δ, detected both patterns of variation, increasing as operational sex ratio deviated from 1:1 in either direction. This index varied less than I_s or Q (showing a three-fold as opposed to a five- to six-fold variation among populations in Experiment 1), which resulted in somewhat lower power to detect treatment effects. Nevertheless, I_δ showed a significant concave relationship with the operational sex ratio overall, and a significant negative relationship when this ratio was female-biased. The pattern of variation in I_δ differed from that for Q primarily in the relative importance of the 10:30 and 30:10 treatments. For I_δ, the increase was less precipitous in the 10:30 treatment and more pronounced in the 30:10 treatment, so that the overall pattern was one of more balanced changes as the operational sex ratio diverged from 1:1 in either direction. This difference between the two indices derives from the extra standardization of Q. Both indices are standardized to the Poisson distribution and hence express contagion relative to the null model of a uniform distribution of mate acquisition probabilities. However, Q also expresses contagion relative to the maximum possible for the given number of competing males. Recall that maximum contagion occurs when one male acquires all the matings and is directly proportional to n. The Morisita index is not standardized to maximum contagion and reaches a maximum of n when one competitor acquires all the resources (Table 1). The pattern that we observed for Q indicates that contagion in mating success was much closer to its maximum in the 10:30 treatment than it was in any of the other treatments, including the 30:10 treatment. However, because the maximum contagion expected with 10 males is less than that expected with 30 males, this difference is not as pronounced when contagion is not standardized to the maximum.

The standardized Morisita index, I_p, has two advantages over I_δ. The first is that, like Q, it is standardized to take a value of zero for randomly distributed resources. Deviations from randomness are thus easily recognizable as positive (overdispersion) or negative (underdispersion) deviations from zero. The second advantage derives from the standardized confidence limits that permit instant evaluation of statistical significance for any independent estimate of I_p. However, conversion of I_δ to I_p requires four different transformations, depending on the actual dispersion in the data set (Smith-Gill, 1975; Krebs, 1999). Three different transformations were required for our 27 populations, and in only one of the nine treatments did all three replicate populations receive the same transformation. This had the unfortunate effect of increasing the variance within treatments, thereby reducing the power of the experiment to detect treatment effects. The requirement of different transformations in different populations would seem to invalidate the standardized Morisita for comparisons among populations differing in the pattern of dispersion of resources. We do not recommend it.

Of the three other indices, which is the most appropriate or valid measure of the potential for sexual selection? The opportunity for selection (I_s) is the variance in relative fitness (relative mating success in our case), and none of the derived indices share this property. Only I_s defines the maximum selection intensity possible during a given episode of selection (Crow, 1958; Wade and Arnold, 1980; Arnold and Wade, 1984; Walsh and Lynch, in press). However, for I_s to translate into selection on any given trait, there must be a consistent relationship between the value of that trait and relative fitness. We argue that indices such as Q and I_δ that take a random distribution of acquired resources as their null model will be better predictors of that relationship than I_s. The basis of this argument lies in defining the appropriate null model for absence of selection. A consistent relationship between fitness and trait values (= selection; Futuyma, 1998, p. 349) presupposes a functional relationship between trait values and the probability of acquiring resources (the gain propensities). If all individuals and hence all trait values have equal gain propensities, realized resource acquisition may vary stochastically in any given population or generation, but there will be no consistent relationship between phenotype and fitness. Therefore, we can define the absence of selection as equality of gain propensities among all competitors. In our case, this translates to an equal probability of mating for all males. However, the opportunity for selection will be non-zero whenever the acquired resources are not uniformly distributed, and it will thus tend to overestimate the potential for phenotypic selection by predicting selection even if gain propensities are equal. Indices that use equality of gain propensities as the null model allow for the sampling error between the propensities (which are assumed to be a function of phenotype) and resources acquired, and hence should be more accurate predictors of phenotypic selection.

Any of our three indices of inequality satisfy this criterion. However, as argued above, we do not recommend the standardized Morisita index for comparisons among populations. The patterns revealed by the other two indices differ primarily because Q is standardized to the maximum variance and I_δ is not. This standardization is useful in analyses of resource monopolization because it quantifies the degree of monopolization relative to the maximum possible when one individual acquires all the resources (Ruzzante *et al.*, 1996). However, the overall strength of selection is determined by the true variance in relative fitness (Crow, 1958; Walsh and Lynch, in press). The positive relationship between the maximum variance and the number of competitors [recall that $E(\sigma^2_{\max}) = n(\mu^2)$] places an upper limit on the opportunity for selection, but this limit is real, not merely a statistical artifact. A given variance in relative fitness signals the same 'overall strength of selection on individuals' (Walsh and Lynch, in press) whether there are 10 or 100 competing males and regardless of mean mating success. Standardization of Q to the maximum expected variance is thus not relevant for predicting the presence and strength of selection. In fact, it may confound such predictions by exaggerating the expected strength of selection when the number of competitors is small, as in our 10:30 treatment. In our data set, this bias is seen in the nearly significant ($P < 0.10$) negative correlation between Q and n. Thus, of the four indices we applied to our data, we conclude that Morisita's index, I_δ, is likely to provide the most accurate measure of the potential for sexual selection.

As in most studies of sexual selection (Thornhill and Alcock, 1983; Andersson, 1994; Choe and Crespi, 1997), our conclusions are based on a limited sampling of mating interactions. The relatively low mean mating success of male *T. molitor* and the strong correlations between the mean and variance are typical of Poisson variables, and resulted in the expected biases in I_s. Our assay was, therefore, representative of standard cross-sectional or short-term assays of sexual selection in laboratory and field populations. These short-term estimators are particularly susceptible to the biases in I_s because of the low mean mating success and high sampling error. Longer-term estimates of relative mating success would be expected to be more accurate and might result in less biased estimates of I_s by virtue of higher cumulative mating success (Ruzzante *et al.*, 1996). Although the indices of inequality are not sensitive to changes in mean mating success, at least when mating is random or contagiously distributed (Kokko *et al.*, 1999), Ruzzante *et al.* (1996) demonstrated that the patterns of monopolization detected by Q may be sensitive to the duration of the mating assay. Thus, estimates of the potential for sexual selection are likely to be context-specific, even when the underlying statistical biases have been removed. Comparisons among populations or studies, therefore, will only be biologically meaningful if based on similar assay techniques.

In addition to serving as a forum for comparisons among indices of the potential for sexual selection, our assays have also provided new information about patterns of sexual selection in captive populations of *T. molitor*. The concave relationship between the potential for sexual selection and the operational sex ratio in these populations is difficult to reconcile with any single mechanism of sexual selection. We postulate instead that sexual selection is mediated by different behavioural modalities when the operational sex ratio is female-biased as opposed to male-biased. Our reasoning is as follows. Female *T. molitor* generally resist mating, as is typical for polygynandrous mating systems. However, when the operational sex ratio is male-biased, they are less discriminatory and less reluctant to mate, and they release less male-attracting pheromone than when the ratio is even or female-biased (Happ and Wheeler, 1969; Gage and Baker, 1991). Thus, females alter their mating behaviour with the operational sex ratio such that sexual selection through female choice becomes less probable as the ratio becomes increasingly male-biased. This is the typical signature of convenience polyandry (Arnqvist, 1992, 1997; Krupa and Sih, 1993; Reynolds, 1996). In contrast, sexual selection through direct male–male competition becomes increasingly probable as the operational sex ratio becomes male-biased. Males actively compete for females (Happ, 1969; Gage and Baker, 1991; Siva-Jothy *et al.*, 1996); we observed many direct physical struggles between males, where one male attempted to push another off or away from a female. Gage and Baker (1991) have shown that males increase their rate of mating, ejaculate volume and tendency to guard females in response to the presence of other males. Thus, when the operational sex ratio is male-biased, we hypothesize that sexual selection operates primarily through male–male competition and should favour traits that enable males to resist takeover attempts [e.g. chitinous penis spines (Siva-Jothy *et al.*, 1996)], prevent remating by females [e.g. inhibitory pheromones (Happ, 1969); post-copulatory guarding] or enhance fertilization success [e.g. copulatory courtship; increased ejaculate volume (Gage and Baker, 1991)]. Although mating interactions have not been studied in populations of *T. molitor* with strongly female-biased sex ratios, we would predict sexual selection under these circumstances to favour traits enabling males to overcome female reluctance and to remate rapidly. Possibilities include pre-copulatory courtship, persistence in mating attempts, and the rapid detection of and response to female pheromones (Thornhill and Alcock, 1983; Brown *et al.*, 1997; Dickinson, 1997). Although physical characteristics such as strong grasping front legs and overall large size could be advantageous for both overcoming female reluctance and displacing rival males, there is little evidence for sexual selection on these traits in *T. molitor* (Gage and Baker, 1991; D.J. Fairbairn, unpublished data). With the exception of these traits, there may be little overlap between the suites of traits favoured by sexual selection at the two extremes of the operational sex ratio. Thus, although the overall potential for selection shows a nearly symmetrical concave relationship with the operational sex ratio, the relationship between the intensity of selection on any given trait and this ratio (i.e. fitness functions) would most likely be linear or at least monotonic. This example serves as a reminder that the potential for selection, no matter how accurately estimated, may be a poor predictor of the pattern of selection on any given trait (Ferguson and Fairbairn, 2001).

In conclusion, our results support the general hypothesis of a causative (i.e. functional) relationship between the operational sex ratio or number of males and the opportunity for sexual selection on males. The conflicting results obtained when we used indices of inequality that standardize contagion in mating success relative to a Poisson null model do not negate this conclusion. However, they call into question the validity of I_s as a predictor of phenotypic selection, particularly in populations with female-biased sex ratios. Although the indices of inequality do not provide a quantitative estimate of the maximum intensity of selection, and so cannot replace I_s in quantitative genetic theory (Crow, 1958; Wade, 1979; Bradbury and Andersson, 1987; Walsh and Lynch, in press), we argue that they more accurately reflect the true probability of sexual selection within populations. Morisita's index appears to be particularly appropriate for this use, and performs well when comparisons must be made among populations that vary in density, sex ratio and mean mating success. Nevertheless, we caution that all indices are likely to be context-specific, and no index of the overall potential for selection can be expected to accurately predict the pattern or intensity of selection on any given trait.

ACKNOWLEDGEMENTS

We thank J. Mueller for technical assistance. We are also grateful to I. Ferguson, J. Grant and J. Reeve for their valuable advice and comments throughout the writing of this paper. The study was supported by a research grant to D.J.F. from the Natural Sciences and Engineering Research Council of Canada.

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