REVIEW

The evolution of polyandry: multiple mating and female fitness in insects

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Theory suggests that male fitness generally increases steadily with mating rate, while one or a few matings are sufficient for females to maximize their reproductive success. Contrary to these predictions, however, females of the majority of insects mate multiply. We performed a meta-analysis of 122 experimental studies addressing the direct effects of multiple mating on female fitness in insects. Our results clearly show that females gain directly from multiple matings in terms of increased lifetime offspring production. Despite a negative effect of remating on female longevity in species without nuptial feeding, the positive effects (increased egg production rate and fertility) more than outweigh this negative effect for moderate mating rates. The average direct net fitness gain of multiple mating was as high as 30–70%. Therefore, the evolutionary maintenance of polyandry in insects can be understood solely in terms of direct effects. However, our results also strongly support the existence of an intermediate optimal female mating rate, beyond which a further elevated mating rate is deleterious. The existence of such optima implies that sexual conflict over the mating rate should be very common in insects, and that sexually antagonistic coevolution plays a key role in the evolution of mating systems and of many reproductive traits. We discuss the origin and maintenance of nuptial feeing in the light of our findings, and suggest that elaborate and nutritional ejaculates may be the result of sexually antagonistic coevolution. Future research should aim at gaining a quantitative understanding of the evolution of female mating rates.
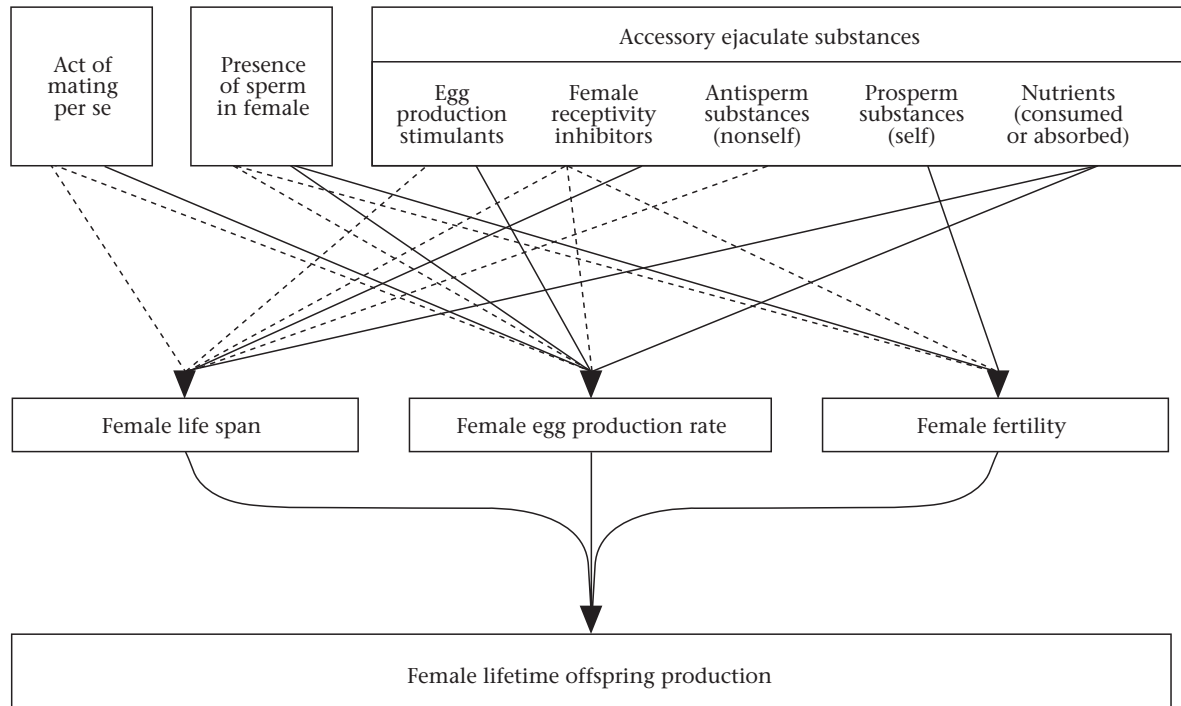
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The primary function of mating is the transfer of sperm to females. Since each mating offers an opportunity to father offspring, males can generally increase their fitness by mating with many mates and high mating rates are thus typically associated with high male reproductive success. Females, in contrast, maximize reproductive success by maximizing the number of viable eggs produced. This basic asymmetry between the sexes suggests that male fitness increases monotonically with increased mating rate, while one or a few matings are sufficient for females to maximize their reproductive success. Contrary to these predictions, however, females of the majority of animal species mate multiply, most often with different males (polyandry) but also with the same male (repeated matings). Since our understanding of the evolution of male and female mating rates is at the heart of reproductive biology, this

apparent discrepancy between theory and empirical observations has generated an extensive body of theoretical and empirical research. A series of additional benefits to females from mating have been suggested, that is, beyond simply receiving sufficient amounts of viable sperm (see e.g. Walker 1980; Thornhill & Alcock 1983; Choe & Crespi 1997; Yasui 1998), and a large number of empirical studies have addressed the effects of multiple mating on female fitness in a variety of different insect species (see Ridley 1988; Vahed 1998).

Novel empirical and conceptual insights, however, suggest that the scenario described above is too simplistic to help us understand the evolution of female mating rates. First, while male insects have often been generally considered to provide females with 'little but sperm' (often motivating a view of direct benefits as being insignificant), we now know that the function of mating goes far beyond that of simply providing females with sperm. Most importantly, a large number of accessory substances are transferred with the ejaculate, and these substances

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Figure 1. A summary of the known effects of mating on female fitness in insects. The act of mating itself, the presence of sperm per se and the transfer of a number of accessory substances with the ejaculate are all known to have various effects on various female fitness components, many of which are antagonistic. Dashed lines represent negative and solid lines positive effects.

have profound effects on female reproductive behaviour (Chen 1984; Gillott 1988; Eberhard & Cordero 1995; Eberhard 1996; Klowden 1999). The importance of direct effects of multiple mating on females may thus be seriously underestimated. Second, even if selection on mating rate may often be sexually antagonistic (Halliday & Arnold 1987; Rice 1996; Holland & Rice 1998; Parker & Partridge 1998; and Discussion below), females are active participants in evolutionary games over mating rates (Hammerstein & Parker 1987). Thus, the near ubiquitous occurrence of multiple mating by females strongly suggests that one or a few matings may not be sufficient to maximize female reproductive success.

Mating may directly affect female fitness in a number of ways. Theoretical studies have suggested that polyandry may also affect female fitness indirectly, by providing various genetic benefits that increase offspring fitness (see Yasui 1998 for a review). However, until the direct effects of multiple mating on female fitness have been generally understood and proven insufficient to account for polyandry, such indirect genetic effects may not need to be invoked (Parker 1984; Yasui 1998). Female lifetime offspring production is principally a product of female life span, egg production rate and fertility. All of these fitness components are known to be affected by mating in various direct ways. The effects can be due to three different factors: the act of mating per se, presence of sperm and transfer of accessory substances (see Fig. 1). First, the act of mating itself is known to carry a number of costs to females. These ecological costs of mating include general time and energy costs (Daly 1978; Thornhill & Alcock 1983; Watson et al. 1998), but also

increased predation rates (Wing 1988; Arnqvist 1989a; Rowe 1994), risk of physical injury (Parker 1979; Helversen & Helversen 1991) and parasite/pathogen infection (Hurst et al. 1995). These costs decrease both female life span and egg production rate. The act of mating itself may, however, also have positive effects on fitness since it may directly stimulate female egg production (Opp & Prokopy 1986). Second, the mere presence of viable sperm in the female reproductive tract is known to stimulate female egg production (Gromko et al. 1984) and an ample and diverse supply of sperm may also increase female fertility (Tregenza & Wedell 1998). However, an excess of sperm may affect both egg production rate (Nilakhe 1977) and fertility negatively (because of polyspermy; see Eberhard 1996).

The large number of accessory substances, typically various proteins, that are transferred to females with the male ejaculate are known to have numerous complex effects on female reproductive performance (for reviews see Eberhard & Cordero 1995; Eberhard 1996; Klowden 1999; see Fig. 1). Certain gonadotropic substances trigger and/or stimulate female egg production and so could increase female fitness by stimulating egg maturation and egg laying. Owing to the cost of reproduction, however, these substances may also decrease female life span (Ikeda 1974; Partridge & Farquhar 1981; Fowler & Partridge 1989; Chapman et al. 1993, 1998). Other substances decrease female remating rate, typically by directly inhibiting female sexual receptivity (see Eberhard 1996) or in some cases by acting as repellents to other males (Andersson et al. in press). These substances may thus reduce female egg production rate and fertility, and may

also affect female life span positively or negatively. Yet other accessory substances are involved in sperm competition, and have negative effects on the sperm of previous mates (Harshman & Prout 1994; Clark et al. 1995). Such substances may have a variety of toxic side-effects to females (cf. Gems & Riddle 1996; Siva-Jothy et al. 1998), and they reduce female life span in *Drosophila* (Fowler & Partridge 1989; Partridge & Fowler 1990; Chapman et al. 1993, 1995). Substances that stimulate and/or trigger female uptake and storage of sperm, and hence act in the interest of the focal male, are also known among the secondary substances (Bertram et al. 1996; Wolfner 1997) and these should often elevate female fertility. Finally, males of some groups of insects provide females with a voluminous ejaculate that is either absorbed or ingested by females. Such nuptial feeding is known sometimes to increase female egg production rate and/or female life span (see Vahed 1998 for a review).

The direct net effects of polyandry on female fitness are inherently difficult to predict from theoretical considerations alone. It is clear from Fig. 1, which summarizes the main known effects of the various factors mentioned above, that different female fitness components are negatively and/or positively affected by a large number of factors in a complex and often antagonistic manner. The intensity and strength of many of these effects are also time and dose dependent (Eberhard 1996), and hence the temporal scale of effects varies between the different factors. The difficulty of making theoretical predictions is further complicated by negative trade-offs between female fitness components, such as that between egg production rate and life span (Chapman et al. 1998). However, two important conclusions can be made at this point. First, it is in no way clear that one or a few matings necessarily maximizes female lifetime offspring production. The direct effects of mating on female fitness are manifold and complex, and reducing mating to a mere sperm delivery act is flawed. Second, empirical studies offer the only viable route to general conclusions concerning the direct net effects of polyandry on female fitness.

Our aim in this review is two-fold. First, we synthesize and analyse experimental research addressing the direct effects of multiple mating on female fitness in insects. Second, we point to new empirical and conceptual domains, and give advice for future research in this area of evolutionary ecology. Many studies have dealt with the effects of varying mating rate on female reproductive performance. The taxa and the experimental design used vary widely across studies (see Appendix), as does the outcome of experiments. Single studies have reported positive, negative or no effects of multiple mating on female fitness. Consequently, results of single studies have been thought 'contradictory' or 'incompatible', and our understanding of the evolution of polyandry in insects 'obscure'. We suggest that this is not necessarily the case. The fact that one study documents a significant effect, while another does not, does not in itself render the results contradictory. Results of single studies are expected to vary because of random sampling error alone. Furthermore, and more importantly, variations in
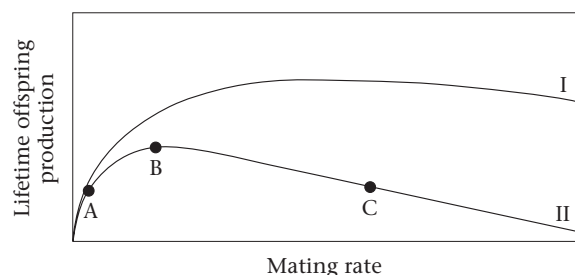
Figure 2. A simple model of the effects of increased mating rate on female fitness. In species in which nuptial feeding occurs (I), female fitness is expected to increase with mating rate. As females become saturated, however, the net effects of further elevated mating rate should be insignificant. In species without nuptial feeding (II), in contrast, female fitness should be maximized at a relatively well-defined optimal mating rate (see text for discussion). Thus, the actual mating rates used in any study relating the degree of multiple mating to female fitness (A, B or C) should be critical to the outcome of the experiment.

experimental design can cause results to differ widely without being contradictory. First, consider a simple model of the direct net effect on female fitness of increased mating rate. Both positive and negative effects of mating (see Fig. 1) are dose dependent. Most of the positive effects (benefits) of mating mentioned above, however, can safely be assumed to generate a gain curve that is asymptotic, owing to diminishing rewards of, for example, additional sperm, gonadotropic substances and nuptial feeding. The negative effects (costs) of mating, in contrast, are likely to be more linearly or exponentially related to mating rate. This is due to the presumably additive or multiplicative negative effects of, for example, time/energy costs, toxic accessory substances, risk of injury/predation and the cost of reproduction. Given these simple assumptions, a net optimal female mating rate is predicted that reflects the trade-off between the various costs and benefits of mating (see Fig. 2 and Discussion). Furthermore, this optimal mating rate will in general tend to be higher in species in which nuptial feeding occurs (Fig. 2, line I) compared to the optimal mating rate in species without such nuptial feeding (Fig. 2, line II), owing to the added positive nutritional effect. Next, consider one study comparing female fitness in singly mated females with near optimally mated females (Fig. 2: A versus B) and another study comparing near optimally mated females with females mated at an even higher rate (Fig. 2: B versus C). The two studies would generate opposing conclusions regarding the effects of polyandry on female fitness, yet they would be neither 'contradictory' nor 'incompatible'. Hence, variations in experimental design could explain a large proportion of between-studies variation in the effects of polyandry on female fitness.

We applied meta-analytical methods to synthesize and analyse experiments addressing the direct effects of varying mating rates in insects on female fitness components (fecundity, fertility and/or longevity). Meta-analysis offers objective and quantitative statistical tools for analysing the results of multiple studies, which are in

many ways superior to the alternative subjective and nonquantitative narrative reviews (see Cooper & Hedges 1994; Arnqvist & Wooster 1995; Adams et al. 1997; Osenberg & St Mary 1998; for recent discussions of meta-analysis). Since the magnitude of the direct effects of polyandry on female fitness may often be fairly small (Yasui 1998), generating a high type II error rate in primary studies, a meta-analysis of these empirical data is particularly well motivated (Arnqvist & Wooster 1995).

METHODS

Data Retrieval and Selection

Search for data

We used four different methods to search for experiments addressing the effects of varying mating rates on female reproductive performance in insects. First, we thoroughly examined the references in previously published narrative reviews on the topic (Thornhill & Alcock 1983; Ridley 1988; Boggs 1995; Choe & Crespi 1997; Vahed 1998). Second, we searched available literature databases (Biological Abstracts, Science Citation Index), using several search strategies. Third, we searched documents available on the World Wide Web, using several search terms and search engines. Fourth, we posted calls for relevant data on four electronic mailing lists on the Internet during September 1997 (Evoldir, Entomo-l, Bugnet, Leps-l), primarily to secure access to relevant unpublished primary studies.

Data selection

Five criteria had to be fulfilled for an experiment to be included in our analyses. First, each study had to involve at least two different experimental treatments: one in which females mated less frequently and one in which females mated more frequently. Many experiments involved one group of females (the control group) that were mated only once, or that had restricted access to males, and another group (the experimental group) where females were mated multiply, or had unlimited access to males. Thus, while the mating frequencies actually used varied between studies, each study included could document/verify a difference in mating frequency between the two groups of females. Second, individual females had to be randomly assigned to the mating treatments mentioned above. This criterion disqualified a surprisingly large number of correlational studies, included in previous reviews (Ridley 1988; Vahed 1998), in which the causes and effects of multiple mating cannot be separated. In such studies, a number of females were typically given the opportunity to mate multiply, and females that mated once were then simply compared with females that mated more than once.

Third, each study had to include a clear and lucid presentation of the materials and methods used. Fourth, studies included had to provide at least one measure of female reproductive performance among the experimental females. This could be fecundity (egg production), fertility (viability or hatching rate of eggs) and/or measures of offspring production. When available, we also recorded female life span. Since measures of offspring production combine the potentially independent effects of mating rate on female fecundity and fertility, we preferentially used measures of fecundity and fertility over offspring production when available. Only in cases where neither fecundity nor fertility was reported did we use offspring production as a measure of female reproductive performance. Fifth, the results sections of primary studies had to allow extraction of the following information: (1) the sample sizes used, that is, number of females in each group; (2) average female reproductive performance in the two groups; and (3) a statistical measure of dispersion for these means. The latter could be either a direct measure of dispersion (SD or SE) or a metric from which a conservative measure of dispersion could be calculated (such as a range or a P value). This information was either retrieved directly from the text or captured from figures in published articles, by means of a digitizing tablet (SummaSketch III).

Statistical Analyses

Grouping variables

To assess heterogeneity among primary studies, and thus to further our understanding of the causes of variation in experimental outcome across studies, we used six grouping variables in our analyses (analogous to factors in conventional ANOVAs), two of which are based on the biology of single species. Since there are several reasons to believe that the experimental design will affect the outcome of single studies, each study was also categorized by four grouping variables based on the experimental design used, to enable us to analyse differences in outcome caused by differing methodology across studies.

First, we used the taxonomic order of the species studied as a grouping variable to assess the overall importance of higher taxonomic affiliation for the outcome of experiments. Second, studies were categorized into two groups, based on the reproductive biology of the species studied. One group consisted of studies performed with species in which nuptial feeding occurs (see Vahed 1998). In this group, we included species in which females ingest male glandular products, regurgitated food or parts of the male ejaculate (spermatophylax and/or spermatophore) prior to, during or after copulation. We also included species in which males transfer an enlarged spermatophore to the female during mating, often constituting several per cent of male body weight. We did not, however, include species in which the ejaculate is not enlarged, even if male-derived substances are incorporated into developing oocytes (see Eberhard 1996; Pitnick et al. 1997; Vahed 1998; and Discussion below, for problems with inferring nutritional effects from radiolabel data). In species in which nuptial feeding occurs, our a priori expectation was a monotonic increase in lifetime reproductive performance with increasing mating rate, at least for moderately high mating rates (see line I in Fig. 2). The other group consisted of species without no nuptial feeding. In such species, we expected a different

relationship between reproductive performance and mating rate (see line II in Fig. 2 and Introduction).

Third, studies in which males were kept continuously with females in the experimental group were contrasted with studies in which males were introduced only intermittently for mating and then removed from females (male cohabitation). Fourth, studies in which female fecundity/fertility was recorded during the entire female lifetime was contrasted with studies in which these parameters were recorded for only a limited part of their life span (duration of experiment). Fifth, studies in which females were provided with adequate/ad libitum food resources were contrasted with studies in which females were food deprived or given a restricted/limited access to food (food level).

Finally, based on the experimental design and the actual mating frequencies used in experiments, we can predict the outcome of an experiment a priori using the simple model presented in Fig. 2 (see Introduction). To assess the accuracy of such a priori expectations, we categorized studies on species not exhibiting nuptial feeding into three types differing in the expected effects of increased mating rate on female reproductive performance in our sixth grouping variable (experimental type). In type I we expected an increase in female reproductive performance (A versus B in Fig. 2). These experiments compared females that were allowed to mate once only with either (1) females that were allowed to mate at a somewhat higher known and controlled rate, and where experiments were performed at any fraction of female life span, or (2) females that were kept continuously with males (male cohabitation), but where the duration of the experiment was less than the female life span. In type II we expected a smaller or no effect of female mating rate (A versus C). These experiments compared females that were allowed to mate once only with females that were allowed to mate at a higher and unknown rate. Experiments of this type used male cohabitation in the experimental treatments and lasted the entire female life span. In type III we expected a decrease in female reproductive performance (B versus C). These experiments compared females that were allowed to mate at an intermediate rate (>1) with females that were allowed to mate at a considerably higher and unknown rate. Experiments of this type also used male cohabitation in the experimental treatments and lasted the entire female life span. Two studies could not be categorized into any of these three groups and were not included in these particular analyses.

Statistical methods

The primary studies used in our meta-analysis cannot strictly be expected to share a single common true effect size, even within orders and grouping variable categories, owing to differences in a number of factors that we could not, or did not, control or account for. Thus, we exclusively used mixed models in our estimations of overall effects of mating rate on female reproductive performance and in our assessments of the importance of grouping variables for experimental outcome. Such models include fixed differences between groups of studies and within-study sampling error, but also allow for random between-studies variation from other sources of variance (Raudenbush 1994; Rosenberg et al. 1997). While the statistical power of mixed models is considerably lower than equivalent fixed-effects models, and hence the type II error rate higher, the assumptions of mixed models are much more likely to be fulfilled in most meta-analyses in ecology and evolution (Gurevitch & Hedges 1993; Rosenberg et al. 1997). Our choice of mixed models, and thus the more conservative inclusion of an additional source of between-studies variance, was further validated by the often significant within-class homogeneities (Q_W) in fixed-effect model analogues of the mixed models reported here.

Since different insect species differ dramatically in absolute fecundities and longevities, we chose to use the response ratio as a measure of effect size (Hedges et al. 1999). This proportional effect size measure is simply the ratio, rather than the difference, of the average outcome in the experimental group to that of the control group (cf. Osenberg et al. 1997; Osenberg & St Mary 1998). To estimate mean effect sizes, and to assess the importance of various grouping variables, we used mixed models where the reciprocal of the sampling variance of each response ratio (ln transformed) was used as weight (Rosenberg et al. 1997). Below, we report mean response ratios and their 95% confidence limits, as $CL_1 \leq RR \leq CL_2$. A ratio significantly different from unity indicates significant effects of the female mating rate treatment. For comparisons between groups of studies, we also report Q_B, the between-groups homogeneity. This statistic is analogous to the between-groups component of variance in conventional analyses of variance, and is χ^2 distributed with N groups minus one degree of freedom (Hedges & Olkin 1985). Owing to the frequent lack of measures of dispersion for fertility data in primary studies as well as the special statistical properties of measures of fertility, our analyses of the effects of multiple mating on fertility differed from those described above in that we used resampling tests, applying nonparametric weights, for statistical inference. In these analyses, we report randomization tests of the between-groups homogeneity and bias-corrected bootstrap 95% confidence limits (5000 iterations) for mean effect sizes (Adams et al. 1997). The statistical software package MetaWin (Rosenberg et al. 1997) was used for all statistical inference.

RESULTS

We were able to locate 122 experiments, on species belonging to 10 insect orders, where all of our five inclusion criteria were fulfilled (see Appendix). As expected, the overall gross effects of multiple mating on female fitness differed between taxa in which nuptial feeding occurs and those in which it does not (see Table 1). Female lifetime egg production, or egg production rate, increased with mating rate in both groups, but to a larger extent in the former. Increased mating rate elevated fertility overall (pooled data for both groups: $1.07 \leq 1.17 \leq 1.32$, $N=48$), but this effect did not differ significantly between the two groups (Table 1). Similarly, in studies reporting only offspring production, increased

Table 1. Comparison of the outcome of experiments addressing the effects of multiple mating on female egg production, fertility, offspring production and longevity

Female fitness component	Group	Number of experiments	Mean response ratio (RR) with 95% confidence limits
Egg production	No nuptial feeding	69	$1.04 \leq 1.11 \leq 1.18$
	Nuptial feeding	28	$1.23 \leq 1.35 \leq 1.49$
	($Q_{B\,1}=11.58$, $P<0.001$)		
Fertility	No nuptial feeding	37	$1.07 \leq 1.20 \leq 1.40$
	Nuptial feeding	11	$1.00 \leq 1.09 \leq 1.22$
	($Q_{B\,1}=0.68$, $P=0.453$)		
Offspring production	No nuptial feeding	26	$1.26 \leq 1.52 \leq 1.84$
	Nuptial feeding	18	$1.44 \leq 1.83 \leq 2.32$
	($Q_{B\,1}=1.38$, $P=0.240$)		
Longevity	No nuptial feeding	37	$0.79 \leq 0.88 \leq 0.98$
	Nuptial feeding	22	$0.93 \leq 1.06 \leq 1.21$
	($Q_{B\,1}=4.37$, $P=0.036$)		

Response ratios higher than unity indicate positive effects of increased female mating rate and those lower than unity indicate negative effects.

mating rate led to a dramatic increase in offspring production (pooled data for both groups: $1.41 \leq 1.63 \leq 1.89$, $N=44$), an effect that did not differ significantly between the groups (Table 1). The effects of increased mating rate on female longevity, in contrast, differed markedly between the two groups of species. While increased mating rate clearly decreases female longevity in species without nuptial feeding, if anything it tends to increase female longevity in those with nuptial feeding (see Table 1). Owing to these fundamental differences in female response to experimentally increased mating rate, we chose to evaluate the effects of various grouping variables separately for the two groups of species.

Species with Nuptial Feeding

The effects of increased mating rate on egg production did not differ significantly between insect orders ($Q_{B\,2}=2.86$, $P=0.239$). While the effects were very similar in magnitude among studies involving Orthopterans ($1.15 \leq 1.35 \leq 1.57$) and Lepidopterans ($1.23 \leq 1.39 \leq 1.57$), they tended to be somewhat lower in Dictyopterans ($0.82 \leq 1.08 \leq 1.41$). The ambient food level did not significantly affect the outcome of experiments ($Q_{B1}=0.003$, $P=0.955$) and neither did the length of the experiment, that is whether experiments were run for the entire female life span or not ($Q_{B1}=0.12$, $P=0.727$). However, studies in which females were kept constantly with males showed a significantly higher positive effect of increased mating rate ($1.41 \leq 1.65 \leq 1.94$), compared with studies in which life-long male–female cohabitation did not occur ($1.12 \leq 1.24 \leq 1.37$; $Q_{B1}=8.88$, $P=0.003$). None of these four grouping variables affected the effects of mating rate on fertility ($Q_{B1} \leq 0.84$, $P \geq 0.092$; in all three cases; cf. Table 1).

The positive effects of increased mating rate on offspring production (Table 1) did not differ significantly between orders ($Q_{B\,3}=1.04$, $P=0.792$) and none of the three design variables affected the outcome ($Q_{B1} \leq 0.21$, $P \geq 0.648$; in all three cases). In terms of female longevity

(Table 1), effects of mating rate did not differ between orders ($Q_{B\,2}=0.88$, $P=0.645$) and neither food availability nor male cohabitation significantly affected the outcome of experiments ($Q_{B1} \leqslant 1.02$, $P \geqslant 0.313$; in both cases).

In summary, multiple mating increases average egg and offspring production in insects with nuptial feeding on average by as much as 35–85%, and these positive effects are fairly homogeneous across orders. Female fertility is elevated by on average 10%, while female longevity is, if at all, only weakly positively affected by multiple mating. Details of the experimental design used did not strongly affect the outcome of experiments among these groups of insects, although studies using male–female cohabitation did show a stronger positive effect of multiple mating on egg production rate than those that did not.

Species Without Nuptial Feeding

Effects of mating rate on egg production

Remating increased female egg production in general (Table 1), and we found no significant differences between orders in the response to increased mating rate ($Q_{B\,3}=7.47$, $P=0.058$; $Q_{B\,2}=1.85$, $P=0.395$ when excluding Dictyoptera from the analysis). Furthermore, neither food availability ($Q_{B1}=2.32$, $P=0.127$) nor experimental duration per se ($Q_{B1}=2.87$, $P=0.089$) significantly affected the strength of the effect. In direct contrast to studies of species with nuptial feeding (see above), studies in which females were kept constantly with males had a significantly lower positive effect of increased mating rate ($0.93 \leq 1.01 \leq 1.10$) than those without constant male–female cohabitation ($1.13 \leq 1.23 \leq 1.35$; $Q_{B1}=9.79$, $P=0.002$). Most importantly, however, the type of experimental design used had a very strong effect on the outcome of primary experiments ($Q_{B\,2}=22.63$, $P<0.001$) and differences between types of experiment corresponded to our qualitative a priori predictions (see Fig. 3 and Methods). The difference between types of experiment remained strong when the analysis was restricted to studies performed during females' complete life span,
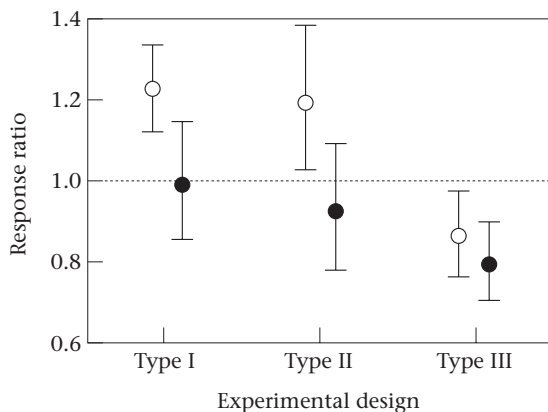
Figure 3. Average effect size (response ratio±95% CL) of the effects of increased mating rate on female egg production (○) and longevity (●) in species where no nuptial feeding occurs. Type I represents studies comparing females mated once versus a few times (A versus B in Fig. 2), type II once versus many times (A versus C in Fig. 2) and type III a few versus many times (B versus C in Fig. 2).
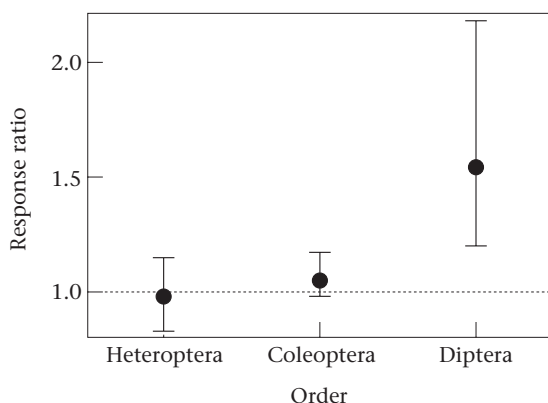
Figure 4. Average effect size (response ratio±95% bootstrap CL) of the effects of increased mating rate on female fertility in three insect orders.

that is, those reporting effects of mating rate on female lifetime fecundity ($Q_{B\,2}=22.09$, $P<0.001$).

Effects of mating rate on fertility

While increased mating rate in general elevates fertility considerably (Table 1), this effect was very variable and differed between orders ($Q_{B\,2}=11.425$, $P=0.019$), being strongest in Dipterans and weakest in Heteropterans (Fig. 4). However, none of the grouping variables affected the outcome of primary experiments in general ($P\geq0.472$; in all four cases).

Effects of mating rate on offspring production

As expected, because of the overall positive effects of multiple mating on egg production rate and fertility mentioned above, studies reporting only female offspring production showed the strongest positive effects of increased mating rate (Table 1). However, neither taxonomic affiliation (effect of orders: $Q_{B\,2}=0.045$, $P=0.977$) nor the length of the experiment ($Q_{B1}=1.17$, $P=0.279$) significantly affected the outcome of experiments.

Effects of mating rate on female longevity

Increased mating rate decreases female longevity in general (Table 1) and orders did not differ significantly in the pattern of this response ($Q_{B\,3}=2.78$, $P=0.426$). Food availability did not seem to affect the outcome ($Q_{B1}=1.83$, $P=0.176$), whereas remating tended to decrease female longevity more in studies where females were kept constantly with males ($0.76\leq0.84\leq0.92$) than in those without male–female cohabitation ($0.85\leq0.99\leq1.15$; $Q_{B1}=3.32$, $P=0.068$). The type of experimental design, however, did affect the outcome in the predicted direction (Fig. 3; $Q_{B\,2}=5.56$, one-tailed $P=0.031$).

Assessment of Sampling Bias

Owing to publication and/or reporting bias, general conclusions from meta-analyses can be flawed (Cooper & Hedges 1994). This will be the case, for example, if studies reporting significant effects are overrepresented among published studies (the 'file-drawer' problem; Rosenthal 1979). In the current analyses, we did not expect this to be a significant problem since (1) data on the effects of mating rate on female fitness components often formed only one restricted part of primary studies and (2) a priori expectations of the outcome were often not obviously directional and the direction of results should hence not be critical to the publication of studies. Nevertheless, we assessed the potential influence of sampling bias by (1) graphical inspection of funnel graphs, that is, plots of sample size versus effect size (Begg 1994) and by (2) computing Spearman rank correlations between the sample size and the effect size (Begg 1994), for all subsets of studies given in Table 1. As expected, however, neither funnel graphs nor rank correlation tests indicated any systematic sampling bias in our data.

DISCUSSION

Our combined analysis of the effects of multiple mating on female reproduction in insects generated a number of important and novel insights. We first discuss the general patterns that emerged from our synthesis, the potential causes of these patterns and some of their implications. We then discuss the evolution of nutritious ejaculates (nuptial gifts) and finally identify areas where future research should be concentrated.

Effects of Polyandry on Female Fitness

It is clear from our analyses that a single mating does not in general maximize female fitness in insects. Despite the overall negative effects of multiple mating on female longevity in species without nuptial feeding, the positive effects of remating documented here more than outweigh this negative effect for moderate mating rates. The positive effect of mating rate on fertility may, at least in part, be due simply to female replenishment of depleted sperm supplies (Thornhill & Alcock 1983). However, certain direct genetic benefits may also contribute to

this effect. In particular, patterns of genetic incompatibility between mates within populations could lead to increased fertility under polyandry (Zeh & Zeh 1996, 1997). To disentangle these effects, we need experiments comparing the fertility of females mated to multiple mates with that of females mated repeatedly to a single male (Tregenza & Wedell 1998). In natural insect populations, multiple mating typically occurs as polyandry, as opposed to repeated matings, owing to the lack of long-term pair bonds (Thornhill & Alcock 1983; Choe & Crespi 1997).

The positive effect of remating on egg production rate in species without nuptial feeding is without doubt due mainly to the well-documented stimulating, or gonadotropic, effects of mating (accessory substances, sperm load and/or simply the act of mating itself), but it could also stem, in part, from a nutritional effect of male ejaculate substances (Pitnick et al. 1997; Rooney & Lewis 1999; see also below). However, the facts that orders did not differ significantly in their response to multiple mating and that food availability during the experiment did not significantly affect the outcome both cast doubts on the validity of the latter possibility (see also Vahed 1998).

Our analyses also demonstrated that female life span decreases with increased mating rate in insects without nuptial feeding. This represents what seems to be a very general cost of polyandry, but because of the complexity of the effects of remating (Fig. 1) it is difficult to make general claims about the causes of this effect. We know that the reduction in female life span can be caused by various ecological or physiological costs of mating, such as those stemming from increased egg production rate or from toxicity of accessory ejaculate substances (see Introduction). The data synthesized here do not allow a general distinction between these alternatives, although it is highly likely that both types of costs are important (cf. Chapman et al. 1998).

Despite the reduction in female survival, the overall net direct fitness gain of mating more than once for females, measured as increase in lifetime offspring production, was as high as 30–70% because of the increased egg production rate and fertility. Hence, the near ubiquitous occurrence of polyandry in insects can be understood solely in terms of direct effects, and observations of true monandry in insects, although rare, may actually be more difficult to understand (see below). In any case, it is clear that we do not need to invoke additional indirect female benefits, such as genetic benefits (Curtsinger 1991; Haig & Bergstrom 1995; Keller & Reeve 1995; Yasui 1998), to explain the evolutionary maintenance of polyandry in insects: females generally gain directly from remating in terms of increased reproductive fitness.

Our analyses, however, also show that female fitness does not increase monotonically with mating rate in species where males do not provide nuptial gifts. Experiments comparing female reproductive performance under moderate and high mating rates in general found negative net effects on female fitness of increased mating rate (type III in Fig. 3). Our results thus collectively strongly support the existence of an intermediate optimal female mating rate in insects in general, a pattern earlier only unambiguously documented in *Drosophila* (Etges &

Heed 1992; Chapman & Partridge 1996). As mentioned above, a single mating is clearly not sufficient to provide females with adequate amounts of sperm and gonadotropins to maintain a high production of viable eggs throughout their life. On the other hand, high mating rates also tend to decrease the net reproductive fitness of females, primarily because of the reduction in life span. In between these two extremes lies an intermediate mating rate at which females maximize their lifetime offspring production (cf. Fig. 2). This pattern is of profound importance, for example for our understanding of female mating patterns and for the evolution of female mate choice (S. Gavrilets, G. Arnqvist & U. Friberg, unpublished data), but has not previously been recognized as a general characteristic of the relationship between mating rate and female fitness (cf. Arnold & Duvall 1994).

The conclusions reported here primarily concern the evolutionary maintenance of polyandry, since all primary studies address current fitness effects of multiple mating (cf. Reeve & Sherman 1993). The factors responsible for the evolutionary origin and maintenance of polyandry may differ, and female mating rate can only be optimal in the sense that it reflects the current trade-off between the various costs and benefits of mating to females (see Introduction). This trade-off, in turn, is determined by the relative efficacy of a suite of female adaptations aimed at gaining the benefits while coping with the costs of mating (Rice 1996, 1998). Females may also incur various additional costs of avoiding matings (Arnqvist & Rowe 1995). In such cases, female mating rates may reflect the 'best-of-a-bad-job' (Arnqvist 1997) and theory suggests that emerging male traits/signals with sexually antagonistic effects may drive female mating rates away from their optimum (Holland & Rice 1998; S. Gavrilets, G. Arnqvist & U. Friberg, unpublished data; see below).

The Evolution of Female Mating Rate

We suggest that optimal female mating rates should be seen as evolving reaction norms, rather than as fixed optima. It is well established that female insects are capable of adaptively modulating their mating rate in response to a series of environmental factors that affect the relative costs and benefits of mating, such as operational sex ratio, population density, presence of predators, food availability and the phenotype of their previous mates (e.g. Gwynne 1986; Heller & Helversen 1991; Simmons & Gwynne 1991; Arnqvist 1992, 1997; Rowe et al. 1994, 1996; Sih & Krupa 1995, 1996; Wiklund & Kaitala 1995). We also know, however, that the factors that determine optimal mating rates tend to evolve relatively rapidly. For example, three lines of evidence from research on *Drosophila* suggest that this is particularly true for male accessory substances and the corresponding female receptors (Eberhard & Cordero 1995). First, there are high levels of genetic variance in accessory substances (Prout & Clark 1996) and male accessory protein genotype is important in postmating sexual selection among males (Clark et al. 1995, 1999; Price 1997; Clark & Begun

1998). Second, comparative and molecular studies have shown that gonadal proteins evolve at high rates and that this evolution is the result of selection (Civetta & Singh 1995, 1998; Tsaur & Wu 1997; Tsaur et al. 1998). Third, and most importantly, artificial selection experiments in *Drosophila* have demonstrated the rapid coevolution of male accessory substances and female receptors (Rice 1996, 1998). Thus, since the signal–receptor system that determines many of the effects of matings on female fitness (Fig. 1) seems to evolve rapidly by antagonistic male–female coevolution (Rice 1996; Holland & Rice 1998), optimal female mating rate should evolve accordingly. Male adaptations that increase the costs of mating to females will decrease the optimal female mating rate, and female adaptations that reduce any of the various costs of mating will increase the optimal female mating rate.

The fact that mating rates beyond the optimum in general tend to be deleterious to female insects strongly suggests that sexual conflicts over the mating rate (Parker 1979, 1984; Hammerstein & Parker 1987; Arnqvist 1997) are much more prevalent and persuasive than previously thought. Two types of conflict can be distinguished (Parker 1984), representing different deviations from the optimal mating rate for females. First, males should generally be selected to seduce (Holland & Rice 1998), entice (Vahed 1998) or coerce (Clutton-Brock & Parker 1995; Arnqvist 1997) already mated females to mate above their optimum, and females should often be selected to resist such attempts (Arnqvist & Rowe 1995; Holland & Rice 1998; S. Gavrilets, G. Arnqvist & U. Friberg, unpublished data). Second, males should generally be selected to induce nonreceptivity in females after mating (e.g. Simmons & Siva-Jothy 1998), thus potentially inducing females to mate below their optimum (see discussion below). Such conflicts and the resultant antagonistic male–female coevolution are likely to be at least partly responsible for the rapid evolution of male accessory ejaculate substances and the corresponding female receptors (Rice 1996; Rice & Holland 1997; Parker & Partridge 1998) as well as for the evolution of male traits that aid in sexual coercion (Arnqvist 1989b; Thornhill & Sauer 1991; Sakaluk et al. 1995; Westlake & Rowe, in press) and female traits that reduce the costs of male harassment (Arnqvist & Rowe 1995). Because of the prevalence of conflicts over the mating rate, our results also suggest that antagonistic seduction/enticement by males may, more generally, be key in the evolution of many classical male display traits, including not only various acoustic, vibratory, sensory, olfactory and/or visual signals but also nuptial offerings (e.g. food items captured by the male; see Vahed 1998), and in the presumed evolution of female resistance to these (Choe & Crespi 1997; S. Gavrilets, G. Arnqvist & U. Friberg, unpublished data).

Nutritional Ejaculates: Nuptial Gifts or Medea Gifts?

The evolution of female mating rate is particularly intriguing in species in which males provide females with so-called nuptial gifts. Our analyses revealed that female reproductive fitness in general increases markedly and monotonically with increased mating rate both in Lepidopterans and Orthopterans, and the general deleterious effects of elevated mating rate found in other insects could not be detected in these groups (but see Cook 1999). Thus, in light of the 35–85% increase in net reproductive fitness experienced by remating females, the maintenance of polyandry is easily understood. The puzzle is rather what constrains the actual mating rate of females in these groups. This problem becomes even more obvious when realized female mating rates are considered. Butterflies are unusual in that we can easily assess natural female mating rate by simply counting the number of spermatophores that wild-caught females carry inside their reproductive tract. Females have been shown to benefit from male ejaculates in several butterfly genera, for example *Colias* (Rutowski et al. 1987), *Papilio* (Watanabe 1988), *Danaus* (Oberhauser 1989) and *Pieris* (Wiklund et al. 1993b). Yet, natural average female mating frequencies in these genera average fewer than two matings per female in the field (Svärd & Wiklund 1988; Wiklund & Forsberg 1991; Karlsson 1995). The true puzzle in species with nuptial gifts is thus why females do not mate more frequently than they actually do, even when experimentally given continuous access to virgin males (Wiklund et al. 1993b; Kaitala & Wiklund 1994). The evolution of monandry (Svärd & Wiklund 1989; Bissoondath & Wiklund 1995) in these insects is currently very poorly understood.

The evolutionary origin and maintenance of nuptial gifts in insects have been the subjects of many empirical studies and of much debate (see Vahed 1998 for a recent review). The experiments synthesized here all concern the current effects of multiple mating, and the main goal of our analyses was to address the evolutionary maintenance of polyandry (see above). Nevertheless, our results can also shed some light on the potential origin of polyandry and nuptial gifts (Reeve & Sherman 1993). The classical view suggests that nutritional investments by males could represent either a paternal investment (Thornhill 1976) or mating effort (Wickler 1985). Males of several species have been shown to benefit from producing large gifts both in terms of increased offspring quality and quantity and in terms of increased relative fertilization success, in apparent accordance with these hypotheses. Although Parker & Simmons (1989) suggested that sexual conflict may be important for the evolutionary origin of nuptial feeding in insects, this possibility has been largely ignored.

Our results are in line with these ideas, and suggest a possible scenario in which sexual conflict over female remating rate, and the resulting antagonistic coevolution between the sexes, may be responsible for the origin and maintenance of nutritional ejaculates (see also Parker & Simmons 1989; Simmons & Gwynne 1991; Wedell 1997). Because of sperm competition, male insects are clearly selected to induce a period of nonreceptivity in females, and accessory substances in male ejaculates are indeed known to induce refractory behaviour in females (see Eberhard 1996). Such refractory behaviour may, of

course, also be beneficial for females under certain circumstances. However, if male induction of female nonreceptivity becomes overly efficient and thus compromises female interests, by reducing female mating rate and hence lowering egg production and fertility, we expect females to evolve resistance to the male refractory-inducing signals. Such female resistance could be achieved either by decreasing the physiological sensibility to male signals or by evolving an increased ability to neutralize the deleterious effects of male signals by metabolizing the transferred substances. In both cases, the refractory effects of male substances on females would tend to be dose dependent, which is indeed the general case in insects (see Eberhard 1996 for a review). Sperm competition would thus select for an increased amount of signals transferred by males (Wedell 1991, 1993a), and we expect females to counter by evolving increased resistance. Male ejaculates may thus become exaggerated by an antagonistic and perpetual coevolutionary arms race between the sexes.

Females may have secondarily evolved an ability to exploit this coevolutionary interaction so that proteins that serve to induce female refractory behaviour in the interest of males are instead metabolized by females and used in somatic maintenance and/or the production of eggs (Boggs 1990, 1995; Wedell 1993b; Wiklund et al. 1993a, b; Vahed 1998), an ability that exists in many insects without elaborate and enlarged ejaculates (Markow & Akney 1984; Boucher & Huignard 1987; Markow et al. 1990; Chapman et al. 1994; Eisner et al. 1996; Pitnick et al. 1997; Vahed 1998; Rooney & Lewis 1999). Several authors have suggested that female use of male-derived substances may be an incidental side-effect of a gift that functions as mating effort (Quinn & Sakaluk 1986; Eberhard 1996; Pitnick et al. 1997; Vahed 1998). We suggest, in contrast, that this effect is not incidental but that it represents a key element in female counter adaptation: females may evolve resistance to male molecular manipulation by actively metabolizing, and thus neutralizing, potentially harmful substances provided by males.

The coevolutionary scenario described above is directly supported in insects with nuptial gifts not only by the seemingly lower than optimal mating rates in females (see above) and the greatly exaggerated size of male ejaculates (up to on average 15% of male body weight in Lepidopterans (Svärd & Wiklund 1989) and 30% in Orthopterans (Wedell 1993a)), but also by ample experimental evidence of positive dose dependency in the refractory-inducing effect of substances in male ejaculates in such species (e.g. Gwynne 1986; Oberhauser 1989; Wiklund & Kaitala 1995; Torres-Vila et al. 1997). Comparative studies are also in agreement with these ideas: several studies have documented a positive relationship between female mating rate, or the degree of female polyandry, and the relative size of the male ejaculate (Svärd & Wiklund 1989; Gage 1994; Bissoondath & Wiklund 1995; Karlsson 1995, 1996; but see Wedell 1993a). Such positive covariance between male traits and female resistance to these traits is predicted under sexually antagonistic coevolution (Hammerstein & Parker 1987; Rice & Holland 1997; Holland & Rice 1998; Parker & Partridge 1998; S. Gavrilets, G. Arnqvist & U. Friberg,

unpublished data), but clearly not under the paternal investment hypothesis (see Vahed 1998, and references therein). Furthermore, the presence of sharp and strongly sclerotized teeth or spines in the bursa copulatrix of female butterflies (signum or lamina dentata) and the often tensile, thick and strong wall of male spermatophores are also both in accordance with such an intraspecific Red Queen scenario.

Three recent experimental findings in polyandrous butterflies lend further support to the sexual conflict hypothesis. First, the rate of spermatophore breakdown in butterfly females is surprisingly low (S. Lindfors & C. Wiklund, personal communication), indicating that spermatophores are not easily metabolized by females. A time span of 1–2 weeks is typically required to reduce ejaculate weight by 50%. It also seems that female size covaries with mating rate in natural populations (C. Wiklund, personal communication). Both findings suggest that spermatophore volume per se may contribute to constraining female remating rate (cf. Nilakhe 1977). Second, Andersson et al. (in press) showed that *Pieris napi* males transfer a highly aromatic substance with the spermatophore that renders females unattractive to subsequent mates. While previously mated females clearly gain from being compliant to courting males, the aromatic substance repels the potential mates, thus suggesting sexual conflict over female remating. Third, two recent studies of gift-giving species (Wedell 1996; Karlsson 1998) have shown that females that receive larger volumes of ejaculate substances increase their lifetime egg production as a result not only of the larger amounts of nutrients transferred by males but also of a higher female reproductive investment. This suggests a dose-dependent female response to male gonadotropic substances in the ejaculate, setting the scene for male exploitation of the female reproductive system and the evolution of female resistance to male manipulations. Males could, in effect, attempt to manipulate females into allocating a higher than optimal share of resources to immediate gamete production. Such sexual conflicts over female reproductive rate will, of course, generate coevolutionary scenarios similar to those of conflicts over female mating rate described above.

In conclusion, nuptial gifts may be a very misleading term for the protein-rich and voluminous ejaculates of many insects, since the evolutionary origin and maintenance of greatly enlarged and elaborate ejaculates may be the result of sexual conflict, manipulation and extortion rather than sexual confluence. They may in fact represent manipulative and sinister superstimuli, or Medea gifts, rather than amicable and nutritional meals. (Medea was a sorceress and the daughter of Aeëtes, king of Colchis. When Jason, the father of Medea's children, fell in love with Glauce, the daughter of King Creon of Corinth, Medea sent Glauce a beautiful but poisoned crimson robe, embroidered with gold and pearls, as a gift, thereby killing her rival.)

Future Research

Most studies of female polyandry in insects have been designed to determine whether female multiple mating is beneficial for females. Our results strongly suggest that

this is not a viable empirical path, since it is clear from our analyses that females generally gain directly from polyandry in terms of increased lifetime offspring production. The maintenance of polyandry is thus not a paradox in itself. The main issues that are currently poorly understood, partly because of the dualistic view of monandry/polyandry in the past, are: (1) the optimal female mating rates under various environmental conditions; (2) the actual female mating rates in natural populations; and (3) the factors that affect the evolution of optimal female mating rates

Experiments determining optimal female mating rates should preferably be performed under conditions where abiotic and biotic factors can be controlled. Females should be mated at a wide range of rates and female reproductive performance should be monitored continuously. Great effort should be made especially at achieving experimental treatments with very high mating rates, as generating a higher than optimal female mating rate is essential but may often be laborious (cf. Fig. 2). To separate the effects of mating rate on female fitness that are due to variance in reproductive rate, fertility and/or longevity, both egg production and egg hatching rate data should be recorded and female reproduction monitored throughout the entire life span of females. Without such data, it is not possible to address the effects of female mating rate on net reproductive fitness. Matings should also be evenly distributed in time, as the temporal distribution of matings per se is likely to affect the outcome of experiments (Markow 1985).

If females are found to mate at a higher than the estimated optimal rate, this might in theory be due either to antagonistic seduction/enticement (Holland & Rice 1998; S. Gavrilets, G. Arnqvist & U. Friberg, unpublished data) or sexual coercion (Clutton-Brock & Parker 1995; Arnqvist 1997) by males, or to additional indirect genetic benefits for females (Yasui 1998). The latter, but not the former, assumes that females will experience a net fitness gain mediated via offspring quality. The importance of these two alternatives could thus be tested for by including the growth rate, survival rate and reproductive success of offspring in measures of female fitness, and subsequently comparing the net performance of females mated at a wide range of rates in natural environments (cf. Arnqvist 1989a; Tregenza & Wedell 1998). We also believe that studies of the role of antagonistic seduction/enticement for the evolution of male display traits have great potential. For example, if females vary in their level of resistance to male stimuli, and if low resistance is associated with higher than optimal mating rate in females, this implies that natural selection on female resistance is generating sexual selection on male display/stimulatory traits (Holland & Rice 1998; S. Gavrilets, G. Arnqvist & U. Friberg, unpublished data).

If, on the other hand, females are found to mate at a lower than optimal rate, this may be due to two different factors. First, the costs of mating might have been underestimated, thus inflating the estimate of optimal mating rate. This is often likely to be the case in laboratory studies, where food is plentiful and the costs of mate searching and predation risk are typically depreciated.

Second, females may be manipulated by males to restrict their mating rate below their optima under natural selection alone. This would be the case if, for example, males transfer either refractory-inducing substances or anti-aphrodisiacs that cause females to mate at a rate below their optima (see above). Distinguishing between these alternatives requires experimental manipulations of the costs of mating and/or experimental separation of the refractory-inducing effects and other effects of male ejaculates.

Most of the experiments on which our analyses are based do not distinguish between the various positive and negative effects of mating (see Fig. 1). Most importantly, when females in the control treatment are mated at regular and controlled intervals and females in the experimental treatment are subject to continuous cohabitation with males, costs generated by the male ejaculate will be indistinguishable from those stemming from the act of mating itself (but see Opp & Prokopy 1986; Chapman et al. 1993, 1995, 1998, for exceptions). Thus, we are unable to unveil any general causal mechanism behind the direct fitness reduction of females at high mating rates. To distinguish between the possible causes, innovative studies are needed that employ artificial selection (Rice 1996), phenotypic (Opp & Prokopy 1986; Chapman et al. 1995, 1998) or genotypic (Chapman et al. 1993) manipulations and/or novel experimental techniques (Watson et al. 1998).

With regard to the evolution of nuptial feeding in insects, studies focusing on the potential role of sexually antagonistic coevolution may yield particularly interesting insights. Both experimental studies, addressing the maintenance, and comparative studies, addressing the origin, of insects with nutritional ejaculates are needed. One obvious task for future experimental research is to identify the substances in the 'gift' and to determine their effects on female reproductive behaviour (Vahed 1998; Andersson et al., in press). For example, Kingan et al. (1995) recently showed that a polypeptide in the spermatophore of *Helicoverpa zea* (Lepidoptera) acts directly or indirectly on female glandular tissue, thereby inducing refractory behaviour in females. Since the gonadotropic hormones are known to differ between Lepidopterans (Ramaswamy et al 1997), comparative studies could compare female endogenous hormones with the substances in male ejaculates across groups. A correlation would imply that males are selected to manipulate females by transferring hormonal 'mimics' (Eberhard & Cordero 1995), rather than arbitrary protein substances. We believe that studies such as these will reveal a central role for sexual conflicts even in these mating systems, which for long have been seen as prime examples of sexual confluence and cooperation (Thornhill 1976; Vahed 1998).

Acknowledgments

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Appendix

Table A1. Experimental studies in which the reproductive performance of female insects mated less frequently (C) and more frequently (E) have been compared

Order	Family	Genus	Species	Nuptial feeding	Food level	Duration of experiment	Male cohabitation	Experimental type	N C	N E	Average number of eggs C	Average number of eggs E
Coleoptera	Anobiidae	*Stegobium*	*paniceum*	0	1	1	1	3	53	51	51.6	32.5
	Bruchidae	*Acanthoscelides*	*obtectus*	0	1	0	0	1	92	86	57.5	78.4
				0	1	0	0	1	69	98	43.1	79.8
		Bruchus	*quadrimaculatus*	0	1	1	1	2	10	10	59.0	79.3
		Callosobruchus	*analis*	0	1	1	0	1	35	36	41.5	59.3
			maculatus	0	1	0	0	1	20	16	93.0	99.0
				0	1	0	1	1	10	10	93.0	93.9
				0	0	1	1	2	48	53	67.9	61.5
				0	0	1	0	1	98	81	85.4	93.1
				0	1	1	0	1	45	37	127.7	142.7
				0	1	1	0	1	40	61	106.7	118.5
				0	1	1	0	1	22	16	52.4	74.6
			subinnotatus	0	1	1	0	1	20	20	95.7	108.6
				0	1	1	0	1	20	20	95.7	92.9
	Cerambycidae	*Hylotrupes*	*bajulus*	0	1	1	0	1	29	14	195.8	195.3
		Tetraopes	*tetraophthalmus*	0	1	0	0	1	21	28	49.3	91.9
	Chrysomelidae	*Labidomera*	*clivicollis*	0	1	0	0	1	13	18	338.7	305.8
		Oulema	*melanopus*	0	1	1	0	1	22	5	315.0	706.8
	Coccinellidae	*Henosepilachna*	*pustula*	0	1	1	0	1	5	7	336.4	377.0
			vigintioctomaculata	0	1	1	0	1	7	3	454.1	805.0
	Curculionidae	*Anthonomus*	*grandis*	0	1	1	1	2	25	25	113.0	144.6
				0	1	1	1	3	6	6	387.5	238.0
		Cylas	*formicarius elegantulus*	0	1	1	1	2	10	10	—	—
	Dermestidae	*Attagenus*	*megatoma*	0	0	1	1	3	15	15	57.8	46.5
				0	1	1	1	3	15	15	130.1	79.7
		Trogoderma	*granarium*	0	1	1	0	1	12	7	65.7	109.3
			parabile	0	1	1	1	2	10	10	77.3	76.8
			versicolor	0	1	1	1	3	20	20	95.0	97.0
	Elateridae	*Conoderus*	*vespertinus*	0	1	1	1	3	7	6	339.0	541.0
	Scarabaeidae	*Cotinis*	*nitida*	0	0	1	0	1	25	25	26.7	27.1
				0	1	1	0	1	25	25	45.1	56.5
	Tenebrionidae	*Tribolium*	*castaneum*	0	1	0	0	1	10	7	—	—
			destructor	0	1	1	1	3	4	17	1141.0	637.2
Dictyoptera	Blattidae	*Periplaneta*	*americana*	0	1	1	1	3	10	20	22.8	28.9
				0	1	1	1	3	6	15	26.0	10.6
	Blaberidae	*Eublaberus*	*posticus*	1	1	1	0	—	12	12	—	—
				1	0	1	0	—	9	27	—	—
	Diplopteridae	*Diploptera*	*punctata*	1	1	1	0	—	44	30	2.8	3.2
				1	1	0	0	—	18	18	11.9	12.4
Diptera	Anthomyiidae	*Coenosia*	*tigrina*	0	1	1	1	2	11	7	71.3	120.7
	Culicidae	*Aedes*	*aegypti*	0	1	0	1	1	10	10	—	—
		Culex	*tarsalis*	0	1	0	1	1	10	10	242.0	285.0
	Diopsidae	*Cyrtodiopsis*	*whitei*	0	1	0	0	1	6	6	—	—
	Drosophilidae	*Drosophila*	*hydei*	0	1	0	0	1	15	15	—	—
				0	1	0	0	1	12	12	—	—
			littoralis	0	1	0	0	1	40	37	—	—
			mauritiana	0	1	1	0	1	22	22	—	—
			melanogaster	0	0	1	1	3	35	35	25.0	20.7
				0	0	1	1	3	35	35	20.2	24.1
				0	0	1	1	3	35	35	35.6	33.9
				0	1	1	1	3	35	35	56.1	58.4
				0	1	1	1	3	35	35	140.3	90.2
				0	1	0	0	1	54	45	116.0	169.7
				0	1	0	0	1	4	2	419.5	368.5
				0	1	0	0	1	6	6	408.8	323.2
				0	1	0	0	1	107	70	—	—
				0	1	0	0	1	26	26	551.0	959.0
			mojavensis	0	1	1	1	2	70	64	33.1	56.3
			montana	0	1	0	0	1	18	24	—	—
			pseudoobscura	1	1	0	0	—	12	24	49.4	31.5
				1	1	1	1	—	40	40	—	—
				1	0	1	1	—	156	198	—	—
			sechella	0	1	1	0	1	25	12	—	—
			simulans	0	1	1	0	1	49	43	—	—
			teissieri	0	1	1	0	1	17	17	—	—
	Tephritidae	*Anastrepha*	*ludens*	0	1	1	0	1	25	25	388.3	215.6
				0	1	1	0	1	25	25	46.9	107.4
				0	1	1	0	1	15	15	457.9	775.5
				0	1	1	0	1	15	15	40.3	40.7

SD eggs		Fertility rate (%)		Average number of offspring		SD offspring		Average female lifespan		SD lifespan		Source
C	E	C	E	C	E	C	E	C	E	C	E	
21.3	20.8	82.1	75.7	42.2	25.9	17.6	18.0	—	—	—	—	Barratt 1977
16.0	39.0	—	—	—	—	—	—	—	—	—	—	Huignard 1974
15.0	18.0	91.0	89.0	39.1	71.1	19.0	22.0	—	—	—	—	Huignard 1974
14.8	8.6	—	—	—	—	—	—	—	—	—	—	Brauer 1944
16.4	16.9	—	—	—	—	—	—	—	—	—	—	Wilson et al. 1999
25.3	18.5	—	—	—	—	—	—	—	—	—	—	Credland & Wright 1989
12.6	16.4	92.2	90.2	—	—	—	—	—	—	—	—	Credland & Wright 1989
15.4	15.7	—	—	—	—	—	—	—	—	—	—	Fox 1993
12.6	14.6	—	—	—	—	—	—	8.4	9.0	1.1	1.1	Fox 1993
19.7	20.5	—	—	—	—	—	—	23.5	22.0	9.2	9.3	Fox 1993
29.9	29.4	—	—	—	—	—	—	—	—	—	—	Wilson et al. 1999
32.5	33.2	—	—	—	—	—	—	—	—	—	—	Wilson et al. 1999
22.8	15.2	—	—	—	—	—	—	—	—	—	—	Mbata et al. 1997
22.8	21.5	—	—	—	—	—	—	—	—	—	—	Mbata et al. 1997
82.4	55.4	85.2	85.7	166.8	167.4	70.4	48.5	12.7	9.3	3.4	1.9	Cannon & Robinson 1981
32.5	63.0	74.5	89.5	69.5	150.3	33.0	40.0	—	—	—	—	Lawrence 1990
375.0	296.0	83.0	85.0	—	—	—	—	—	—	—	—	Dickinson 1988
144.0	262.0	63.1	72.4	—	—	—	—	30.0	57.0	15.7	21.5	Wellso et al. 1975
254.4	250.0	49.5	52.5	—	—	—	—	—	—	—	—	Nakano 1985
255.1	483.0	42.2	58.1	—	—	—	—	—	—	—	—	Nakano 1985
56.5	72.3	85.5	94.6	—	—	—	—	33.9	32.4	16.9	16.1	Mayer & Brazzel 1963
69.1	155.3	—	—	—	—	—	—	63.3	38.3	1.3	7.3	Nilakhe 1977
—	—	—	—	11.5	74.9	5.5	37.4	105.5	79.4	57.7	39.7	Mullen 1981
19.4	17.1	—	—	—	—	—	—	15.3	15.1	2.3	1.8	Kirtani & Kawhara 1963
31.8	22.9	—	—	—	—	—	—	28.4	28.8	8.1	7.6	Kirtani & Kawhara 1963
11.9	19.4	—	—	—	—	—	—	—	—	—	—	Karnavar 1972
33.2	33.2	—	—	—	—	—	—	—	—	—	—	Loschiavo 1968
26.7	26.7	75.5	75.8	—	—	—	—	12.6	11.8	3.1	3.1	Norris 1936
77.0	77.0	61.3	81.4	—	—	—	—	—	—	—	—	Turnipseed & Rabb 1963
26.0	26.5	51.8	76.3	13.8	20.7	15.0	22.0	14.9	13.9	4.5	5.0	Domek & Johnson 1991
26.0	26.5	65.7	57.4	29.6	32.4	21.0	21.0	23.1	23.0	6.5	6.5	Domek & Johnson 1991
—	—	—	—	35.5	50.4	12.3	12.4	—	—	—	—	Lewis & Austad 1994
353.6	325.5	35.0	59.0	324.0	385.4	191.0	250.0	500.0	295.0	58.3	58.5	Reynolds 1944
13.6	11.2	—	—	—	—	—	—	267.0	223.0	117.4	79.0	Griffiths & Tauber 1942
5.9	5.3		—	—	—	—	—	219.0	125.0	21.5	31.6	Griffiths & Tauber 1942
—	—	—	—	81.4	892.0	25.6	31.9	572.0	512.0	111.8	194.0	Roth 1968
—	—	—	—	25.5	35.9	11.4	31.2	239.0	244.0	60.0	52.0	Roth 1968
0.86	1.2	—	—	—	—	—	—	339.0	340.0	113.0	113.3	Stay & Roth 1958
0.8	0.6	86.0	99.0	10.2	12.3	3.9	0.6	—	—	—	—	Woodhead 1985
38.8	51.6	33.5	63.8	23.9	77.0	20.0	38.0	58.6	58.1	21.8	19.2	Morris & Cloutier 1987
—	—	—	—	94.1	184.2	18.7	26.2	—	—	—	—	Young & Downe 1982
83.0	81.0	56.7	73.7	—	—	—	—	—	—	—	—	Young & Downe 1983
—	—	—	—	18.3	25.6	16.4	16.0	—	—	—	—	Lorch et al. 1993
—	—	—	—	56.0	96.3	27.1	32.6	—	—	—	—	Markow 1985
—	—	—	—	55.3	55.2	20.5	23.5	—	—	—	—	Markow 1985
—	—	—	—	36.0	57.6	28.4	38.0	—	—	—	—	Aspi 1992
—	—	—	—	165.0	195.0	73.0	65.0	—	—	—	—	Price 1997
16.9	10.7	—	—	—	—	—	—	13.5	14.5	3.7	5.2	Chapman & Partridge 1996; T. Chapman, personal communication
8.9	16.1	—	—	—	—	—	—	18.0	21.1	10.9	9.8	Chapman & Partridge 1996; T. Chapman, personal communication
14.6	21.7	—	—	—	—	—	—	36.2	27.4	11.5	10.6	Chapman & Partridge 1996; T. Chapman, personal communication
14.6	30.1	—	—	—	—	—	—	27.5	23.2	14.4	10.9	Chapman & Partridge 1996; T. Chapman, personal communication
14.6	49.7	—	—	—	—	—	—	30.5	19.5	9.0	10.3	Chapman & Partridge 1996; T. Chapman, personal communication
30.9	39.6	—	—	—	—	—	—	—	—	—	—	Gromko & Pyle 1978
129.2	96.9	—	—	—	—	—	—	—	—	—	—	Lefevre & Jonsson 1962
65.5	35.5	—	—	—	—	—	—	—	—	—	—	Lefevre & Jonsson 1962
—	—	—	—	528.0	1053.0	264.0	526.5	—	—	—	—	Pyle & Gromko 1978
225.0	479.5	76.0	91.0	—	—	—	—	—	—	—	—	Pyle & Gromko 1978
81.0	81.0	—	—	—	—	—	—	21.2	17.1	14.5	14.5	Etges & Heed 1992
—	—	—	—	16.9	30.3	14.0	21.7	—	—	—	—	Aspi 1992
21.0	31.5	—	—	—	—	—	—	—	—	—	—	Pruzan-Hotchkiss et al. 1981
—	—	—	—	484.0	587.0	177.0	177.0	—	—	—	—	Turner & Anderson 1983
—	—	—	—	45.0	145.0	124.0	124.0	288.0	142.0	152.0	85.4	Turner & Anderson 1983
—	—	—	—	146.0	178.0	44.0	50.0	—	—	—	—	Price 1997
—	—	—	—	220.0	252.0	67.0	65.0	—	—	—	—	Price 1997
—	—	—	—	170.0	209.0	101.0	52.0	—	—	—	—	D. Joly, personal communication
371.3	247.3	74.0	85.0	—	—	—	—	39.4	27.2	23.6	18.8	Mangan 1997
110.5	157.2	13.0	53.0	—	—	—	—	61.7	50.9	39.7	37.9	Mangan 1997
367.7	800.4	67.0	67.0	—	—	—	—	55.2	50.9	30.7	22.9	Mangan 1997
119.1	111.5	72.0	70.0	—	—	—	—	123.0	76.7	61.5	45.5	Mangan 1997

Table A1. *Continued*

Order	Family	Genus	Species	Nuptial feeding	Food level	Duration of experiment	Male cohabitation	Experimental type	N C	N E	Average number of eggs C	Average number of eggs E
		Dacus	*tryoni*	0	1	0	1	1	40	40	859.6	871.2
		Rhagoletis	*cerasi*	0	1	1	1	2	13	11	209.7	188.1
			completa	0	1	0	1	1	11	14	17.2	49.1
			pomonella	0	1	1	1	3	11	4	359.0	395.0
				0	1	0	0	1	10	20	224.1	120.5
				0	1	1	0	1	27	19	52.1	143.9
				0	1	1	1	3	19	15	143.9	177.0
Heteroptera	Alydidae	*Reptortus*	*clavatus*	0	1	1	1	2	25	11	215.7	372.6
	Gerridae	*Aquarius*	*remigis*	0	1	0	0	—	10	10	51.8	57.5
		Gerris	*odontogaster*	0	1	0	1	—	11	11	35.3	44.9
	Miridae	*Antestiopsis*	*lineaticollis*	0	1	1	1	2	12	13	66.2	95.1
	Pentatomidae	*Nezara*	*viridula*	0	1	1	1	2	175	59	632.0	724.3
		Oebalus	*pugnax*	0	1	1	1	2	8	12	742.5	884.7
		Plautia	*stali*	0	1	0	1	1	26	4	140.0	221.0
	Pyrrhocoridae	*Dysdercus*	*koenigii*	0	1	0	1	1	6	6	101.5	103.8
			cardinalis	0	1	1	1	3	26	27	390.9	381.1
	Reduviidae	*Triatoma*	*brasiliensis*	0	1	1	1	2	15	15	138.3	292.9
Homoptera	Psyllidae	*Tyora*	*tessmanni*	0	1	1	0	1	10	10	48.1	48.2
Lepidoptera	Danaidae	*Danaus*	*plexippus*	1	0	1	0	—	7	6	477.7	620.1
				1	1	1	0	—	5	7	285.0	526.0
				1	1	1	0	—	12	19	640.0	678.0
	Noctuidae	*Earias*	*insulata*	1	1	1	1	—	20	21	98.0	374.0
		Pseudaletia	*unipuncta*	1	1	1	0	—	23	24	1618.0	2043.0
		Trichoplusia	*ni*	1	1	1	0	—	12	10	1376.0	1708.0
				1	1	1	0	—	24	17	1470.0	1799.0
	Papilionidae	*Papilio*	*xuthus*	1	1	0	0	—	22	15	37.6	50.1
	Pieridae	*Pieris*	*napi*	1	1	1	1	—	22	25	284.3	489.7
				1	0	1	1	—	13	11	149.0	375.0
				1	1	1	0	—	10	7	342.0	461.0
				1	1	1	1	—	7	7	320.8	501.7
	Pyralidae	*Plodia*	*interpunctella*	1	0	1	0	—	32	26	222.6	137.7
	Saturniidae	*Antheraea*	*mylitta*	1	1	0	0	—	30	30	215.2	282.4
	Tortricidae	*Epiphyas*	*postvittana*	1	1	1	1	—	40	40	493.0	623.0
Orthoptera	Acrididae	*Chorthippus*	*brunneus*	1	0	0	1	—	14	10	0.250	0.411
				1	1	0	1	—	10	13	0.441	0.477
		Eyprepocnemis	*plorans*	1	1	0	1	—	10	8	2.2	5.4
	Gryllidae	*Acheta*	*domesticus*	1	0	1	0	—	56	27	—	—
				1	1	1	1	—	26	23	—	—
		Allonemobius	*socius*	1	1	1	0	—	15	9	240.6	265.8
		Gryllodes	*sigillatus*	1	1	1	1	—	15	15	—	—
				1	0	1	1	—	15	15	—	—
				1	1	0	0	—	6	6	1451.0	2328.0
		Gryllus	*bimaculatus*	1	0	1	0	—	10	10	2256.0	2663.0
			integer	1	0	1	0	—	8	8	—	—
				1	1	1	0	—	22	44	—	—
			veletis	1	1	1	1	—	15	15	—	—
				1	0	1	1	—	15	15	—	—
		Truljalia	*hibinonis*	1	1	0	0	—	20	19	213.3	200.6
	Tettigoniidae	*Conocephalus*	*nigropleurum*	1	1	1	0	—	8	7	30.6	65.1
		Requena	*verticalis*	1	1	0	0	—	12	13	45.8	70.7
Plecoptera	Perlodidae	*Megarcys*	*signata*	0	1	1	1	2	20	20	267.9	202.0
Trichoptera	Leptoceridae	*Mystacides*	*azurea*	0	1	1	0	1	19	17	61.6	67.3
Zoraptera	Zorotypidae	*Zorotypus*	*barberi*	1	1	0	0	—	20	70	6.6	17.7

SD eggs		Fertility rate (%)		Average number of offspring		SD offspring		Average female lifespan		SD lifespan		Source
C	E	C	E	C	E	C	E	C	E	C	E	
86.8	96.7	92.1	92.3	—	—	—	—	—	—	—	—	Barton Brown 1957
111.3	138.1	34.0	95.0	—	—	—	—	29.3	23.8	8.4	8.2	Boller 1966
108.0	108.0	29.0	76.0	—	—	—	—	—	—	—	—	Telang et al. 1996
157.9	50.9	46.1	94.7	165.8	373.8	73.6	45.7	120.6	106.8	29.1	35.6	Neilson & McAllan 1965
168.9	111.4	—	—	—	—	—	—	—	—	—	—	Myers et al. 1976
46.8	126.4	13.4	16.5	—	—	—	—	38.6	80.7	21.0	23.3	Opp & Prokopy 1986
126.4	147.2	16.5	43.9	—	—	—	—	80.7	52.3	23.3	25.2	Opp & Prokopy 1986
84.3	133.4	48.4	47.3	104.4	176.4	62.9	116.4	77.4	89.1	520.3	14.7	Sakurai 1996 a, b
13.6	10.8	88.5	89.4	45.8	51.4	4.4	5.0	—	—	—	—	D. J. Fairbairn, personal communication
11.3	24.8	94.0	96.0	—	—	—	—	—	—	—	—	Arnqvist 1989a
109.0	107.0	67.8	69.9	—	—	—	—	60.5	80.3	40.9	23.1	Abasa 1973
451.4	355.1	—	—	—	—	—	—	—	—	—	—	McLain et al. 1990
	94.8	386.4	68.2	92.2	—	—	—	48.8	48.2	13.3	13.3	Nilakhe 1976
41.0	6.0	47.0	57.0	65.8	125.9	19.2	3.4	—	—	—	—	Mau & Mitchell 1978
41.4	38.8	86.3	95.0	—	—	—	—	—	—	—	—	Harwalkar & Rahalkar 1973
35.5	29.7	—	—	—	—	—	—	26.5	19.2	5.8	3.9	Kasule 1986
144.0	285.0	93.3	59.9	—	—	—	—	201.4	164.1	247.0	139.0	Brasileiro 1982
8.6	8.4	—	—	—	—	—	—	—	—	—	—	Igboekwe & Adenuga 1983
151.1	194.9	79.3	81.6	378.8	506.0	137.0	165.0	35.6	28.1	2.7	3.8	Oberhauser 1989
250.4	181.5	81.7	84.6	232.8	445.0	206.0	167.0	26.7	29.1	7.1	2.9	Oberhauser 1989
326.0	572.0	—	—	—	—	—	—	—	—	—	—	Svärd & Wiklund 1988
87.0	187.0	64.5	72.6	63.0	272.0	60.0	162.0	15.5	21.5	3.5	5.3	Tamhankar 1995
472.0	514.0	85.0	81.2	1375.0	1659.0	429.0	503.0	15.8	18.8	2.7	2.9	Svärd & McNeil 1994
305.0	285.0	—	—	—	—	—	—	18.4	14.0	3.6	3.5	Ward & Landolt 1995
269.0	371.0	—	—	—	—	—	—	14.7	15.3	4.1	2.8	Ward & Landolt 1995
18.0	23.0	88.0	92.0	—	—	—	—	—	—	—	—	Watanabe 1988
142.8	130.8	—	—	—	—	—	—	17.0	23.0	8.6	6.1	Wiklund et al. 1993a; C. Wiklund, personal communication
108.0	189.0	—	—	—	—	—	—	—	—	—	—	Wiklund et al. 1993a; C. Wiklund, personal communication
152.0	111.0	—	—	—	—	—	—	18.3	24.3	6.6	3.4	Wiklund et al. 1993b
96.0	46.8	—	—	—	—	—	—	13.3	20.0	3.6	4.0	Karlsson 1998
96.2	158.0	91.5	91.0	—	—	—	—	9.4	9.1	1.9	2.5	Cook 1999; P. A. Cook, personal communication
17.3	22.6	72.1	95.6	155.1	270.1	22.0	24.0	—	—	—	—	Ravi Kumar et al. 1995
316.0	246.0	62.2	57.7	307.0	359.7	342.0	378.0	17.2	17.4	5.1	4.4	Danthanarayana & Gu 1991
0.056	0.030	—	—	—	—	—	—	—	—	—	—	Butlin et al. 1987
0.058	0.106	—	—	—	—	—	—	—	—	—	—	Butlin et al. 1987
2.0	2.0	84.0	92.0	—	—	—	—	—	—	—	—	Pardo et al. 1995
—	—	—	—	61.9	87.3	62.2	62.3	—	—	—	—	Sakaluk & Cade 1980
—	—	—	—	512.9	745.3	323.4	425.4	—	—	—	—	Sakaluk & Cade 1983
101.6	198.6	—	—	—	—	—	—	46.1	35.8	16.4	11.3	P. Lorch, personal communication
—	—	—	—	473.3	600.1	340.1	419.0	49.8	58.6	18.3	18.0	Burpee & Sakaluk 1993
—	—	—	—	37.7	63.3	25.5	48.1	12.6	25.3	1.5	2.5	Burpee & Sakaluk 1993
410.0	248.0	—	—	—	—	—	—	—	—	—	—	Subramaniam et al. 1988
855.0	1102.0	30.1	54.8	—	—	—	—	44.5	39.3	10.8	14.8	Simmons 1988
—	—	—	—	121.0	172.5	136.8	107.5	—	—	—	—	Sakaluk & Cade 1980
—	—	—	—	485.2	834.2	354.8	515.4	—	—	—	—	Sakaluk & Cade 1983
—	—	—	—	17.7	56.4	35.4	126.4	55.6	62.7	14.3	16.5	Burpee & Sakaluk 1993
—	—	—	—	—	—	—	—	20.0	21.8	4.1	3.5	Burpee & Sakaluk 1993
46.5	28.6	—	—	—	—	—	—	—	—	—	—	Ono et al. 1995
29.3	24.7	—	—	—	—	—	—	53.9	69.1	13.5	16.1	P. Lorch & L. Bussière, personal communication
10.7	16.9	—	—	—	—	—	—	—	—	—	—	Gwynne 1984
127.2	69.5	—	—	—	—	—	—	22.3	16.3	7.5	7.4	Taylor et al. 1998
25.4	32.0	93.0	97.8	57.3	65.8	31.4	24.4	3.9	3.6	3.1	2.4	Petersson 1991
5.0	6.0	—	—	—	—	—	—	—	—	—	—	Choe 1995