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Evolutionary significance of promiscuity in an aphidophagous ladybird, *Propylea dissecta* (Coleoptera: Coccinellidae)

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Abstract

The short- and long-term consequences of monogamy and promiscuity in an aphidophagous ladybird, *Propylea dissecta* (Mulsant) in terms of reproductive performance and offspring fitness were investigated. Promiscuous females were more fecund and laid more viable eggs than monogamous ones. Amongst promiscuous females, those mated with multiple males (freedom for mate choice) had significantly higher reproductive output than those mated daily with a new unmated male. The increased reproductive output of females mated with an unmated male each day in comparison to monogamous ones might possibly be a result of their increased ejaculate size. The further increase in reproductive output, when a female was allowed to choose a mate, may be because of repeated preferential mating with the fitter males. Results on long-term consequences of promiscuity revealed faster development and increased survival in offspring of promiscuous females at 25, 27 and 30°C. The percent adult emergence was more strongly influenced than development by the mating regime. There were no statistically significant differences in survival of offspring of promiscuous females (mate choice) at the three temperatures, while the percent survival of offspring of monogamous females differed significantly. Offspring of promiscuous females (mate choice) were fittest in terms of development and survival, which indicates their probable better genetic constitution and subsequently that of chosen mates. Thus, promiscuity has both short- and long-term benefits and is advantageous to ladybirds. The presence of long-term benefits in terms of fitter offspring probably indicates the evolutionary rationale behind the prevalence of promiscuity in ladybirds.

Keywords: promiscuity, evolution, *Propylea dissecta*, ladybirds

Introduction

Female mating patterns have broad implications for conflicts of interest between the sexes (Parker, 1979), sexual selection (Eberhard, 1996), and speciation (Arnqvist *et al*., 2000) yet they are not so well understood. Repeated matings and promiscuity are well-recorded phenomena in insects and their occurrence has been of great interest to scientists the world over. This is so because matings are known to have high costs, such as time and energy consumption (Thornhill & Alcock, 1983), increased predation risk owing to decreased vigilance (Arnqvist, 1989), increased risk of disease transmission (Hurst *et al*., 1995) and decrease in longevity (Chapman *et al*., 1995; Omkar and G. Mishra, unpublished data), yet repeated matings occur in nature. However, in those insect species where females benefit through either nutritional gifts or protection or parental care by the male, repeated matings seem advantageous (Fox *et al*., 1995; Eberhard, 1996; Arnqvist & Nilsson, 2000; Hosken & Stockley, 2003). In recent years, research has revealed numerous other direct and indirect genetic benefits associated with increased number of matings.

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The increased benefits in comparison to the costs of repeated matings explain their occurrence in insects. What is still not clear is why do females not usually mate repeatedly with a single male and why with multiple males? This is despite the fact that in most insect species, females are not known to derive many benefits from promiscuity but rather, frequently incur direct costs (Chapman *et al*., 1995; Blanckenhorn *et al*., 2002). Exposure to more males is likely to make the female more susceptible to increased time and energy expenditure, disease transmission and genetic incompatibility.

Nevertheless, promiscuity is widespread, with females mating with multiple males (Birkhead & Møller, 1998). The possible reason behind this widespread incidence of promiscuity in female insects in the absence of direct benefits, is the presence of indirect benefits to the offspring (Jennions & Petrie, 2000; Tregenza & Wedell, 2002; Hosken & Stockley, 2003; Hosken *et al*., 2003). One hypothesis discusses promiscuity as a means to avoid costs of inbreeding depression, leading to increased egg viability (Tregenza & Wedell, 2002), and fitter offspring of higher quality (Sakaluk *et al*., 2002; Hosken *et al*., 2003).

The production of high quality offspring by promiscuous females has been attributed to a probable correlation between the male's success in sperm competition and genetic quality; with the sperm of more successful males being of higher genetic quality, i.e. the good sperm hypothesis (Birkhead *et al*., 1993; Hosken *et al*., 2003). Offspring of such males might be more competitive/attractive (sexy sons) or may be genetically more viable (good genes) (Jennions & Petrie, 2000). Though these hypotheses have not yet been subjected to extensive experimentation, there have been reports both for (Madsen *et al*., 1992; Hosken *et al*., 2003) and against (Olsson *et al*., 1996; Simmons, 2001).

Despite the interest in promiscuity in insects, the benefits thereof and the reasons for its occurrence are still not clear. In ladybirds, this aspect still remains untouched, despite their highly promiscuous nature (Majerus, 1994). Repeated matings as such have been well studied in ladybirds (Bind, 1998; Omkar & Srivastava, 2002; Omkar, 2004; Omkar & James, 2005; Omkar & Pervez, 2005) but studies on promiscuity are still lacking. It was therefore decided to undertake a study on the evolutionary significance of the occurrence of promiscuity in ladybirds, with emphasis on both the possible direct and indirect benefits. For the purpose, an Oriental, aphidophagous locally abundant ladybird, *Propylea dissecta* (Mulsant) (Coleoptera: Coccinellidae) was selected as the experimental model. The primary reason behind its selection as an experimental tool was its prominent sexual dimorphism (Omkar & Pervez, 2000) and relatively scarce literature (Omkar & Mishra, 2003, 2005; Omkar & Pervez, 2003, 2005; Mishra & Omkar, 2004a,b, 2005; Pervez & Omkar, 2003, 2004a,b,c; Pervez *et al*., 2004).

Materials and methods

Maintenance of stock

Adults of *P. dissecta* were collected from the agricultural fields in the suburbs of the city of Lucknow, India, brought to the laboratory and reared in pairs on an *ad libitum* supply of *Aphis craccivora* Koch (Hemiptera: Aphididae) from bean (*Dolichos lablab* L.) in Petri dishes (9.0 × 1.5 cm) at 25 ± 2°C and 65 ± 5% R.H. The pairs were checked daily for oviposition, the eggs collected and observed for hatching. The neonates were transferred to muslin-covered beakers containing *A. craccivora* and reared till adult eclosion. Rearing was continued and the emerging F_2 adults were sexed and isolated on the basis of pronotal characteristics (Omkar & Pervez, 2000). The F_2 adults were used for experiments to dilute the possible effects of variations in fitness owing to varying diets of field collected adults.

Experimental design

Reproductive performance

Three experiments were designed by modifying the method of Sakaluk *et al*. (2002) for studying effects of monogamy and promiscuity in *P. dissecta*. The experiments were: (i) 5-day-old virgin female paired with a 5-day-old unmated male, allowing only a single mating per day (monogamous, limited matings); (ii) 5-day-old virgin female provided daily with a new unmated male of the same age as female (allowing change in male age with female age) for a single mating (promiscuous, no-choice); and (iii) 5-day-old female paired with five 5-day-old unmated males, thus allowing free will to choose her mate (promiscuous, mate choice). The mating treatments were maintained for five days. Though the last experiment seemingly allowed unlimited matings, there is very little chance of such an occurrence because of the observation of not more than a single prolonged mating (5–6 h) in a day (Mishra & Omkar, 2004a); thus the probability of a total of approximately 5–6 matings in the experimental duration was high. The pairs were formed in Petri dishes (9.0 × 1.5 cm) and were provided *ad libitum* with *A. craccivora* (most preferred; Omkar & Mishra, 2005) on *D. lablab* twigs (25 ± 2°C; 65 ± 5% R.H.). After the five-day mating treatment, the females were isolated and observations on daily oviposition and percent egg viability for all the experiments made for 20 days post-treatment. There were ten replicates per experiment with individuals in a single Petri dish forming a replicate.

Offspring fitness

For the purpose of studying the long-term effects of monogamy and promiscuity, offspring fitness in terms of development and survival was studied at three different temperatures, 25, 27 and 30°C.

Fifty eggs were selected randomly from each of the three mating treatments and placed at each of the three temperatures (25, 27 and 30°C). They were observed for hatching and the neonates placed in a beaker (6.5 × 9.5 cm) covered with muslin fastened with a rubber band, at a maximum of five insects per beaker to avoid overcrowding, with one beaker constituting a replicate. A total of ten beakers containing a maximum of five larvae each were placed at the three temperatures. Insects were provided with an *ad libitum* supply of aphid *A. craccivora* on the twigs of *D. lablab*. The duration required for development from egg to adult emergence (observations taken twice every 24 h) and the number of individuals surviving were recorded. Since there were five insects per beaker, the mean values per beaker were considered as observation of a replicate.

Table 1. Effect of monogamy and promiscuity on reproductive performance of *Propylea dissecta*.

Treatments	Fecundity	Percent egg viability
5 matings, 1 male	455.00 ± 26.36a	83.13 ± 2.07a
5 matings, 5 males	516.20 ± 23.57b	88.81 ± 3.29b
Unlimited matings, 5 males (mate choice)	561.50 ± 14.80c	95.32 ± 1.99c
F-value	108.24	96.62

Values are mean ± SD.

Statistical analysis

Data on fecundity and percent egg viability were subjected to one-way ANOVA and post hoc comparison of means using Tukey's test of significance. All percent data were subjected to arcsine square root transformation to normalize the data prior to being subjected to ANOVA. Treatment effects were assessed with respect to two measures of offspring fitness: total developmental time (duration from egg to adult emergence) and percent adult emergence (percentage of adults emerging from the initial egg batch). To examine the effects of female promiscuity and offspring rearing environment, the data were subjected to two-way ANOVA with mating treatments as row factor and temperature regimes as column factor. Analyses within mating treatments and within temperature regimes were also conducted. All analyses were done using statistical software MINITAB.

Results

Reproductive performance

There were statistically significant differences in fecundity of experimental females across the mating treatments ($F = 108.24$; $P < 0.001$; table 1), with promiscuous females having mate choice being highly fecund in comparision to the monogamous females with limited matings. Comparison within the two promiscuous groups revealed that females with mate choice had significantly greater egg output than those with no mate choice (table 1). The differences in individual means of fecundity across the three treatments were significant.

The percent viability of eggs was also significantly affected by the mating treatment ($F = 96.62$; $P < 0.001$; table 1). Eggs of females that mated with different males and also had multiple mate choice were most viable while monogamous ones with limited matings laid least viable eggs. The differences between individual means across treatments were significant for all the three experiments, as revealed by comparison of means (table 1).

Offspring fitness

The developmental time changed significantly in response to both mating treatments ($F = 13.34$; $P < 0.001$) and temperature regimes ($F = 311.00$; $P < 0.001$) (table 2). The interaction between these two was, however, not significant ($F = 1.73$; $P > 0.05$). The number of neonates surviving till adult emergence were also significantly influenced by the mating treatments ($F = 11.90$; $P < 0.001$) and temperature regimes ($F = 23.07$; $P < 0.001$). There was a small but statistically significant interaction between temperature regime and mating treatments on the percent adult emergence ($F = 5.37$; $P < 0.01$); separate analyses of treatment effects within temperature regimes failed to identify the source of interaction.

Both the mating treatments and temperature regimes significantly affected the development and percent adult emergence. Specifically, while the increase in temperature led to a statistically significant decline in developmental time of immature stages of a mating treatment, the development of immature stages at a particular temperature was fastest in the offspring of promiscuous females with mate choice and slowest in offspring of monogamous females (fig. 1). In the case of percent adult emergence, the maximum emergence was seen at 27°C in all mating treatments. However, at each temperature, the highest survival was found for the offspring of promiscuous females (fig. 2). The differences in percent adult emergence of offspring of promiscuous females with mate choice were not statistically significant at the three temperatures (fig. 2).

Discussion

The results reveal that promiscuous females had high fecundity and percent egg viability, thus revealing apparent short-term benefits of promiscuity. Increase in number of eggs with repeated matings is well documented (Fox *et al.*, 1995; Eberhard, 1996; Omkar & Srivastava, 2002; Omkar, 2004), but the effects of promiscuity have not yet been confirmed, at least in ladybirds.

The decreased fecundity and percent egg viability in monogamous *P. dissecta* even after repeated matings may be a result of the decreased ejaculate size of males on being subjected to subsequent matings, as has been previously reported for other insects (Fox *et al.*, 1995; Savalli & Fox, 1999). It is possible that females in nature may preferentially select quality mates by mating more often or by mating each time with unmated ones, so as to increase her reproductive fitness and the number and quality of offspring

Table 2. Effect of mating treatments and temperature regimes on offspring fitness in *Propylea dissecta*.

Variable	Source	df	MS	F	*P* values
Developmental time	Mating treatment	2	1.76	13.34	< 0.001
	Temperature regime	2	41.05	311.00	< 0.001
	Treatment × temperature	4	0.23	1.73	> 0.05
Adult emergence	Mating treatment	2	364.20	11.90	< 0.001
	Temperature regime	2	706.00	23.07	< 0.001
	Treatment × temperature	4	164.30	5.37	< 0.01

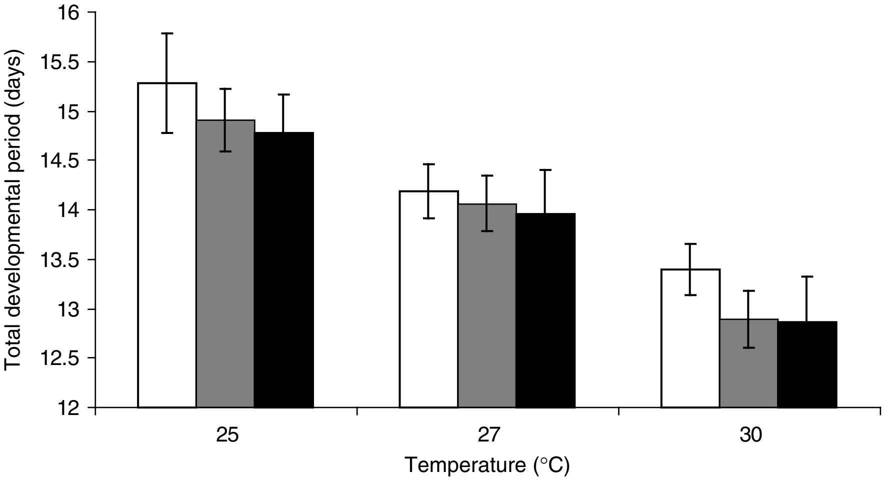

Fig. 1. Total developmental period of offspring of *Propylea dissecta* subjected to monogamy and promiscuity at three temperatures: □, monogamous setup with five matings; ▨, promiscuous setup with five matings; ■, promiscuous setup with mate choice.

(Fox & Hickman, 1994). The status of males in some insects is determined by the quality and quantity of ejaculate size (Savalli & Fox, 1999). The quality is determined by genetic composition of individuals and intra- as well as inter-specific variations (Sakaluk & Smith, 1998; Schaus & Sakaluk, 2002), while quantity is mating history dependent (Fox *et al*., 1995; Savalli & Fox, 1999). This variation in male ejaculate size may be responsible for mate choice as well as the reproductive output. It is also likely that a female that has mated with males having small ejaculate size might go on to mate again more rapidly to fulfill her sperm/nutritional requirements.

Female *P. dissecta* which mated with five males provided one at a time had lower fecundity and egg viability than those paired with five males (all males together), i.e. promiscuity along with probable mate choice increased reproductive output. It is possible that the latter females may have mated with the more desirable and potent males more than once to increase her fitness and number of progeny. Thus, the higher levels of fecundity and percent egg viability could be a possible result of repeated matings with higher quality males in the group. Though this experimental treatment allows the female to exercise her opportunity to mate with multiple mates, it may not always be the case. Selective matings, if they occur, may be a result of either female choice based on male quality or of male competition. The latter reason seems more plausible in *P. dissecta*, where copulation is a male dominated event, with young females being forced to mate by older males despite their reluctance, at least under laboratory conditions (Omkar & Pervez, 2005). During forced matings with a different male each time, it is possible that there might have been genetic

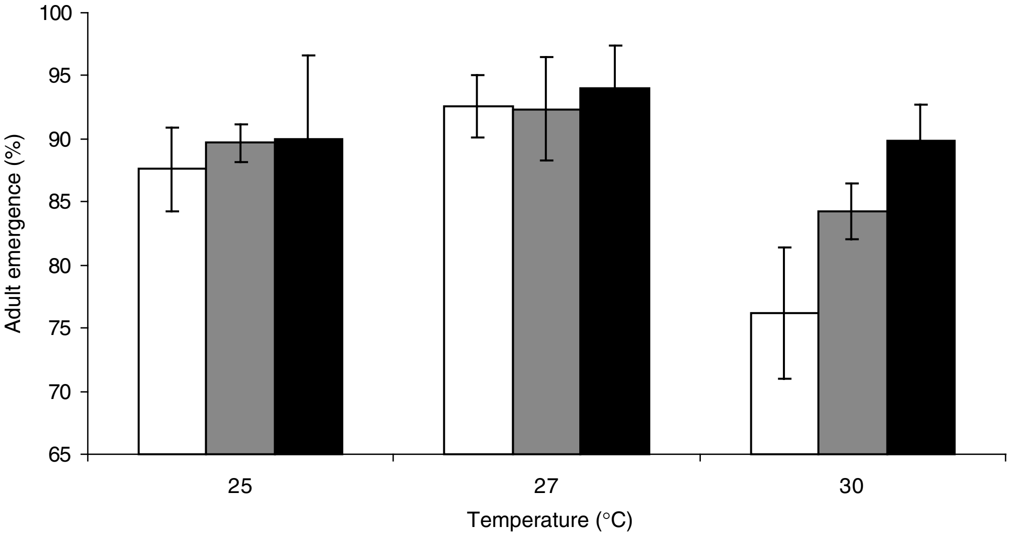

Fig. 2. Percent adult emergence in offspring of *Propylea dissecta* subjected to monogamy and promiscuity at three temperatures: □, monogamous setup with five matings; ▨, promiscuous setup with five matings; ■, promiscuous setup with mate choice.

incompatibility between the females and males leading to lesser reproductive output (Olsson *et al*., 1996). A recent study indicates that promiscuity is also a means of reducing the costs of inbreeding depression (Tregenza & Wedell, 2002). Further, it is not possible that females in nature would mate with an unmated male each and every time and thus the experiment allowing mate choice is a more realistic experimental interpretation of natural conditions.

The present results reveal an increase in both fecundity and hatching success in *P. dissecta* while in crickets an improvement in either fecundity (Simmons, 1987) or percent egg viability (Tregenza & Wedell, 1998) is observed with increased levels of promiscuity. The difference in results in these two studies on crickets perhaps owes to the difference in experiments, with Simmons (1987) being a more realistic design having increased number of matings. The number of matings might also influence the benefits of polyandry. A few studies on the benefits of optimal mating rates have been conducted in insects (Leather, 1990; Tregenza & Wedell, 1998; Arnqvist & Nilsson, 2000; Wedell *et al*., 2002). Arnqvist & Nilsson (2000) suggest that like optimal mating rates there might be an optimal degree of polyandry beyond which female fitness declines. Notably, in the pine beauty moth, *Panolis flammea* Denis & Schiffermüller (Lepidoptera: Noctuidae), the sex ratio leading to optimal fecundity was three males paired with a female, though optimal fertility required a sex ratio of one male/female (Leather, 1990). Optimal mating rates of one and three matings with suboptimal reproductive performance at two matings have been reported in *Callosobruchus maculatus* (Fabricius) (Coleoptera: Bruchidae) (Nilsson, 2004).

The experiments on the effect of promiscuity on offspring fitness (developmental durations and adult emergence) at different temperatures were designed for the purpose of the evaluation of long-term benefits. Different temperatures were considered as indicators of environmental stressors. Results revealed that the differences in survival of offspring of promiscuous females with mate choice were insignificant at the three temperatures, revealing them to be more fit at dealing with environmental stresses. Though the developmental durations of offspring of promiscuous females with mate choice were lowest, the effect was more substantial on the survival of offspring.

The efficacy of offspring with different parental mating histories in dealing with environmental stresses has previously been studied in crickets with nutrition deprivation acting as a stressor (Sakaluk *et al*., 2002). While the development time and survival of offspring did not differ with the levels of promiscuity (Sakaluk *et al*., 2002), weight and size of adult male offspring increased (Sakaluk *et al*., 2002). This variation in crickets is important and has a probable evolutionary rationale since larger males are preferred over smaller ones as mates in crickets (Sakaluk, 1985; Burpee & Sakaluk, 1993) while there are no known advantages of larger size to females (Will & Sakaluk, 1994). Larger male crickets may enjoy increased mating success owing to their success in agonistic interactions with smaller opponents (Souroukis & Cade, 1993; Hack, 1997) and their increased attractiveness to females (Brown *et al*., 1996; Bateman *et al*., 2001). This reason, however, does not apply in the case of ladybirds where smaller males are considered more efficient mates in prey-deprived conditions (Yasuda & Dixon, 2002). Larger size of female progeny may be more beneficial in ladybirds since number of ovarioles and egg output are size dependent (Stewart *et al*., 1991). Though no apparent differences in the sizes were found in the adults, the effects of parental promiscuity on offspring size needs to be further investigated.

The study does reveal that promiscuity in ladybirds provides both short- and long term benefits in the form of increased reproductive performance and better adaptability of the offspring to counter environmental stresses supporting the evolutionary significance of incidence of promiscuity in nature.

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