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Benefits of polyandry in Parthenium beetle, *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae)

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ABSTRACT

The influence of polyandry on the reproductive performance of females and on offspring fitness in *Zygogramma bicolorata* Pallister was investigated using four experimental treatments, viz. (A) monandrous, limited mating, (B) monandrous, unlimited mating, (C) polyandrous, no-choice limited mating, and (D) polyandrous, mate choice unlimited mating. Polyandrous females had higher reproductive performance than monandrous ones. Monandrous females subjected to unlimited matings had higher egg viability than those subjected to limited matings, but fecundity did not differ significantly. In polyandrous females, the freedom to choose mates did not affect reproductive performance. However, offspring of polyandrous females allowed mate choice developed fastest and had the highest survival at 25, 27, and 30 °C. Thus, polyandry in *Z. bicolorata* appears to provide both direct (material) and indirect (genetic) benefits resulting in better reproductive performance and increased adaptability of the offspring to counter environmental stresses. The present study not only adds to the knowledge of reproductive biology of *Z. bicolorata* but it could also be of economic value as it may help in the mass rearing of *Z. bicolorata* and in the management of *Parthenium hysterophorus*.

Introduction

Promiscuity is common among, animals and males and females are both likely to mate with more than one individual of the opposite sex. The mating of a single female with several males is termed polyandry whereas the mating of a single male with several females is polygyny. However, for generations, most reproductive biologists had assumed females were sexually monandrous (Tang-Martínez and Ryder, 2005) because it was assumed that mating with multiple partners had little or no benefit to females (Trivers, 1972) and because females were thought to be passive in the mating process. In addition, polyandry was thought to be a result of forced copulation by multiple males or non-resistant acceptance of multiple males (Simmons, 2001; Arnqvist and Rowe, 2005). However, recent evidence indicates the prevalence of polyandry in many species of insects, birds and reptiles (Birkhead, 2000). Further detailed studies indicate that obtaining sperm from multiple mates has reproductive benefits (Parker, 1992; Eberhard, 1996). The benefits of polyandry to the female can be either direct (those important for themselves: material benefits) and/or indirect (those important for their offspring: genetic benefits). Many studies related to polyandry have been performed in recent years (Birkhead, 2000; Jennions and Petrie, 2000; Hosken and Stockley, 2003).

Direct benefits of polyandry include fertility insurance, additional resources or paternal care, protection against predators or infanticidal males, or avoiding rejection costs of coercing or harassing males (Birkhead, 2000; Arnqvist and Nilsson, 2000). Females are also likely to obtain some genetic benefits, such as increased genetic diversity of the offspring, minimized chance of being fertilized by a genetically incompatible male, acquisition of genes promoting viability or attractiveness of the offspring (Birkhead, 2000; Tregenza and Wedell, 2002). Polyandry is also recognized as a means of reducing the cost of inbreeding depression, leading to increased egg viability (Tregenza and Wedell, 2002), high quality offspring (Sakaluk et al., 2002; Hosken et al., 2003) and increased resistance from disease (Cornell and Tregenza, 2007). In insects, the impact of polyandry is well documented, especially in cricket *Gryllus bimaculatus* De Geer (Simmons, 2001; Tregenza and Wedell, 2002), red flour beetle *Tribolium castaneum* (Herbst) (Pai and Bernasconi, 2007), common fruit fly *Drosophila melanogaster* (Brown et al., 2004), yellow dung fly *Scathophaga stercoraria* (Linnaeus) (Tregenza et al., 2003), honeybee *Apis andreniformis* Smith (Oldroyd et al., 1997; Kraus et al., 2004), ladybird beetles *Propylea dissecta* (Mulsant) (Omkar and Mishra, 2005), *Coccinella septumpunctata* Linnaeus (Srivastava and Omkar, 2005), and Japanese beetle *Popillia japonica* Newman (Kruse and Switzer, 2007). Studies on arthropods provide further evidence of both direct and indirect benefits (Newcomer et al., 1999).

Although the benefits of multiple mates are clear, it is difficult to ascertain whether material benefits, genetic effects, or both are

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responsible for the elevated fitness levels of polyandrous females and their role in maintaining polyandry (Møller and Jennions, 2001). While a few studies (Newcomer et al., 1999; Ivy and Sakaluk, 2005) suggest only a genetic benefit of polyandry, other explanations cannot be completely ruled out, as the number of mates is also correlated with some aspects of offspring viability or quality (Madsen et al., 1992; Olsson et al., 1994). These differences are due in part to a few experimental anomalies, such as not controlling for the number of matings experienced by females (Sakaluk et al., 2002), or not including treatments involving females mating repeatedly with the same/different males (Vahed, 2003). A few studies indicate that mate choice may influence polyandry (Zeh et al., 1998; Konior et al., 2001). One study revealed that female fitness increases markedly with increased number of matings in insects (Arnqvist and Nilsson, 2000).

The ambivalence in literature regarding patterns, costs and benefits of polyandry, and the lacunae in experimental design suggested a need for more study. The present study is novel in that that it adds information on direct and indirect benefits of polyandry as well as the impact of environmental variation. We hypothesized that polyandry would not only increase the females' reproductive performance, but also the fitness of offspring by providing better genes from competitive mates. We also hypothesized that mate choice would further enhance these benefits. Thus, in the present study, experiments were designed to evaluate the influence of polyandry on direct and indirect benefits in Parthenium beetle, *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae). Reproductive performance was studied for direct benefits while progeny fitness under different temperature regimes (temperature as a stressor) was studied for indirect benefits. This beetle is an effective biological control agent of the noxious weed *Parthenium hysterophorus* Linnaeus (Jayanth, 1987; Dhileepan et al., 2000). Previous studies of this beetle have been conducted on the effects of temperature on variation in life history traits (Bhoopati and Gautam, 2006; Omkar et al., 2008, 2009a), day–night cycle (Omkar et al., 2009b) and crowding (Omkar and Afaq, 2009). This is the first attempt to study the influence of polyandry on reproductive performance and offspring fitness in this beetle. In addition to identifying the benefits or costs of polyandry, it also will elucidate the evolutionary rationale behind its occurrence and assess the adaptability of offspring to a wide range of abiotic conditions.

Materials and methods

Insect stock maintenance

Different stages of *Z. bicolorata* were hand collected from Parthenium plants on the campus of the University of Lucknow, India. A stock culture of *Z. bicolorata* was maintained in beakers (11.0 × 8.5 cm) under controlled abiotic conditions (27 ± 1 °C; 65 ± 5% RH; 14L:10D) in Environmental Test Chambers (ETC) (CH-6S Remi Instruments, India). The life stages were provided with fresh excised leaves of *P. hysterophorus*, which were replenished daily and reared until adult emergence.

Reproductive performance of female

Four experimental treatments were designed by modifying the method of Sakaluk et al. (2002) for studying influence of polyandry in *Z. bicolorata*. The treatments were: (A) 10-day-old virgin female paired with a 10-day-old unmated male for 5 days, allowing only a single mating per day after which the male was removed (monandrous, limited mating), (B) 10-day-old virgin female paired with a 10-day-old unmated male for 5 days, allowing unlimited mating (monandrous, unlimited mating), (C) 10-day-old virgin female provided daily with a new unmated male of the same age (the age of introduced male was allowed to correspond with the female age) for a single mating per mate only (polyandrous, no-choice; limited five matings), and (D) 10-day-old virgin female paired with five 10-day-old unmated males, thus allowing to choose mate (polyandrous, mate choice; unlimited matings). All mating treatments were maintained for 5 days in Petri dishes (9.0 × 2.0 cm) and insects were provided with fresh Parthenium leaves. After mating treatments, the females were isolated and daily observations were made on oviposition and percent egg viability for 20 days. There were 10 replicates per treatment with individuals in single Petri dish forming a replicate.

Offspring fitness

The indirect and long-term benefit of polyandry was studied by observing offspring developmental attributes at three different temperatures. Here, temperature was supposed to work as a stressor, which would help in assessing offspring fitness and adaptability to a wide range of abiotic conditions. For each of the four treatments, a total of 150 eggs per female (10 females per mating treatment) were selected, divided at random into three groups and then reared at one of three temperatures (25, 27, and 30 °C). The 50 eggs from each female were reared in a single batch. Eggs were observed daily for hatch. Neonates were placed in Petri dishes (five larvae per Petri dish) with fresh Parthenium leaves which were replenished daily. During larval development, cast exuviae were noted and removed daily in order to determine the number of molts, the duration of each stage and the survival rate of various developmental stages. Fully grown grubs were transferred from Petri dishes to glass beakers (6.5 × 9.5 cm) filled with moist sand for pupation. The periods of different life stages and the number of survivors per stage were recorded.

Statistical analysis

All data were checked for normality using *Bartlett's* test. All percent data were arcsine square root transformed prior to further analysis. Fecundity and percent egg viability were subjected to analysis of variance (ANOVA) followed by *Tukey's post hoc* test. Treatment effects were evaluated with respect to developmental period (duration from egg to adult emergence), percent larval survival, and percent pupal survival (percentage of adults emerging from the pupae). To examine the effects of polyandry and offspring rearing environment, the data were subjected to two-way ANOVA, with mating treatments as row factor and temperature as column factor. All analyses were done using statistical software Minitab (2003) on PC.

Results

Reproductive performance

Results revealed that fecundity of *Z. bicolorata* was significantly influenced by different mating treatments ($F = 7.65$; $P < 0.001$ $df = 3, 39$). Females of *Z. bicolorata* were most fecund under polyandrous conditions. Monandrous females that were allowed a limited number of matings laid the fewest eggs (Fig. 1) but were not statistically different from monandrous females with unlimited matings. Polyandrous females without mate choice laid fewer eggs than polyandrous females with mate choice, though this difference was not statistically significant. However, fecundity of polyandrous females without mate choice was significantly higher than monandrous females with either limited or unlimited matings.

The percent egg viability also showed statistically significant differences across the four mating treatments ($F = 13.13$; $P < 0.001$; $df = 3, 39$). Polyandrous females with mate choice laid the highest number of viable eggs while the lowest number of eggs was laid by monandrous female with limited mating. Monandrous females with