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No sex, no job: sexual abstinence reduces feeding rates of *Cryptolaemus montrouzieri*

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Abstract

In insects that copulate several times, females are responsible for obtaining nutritional resources for eggs. In certain species, males transmit nuptial gifts to increase the reproductive fitness of the females. The presence or absence of such investments is an important factor in defining the frequency of copulations and the search for resources for reproduction. The existence of a balance between foraging for food and reproduction shows that both factors have an influence on each other. However, it is not known whether females that copulate multiple times consume significantly more prey to increase fertility than females with a limited number of copulation opportunities. It is also unknown how such as copulation limitations affect the consumption rates of males. The aim of this experiment was to determine whether the number of copulations affects the rate of food consumption and fertility of the predatory ladybug *Cryptolaemus montrouzieri* Mulsant (Coleoptera Coccinellidae). The experiment consisted of three treatments: 1) adults who copulated only once, 2) adults who copulated twice, and 3) adults who copulated four times. In treatments with more than one copulation, the refractory period was one week. The ladybugs were fed with adult *Maconellicoccus hirsutus* (Green) (Hemiptera Pseudococcidae) females and consumption was evaluated every two days. Egg-laying and fertility were also evaluated. The results showed that there was a significant decrease in the number of eggs of females that copulated only once compared to females that copulated two and four times. Fertility was also compromised. Females that copulated only once consumed less than those that copulated two or more times. The copulation of males also affected consumption.

Key words: ladybug, biological control, mealybug, mating rate, consumption rate.

Introduction

The mating systems of insects vary depending on their reproductive strategies. Some species copulate only once in their lifetime (Wedell *et al.*, 2002; Monceau and van Baaren, 2012), while some species present high copulation rates to maintain fertility (Arnqvist and Nilsson, 2000; Gershman, 2010).

The investment of both sexes on reproduction influences the development of different types of copulation strategies. For example, in species that copulate a few times, females are primarily responsible for obtaining the nutritional resources to produce eggs (Osawa, 2005), whereas males contribute only to sperm transfer (Svärd and Wiklund, 1989). On the other hand, there are species in which males transmit highly nutritious resources to females via ejaculate enriched with proteins produced during copulation (Snook, 2014). Such donations serve as an investment by males in the reproductive fitness of females and are known as "nuptial gifts" (Parker and Simmons, 1989). The presence or absence of such investments by males is an important factor in defining the frequency of copulation of a species (Villarreal *et al.*, 2018).

The main goal of an adult insect is to consume food and allocate energy for reproduction. This activity demands energy and time (Thornhill and Alcock, 1983). Energy expenditure for searching for prey and finding mates for copulation and sites for oviposition is related to the availability and consumption of resources (Boggs, 1992). The existence of a balance between the time spent foraging for food and reproductive activities (e.g., courtship and copulation) shows that both factors influence each other (Perry and Tse, 2013). If this influence is especially significant for one sex and the number of copulations interferes with the predatory rates of a natural enemy, pest control efficiency can be expected to depend on the sex ratio of a population of predators in the environment (Ottehnheim *et al.*, 1992; Heimpel and Lundgren, 2000; Šipoš *et al.*, 2012).

Many coccinellid species copulate multiple times (Nalepa and Weir, 2007; Pervez and Maurice, 2011). In several species, resources obtained by females are used for oocyte maturation and egg production (Osawa, 2005). Males also play an important role in stimulating females to lay more eggs (Omkar and Mishra, 2005). However, the high frequency of copulations may not necessarily be related to an investment by males in female fecundity, as occurs with *Hippodamia convergens* Guerin-Meneville (Coleoptera Coccinellidae); males are limited to just transferring sperm (Bayoumy and Michaud, 2014). Thus, the role of males in the progeny of coccinellids depends on the level of protein transferred by copulation (Michaud *et al.*, 2013).

Males of the predatory ladybug *Cryptolaemus montrouzieri* Mulsant (Coleoptera Coccinellidae) form a gelatinous and inconsistent spermatophore, which is absorbed by the female's reproductive tract shortly after copulation (Kaufmann, 1996). Other coccinellid species produce similar spermatophores. It has been suggested that they have a non-nutritive role and instead help the sperm move towards the spermatheca (Katakura, 1985; Obata, 1987). Despite the apparent lack of nutritional value, the spermatheca require a considerable amount of male resources to be produced, which makes them highly costly (Perry and Rowe, 2010; Perry and Tse, 2013). If males produce large spermatophores for transfer during copulation, in a multiple copulation system in which there is a high frequency of copulation opportunities, the production of ejaculate requires greater energy expenditure for the secretion of nutritious spermatophores, and thus should stimulate prey consumption. In this scenario, males that are deprived of copulations may have less demand for nutrients to form spermatophores, and therefore, a reduced appetite.

The ladybug *C. montrouzieri* consumes a wide variety of prey (Kaur and Virk, 2011; Solangi *et al*., 2012), although some of which are not nutritionally adequate (Maes *et al*., 2014). Owing to its high voracity (Afifi *et al*., 2010), it is considered an efficient organism for the biological control of insect pests (Gravena, 2003). The adult consumption rate of females is important for maintaining high fertility (Xie *et al*., 2015), and together with copulation encourages females to feed (Xie *et al*., 2014). In addition, the egg production of females that copulate only once is lower than that of females that copulate several times (Jayanthi *et al*., 2013).

If there is evidence that both sexes of *C. montrouzieri* invest in reproduction by transferring large spermatophores (Kaufmann, 1996) or though prey consumption (Jayanthi *et al*., 2015), we hypothesized that the decrease in copulation opportunities for this species, which has a high copulatory frequency (Kaufmann, 1996), would reduce its consumption rate, since there would be less demand for the production of eggs and spermatophores. Thus, we investigated whether females and males performing limited copulations tend to consume significantly less prey compared to adults that have greater copulation availability, and how copulation affects the fertility and fecundity of *C. montrouzieri*.

Materials and methods

The experiment was conducted at the Laboratório de Entomologia Aplicada of the Universidade Federal de Pernambuco, Recife, Brazil. Experimental conditions and breeding of insects were carried out in an environment with controlled temperature and humidity (25 ± 5 °C, 70 ± 5% RH, 12:12 photoperiod).

C. montrouzieri individuals used in this experiment were obtained from a laboratory colony. Breeding was performed in acrylic cages (30 × 40 × 50 cm) with voil to allow gas exchange. Fruits of *Cucurbita moschata* (Cucurbitaceae) var. "Jacarezinho" were infested with the mealybug *Maconellicoccus hirsutus* (Green) (Hemiptera Pseudococcidae) and later stored inside the breeding cage. The methodology was adapted from that of Sanches and Carvalho (2010).

Pupae of *C. montrouzieri* from the laboratory colony were separated individually in Petri dishes (5 × 1 cm) covered with film paper. The pupae were observed daily until adult emergence. Males and females were sexed by morphological differentiation of the first pair of legs (Pang and Gordon, 1986). The adults used in the experiment were aged 2-5 days old and fed *ad libitum* with adult females of *M. hirsutus*.

To test the effects of copulation on the fecundity and consumption rates of *C. montrouzieri*, the treatments were divided into 1) females performing one copulation, 2) females performing two copulations, and 3) females performing four copulations. In the first part of the experiment, all females were paired with one male in 10-mL transparent cylindrical plastic pots and observed until the first copulation. At the end of copulation, which lasts approximately 30 minutes (Kaufman, 1996), males and females were separated.

The treatments were divided according to the number of copulations performed. In the first treatment, the females were allowed to copulate only once (n = 11). The second treatment consisted of females copulated twice (n = 11), and the third treatment consisted of females copulated four times (n = 11). The interval between the copulas was six days. All males used to copulate with females were virgins. Females did not copulate with the same male, nor did the same male copulate with different females. The same copulation procedure was performed with *C. montrouzieri* males to assess whether the quantity of copulation influenced food consumption. Males and females were fed six adult females of mealybug females every two days. The number of mealybugs consumed was recorded every two days for 33 days.

To assess fecundity, eggs were counted every three days for 33 days. To record fertility, eggs were removed and placed in a Petri dish containing filter paper and a piece of moist cotton to avoid egg desiccation every three days. To avoid cannibalism among newly hatched *C. montrouzieri* larvae (Dinesh and Venkatesha, 2014), mealybug nymphs were placed on each Petri dish as a food supply. Additionally, each dish was carefully inspected to observe whether there were partially eaten eggs of *C. montrouzieri*. The eggs were observed for six days and larvae was counted. Eggs that did not hatch for more than six days were considered infertile.

Statistical analysis

The data were analysed for normality using the Shapiro-Wilk test and homogeneity of variance using the Kolmogorov-Smirnov test. Data considered normal and with homogeneous variation were analysed using ANOVA. Data that were not considered normal by the tests mentioned above were analysed using non-parametric statistical tools.

The mean number of eggs was tested using Generalized Linear Models (GLM) assuming Poisson dispersion for counting data. Fertility, as percentage data, was assessed using a GLM with a binomial distribution.

The mealybug consumption results were analysed using generalized linear models (GLM). The results of daily oviposition were analysed by mixed models by fixing the variable "day". The data were analysed using statistical software R (version 2.1.4) and SAS (version 1.4).

Results

There was a significant decrease in the number of eggs in females that performed only one copulation (12.9 ± 5.07 eggs) compared with females that performed two

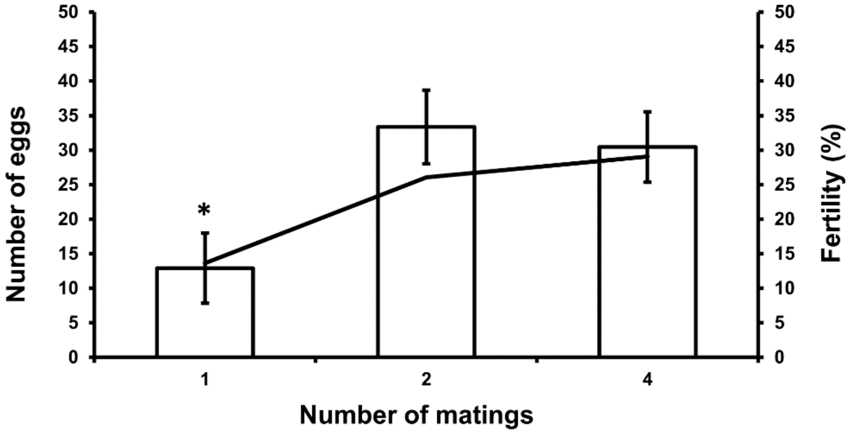

Figure 1. Number of eggs (± SE) (in bars) and fertility (line) of *C. montrouzieri* with different numbers of copulations (n = 11). (*) significant difference at $p < 0.05$.

(33.36 ± 5.32 eggs) and four copulations (30 ± 5.10 eggs) ($F_{2.30} = 2.74$, $p < 0.01$) (figure 1). The number of copulations was observed to affect fertility. Females performing a single copulation showed lower fertility (13.61%) than females that performed two (26.05%) and four copulations (29.07%) ($F_{2.30} = 3.63$, $p = 0.038$) (figure 1).

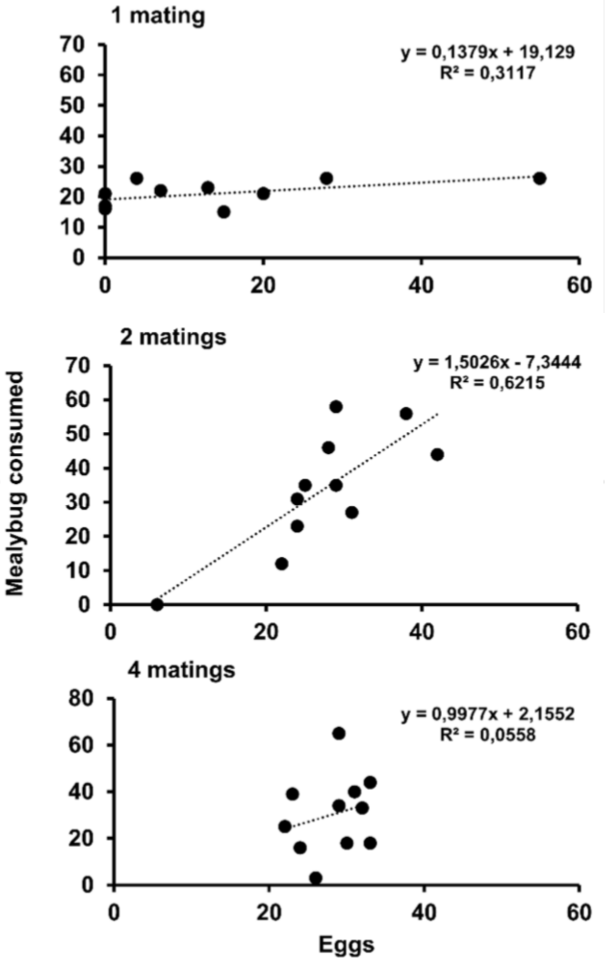

Figure 2. Correlation between mealybugs consumed and production of eggs by females of *C. montrouzieri* with different numbers of copulations (n = 11).

The number of mealybugs consumed was significantly related to the number of eggs laid by females that performed more than one copulation (GLM $\chi^2 = 25.85$, $df = 1$, $p < 0.01$), that is, when more mealybugs were consumed, means that more eggs were laid (figure 2).

The limited opportunity for copulation significantly reduced mealybug consumption. Females that performed only one copulation consumed less adult mealybugs (20.90 ± 1.25) than females that performed two (27.09 ± 2.79) and four copulations (28.36 ± 1.20) (GLM $\chi^2 = 8.35$, $df = 2$, $p = 0.01$) (figure 3). Males that performed one copulation consumed an average of 24 ± 1.06 mealybugs compared to males that copulated two (28.36 ± 1.76) and four times (29.18 ± 1.75) (GLM $\chi^2 = 6.40$, $df = 2$, $p = 0.040$) (figure 3).

Females that copulated only once laid eggs shortly after the copulatory event, followed by a few days with low oviposition, and then an increase in the oviposition rate on the 20th day of the experiment. Females that copulated two and four times showed peaks in oviposition over time. Differences in the daily oviposition rhythm occurred only among females that copulated once in relation to all other females that copulated more than once ($F_{20,30} = 2.74$, $p < 0.01$) (figure 4).

Discussion and conclusion

Females of *C. montrouzieri* that copulated at least twice consumed more mealybugs than those that copulated only once. *C. montrouzieri*, which is a species with multiple copulations (Kaufman, 1996), had increased fertility due to an increase in the number of copulations (Xie *et al*., 2014; 2015). There was a reduction in consumption rates following a reduction in copulation opportunities. Copulation frequency can stimulate ovarian development (Shahid *et al*., 2016) and, consequently, increase the impetus to seek food for egg maturation (Perry, 2011).

The energy demand for the production of female reproductive tissues, such as oogenesis, is high, leading to greater demand for nutrients for the development of these tissues (Hayward and Gillooly, 2011). In some predatory coccinellid species such as *Brumoides foudrasii* (Mulsant)

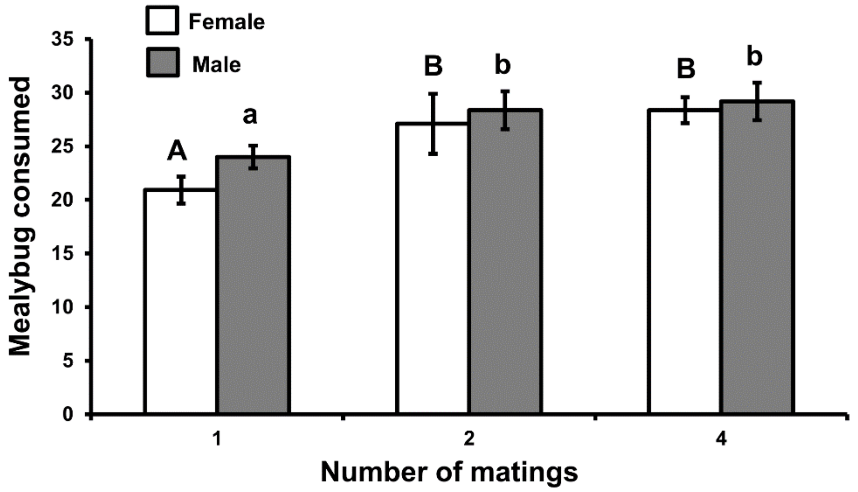

Figure 3. Mealybugs consumed by males and females of *C. montrouzieri* with different numbers of copulations (n = 11). Same letters (uppercase for females and lowercase for males) indicate no significant differences ($p > 0.05$).

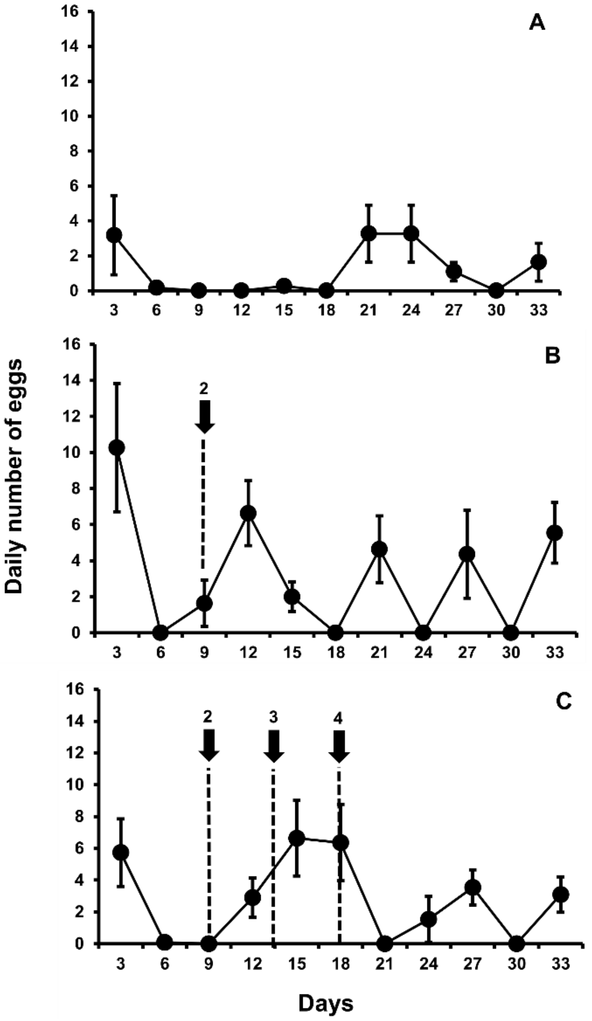

Figure 4. Daily number of eggs (± SE) laid by *C. montrouzieri* with different numbers of copulations (n = 11). (**A**) Females that copulated only once; (**B**) females that copulated twice; (**C**) females that copulated four times. Dashed lines show the day of copulation after the first mating. Numbers above arrows indicate how many times each female copulated.

(Coleoptera Coccinellidae), the supply of prey is directly related to ovarian maturation (Lima *et al.*, 2020). This suggests that energy demand for reproduction comes from food obtained in adulthood (Osawa, 2005; Kajita and Evans, 2009). This method of obtaining resources characterizes this species as an "income breeder" (Tammaru and Haukioja, 1996).

The decrease in the number of eggs laid by females that copulated only once between 6 and 18 days could not be explained by the absence of males because of the need for sperm replacement. Females of *C. montrouzieri* has been found to maintain fecundity, even with irregularity, for more than 20 days, with one complete copulation (De Lima, 2022). How can this period be explained without oviposition? One hypothesis could be that during copulation, males transfer substances that are stimulants for females to lay eggs (Avila *et al.*, 2011). Without access to males, even in the presence of sperm in the spermatheca, the number of eggs laid could significantly decrease because of the lack of stimulants associated with the presence of males (Xu and Wang, 2011).

Another hypothesis is that this daily egg production pattern is characteristic of this species. Coccinellids exhibit different oviposition patterns. They range from an initial peak with high egg production followed by an abrupt or continuous drop to high oviposition peaks interspersed with minimal or total absence of eggs for a few days (Nedved and Honek, 2012). However, our results suggest that the daily oviposition pattern of *C. montrouzieri* can change and fit more than one model, according to the availability for copulation. For example, when females were limited to only one copulation, their daily oviposition pattern resembled that of a polymodal model, as observed for the ladybird *Chilocorus nigritus* (F.) (Coleoptera Coccinellidae) in the face of a low supply of prey (Ponsonby and Copland, 2007).

Many insects require multiple copulations to maintain their fertility and fecundity over time due to sperm transfer (Wang and Davies, 2006), seminal fluids, or both (Jin and Gong, 2001). The absence of sexual encounters with males experienced by females that copulated only once influenced the female's decision to return to oviposition. Species that experience frequent periods of food restriction can retain their egg stock until conditions become suitable again and then retake oviposition (Boggs, 1992; Nedved and Honek, 2012).

Males showed a similar pattern. Individuals that copulated only once consumed less mealybugs than did males that copulated at least twice. The increase in consumption may be a consequence of the cost of copulations for males, which is significantly higher in some coccinellids (Perry and Tse, 2013). Previously, the energy expenditure of males was thought to be superfluous because of the large number of wasted male gametes. However, experiments have shown that males often contribute significantly to reproduction (Paukku and Kotiaho, 2005; Janowitz and Fischer, 2010; Perry and Tse, 2013).

The increase in consumption rates being dependent on sexual encounters in males may reflect two hypotheses: 1) that the sexual event is stressful to the point of inducing males to seek more food to compensate for the energy expenditure after the sexual event (Perry and Tse, 2013), or 2) that the males transmit nutritious substances through the ejaculate that needs to be replenished through food consumption so that they remain competitive for the available females (Thornhill and Alcock, 1983). Although females of some coccinellid species ingest spermatophores after copulation, it does not seem to be a clear indication that spermatophores have a nutritional component that directly affects their fertility (Perry *et al.*, 2009). In this case, the production and transfer of a large spermatophore can be related to the mobility of spermatozoa towards the spermatheca and not necessarily to the transfer of nutrients (Katakura, 1985).

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