

Polyandry and trade-off between fecundity and longevity in female *Dichelops furcatus* (Hemiptera: Pentatomidae)

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Abstract

A trade-off is a relationship between two life history characteristics principally reproduction and adult longevity that are fundamental in predicting the optimal life history in any given environment. Mating is indispensable for sexual reproduction, but also can impose risks to females. Nevertheless, in the majority of insects, females allow multiple mating. *Dichelops furcatus* (Hemiptera: Pentatomidae) is a pest of wheat and corn in Argentina and southern Brazil, but little is known about its reproduction (i.e., the characteristics of the process that results in offspring). We analyzed reproductive attributes of *D. furcatus*, and the effect of single mating vs. multiple matings, evaluating the trade-off between fecundity and adult female longevity. We found that mating is not required for *D. furcatus* to oviposit, and multiple copulations were costly in terms of reduced longevity. Although multicopulated females lived a shorter period, only the pre- and post-reproductive periods were shortened. Fecundity was not affected but fertility was incremented in multicopulated females. Females copulated only once oviposited most of the eggs in the first half of the reproductive period, while eggs oviposited in the second half were all inviable (did not hatch). Studying demographic attributes of phytophagous insects provides relevant information to better understand the population dynamics of pests.

Keywords: green belly stink bug, life history traits, polyandry, fertility, multiple copulations

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Introduction

A trade-off is a negative relationship between two life history traits in which increases in one are associated with decreases in the other as a result of a compromise allocation of the limited resources that are available to it (Begon *et al.*, 2006). A trade-off can be revealed through experimental manipulation in which individuals are randomly assigned to different treatments. This procedure is better than simple field observation of negative phenotypic correlation because

individuals may differ, for instance, in the quantity of resources they have available. Trade-offs are fundamental in predicting the optimal life history in any given environment, and traits commonly considered are reproduction and adult longevity (Zera & Harshman, 2001).

Reproduction is a life history trait that may occur in one terminal burst (semelparity) or as a series of repeated events (iteroparity), whose costs are eggs production and mating (De Loof, 2011). In insects, eggs production is coordinated with the availability of food, duration of the photoperiod and mating, among other factors (Gullan & Cranston, 2010). Concerning mating, it is indispensable for the transfer of sperm in species with sexual reproduction. However, apart from the investment in energy and time that it requires, mating can impose risks to females due to physical injuries, pathogen infection, and predation. Nevertheless, in the majority of

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insects, females permit multiple mating with the same or with multiple males (i.e., polyandry) even when males provide no other benefits to females such as food or parental care (Arnqvist & Nilsson, 2000). Suggested positive effects of mating on female fitness are: sperm supply can maintain egg fertility, accessory substances can increase egg production rate, the mating act itself can stimulate egg production (Bradshaw & McMahon, 2008) and extend female lifespan (Burpee & Sakaluk, 1993). For males, each copulation offers the opportunity to produce new offspring, so that their reproductive success is closely related to the number of females that they have the possibility of inseminating. Copulations can last a long time, and long-lasting copulations increase males' fertilization success relative to their rivals, in response to high sperm competition intensity under high population density and male-biased sex ratio (Sillén-Tullberg, 1981).

Stink bugs are iteroparous and they exhibit multiple copulations (MC) throughout their lifespan (Panizzi, 2000). The green belly stink bug *Dichelops furcatus* (F.) (Hemiptera: Penatatomidae) is a Neotropical phytophagous stink bug common in Argentina and southern Brazil (Pereira et al., 2013). It is a pest on wheat and corn: when feeding injects toxins in the stem of the seedlings harming the vigor of the plant, and the pest status was attributed to the massive adoption by growers of the no-tillage cultivation system (Panizzi, 2000). The adults overwinter in the fallow of maize and soybean crops, and in mid spring the post-hibernating adults disperse to wheat and later to young maize. Despite being a pest, very little is known about the population dynamics of *D. furcatus* and the characteristics of the process that results in offspring production.

Our objectives were: (1) to estimate demographic attributes of *D. furcatus* optimal reproduction (i.e., allowing females to copulate freely), (2) to analyze the effect of only one mating vs. multiple matings, and (3) to evaluate the trade-off between fecundity and adult female longevity.

Methods

Colonies of stink bugs were established from wild individuals collected from the Experiment Station 'Julio Hirschhorn' of the Faculty of Agricultural Sciences and Forestry of the National University of La Plata (34°59'24.32"S, 58°0'18.51"W; 27 ms. n. m.). Adults of *D. furcatus* were maintained in wired cages (20 × 20 × 30 cm), fed with *Phaseolus vulgaris* (L.) (Fabales: Fabaceae) pods, and kept at 24 ± 1°C, 70 ± 10% relative humidity, and a photoperiod of 14:10 h (L:D). Once the stink bugs reached the last (fifth) nymphal instar, they were kept separately until they molted into the adult stage. Then, adults were assigned to one of the following three treatments: (1) MC: each female was allowed to mate repeatedly with a single male until female's death ($n = 20$). Every time a male is dead before female's death, the male was replaced. (2) Single copulation (SC): each female was kept together with one male only until the first copulation was observed. We performed 18 replicates ($n = 18$), registering also the duration of the copulation process. (3) Virgin females (VF): each female was kept singly without copulation until its death ($n = 20$). The individuals were maintained in the same conditions as mentioned for insect culture. Every replicate was checked daily, and egg masses were collected and kept separately in a Petri dish until the emergence of nymphs. We recorded the date in which each oviposition was made, the number of egg masses oviposited by each individual female,

the number of eggs per egg mass (egg mass size), and the number of viable (hatched) and inviable (unhatched) eggs, as well as females' mortality. For each female, we recorded the entire reproductive period (i.e., the time elapsed between the first and the last oviposition made), the time interval between two successive ovipositions, as well as the duration of the pre-reproductive (time until start of oviposition) and post-reproductive (time from last oviposition to death) periods. We estimated the mean longevity of females in the j th group, $L_{(G_j)}$, based on the duration of the adult life of each individual female, $l_{(n, G_j)}$, as $L_{(G_j)} = [\sum_{n=1, N} l_{(n, G_j)}] / N_{(G_j)}$, where $N_{(G_j)}$ represents the total number of females in the j th group.

The mean fecundity of females in the j th group, $Fec_{(G_j)}$, was estimated as $Fec_{(G_j)} = [\sum_{n=1, N} fec_{(n, G_j)}] / N_{(G_j)}$, where $fec_{(n, G_j)}$ is the fecundity of each individual female.

We estimated the total egg fertility of females in the j th group, $F_{(G_j)}$, dividing the total number of eggs from which nymphs emerged by the total number of eggs laid. For each female, we divided the reproductive period into two equal halves: first half (i.e., from the first oviposition to the mid time of the reproductive period) and second half (i.e., from the mid time of the reproductive period to the last oviposition). We compared fecundity and fertility between the first and the second halves.

Number of lived days equivalent to one deposited egg:

For answering this question, we assumed that the resources available to *D. furcatus* adult females would be allocated into reproduction and survival. We also assumed that the resource requirements to produce and oviposit a viable (fertilized) or an inviable (not fertilized) egg are the same, as well as that the requirements of a female to survive on a daily basis are independent of her age.

Taking into account the mean values of longevity and fecundity of MC females ($L_{(MC)}$ and $Fec_{(MC)}$) and of VF females ($L_{(VF)}$ and $Fec_{(VF)}$), we considered that, from the total amount of resources required for the development of an adult of *D. furcatus*, the amount invested by an MC female in its possible greater number of laid eggs is proportional to the amount invested by a VF female in its possible greater longevity. That is to say, $k[Fec_{(MC)} - Fec_{(VF)}] = [L_{(VF)} - L_{(MC)}]$, where k is the coefficient of proportionality. Therefore, $k = (L_{(VF)} - L_{(MC)}) / (Fec_{(MC)} - Fec_{(VF)})$ represents the number of lived days equivalent to one deposited egg, and the inverse of the coefficient $1/k = (Fec_{(MC)} - Fec_{(VF)}) / (L_{(VF)} - L_{(MC)})$ represents the number of deposited eggs that are equivalent to one lived day. If, as a result of the trade-off between longevity and reproduction, $Fec_{(MC)}$ is expected to be greater than $Fec_{(VF)}$ and $L_{(VF)}$ is expected to be greater than $L_{(MC)}$, then the coefficient k takes values in the interval (0, infinite). On the contrary, if $L_{(VF)} \sim L_{(MC)}$ and $Fec_{(MC)} \sim Fec_{(VF)}$, k gets an undetermined value.

If the total amount of resources required for a *D. furcatus* adult female were independent of the treatment to which it was subjected, we expressed it for the n -th female of the SC group in units of days, $TRd_{(n, SC)}$, adding to the observed longevity, $l_{(n, SC)}$, the number of days equivalent to its fecundity, $k \cdot fec_{(n, SC)}$, symbolically: $TRd_{(n, SC)} = l_{(n, SC)} + k \cdot fec_{(n, SC)}$. In a similar way, we expressed the total amount of resources required for the n -th female of the SC group in units of eggs, $TRe_{(n, SC)}$, adding to the observed fecundity, $fec_{(n, SC)}$, the number of eggs equivalent to its longevity, $(1/k) \cdot l_{(n, SC)}$, symbolically: $TRe_{(n, SC)} = fec_{(n, SC)} + (1/k) \cdot l_{(n, SC)}$. We would expect that the corresponding mean values, $TRd_{(SC)} = [\sum_{n=1, N} TRd_{(n, SC)}] / N_{(SC)}$, and $TRe_{(SC)} = [\sum_{n=1, N} TRe_{(n, SC)}] / N_{(SC)}$, where $N_{(SC)}$ represents the total number of females in the SC

group, did not differ significantly from the mean values calculated from MC (values from the VF group equals values from the MC group): $TRd_{(MC)} = L_{(MC)} + k \cdot Fec_{(MC)}$, and $TRe_{(MC)} = Fec_{(MC)} + (1/k) \cdot L_{(MC)}$.

Statistical analysis

Differences in longevity, duration of the reproductive period, fecundity, fertility, and time interval between two successive ovipositions were tested by one-way analysis of variance and differences among treatments were analyzed by means of the Tukey's HSD test. In cases where the assumptions of parametric tests were not reached, even after data transformation, we performed the non-parametric Kruskal–Wallis test and differences between pairs of treatments were analyzed by means of the Mann–Whitney *U* test.

We performed a correlation by the Pearson product-moment correlation test, between longevity and fecundity, for each one of the treatments. Differences between TRd and $TRd_{(SC)}$ and between TRe and $TRe_{(SC)}$ were evaluated by a *t* test. All statistical analyses were carried out using the free software R (R Core Team, 2014) and $P < 0.05$ values were considered significant (Zar, 1996).

Results

For MC females, the more and the less long-lived individuals lived 205 and 73 days, respectively (the difference between them was almost 4 and a half months). Maximum and minimum fecundities were 415 and 83 eggs/female, and the lowest fertility was five times less than the highest. Longevity and fecundity of all MC females were positively correlated: $r = 0.50$; $t_{(df=19)} = 2.458$ ($P = 0.024$).

For SC females, maximum and minimum longevity were 280 and 34 days, respectively (the difference between them was more than 8 months). Fecundity also fluctuated widely: maximum and minimum fecundity were 445 and two eggs/female, respectively. The lowest fertility was more than 200 times less than the highest. Longevity and fecundity of all SC females were not significantly correlated: $r = 0.261$; $t_{(df=16)} = 1.082$; $P = 0.295$.

For VF females, maximum and minimum longevity were 396 and 20 days, respectively. Regarding fecundity, four of the females did not reproduce, and another four females laid only one egg mass. Without considering the females that did not lay eggs, maximum and minimum fecundity were 154 eggs/female (this female lived 265 days) and three eggs/female (oviposited by a female that lived 258 days).

The lowest fertility was more than 50 times less than the highest. As for SC, longevity and fecundity of all VF females were not correlated: $r = 0.215$, $t_{(df=19)} = 0.933$; $P = 0.363$.

Longevity was different among treatments ($H_{(2, n=58)} = 13.438$; $P = 0.001$), being lower on females of the group MC (table 1). When we differentiated the duration of the pre- and post-reproductive and reproductive periods, we also found differences among treatments. The pre-reproductive period was similar for MC and SC females, and it was shorter than the period recorded for VF ($H_{(2, n=54)} = 23.392$; $P < 0.001$). Contrarily, there were no differences in the duration of the reproductive period among treatments ($H_{(2, n=54)} = 3.357$; $P = 0.197$). However, the post-reproductive period of MC females was shorter than the one of SC and VF ($H_{(2, n=54)} = 10.989$; $P = 0.004$) (table 1).

We also found differences in the fecundity of females among treatments ($H_{(2, n=58)} = 26.114$; $P < 0.001$): females of the groups MC and SC were more fecund than females of the group VF (table 1). The size of egg masses differed among treatments ($H_{(2, n=2)} = 7.556$; $P = 0.023$): VF = 9.716 eggs/egg mass (SD = 3.182, $n = 16$), SC = 14.329 eggs/egg mass (SD = 4.355, $n = 18$), and MC = 12.543 eggs/egg mass (SD = 0.980, $n = 209$), and the differences between SC and MC were not significant (0.073). The mean egg mass size of SC females was somewhat greater than MC (although not significantly) and each SC female oviposited a lower number of masses than MC (although not significantly). Overall fecundity of SC females did not differ significantly from MC ($F = 2.715$; $df = 41$; $P = 0.107$) (table 1). Regarding eggs' fertility, VF only oviposited unfertile eggs, and when VF was excluded from the analysis, we found differences in the fertility of eggs oviposited by SC or MC females ($F = 8.773$; $df = 35$; $P = 0.005$).

In general, MC and VF females represented contrasting results in terms of longevity and fecundity, and SC females showed intermediate values (fig. 1).

Finally, the time interval between two successive ovipositions was significantly different among treatments ($H_{(2, n=47)} = 28.305$; $P < 0.001$), being the shortest for MC, and SC shorter than VF.

Analyzing the effect of only single copulation vs. multiple copulations

During adulthood, MC females spent a pre-reproductive period of almost a fortnight, which represented 13.48% of the total longevity. The reproductive period represented 62.81% and the post-reproductive period represented the remaining 23.71% of the total longevity (table 1). When we

Table 1. Effect of mating frequency on demographic attributes of *Dichelops furcatus* females multicopulated (MC), copulated once (SC), or virgin (VF) (means \pm SD).

	MC	SC	VF
Longevity	109.45 \pm 39.96 days a	177.06 \pm 80.34 days b	214.40 \pm 99.65 days b
Pre-reproduction	14.75 \pm 6.14 days a	13.11 \pm 1.36 days a	44.94 \pm 37.63 days b
Reproduction	68.75 \pm 37.10 days a	84.33 \pm 59.35 days a	109.63 \pm 76.30 days a
Post-reproduction	25.95 \pm 29.49 days a	79.61 \pm 67.53 days b	64.43 \pm 46.00 days b
Fecundity	192.60 \pm 94.82 eggs/♀ a	166.89 \pm 194.35 eggs/♀ a	40.85 \pm 42.57 eggs/♀ b
	15.15 \pm 6.84 egg masses/♀ a	12.50 \pm 8.81 egg masses/♀ a	4.15 \pm 3.94 egg masses/♀ b
Fertility	60% of eggs a	40% of eggs b	0% of eggs c
Time interval between two successive ovipositions	4.79 \pm 6.27 days a	8.52 \pm 5.25 days b	33.25 \pm 18.41 days c

Different letters indicate significant differences among treatments.

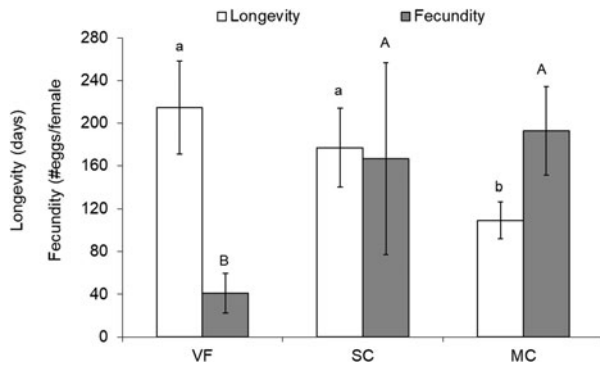


Fig. 1. Mean longevity and fecundity of adult multicopulated (MC), copulated once (SC), or virgin (VF) females of *Dichelops furcatus*. Bars indicate confidence intervals (95%). Different letters indicate significant differences in longevity (lowcase letters) or fecundity (capital letters) among treatments.

divided the reproductive period into two equal parts, females laid 59.61% of all the eggs oviposited in their life in the first half, with a fertility of 60%. The time interval between two successive ovipositions was 4.30 days on average (SD = 1.65). We found no significant differences on the number of oviposited eggs, the fertility, and the duration of time intervals between successive ovipositions, between the first and the second half of the reproductive period (fecundity: $F = 3.081$; $df = 38$; $P = 0.087$, fertility: $F = 0.134$; $df = 35$; $P = 0.716$, time interval between successive ovipositions: $U_{(n1=20, n2=20)} = 131.00$; $P = 0.062$).

During adulthood, SC females spent a pre-reproductive period of 13.11 days on average, which represented 7.405% of the total longevity. The reproductive period represented 47.631% and the post-reproductive period represented the remaining 44.965% of the total longevity (table 1). When we divided the reproductive period into two equal parts, SC females laid 57.53% of all the eggs oviposited in their life in the first half, with a fertility of 56%. The time interval between two successive ovipositions was 6.76 days on average (SD = 5.04). In the second half of the reproductive period, females oviposited a significantly lower number of eggs (52.18 ± 40.20) ($U = 58$; $P = 0.014$), with a lower fertility ($U = 37$; $P < 0.001$) (fig. 2) and with longer time intervals between successive ovipositions ($U = 54.5$; $P = 0.014$). Each copulation recorded in the SC group lasted between 5 and 20.9 h and the mean value was 18.27 h (SD = 4.93; $n = 18$).

Females of the VF group showed a significantly higher (almost double) longevity than MC females (table 1). During adulthood, VF females spent a pre-reproductive period of 44.94 days on average, which represented 20.52% of the total longevity. The reproductive period represented 50.06% and the post-reproductive period represented the remaining 29.42% of the total longevity (table 1). Due to the scarce oviposition events recorded for females of the group VF, we did not divide the reproductive period into two halves for further analysis.

Number of lived days equivalent to one deposited egg

Mean longevity of VF females was 1.96 times greater than the longevity of MC females. On the contrary, mean fecundity of MC females was 4.71 times greater than fecundity of VF

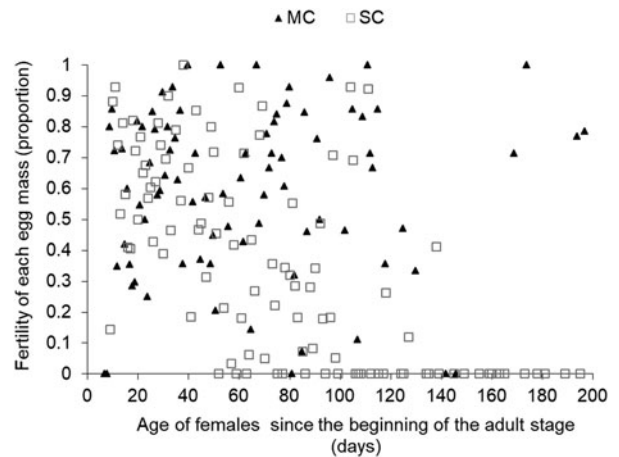


Fig. 2. Fertility of individual egg masses oviposited by multicopulated (MC) and copulated once (SC) females of *D. furcatus*.

females. The coefficient $k = 0.69$ indicates that the amount of resources that would be needed to produce one egg is only enough to live 0.69 days. Consequently, $1/k = 1.45$ indicates that the amount of resources that would be needed to live 1 day allows to produce almost one and a half egg.

For the MC group, the calculated total amount of resources utilized by an adult female expressed in 'days equivalent' and in 'eggs equivalent' were: 242.65 and 350.86, respectively, and the corresponding estimated mean values for SC group were: $TRd_{(SC)} = 277.86$ 'days equivalent' (SD = 161.89, $n = 18$), and $TRe_{(SC)} = 460.01$ 'eggs equivalent' (SD = 268.39, $n = 18$) (fig. 3) which did not differ from the former values: $t_{(df=17)} = -0.923$ ($0.2 > P > 0.1$) for 'days equivalent', and $t_{(df=17)} = -1.725$ ($0.1 > P > 0.05$) for 'eggs equivalent'.

Discussion

Life-history evolution can be constrained by trade-offs among various traits that contribute to fitness, and fitness can be defined as a measure of the proportion of individuals that are propagated into the following generations. Traits commonly considered are reproduction and adult longevity and reduction of life span as a result of mating has been reported for many species of arthropods of diverse orders and families (de Loof, 2011 and references therein).

Reproductive costs can imply ecological costs, as increased vulnerability to parasitism of mating pairs, and physiological costs when resources are diverted into reproduction and away from other essential processes (Reguera *et al.*, 2004).

Besides, mating itself is an energy-demanding process which can represent a major reproductive cost and may directly and indirectly affect female fitness in a number of ways (Arnqvist & Nilsson, 2000). In effect, females may suffer male harassment during courting, physical damage by male genital barbs and spines (Crudginton & Siva-Jothy, 2000), and reduction of life span and foraging time (de Loof, 2011 and references therein). Nevertheless, mating can function as a necessary stimulus for the initiation of vitellogenesis or ovary development (Gillott, 2003), and can affect female's fecundity through three different mechanisms: the act of mating *per se*, the presence of sperm, and the transfer of accessory

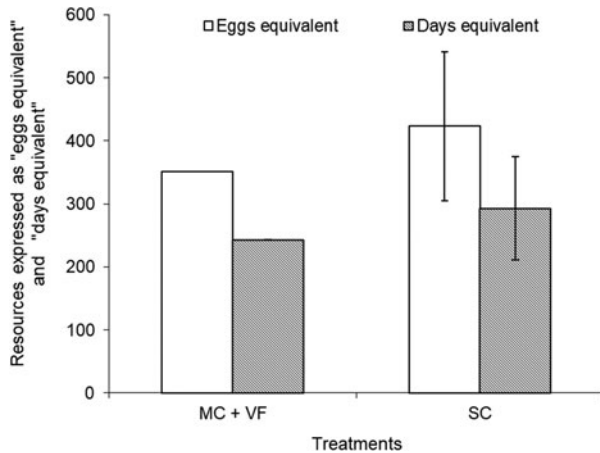


Fig. 3. Total amount of resources invested by each female of *D. furcatus* in producing eggs (columns on the left side) or in surviving (columns on the right side), expressed in 'equivalent eggs' and 'equivalent days', respectively. Bars represent 95% confident intervals.

substances (Arnqvist & Nilsson, 2000). Anyway, multiple mating is widespread in insect species (Arnqvist & Nilsson, 2000). The adaptive significance of multiple mating has been extensively debated and the general idea is that, to be adaptive, the costs of multiple mating must be offset by benefits that enhance female's fitness. Two types of benefits are commonly used to explain the adaptive value of multiple mating: non-genetic benefits (Arnqvist & Nilsson, 2000) and genetic benefits (Jennions & Petrie, 2000). The former, also denominated direct or first generation benefits, derive from the quality of the sperm of certain males that may increase female's fecundity, longevity, or mating rate. In this sense, Okada *et al.* (2015) demonstrated that irrespective of whether females mated with one or four males, mating multiply improved female fecundity and lifetime reproductive success in horned flour beetles (*Gnatorcerus cornutus*, Coleoptera: Tenebrionidae). Additionally, if males transfer insufficient sperm, females may mate multiply to ensure all eggs are fertilized, hence obtaining fecundity benefits (García-González, 2004). The latter also denominated indirect or second generation benefits result in an increase in the genetic diversity of the offspring, avoiding genetic incompatibilities derived from incestuous matings and inbreeding (Jennions & Petrie, 2000). In this way, if future environmental conditions change, the chances that at least part of the offspring will be able to cope with the changes are increased.

Arnqvist & Nilsson (2000) performed a meta-analysis to address the effects of multiple mating on the fitness of female insects, and concluded that a single mating does not maximize female fitness in general, and that beneficial effects of remating (increased fecundity and fertility) outweigh its detrimental effects on female longevity. Particularly among the Heteroptera, the effects of mating on egg development and oviposition appears to be variable (Fortes *et al.*, 2011 and references therein). It was shown that *N. viridula* does not need mating-derived stimuli for ovary maturation, as already observed for other stink bug species (Masner, 1966; Wightman, 1973; Davey *et al.*, 1986; Adams, 2000) in which VF never laid eggs. However, multiple mating increased reproduction in *N. viridula* and *Edessa meditabunda* (Hemiptera: Pentatomidae) and

the cost of increasing fecundity was the reduction of longevity (Mitchell & Mau, 1969; Silva *et al.*, 2012).

In our study, we found that mating is not required for *D. furcatus* to oviposit, as VF were able to lay eggs. The same situation was denoted for *Halyomorpha halys* (Hemiptera: Pentatomidae) (Chu *et al.*, 1997; Cambridge, 2016). The effects of mating on egg development and oviposition are variable, and even when VF lay eggs, alterations in the ovarian developmental period, oocyte size and composition, and/or number of eggs laid may occur (Fortes *et al.*, 2011).

MC were costly in terms of reduced longevity for *D. furcatus* compared with once mated and VF. However, although multicopulated females lived a shorter period, only the pre- and post-reproductive periods were shortened and the time interval between consecutive ovipositions was reduced, agreeing with the observations made for *E. meditabunda* (Silva *et al.*, 2012). Although the total number of eggs laid by a *D. furcatus* female was not affected by the number of copulations, *D. furcatus* females copulated only once concentrated ovipositions in the first half of the reproductive period while multicopulated females oviposited a similar number of eggs in the first and second halves of the reproductive period. Congruent results in terms of the moment of the reproductive period in which ovipositions were made were found for *N. viridula*: females mated once or twice produced more egg clusters and concentrated egg-laying activity in the early part of adult life, whereas those mating more often laid eggs throughout the life span, with fewer egg clusters (Fortes & Cónsoli, 2011). These authors also found that mating did not stimulate oocyte development in *N. viridula*, but the lack of mating activity appeared to have stimulated oocyte resorption in 17-day-old females. Oocyte resorption may explain the lower fecundity of virgin *D. furcatus*, when compared to multi or once-copulated females.

Coefficients k and $1/k$ indicate that the amount of resources needed to produce one egg is only enough to live 0.69 days, or in other words, that the amount of resources needed to live 1 day allows producing more than a single egg. This was another way to analyze the amount of resources invested by MC females compared with VF females: while the reduction in the number of days lived was 104.95 days, the increase in fecundity was 151.75 eggs: more than one egg per day lost.

Concerning egg fertility, we found a significant increase in *D. furcatus* females with a higher number of copulations. Similarly, Kawada & Kitamura (1983) found that an increase in the number of copulations moderated the decline of fertility of *Halyomorpha mista* (Hemiptera: Pentatomidae). In a congruent way, *D. furcatus* females copulated only once concentrated viable eggs in the first half of the reproductive period, while in the second half all eggs were inviable, indicating that females mated only once received insufficient sperm to ensure all eggs to be fertilized, or that sperm quality deteriorated over time leading to a decrease in fertilization capacity. The relatively long time that each copula lasted suggests that it is a strategy of the males tending to ensure that their sperm fecundates all or the largest number of oocytes. In polyandric females, the competition between males continues after the copulation in the form of competition between ejaculates of different males, a process that is known as 'spermatic competition'. Males may try to avoid or minimize sperm competition by defending the female from other males' copulation attempts. This defense can take different forms, one of which is the prolonged copulations with the female that physically prevent copulation by other males. This behavior was rather common among Pentatomidae, as with *N. viridula* (McLain, 1992).

MC reduced the longevity of *D. furcatus* females, and although fecundity was not affected, fertility was incremented in multicopulated females. These findings provide information about the reproduction of this phytophagous insect, relevant to improve our understanding of the population dynamics of this pest.

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