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Mating and social contact change egg production and longevity in adult females of the mirid *Lygus hesperus*

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Abstract

There is frequently a tradeoff between fecundity and longevity, but the relationship is inconsistent across species and influenced by various exogenous and endogenous factors. Previous studies of *Lygus hesperus* Knight (Hemiptera: Miridae) established that egg production is promoted by insemination, at least temporarily, but little is known about the long-term effects of mating and nonsexual interactions with conspecifics on egg production and female lifespan. To elucidate these relationships, survivorship and oviposition rate were tracked daily in females that were isolated or paired with a fertile male or another female throughout their adult lives. Mating rates were determined by postmortem examination. Results indicate that male-specific stimuli accelerate female reproductive maturation, and that mating elevates oviposition rate. However, females paired with either a female or male companion had shortened lifespans, suggesting that social contacts exact a significant cost in this solitary species. Despite the negative impact of conspecific interactions and the finding that a singly mated female has sufficient sperm to fertilize a lifetime supply of eggs, many females were found to have mated more than once. Multiply mated females had higher sustained oviposition rates, lived longer, and had greater lifetime fecundities. Collectively, no strong evidence was found of a direct physiological link between fecundity and longevity, but environmental factors and mating were found to significantly influence both traits.

Introduction

For many insects, reproduction has an associated metabolic cost that can impact various life-history traits. An increased allocation of resources toward gamete production, particularly in females, can result in a shortened lifespan (Partridge et al., 1986; Partridge et al., 1987; Ohgushi, 1996; Chapman et al., 1998). Shunting resources away from somatic maintenance may reduce the capacity to adequately guard against environmental stressors or pathogens (Djawdan et al., 1996; Salmon et al., 2001), with more stressful conditions exacerbating the tradeoff costs (Tatar & Carey, 1995; Manrakhan & Lux, 2006; Fricke et al., 2010). In some species, lifetime fecundity does not impact longevity, but the rate of egg production does (Rowe & Scudder, 1990; Rönn et al., 2006; but see Müller et al., 2001). Although a tradeoff has been observed in numerous insects, not all species exhibit a negative association between fecundity and longevity (Chapman et al., 1998; Arnqvist & Nilsson, 2000; Papanastasiou et al., 2013; Schrempf et al., 2017). Notably, some highly fecund queens of social insect colonies can live considerably longer than their own 'sterile' progeny (Keller & Jemielity, 2006; Heinze & Schrempf, 2008; Flatt et al., 2013; Rodrigues & Flatt, 2016), and exhibit positive associations between lifespan and egg production (Lopez-Vaamonde et al., 2009; Heinze et al., 2013). However, workers may buffer queens from these costs (Lopez-Vaamonde et al., 2009), and reproductively active workers have shortened lifespans (Blacher et al., 2017).

It is not just the process of oogenesis that can be costly to a female, but non-sexual and sexual interactions can also reduce longevity. Exposure to male behavioral stimuli can negatively impact female health (Partridge & Fowler, 1990; Fielding & Knisley, 1995; Cordts & Partridge, 1996; Chapman et al., 1998), possibly due to stress from the constant harassment of prospective mates, or from competition for or contamination of food sources (Partridge & Fowler, 1990). In species of Diptera, especially those that

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mate multiple times, insemination by itself can diminish female lifespan (Fowler & Partridge, 1989; Chapman et al., 1993, 1995, 1998; Holland & Rice, 1999; Civetta & Clark, 2000). Mating always carries inherent risks, such as the enhanced likelihood of predation, physical damage, or the exchange of pathogens (Arnqvist & Nilsson, 2000; Rolff & Siva-Jothy, 2002; Knell & Webberley, 2004).

The deleterious effects of mating in *Drosophila* spp. appears to be due to seminal components (Chapman et al., 1993, 1995; Wigby & Chapman, 2005). Seminal products often drive post-copulatory behavioral shifts and egg production, with males contributing limiting resources (Boggs, 1990; Andersson, 1994; Arnqvist & Nilsson, 2000; Gioti et al., 2012) or chemical triggers that promote oogenesis or ovipositional behavior (Loher et al., 1981; Heifetz et al., 2000; Chapman et al., 2003; Worthington et al., 2015). The compounds increase male fitness by displacing or incapacitating the sperm of competitors (Harshman & Prout, 1994; Clark et al., 1995; Holland & Rice, 1999), decreasing female receptivity, supporting sperm storage, and enhancing egg production (Chen et al., 1988; Herndon & Wolfner, 1995).

The relationship between fecundity and longevity is varied across mirid species. For some, there is a negative correlation between the two traits, whereas in others, there is no correlation or even a positive association (reviewed in Wheeler, 2001). Given the potential implications for predicting pest populations, or developing novel control approaches, it is essential to understand the cost and benefits of mating and egg production on an individual species basis. For one key pest of the southwestern USA (Jackson et al., 1995), *Lygus hesperus* Knight (Hemiptera: Miridae), mating has been shown to enhance egg laying, at least for short periods (Brent, 2010a,b). Virgin females will oviposit non-viable eggs at a steady low rate, whereas inseminated females lay fertile eggs in a rapid burst. However, the long-term benefits and costs of mating, especially if repeated over a female's lifetime, remain to be determined. *Lygus hesperus* females have been observed to mate multiple times (Strong et al., 1970; Brent, 2010a,b). This is possibly due to a need to replenish their sperm supply, although there is limited evidence that a single spermatophore may have sufficient sperm for a female's lifetime egg production (Strong et al., 1970). Average remating time for a female is 5–7 days under laboratory conditions (Strong et al., 1970; 2010a,b), suggesting sperm may be used up or become non-viable within a week. During insemination, *L. hesperus* males deliver a spermatophore that includes a complex blend of chemicals which may be of additional benefit or detriment to the female. This mix includes pheromones (Brent & Byers, 2011; Brent et al., 2017), hormones (Brent et al., 2016), trace amounts of micro- and macronutrients (Brent et al., 2011), and other modulators of behavior and physiology that could impact long-term female health. Frequent mating may also maintain an elevated rate of egg production, which may influence female longevity (Strong & Sheldahl, 1970).

To elucidate the relationship between fecundity, longevity, and mating in *L. hesperus* females, survivorship and oviposition rate were tracked daily in isolated virgin females and females paired with either a fertile male or another female. These tests were conducted with laboratory populations reared entirely in a controlled environment on a strict diet.

Materials and methods

Stock colony insects

Test subjects were taken from a stock *L. hesperus* colony that has been under continuous culture for >10 years, with periodic outbreeding to ensure vitality. Colony insects were reared at 27.5–29.0 °C and L14:D10 photoperiod. They were provisioned with artificial diet (Debolt, 1982) packaged in Parafilm M (Pechiney Plastic Packaging, Chicago, IL, USA) (Patana, 1982). Eggs were obtained by placing oviposition packets (agarose gel packaged with Parafilm M) on the screened tops of rearing cages for 6–8 h. Egg-filled packets were placed in 1 890-ml waxed chipboard cups (Huhtamaki, De Soto, KS, USA), and held in an environmental chamber maintained at L14:D10 photoperiod and 27.0 ± 1 °C. Emerging nymphs were reared in groups and provided an ad libitum diet of green bean pods (*Phaseolus vulgaris* L.) and raw sunflower seeds (*Helianthus annuus* L.). Beans and seeds were replenished 3× weekly or more often if their quality deteriorated. Shredded paper was provided as a refuge. Beginning when fifth instars were first observed, nymphs were monitored daily to detect adult eclosion. Adults emerging on the same day were separated by gender, based on the presence or absence of an ovipositor, and placed into separate rearing containers.

Oviposition and longevity of laboratory insects

To determine the effects of social interactions and mating on reproductive development, lifetime egg production, and longevity, newly emerged virgin adult females were observed under three experimental conditions: in isolation, paired with a virgin 2- to 4-day-old female, or with a virgin 8- to 10-day-old male. Pairing with females permitted the assessment of the effects of companions without male-specific stimuli. Because not all of the females paired with a male chose to mate, a fourth treatment was unintentionally created. Companion ages were chosen to

ensure that the females were not actively ovipositing and that the males were sufficiently mature to mate (Brent, 2010a,b). Companions were replaced every other day to ensure these criteria were constantly met. Companions were marked with paint on the thorax so that they could be readily distinguished from the test subjects. For each of the three treatments, 200 individuals were monitored. All subjects were from the same cohort and monitored simultaneously. They were housed in covered plastic Petri dishes (1.5 cm high, 5 cm diameter) supplied with a 2.5-cm section of green bean and two sunflower seeds. This diet is sufficient for development and gamete production, but is restrictive relative to the artificial diet provided to nymphs. This switch was made to ensure that any benefits or costs of mating were not obscured or offset by an overabundance of resources, as has been previously observed in *Callosobruchus maculatus* (Fabricius) (Tatar & Carey, 1995; Messina & Slade, 1999; Messina & Fry, 2003). Petri dishes were maintained in environmental chambers (I30BLL; Percival Scientific, Perry, IA, USA) with a L14:D10 photoperiod. Temperature was maintained at 27 ± 0.5 °C and monitored twice weekly using portable loggers (U10-003; Onset Computer, Bourne, MA, USA). A daily census assessed female survivorship and counted the eggs laid in the bean section using a dissecting scope. Beans were replaced daily and seeds as needed. Upon death, females were dissected to count spermatophores, an accurate indicator of lifetime insemination events. Females dying prior to ovipositing were excluded from analyses.

Sperm viability duration

To verify how long a female can utilize the sperm from a single insemination event to produce viable offspring, 200 virgins of each sex, aged 7 days, were allowed to mate overnight as a group in a single fully provisioned chipboard container under standard rearing conditions described above. On the following morning, female mating status was non-invasively determined using a dissecting scope to look for the presence of a spermatophore. These large y-shaped bodies are readily discernable just under the ventral abdominal cuticle (Cooper, 2012). No female was observed to have mated more than once. Mated females were separated into 12 groups of 10 individuals each, housed in 355-ml chipboard cups containing seeds and paper. Groups rather than single females were tested to reduce noise created by individual variation in egg production. One oviposition packet was placed in each container for 6 h, after which the females were provided with green beans. The number of eggs laid in each packet was determined under a dissecting scope, and the packs placed individually into mesh-covered cups, labeled with the group number and collection day. Containers were examined daily until 2 days after the last egg hatch was observed; emerging nymphs were counted then removed to ensure they were assayed only once. New packets were supplied each morning, until all the females had died or had stopped ovipositing (20 days after insemination).

Statistical analysis

For all experiments the data were non-normally distributed, necessitating the use of a Kruskal–Wallis (KW) test on ranks for comparison between treatment groups for age of first oviposition, mean daily oviposition rate, peak oviposition rate, and lifetime fecundity. Dunn's test for multiple comparisons was used where the analysis indicated significance. Kaplan–Meier survival analysis was used to compare longevities, using the Holm–Sidak method for multiple comparisons. For all tests, $\alpha = 0.05$ and adjusted P-values are provided. Tests for association between fecundity, longevity, and mating frequency used Spearman Rank Correlation. All analyses were conducted with SigmaPlot v.13.0 (Systat Software, Chicago, IL, USA).

Results

The social rearing conditions to which females were exposed significantly influenced the onset of egg laying (Figures 1A and 3; KW-ANOVA: $H = 44.74$, d.f. = 2, $P<0.001$). Females took several days after adult emergence before they began to lay eggs, a typical pre-oviposition period for this species (Strong et al., 1970; Brent, 2010a,b). Those paired with a male (n = 178) took 1 day less to begin ovipositing compared to those left isolated (Dunn's: $Q = 4.78$, $P<0.001$; n = 175) or paired with another female ($Q = 6.28$, $P<0.001$; n = 161).

The daily rate of egg production averaged across the entire span of ovipositional activity was also impacted by treatment (Figure 1B; KW-ANOVA: $H = 83.67$, d.f. = 2, $P<0.001$). Relative to the rates of females paired with a male, which were highest, isolated females were 24% lower ($Q = 5.26$, $P<0.001$), whereas those paired with another female were 40% lower ($Q = 9.10$, $P<0.001$). The latter two groups also differed significantly ($Q = 3.96$, $P<0.001$). The highest number of eggs laid by an individual during a single 24-h period (Figure 1C) also varied by treatment ($H = 29.80$, d.f. = 2, $P<0.001$) and followed a similar pattern. Again, females paired with a male had the highest median peak rate, although this did not differ from that of isolated females ($Q = 2.31$, $P = 0.063$). Both groups had higher peak rates than females paired with another female ($Q = 5.43$ and 3.18, both $P<0.001$). The timing of the peak oviposition rate also differed across treatments ($H = 27.25$, d.f. = 2, $P<0.001$); those paired with a male had their peak production at a median age of 11 days,

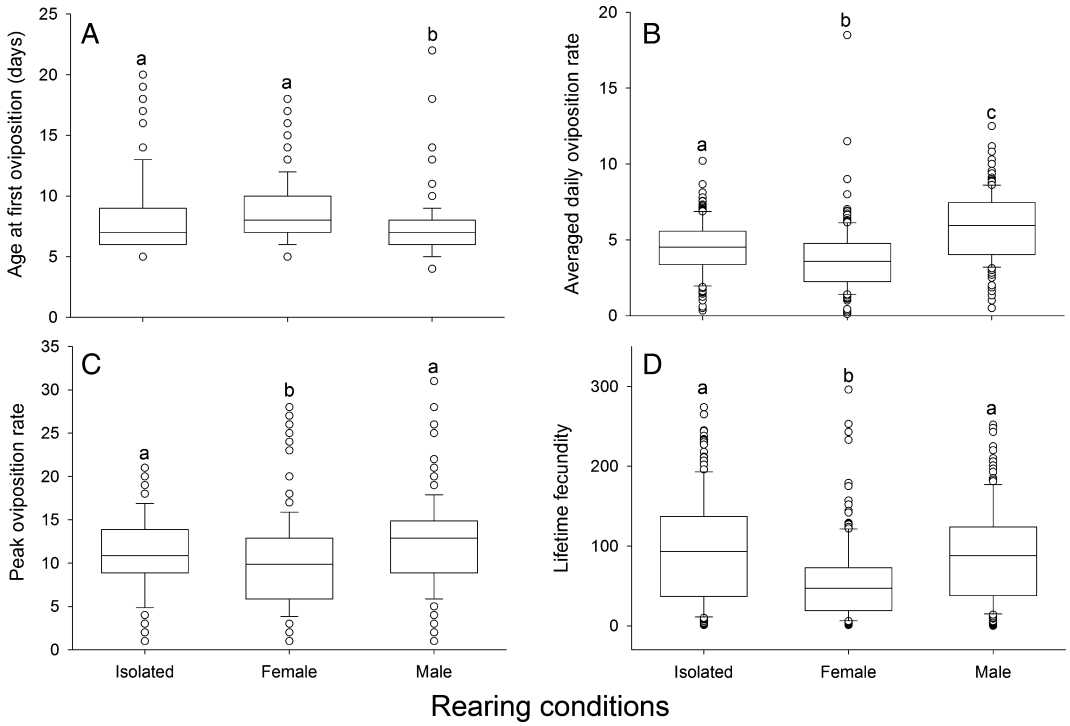

Figure 1 Effect of rearing conditions on the (A) number of days from eclosion until the start of the oviposition, (B) average daily number of eggs produced across the entire period of active ovipositing, (C) peak number of eggs laid in a single 24-h period, and (D) lifetime fecundity of laboratory-reared females that matured as adults in isolation (n = 175), paired with another female (n = 161), or with a male (n = 177). Presented are the medians, interquartile ranges, 90th and 10th percentiles (whiskers), and any outlier data points exceeding these outer bounds (dots). Significant differences between groups are indicated by different letters over the boxes (Kruskal–Wallis ANOVA on ranks followed by Dunn's post hoc analysis: P<0.05).

2 days sooner than for those in isolation (Q = 4.72) or paired with a female (Q = 4.23, both P<0.001).

Differences between treatment groups were also observed in the pattern of oviposition across the entire study period of roughly 50 days (Figure 2). Those paired with a female settled into a relatively constant rate of egg production that lasted until death. Females left isolated or paired with a male had rates that gradually decreased during their last week of life. One result of these varied oviposition rates was differences in lifetime fecundity across treatments (Figure 1D; KW-ANOVA: H = 43.43, d.f. = 2, P<0.001). Females housed with a male had egg totals similar to those of isolated females, but both produced almost twice as many eggs as females housed with another female (Q = 5.56 and 5.92, both P<0.001).

Longevity was another attribute effected by rearing conditions (Figure 3; Kaplan–Meier survival analysis, Log-Rank Statistic = 80.42, P<0.001). The longest-lived group was isolated females, with a mean (± SD) survival of 27.2 ± 0.8 days. Isolated females lasted longer than females paired with females (22.5 ± 0.7 days; Log-Rank Statistic = 66.15, P<0.001) or males (21.0 ± 0.6 days; Log-Rank Statistic = 53.02, P<0.001). The difference between the latter two groups was also significant (Log-Rank Statistic = 4.48, P = 0.034), albeit less pronounced.

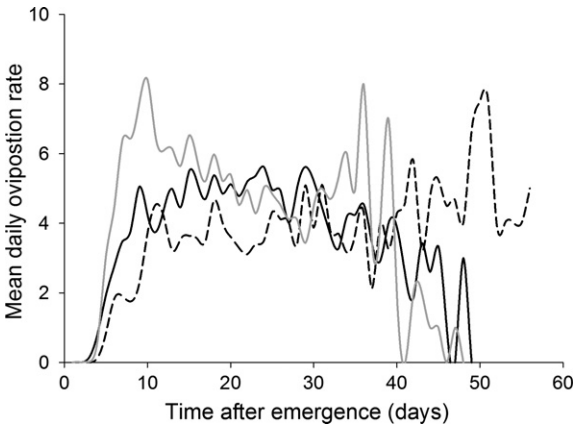

Figure 2 Mean rate of oviposition for each day of the entire sampling period for females in isolation (solid black line), paired with another female (dashed line), or with a male (solid grey line). Sample sizes varied across treatments and over time.

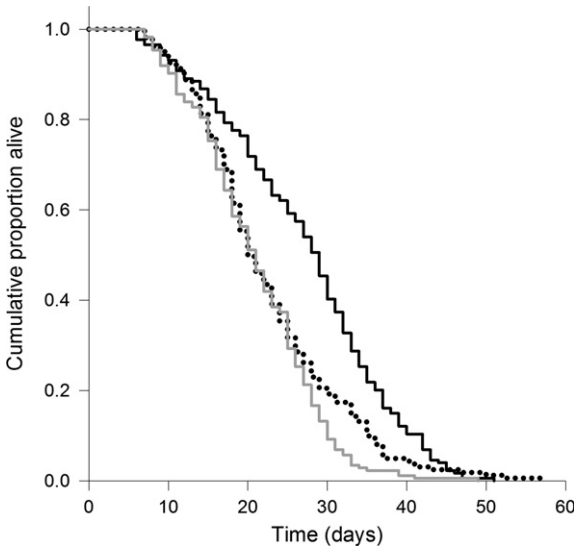

Figure 3 Survival curves showing the cumulative proportion of females alive over time while in isolation (solid black line), paired with another female (dashed line), or with a male (solid grey line). The experiment was ended only after all females had died, so there were no censored values. Significant differences were found between all treatments (Kaplan–Meier survival analysis: $P<0.001$).

Resources allocated toward oogenesis did not appear to negatively impact lifespan; there were positive associations between total fecundity and longevity for females in isolation (Spearman Rank Correlation; $r = 0.79$, $P<0.001$), paired with another female ($r = 0.80$, $P<0.001$), or with a male ($r = 0.80$, $P<0.001$). The association between oviposition rate and longevity was weaker, but still positive for isolated females ($r = 0.29$, $P<0.001$) or for those paired with a male ($r = 0.20$, $P = 0.009$) or another female ($r = 0.15$, $P = 0.05$).

Mating rates of females given access to males varied; 19% remained virgins, 54% mated once, and 27% mated more than once. Several females mated 5×. Given that the hatch rate of eggs remained relatively constant throughout the reproductive life of a singly mated female (Figure 4), there does not appear to be a need for *L. hesperus* to mate more than once. Only toward the end of the collection period, when fewer eggs were produced, did hatch rate become more variable. There were significant positive associations between the number of times mated with both the daily rate of egg production (Spearman Rank Correlation; $r = 0.32$) and total egg production ($r = 0.35$, both $P<0.001$).

Further evidence of the impact of mating is found when comparing virgin and mated females that had been continuously exposed to male stimuli. Although a male presence appeared to promote egg production, this was only true for inseminated females. Virgins oviposited less than half the median number of eggs over their lives compared to mated females (42.5 vs. 94.0 eggs; Mann–Whitney test: $T_{32,140} = 1949$, $P<0.001$), the result of a lower daily production rate (4.0 vs. 6.1 per day; $T_{32,140} = 1894$, $P<0.001$). The difference may have been exacerbated by a suggestively shorter lifespan for non-mated females (18.0 vs. 22.0 days; $T_{32,140} = 2280$, $P = 0.055$).

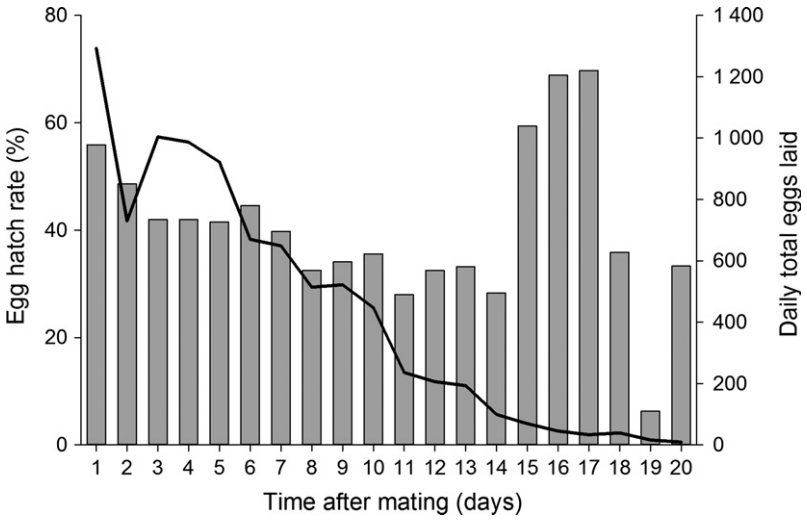

Figure 4 Sperm viability, as indicated by the percentage of eggs that successfully hatched after being collected from singly mated females each day after insemination until oviposition had stopped (columns), and the total number of eggs laid each day (solid line).

Discussion

The results of this study show that the fecundity and longevity of *L. hesperus* females are sensitive to conspecific stimuli. Males in particular had broad impact, enhancing the rate at which females matured, produced eggs, and senesced relative to isolated laboratory females. These findings are similar to those of other species in which interactions with males promote egg production seemingly at the expense of lifespan (Partridge et al., 1986; Djawdan et al., 1996; Ohgushi, 1996). However, the observed negative responses to the presence of another female suggest that more is occurring here than a direct tradeoff. Compared to females living alone, those paired with another female produced eggs at a slower rate and diminished lifetime fecundities, but still had shorter lifespans. These data suggest that in *L. hesperus* the link between fecundity and longevity is either non-existent, or highly conditional.

The positive influence males had on oviposition rate appears attributable to insemination rather than non-sexual interactions. Females paired with a male that remained virgins did not lay eggs as quickly as those that mated, producing eggs at the same suppressed rate as females paired with another female. In contrast, multiply mated females had added gains in egg production rate. As is the case with numerous other insects (Gillot, 2003; Wolfner et al., 2005), male accessory gland products transferred in the *L. hesperus* spermatophore appear to trigger this rate increase (Brent, 2010a,b; Brent et al., 2011). However, spermatophores of *L. hesperus* have limited macro- and micronutrient content (Brent et al., 2011), in contrast to the numerous species in which males provide 'nuptial gifts' of nutrients along with their sperm (Boggs, 1990; Arnqvist & Nilsson, 2000). This suggests that the stimulatory effect of mating on egg production may be hormonally driven, which coincides with the finding that one of the seminal components is juvenile hormone (Brent et al., 2016), a common systemic regulator of insect gonadal activity and reproductive behavior (Raikhel et al., 2005).

The enhanced rate of egg production promoted by multiple matings is a common response among insects (Arnqvist & Nilsson, 2000) and has been observed in another mirid (Smith, 1977). In contrast, some mirids are either monandrous or gain no fecundity benefits from multiple matings (Abasa, 1973; Blommers et al., 1997; Groot & Smid, 2000; Wheeler, 2001; Takahashi & Higuchi, 2006; Gemeno et al., 2007; Okutani-Akamatsu et al., 2009; Siswanto et al., 2009). Many *L. hesperus* in this study mated more than once, and previous dissections of females from this stock colony have found as many as nine spermatophores (unpubl.). The multiple matings of *L. hesperus* appear to be necessary only to sustain an elevated oviposition rate as there is no evident need to replenish sperm. Supporting the tenuous conclusion of Strong et al. (1970), a single mating was found to be sufficient to ensure that a female could produce viable eggs throughout her reproductive life. Mating multiple times may ensure that male-derived promoting factors are in sufficient supply to maximize a female's output potential.

The effects of mating in promoting egg production are limited; compared to isolated virgins, inseminated females have similar lifetime fecundities. This limitation may be caused by equivalent resources being available for oogenesis, given that females under both conditions had access to the same diet throughout their lives. Mated females, with their enhanced rate of oviposition, achieved their reproductive potential sooner, but this was accomplished by expending limited endogenous resources more rapidly, which could have caused their reduced survivorship. Field populations, which can access more varied and nutritive food sources, might have very different limitations, given that diet during development can have long-lasting consequences on fecundity and lifespan (Zwaan et al., 1991; Kaspi et al., 2002; Boggs & Freeman, 2005; Barrett et al., 2009; Colasurdo et al., 2009; Zajitschek et al., 2009; Adler et al., 2013; May et al., 2015). Adult stage resource access has also been shown to influence a sister species, *Lygus lineolaris* (Palisot de Beauvois), in which enriched diets produce higher fecundities (Fleischer & Gaylor, 1988; Fleming et al., 2015), including a large boost from a field diet (Gerber, 1995). Had a richer diet been provided in this study, higher fecundities might have resulted.

Although insemination appears to be generally beneficial to *L. hesperus* females, non-sexual interactions with conspecifics, regardless of sex, appear to have negative consequences. Contact with companions is unavoidable as they move in the rearing dish. Females typically respond to unwanted interactions by moving away (Strong et al., 1970; Brent et al., 2010a), causing a caloric expenditure and disrupting feeding and ovipositing (Cordts & Partridge, 1996; Bateman et al., 2006). Chronic interruptions can reduce a female's ability to cope with other stressors, thereby reducing survivorship (Partridge & Fowler, 1990). Another potential cost of cohabitation, is the enhanced risk of disease (Arnqvist & Nilsson, 2000). Despite being from the same stock colony, paired animals could carry different pathogen loads which they can then transmit. In addition, doubling the number of dish occupants amplifies resource contamination and depletion (Partridge & Fowler, 1990). The cost of such interactions is most evident in the reduced fecundity and longevity of females paired with females as compared to isolated females.

Being paired with a male would likely amplify some of these social interaction costs. First, pathogen transmission may be exacerbated by intromission and insemination (Hurst et al., 1995; Rolff & Siva-Jothy, 2002; Knell & Webberley, 2004). Second, directed courtship behavior would increase the frequency of unwanted contacts. Males approach females that have not mated recently and attempt to mount (Strong et al., 1970; Brent, 2010a,b). Under the conditions used here, this behavior can be observed dozens of times in the course of an hour (pers. obs.). Recently mated females would not suffer as badly as virgins; along with sperm, an *L. hesperus* spermatophore contains an antiaphrodisiac that the female slowly externalizes to reduce male courtship for several days (Brent, 2010a,b; Brent & Byers, 2011; Brent et al., 2017). Although this pheromone is effective, male harassment would resume once the emitted concentration dropped below an activational threshold (Brent et al., 2017).

Despite the potential added costs of a male companion, inseminated females appear to compensate to the extent that there is a positive correlation between mating frequency and longevity. This increased longevity could result from the antiaphrodisiac-driven reduction in harassment or it might be attributable to secondary effects of the heightened oogenesis induced by insemination. Vitellogenin, the egg yolk protein precursor, has a variety of protective properties in both vertebrates and invertebrates (reviewed in Zhang et al., 2011). In honey bees, high titers of vitellogenin can enhance immunity (Amdam et al., 2004) and reduce aging effects (Seehuus et al., 2006). Mating-induced increases in oviposition could similarly promote circulating vitellogenin in *L. hesperus*, enhancing stress resistance. Alternatively, the females in this study that were willing to mate more than once may have also had more resources to allocate toward both somatic maintenance and fecundity.

In summary, mating just once provides adequate sperm for a lifetime of egg production in *L. hesperus*, but females benefit from a sustained increase in their oviposition rate achieved by mating multiple times. However, the number of matings does not appear to increase the total number of eggs a female produces. Lifetime fecundity may be fixed by nutritional conditions during early development and the period of egg production, setting reproductive potential. Müller et al. (2001) have suggested that the onset of senescence occurs once this potential is reached, so that a faster rate of egg production could lead to a reduced lifespan. This does not seem to be the case here given that females paired with females produced fewer eggs and died just as soon as mated females. Instead, interactions with conspecifics may have costs unrelated to oogenesis that provide greater limitations to longevity. Further study is needed to clarify the physiological linkage between fecundity and longevity and how both may be influenced by rearing environment during early development and reproductive stages.

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