FEMALE CHOICE OF MATES IN THE APHIDOPHAGOUS LADYBIRD BEETLE, *HIPPODAMIA VARIEGATA* (COLEOPTERA: COCCINELLIDAE): THE EFFECT OF MALE AGE, SEXUAL STATUS AND FAMILIARITY

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ABSTRACT

Mating involves the transfer of sperm to females. Female reproductive investment is based on gamete numbers as well as gamete size. Females are more selective than males and this selection is based on numerous factors, like a male's age, sexual status and familiarity. *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) is an important natural enemy of many insect pests such as aphids, psyllids, whiteflies and mealybugs in many countries. We investigated female mate choice in *Hippodamia variegate* caging females with: (i) a young and a middle-aged male, (ii) a virgin and mated male and (iii) a novel and a familiar male. Time to and duration of copulation were recorded. Females preferred to mate with middle-aged and familiar males and did not differentiate between previously mated and virgin males. Females copulated quicker and for longer with young or familiar males.

Keywords: copulation duration; copulation latency; familiarity; female choice; individual recognition; mating experience

Introduction

Sexual selection involves competition between members of one sex for access to mates or gametes of the opposite sex, which involves either mate choice or intrasexual competition (Darwin 1888; Andersson 1994). It is the main driving force for many evolutionary changes in organisms and the reasons for these changes has been studied in various species of animals (Thornhill and Alcock 1983; Eberhard 1996; Simmons 2001). The main function of mating is the transfer of sperm from males to females (Arnqvist and Nilsson 2000) and because of the larger investment in gametes of females (Bateman 1948), they are more selective than males (Trivers 1972). Mate choice helps females to choose among qualitatively different mates that could affect their reproductive output, provide better resources, genes and parental care (Kokko et al. 2003). Despite being costly in terms of energy and time invested in finding suitable mates (Johnstone et al. 1996; Watson et al. 1998), risk of injury and predation (Rowe 1994; Bonduriansky and Brooks 1998), of rejecting good mates (Real 1990) and choice of high-quality mates can greatly affect their fitness (Rosenthal 2017). Males have certain traits that benefit females (Holland and Rice 1998; Gavrilets et al. 2001) eventually leading to the co-evolution of certain mating preferences of males and females (Kirkpatrick and Ryan 1991; Jennions and Petrie 2000). Numerous abiotic (Gamble et al. 2003; Borg et al. 2006) and biotic (Mautz and Sakaluk 2008) factors influence mate choice. Studies on ladybirds have demonstrated the occurrence of age-based mate choice and its effect on parental reproduction and fitness of their progeny (Omkar and Pervez 2005; Omkar et al. 2006b; Avent et al. 2008; Omkar et al. 2010; Prathibha et al. 2011; Pandey and Omkar 2013), thus age is considered to be one of the most crucial factors.

Likewise, the mating status of males plays a crucial role (Wedell and Ritchie 2004). Females of the seed beetle, *Callosobruchus maculatus* (Fabricius 1775) (Coleoptera: Bruchidae) are more fecund when they mate with virgin than mated males (Savalli and Fox 1999). Though a single mating is sufficient for female insects to ensure fertilization and achieve reproductive success, multiple matings are reported for most species (Arnqvist and Nilsson 2000; Eberhard 2009; Parker and Birkhead 2013), including ladybirds (Haddrill et al. 2008). But in general, the costs of re-mating are high in terms of energy expenditure (Watson 1993), risk of predation or disease (Watson et al. 1998; Blanckenhorn et al. 2002), injury (Eberhard 1996) and reduction in life span (Maklakov et al. 2006). In addition, various benefits, such as genetic diversity (Arnqvist and Nilsson 2000) and ability of females to influence the outcome of sperm competition and offspring fitness (Eberhard 1996) are also reported.

Arthropods recognize each other (Liu et al. 2010) and in species that mate more than once, many females avoid copulating with familiar males (Ivy et al. 2005, Ödeen and Moray 2008) in order to ensure they gain superior genes for their offspring (Bateman 2004).

Mate choice is well studied in a range of insects (Reid 1991; Arnaud and Haubruge 1999; Birkinshaw and Smith 2001; Kobayashi and Ueda 2002; McNamara et al. 2004; Fedina and Lewis 2008; Maklakov and Arnqvist 2009; Suzuki 2009; Watson and Simmons 2010; Omkar and Afaq 2013; Pandey and Omkar 2013).

In ladybirds mate choice is reported to be based on morph (Osawa and Nishida 1992; Mishra and Omkar 2014), age (Bista and Omkar 2015), body size (Dubey et al. 2016), mating status (Dubey et al. 2018) and familiarity (Saxena et al. 2018). *Hippodamia variegata* (Goeze)

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(Coleoptera: Coccinellidae) is an aphidophagous ladybird native to Asia and a potential biological control agent (Tan et al. 2014). Mainly only the effect of polyandry and male body size (Pervez and Navodita 2011; Pervez and Singh 2013) are studied in this ladybird and little is known about its sexual behaviour. The present study is on mate choice and mating parameters based on age, mating status and familiarity of males.

Material and Methods

Establishment of stock culture

A stock colony was established using *Hippodamia variegata* ladybirds from the College of Agriculture and Natural Resources field of University of Tehran in Karaj, Alborz Province, Iran (35°48′04.6″N, 50°57′39.6″E, at an altitude of 1315 m) in May 2019. Following the transfer of them to the laboratory, the colonies of *H. variegata* were fed *A. fabae* in plastic containers (18 × 15 × 5 cm). They were maintained in the laboratory conditions at 25 ± 1 °C, 55 ± 5% RH and under a 16L: 8D photoperiod. Eggs were laid on the inner surfaces of the containers or on leaves and were collected daily by transferring the beetles or the leaves on which they laid their eggs to new containers. All larvae were fed an *ad libitum* supply of *Aphis fabae* and kept in the same conditions as the adults. Adults were separated based on sex within a few hours of emergence from the pupae to prevent them from mating. All the experiments were carried out in the same containers and conditions.

Experimental design

The effect of age on female mate choice

In this experiment, young and unmated females and unmated males of two different ages (young: 10–15 days post-emergence and middle aged: 30–40 days old) (Bista and Omkar 2015) of *H. variegata* were used. Each female was provided with two males (young and middle aged) in a container. Mate choice was recorded. Once the mating commenced, the other male was removed in order to avoid male-male competition. To discriminate between the males, one elytron of each male was marked blue or white (Dubey et al. 2018). Colours were changed to avoid colour biases. The pairs were given 3 h to mate (from 12:00 to 15:00), after which they were separated. The pairs that did not mate within 3 h were not included in the experiment. In addition, we recorded time to copulation (i.e., time to genital contact) and duration of copulation (i.e., time from the insertion of the male's aedeagus into the female's genitalia until its removal). There were 25 replicates of this experiment.

The effect of mating status of males on female mate choice

In this experiment, young and unmated females were paired with young males of different sexual status (virgin and mated). Each female was provided with two males (virgin and mated) in a container. The mated male had copulated several times previously and was isolated 24 h before the experiment. Mate choice was recorded as above. Once mating commenced the other male was removed. Time to and duration of copulation were also recorded. There were 25 replicates of this experiment.

The effect of male familiarity on female mate choice

In this experiment, young and unmated males and females of *H. variegata* were used. Initially, a female was placed in a container with a male. The pairs that successfully completed a first mating were used in the following experiment after 24 h. The females were then given an opportunity to select between two males: a 'familiar male' with which the female had previously copulated and a 'novel male' that the female had not encountered before, but had mated with another female and isolated 24 h before the experiment. Mate choice was recorded. In addition, time to and duration of copulation were recorded. There were 25 replicates of this experiment.

Statistical analysis

All analyses were done using IBM SPSS Statistics V22.0 software. A binomial test was used to evaluate mating occurrence. Since the distributions of the results of these experiments was not normal, the Mann-Whitney U test was used to compare the means of the times to and duration of copulation.

Results

The effect of age of males on female mate choice

Females preferred to mate with middle-aged males rather than young males (two-tailed binomial test: $p = 0.043$) (Table 1). Out of 25 females, 18 (72%) mated with the middle-aged males and only 7 (28%) mated with young males. The time to copulation was shorter for young males ($U = 18.5$, $p = 0.006$) but there was no significant difference in the duration of copulation ($U = 55$, $p = 0.623$).

The effect of sexual status of males on their choice of females

The choice of females of virgin and mated males did not differ (two-tailed binomial test: $p = 1.000$) (Table 2). Out of 25 females, 13 (52%) mated with virgin and 12 (48%) with mated males. The time to copulation was shorter ($U = 10.000$, $p = 0.0005$) and duration of copulation was longer for mated males ($U = 0.0005$, $p = 0.0005$).

The effect of male familiarity on female mate choice

Females preferred to re-mate with familiar than unfamiliar males (two-tailed binomial test: $p = 0.015$) (Table 3). Out of the 25 females, 19 (76%) mated with familiar and only 6 (24%) with males they had not previously encountered. The time to copulation was shorter for fa-

Table 1 The percentage of females of *Hippodamia variegata* that mated, mean (± SE) time to and duration of copulation when mated with a middle-aged or young male.

Treatment	Mating Occurrence (%)	Time to mating (Seconds)	Duration of copulation (Seconds)
Middle-age	72	438.06 ± 85.877	7019.00 ± 173.356
Young	28	15.14 ± 6.010	7225.14 ± 222.407
Test statistics	Two-tailed binomial test	Mann-Whitney U U = 18.5	Mann-Whitney U U = 55
P-values	$p = 0.043$	$p = 0.006$	$p = 0.623$

Table 2 The percentage of females of *Hippodamia variegata* that mated and mean (± SE) time to and duration of copulation when mated with a virgin or previously mated male.

Treatment	Mating Occurrence (%)	Time to mating (Seconds)	Duration of copulation (Seconds)
Unmated	52	1253.92 ± 364.129	5066.08 ± 153.916
Mated	48	315.08 ± 23.266	6742.58 ± 121.332
Test statistics	Two-tailed binomial test	Mann-Whitney U U = 10.000	Mann-Whitney U U = 0.0005
P-values	$p = 1.000$	$p = 0.0005$	$p = 0.0005$

Table 3 The percentage of females of *Hippodamia variegata* that mated and mean (± SE) time to and duration of copulation when mated with a familiar or unfamiliar male.

Treatment	Mating Occurrence (%)	Time to mating (Seconds)	Duration of copulation (Seconds)
Familiar	76	314.16 ± 34.502	6524.83 ± 398.288
Novel	24	568.67 ± 127.192	6671.74 ± 104.356
Test statistics	Two-tailed binomial test	Mann-Whitney U U = 24	Mann-Whitney U U = 45
P-values	$p = 0.015$	$p = 0.035$	$p = 0.442$

miliar males (U = 24, $p = 0.035$), but there was no difference in the duration of copulation (U = 45, $p = 0.442$).

Discussion

Mate choice is well studied in Coleoptera such as *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) (Arnaud and Haubruge 1999; Fedina and Lewis 2008), bark beetle, *Ips pini* (Say) (Coleoptera: Scolytidae) (Reid 1991), oak ambrosia beetle, *Platypus quercivorus* (Murayama) (Coleoptera: Platypodidae) (Kobayashi and Ueda 2002), grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) (Birkinshaw and Smith 2001), hide beetle, *Dermestes agittari* De Geer (Coleoptera, Dermestidae) (McNamara et al. 2004), burying beetle, *Nicrophorus quadripunctatus* Kraatz (Coleoptera: Silphidae) (Suzuki 2009), seed beetle, *Callosobruchus chinensis* L. (Coleoptera: Bruchidae) (Maklakov and Arnqvist 2009), dung beetle, *Onthophagus sagittarius* Fabricius (Coleoptera: Scarabaeidae) (Watson and Simmons 2010) and parthenium beetle, *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae) (Omkar and Afaq 2013; Pandey and Omkar 2013), but there is little information on mate choice based on morph, age, body size, mating status and familiarity in ladybirds .

The results of the first experiment on *H. variegata* revealed that the females preferred middle-aged males as sexual partners. This is consistent with what Pervez et al. (2004) and Sahu and Omkar (2013), respectively, report for *Propylea dissecta* (Coleoptera: Coccinellidae) and *Anegleis cardoni* (Coleoptera: Coccinellidae) with a sigmoidal increase in willingness to mate with age. This could be due to prolonged mate deprivation as is documented for *Coccinella septempunctata* (Srivastava and Omkar 2004).

In many species, middle-aged males are known to transfer more sperm (Parker 1974; Ueno 1994; Bonduriansky and Brassil 2002; Jones and Elgar 2004) and have higher reproductive output than other aged individuals (Hansen and Price 1995; Beck and Powell 2000). This is in accordance previous studies on ladybirds (Pervez et al. 2004; Srivastava and Omkar 2004; Bista and Omkar 2015). However, numerous studies imply that females tend to choose older males as partners in order to gain indirect benefits, as older males are likely to be of superior genetic quality (Trivers 1972; Manning 1985; Andersson 1994; Hansen and Price 1995; Kokko and Lindström 1996). Since gamete production and fertilization are costly, a way of optimizing the allocation of gametes is to choose mates based on their sexual status (Trivers 1972; Savalli and Fox 1999; Koene et al. 2008; Simmons and Beveridge 2011). In this context, numerous authors imply that unmated males can better enhance a female's fecundity than previously mated males (Jiménez-Pérez and Wang 2004; McCartney and Heller

2008; Michaud et al. 2013; Jiaqin et al. 2014; Mirhosseini et al. 2014; Colares et al. 2015; McDonald and Pizzari 2016) and females tend not to copulate with recently mated males (Markow et al. 1978; Nakatsuru and Kramer 1982; Gerofotis et al. 2015).

The results of the second experiment did not reveal a significant difference in female's choice between virgin and mated males; although previously mated males had a shorter time to copulation. This may be due to experienced males being more competitive in mating (Milonas et al. 2011) than virgin males (Wiklund and Kaitala 1995). The results demonstrated that mating with experienced males continued for a longer, which could be attributed to repeated mating as many studies report that experienced males produce less ejaculate than virgin males (Kaitala and Wiklund 1994; Wedell and Ritchie 2004; Torres and Jennions 2005; Lauwers and Van Dyck 2006; McNamara et al. 2007; Dowling and Simmons 2012). As mentioned in (Omkar et al. 2006a), prolonged mating may increase sperm transfer and result in an increase in fecundity and fertility and assure paternity (Dubey et al. 2018). In contrast, the studies on *Coccinella septempunctata* (Omkar and Srivastava 2002) and *Anegleis cardoni* Weise (Coleoptera: Coccinellidae) (Omkar and Afaq 2013) indicate that the duration of copulation is longest for virgin males.

The results of the third experiment revealed that females of *H. variegata* preferred familiar males over unfamiliar males and preferred to re-mate quickly with them. These results are consistent with the studies on *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) (Jiaqin et al. 2014); *Tenuis valvaenotata* (Mulsant) (Coleoptera: Coccinellidae) (Túler et al. 2018) and cabbage beetle, *Colaphellus bowringi* (Baly) (Coleoptera: Chrysomelidae) (Liu et al. 2010), where females prefer to remate with familiar males.

Contrary to this, there are studies in which females prefer mating with unfamiliar males: hide beetles, *Dermestes maculatus* (Coleoptera: Dermestidae) (Archer and Elgar 1999), *Menochilus sexmaculatus* (Coleoptera: Coccinellidae) (Saxena et al. 2018) and see also Hosken et al. 2003; Bateman 2004; Ivy et al. 2005; Harris and Moore 2005 and Ödeen and Moray 2008. This may be in order to gain genetic benefits from different males, which ensures the genetic diversity of their progeny and avoids genetic incompatibility (Arnqvist and Nilsson 2000).

In conclusion this study revealed previously unknown aspects of the mating behaviour of *H. variegata*. Females of *H. variegata* preferred to mate with familiar and middle- aged males and show no preference for mates based on mating status. Some research indicates that females of some insects do not prefer previously mated males (Archer and Elgar 1999; Bateman 2004) and of other species prefer to mate many times with mated familiar males (Liu et al. 2010). Further studies are needed to confirm these preferences by subjecting males and females to different combinations of the parameters. Also, the measure of the success in gaining access to mates is incomplete as competition also occurs in the reproductive tract of females, which could be better understood by studying post-copulatory sexual selection.

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Authors' contributions

MS and MRF conceived the idea. MRF performed fieldwork and collected material. MRF, MS and O performed experiments and statistical analysis. MRF, MS and O contributed to writing the manuscript. All authors read and approved the final version of the manuscript.

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