



Original article

Reproductive success in *Zygogramma bicolorata*: A role of post-insemination association of male and female



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ABSTRACT

Reproductive success is attained by various mechanisms in insects. Prolonged post insemination association is one such mechanism to increase the reproductive success. The present study was conducted to assess the role of post insemination association of mating partners on reproductive performance in Chrysomelidae beetle, *Zygogramma bicolorata* Pallister. The matings were disrupted at different time intervals and fecundity and percent egg viability of the females were recorded. In addition, the mounting attempts, mating attempts, time to commencement of mating and latent period were also recorded. It was hypothesized that: (1) the mounting and mating attempts would not exist, (2) copulation duration, would not affect the reproductive performance, and (3) the beetle would not exhibit the mate guarding behaviour. Interestingly, results revealed that 6.00 ± 1.3 and 6.59 ± 0.93 mounting and mating attempts are needed to establish successful mating. The results revealed that males improved their percent egg viability with a mating duration ranging from nearly 30–50 min. While fecundity increased with a mating duration of above 30 min and up to a duration of 60 min. This result concluded that males of this beetle display post copulatory mate guarding behaviour after 60 min in which male rides on female's back with his aedeagus inserted in the female genital tract.

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1. Introduction

Reproductive success is the maximum number of offspring sired by a male from early life till its reproductive senescence (Hsu et al., 2017). The complex behaviours of mating partners and processes that occur during pre and post mating leads to huge variation in reproductive success (Boorman and Parker, 1976). The pattern of reproductive success in insect species where females mate multiple times within a single reproductive cycle is often highly variable (Lewis and Austad, 1990). Insects either show mixed paternity to varying degrees, or the last male fertilizes most

of the female's eggs (Simmons and Siva-Jothy, 1998). A last male advantage can arise by males removing previous ejaculates. However, the mechanisms by which the last male achieves high paternity are unknown for most species where the males do not remove sperm.

Recent studies have observed the effects of specific behavioural or morphological characters on the reproductive success (Hosken et al., 2008; South and Lewis, 2012). For some species, it has been shown that male body size in case of *Pieris napi* and *Nephila edulis* (Bissoondath and Wiklund, 1997; Schneider et al., 2000), copulation duration in case of *Gerris lateralis* and *Argiope keyserlingi* (Arnqvist and Danielsson, 1999a,b; Elgar et al., 2000), courtship behaviour in case of *Linyphia litigiosa*, *Scathophaga stercoraria* and *Dryomyza anilis* (Watson, 1991b; Otronen, 1997; Otronen et al., 1997), re-mating interval in case of Pseudoscorpions and *Gerris lacustris* (Zeh and Zeh, 1994; Danielsson and Askenmo, 1999), biochemical compatibility in case of *Diplosoma listerianum* (Bishop et al., 1996; Zeh and Zeh, 1996), morphology of male genital organ in case of *Gerris lateralis* and *Gerris lacustris* (Arnqvist and Danielsson, 1999b; Danielsson and Askenmo, 1999) and sperm size

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in case of *Rhizoglyphus robini* and *Caenorhabditis elegans* (Radwan, 1996; LaMunyon and Ward, 1998) affects the male fitness.

The body size of male is directly associated with the size of spermatophore transfer to female genital tract which is one of the crucial factor significantly affecting the reproductive success (Sakaluk and Eggert, 1996; Bissoondath and Wiklund, 1997; Schneider et al., 2000). In some cases, rapid and divergent evolution in the male genital structure is also one of the important factor which directly influences the reproductive success (Arnqvist and Danielsson, 1999b; Danielsson and Askenmo, 1999). Apart from the male genital morphology, sperm size also plays a vital role in the paternity success, i.e. large sperm compete more and favour fertilization than the smaller one (Radwan, 1996; LaMunyon and Ward, 1998). Moreover, somatic and genetic incompatibility mechanisms regulate mating, and this may involve differential phagocytic removal in oviduct of sperm. (Bishop et al., 1996; Zeh and Zeh, 1996).

Among different factors, copulation duration is one of the most important factor influencing the reproductive success because copulation duration is directly related to the number of spermatophore deposition and degree of sperm displacement (Simmons and Parker, 1992; Elgar et al., 2000). Copula duration shows vital effects on overall fitness of both partners (Edvardsson and Canal, 2006; Perez Staples et al., 2010). Although sperm transfer requires only a few seconds in some insects (Seth et al., 2002), still it has been observed that they continue to mate for several hours. This variability in copula duration is usually correlated with one or the other functions or combination of, such as the transfer of nutrients or other seminal fluid compounds along with sperm to the female (Riemann et al., 1967), the production and placement of spermatophore in male reproductive organ (Gregory and Howard, 1994), mating plug formations to prevent chances of other male's sperm to reach the ovum (Labine, 1964), mate guarding from other competitors (Emily et al., 2014) and the displacement of rival sperm (Parker, 1970c).

Mate guarding is a term for prolonged periods of male and female association beyond the time span required for fertilization (Simmons, 2001). This post mating interaction might have other benefits to engaged partners (Alcock, 1994). Mate guarding behaviour is basically to reduce the sperm competition (Vahed et al., 2011). It can be either reduced by preventing female from mating with multiple males or by obtaining last male advantages (Adler and Adler, 1991). It is expected that mate guarding will always be favoured when the risk of sperm competition is maximum. Male insects probably assess the risk of sperm competition from other competing males (Carazo et al., 2007), according to which they generally adjust their mate guarding duration (Burdfield-Steel and Shuker, 2014; Shuker and Simmons, 2014). Mate guarding duration might be affected by different factors which includes male resistivity to takeover, receptivity of female post copulation, degree of sperm superiority, male density, re-mating intervals, oviposition and predation risk, age and body size of mating partners (Alcock, 1994; Elgar and Bathgate, 1996).

Mate guarding has both advantages and disadvantages. Its advantage is that it avoids or decreases sperm competition and permits a male to assure its paternity (Parker, 1970; Henar and Papaj, 1999). The disadvantages, conversely, are more diverse (Simmons 2001). It includes: (i) greater risks of predation (Alcock, 1994), (ii) increased energy expenditure (Saeki et al., 2005), (iii) lower sperm formation (Ward and Simmons, 1991), (iv) diminished development rate (Robinson and Doyle, 1985), (v) reduced egg size of guarded females (Jormalainen et al., 2001), and (vi) lost opportunity for feeding or mating with other mates (Dodson and Marshall, 1984).

Although there are several studies on mate guarding and its effects on paternity success in insect species (Hockham and

Vahed, 1997; Stoks et al., 1997; Chaudhary et al., 2015) however similar studies are lacking in *Zygogramma bicolorata*. In addition to it a few number of trials/attempts have been observed for successful mating establishment which might be considered as mounting and mating attempts in *Zygogramma bicolorata* (data collected from lab observations). So the present study is an attempt to examine and establish the post-copulatory mate guarding behaviour in *Z. bicolorata* Pallister (Coleoptera: Chrysomelidae), if any? And find out the required number of mounting and mating attempts for successful mating.

Therefore, it is hypothesized that (1) mounting attempts and mating attempts do not exist in *Z. bicolorata* (2) Parthenium beetle does not exhibit mate guarding (3) if it exists then it would not show any effect on reproductive success. It is further expected that the present study would develop the base for research on sexual selection in this beetle.

2. Materials and methods

2.1. Study species

Zygogramma bicolorata, commonly known as the Mexican beetle or Parthenium beetle, is a potential biocontrol agent of *Parthenium hysterophorus*. The beetle was first introduced in Australia from Mexico in 1998 (McFadyen and McClay, 1981). It was introduced in India from Mexico in 1983 by the Indian Institute of Horticultural Research for the biocontrol of noxious weed, *P. hysterophorus*. Both male and females take about 11 ± 01 days to mature sexually after emergence (Jayanth and Bali, 1993). The average life cycle of *Z. bicolorata* ranged from 27 ± 03 days.

2.2. Stock maintenance

The laboratory culture of *Zygogramma bicolorata* was established from adults and larvae collected from the agricultural fields of Amarkantak ($22^{\circ} 40'N, 81^{\circ} 45'E$), India and fed on ad libitum supply of fresh excised leaves of *Parthenium hysterophorus* in plastic Petri dishes ($14.5 \times 1.5 \text{ cm}^2$), kept under constant abiotic conditions ($25 \pm 2^{\circ} \text{C}$, $65 \pm 5\% \text{ R.H}$ and 14L: 10D) in a BOD incubator (Matrix Scientific Instruments; CAT No.MBI-50; Sr. No. F/11/913). The wilted leaves were replaced daily with fresh ones. Newly hatched larvae were reared in Petri dishes till fourth instar stage. After that fourth instar larvae were transferred to glass beakers (500 ml) filled with moist sand, for pupation. The 10 day old adults were taken out from the stock culture for further experimentation.

2.3. Experimental design

For the control treatment 10 day old unmated adults (male and female) were paired for single mating in new plastic Petri dish (size as above) and allowed to complete mating, the mating duration was recorded using a stopwatch. Post mating, the females were isolated and kept on excised leaves of *Parthenium* in fresh Petri dish, replenished daily, the oviposition and egg viability was recorded every 24 h for the next five days. A total of 10 replicates were conducted.

For the experimental treatments, 10 day old unmated adults were paired in fresh plastic Petri dish and mounting attempt (MoA), mating attempt (MA), time to commencement of mating (TCM) and latent period (LP) were recorded (Table 1). After the mounting, mating was disrupted at different mating intervals, (i) 5 min, (ii) 10 min, (iii) 15 min, (iv) 20 min, (v) 30 min, (vi) 40 min, (vii) 50 min, (viii) 60 min, (ix) 120 min, and (x) 180 min.

All treatments were replicated 10 times. Post mating, the females were isolated and kept on excised leaves of *Parthenium*

Table 1
Definitions of different mating parameters.

Sr. No.	Terms	Definition	References
1.	MoA	It is defined as the no. of trials accomplished by the male to mount the back of female	Sales et al. (2018)
2.	MA	It is defined as the number of mating position assume by male after mounting and extrude his genitalia for mating	Sales et al. (2018)
3.	TCM	It is the time in minutes taken by the male to first mount on the female after its introduction to the arena	Han and Jablonski (2018)
4.	LP	It is the duration between the mounting and first stroke after the insertion of the aedeagus	Han and Jablonski (2018)

in fresh Petri dish, replenished daily and fecundity and egg viability recorded every 24 h for the next five days.

2.4. Statistical analysis

All the collected data on MA, MoA, TCM, LP, mating duration, fecundity and percent egg viability were checked for normality with the help of Kolmogorov-Smirnov's test, which revealed normal distribution. Heterogeneity of variance of data was checked by Bartlett's test, which revealed homogenous variances. Fecundity and percent egg viability were subjected to one-way ANOVA followed by Tukey's post hoc honest test of significance at 5% level. Percent data were arcsine transformed prior to being subjected to ANOVA. All statistical analyses were done using MINITAB-16 as statistical software (Minitab Inc., State College, Pennsylvania, USA).

3. Results

Our study revealed that for the proper establishment of mating association by adults, it requires 6.00 ± 1.3 and 6.59 ± 0.93 mounting and mating attempts respectively. After 114.86 ± 12.75 s, adults established their copulation i.e. TCM. Latent period was 98.60 ± 8.09 s.

Results of one-way ANOVA revealed the significant influence of copula duration on fecundity ($F = 23.87$, $df = 1.19$, $P < 0.05$; Fig. 1). Comparison of means revealed insignificant differences in fecundity at mating durations between 5.00 and 20.00 min, 30.00–50.00 min, and 60.00–complete mating (240.34 ± 8.07 min: Fig. 1).

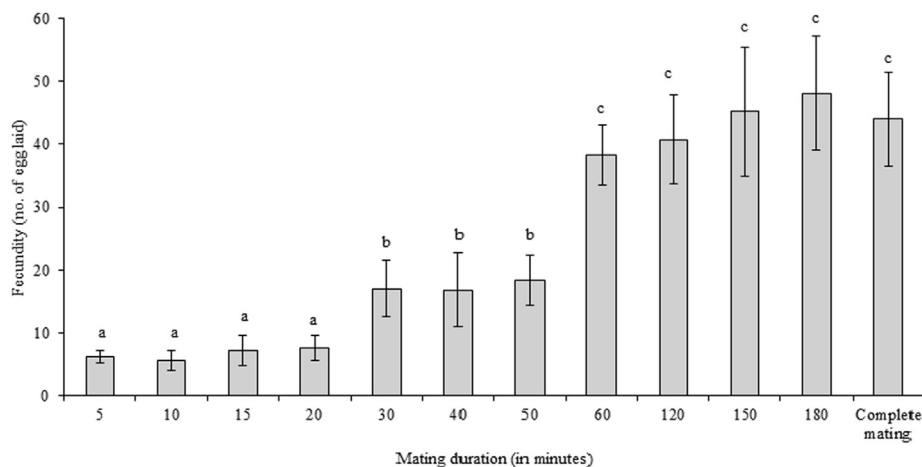


Fig. 1. Effect of mating duration on the fecundity of *Zygogramma bicolorata*.

A significant effect of copula duration was also observed on percent egg viability ($F = 34.29$, $df = 1.19$; $P < 0.05$; Fig. 2). Percent egg viability did not vary significantly at mating durations between 5.00 and 20.00 min, 30.00–40.00 min, and 50.00–complete mating (Fig. 2).

4. Discussion

The results of the present investigation revealed that this beetle requires few mounting and mating attempts for successful mating establishment. It may be due to the active courtship behaviour as observed in the case of *Manacus vitellinus* (Chiver and Schlinger, 2017), aggressive behaviour as observed in case of *Drosophila melanogaster* (Bath et al., 2017) and female choice before mating. For the mating, this beetle requires 114.86 ± 12.75 s of time to commencement of mating and 98.60 ± 8.09 s of Latent period. The same behaviour has been observed in case of *Coleomegilla maculata* which was due to the non-familiarity with mate or with mating process (Harmon et al., 2008), female resist to mate with male and activeness or passiveness of the mating partners (Eberhard, 1985).

Our result also revealed that the fecundity was significantly influenced by the copula duration. The fecundity increased with increase in copula duration. Similar observations were recorded earlier in *M. Sexmaculatus* by Chaudhary et al. (2015). This increase in copula duration might be for: (1) the sufficient number of sperm transferred to fertilized more eggs as the amount of sperm transfer is directly proportional to the copula duration (Simmon and Siva Jothy, 1998; Simmon, 2001; Engqvist, 2007; Himuro and Fujisaki, 2015), (2) male partner of many insects transfer substances in their ejaculate during copulation that play important role in induction of oviposition in female partner (Riemann et al., 1967), (3) during copulation some seminal fluid proteins are transferred which are known to accelerate ovarian development and egg production in some species (Shahid et al., 2016), and provide fitness benefits to both the mating partners (Savalli and Fox, 1999).

The increase in percent egg viability with increase in copula duration might be because of the prolonged copula durations providing maximum sperm quantity to fertilize eggs. The present outcomes obey many earlier reports in beetles (Omkar et al., 2006; Chaudhary et al., 2015). The comparative increase in percent egg viability with copulation duration might be due to the uninterrupted sperm deposition and numerous ejaculation during mating (Riemann et al., 1967). It has been shown in various studies in insects that protein from seminal fluids (Chen, 1984; Simmons

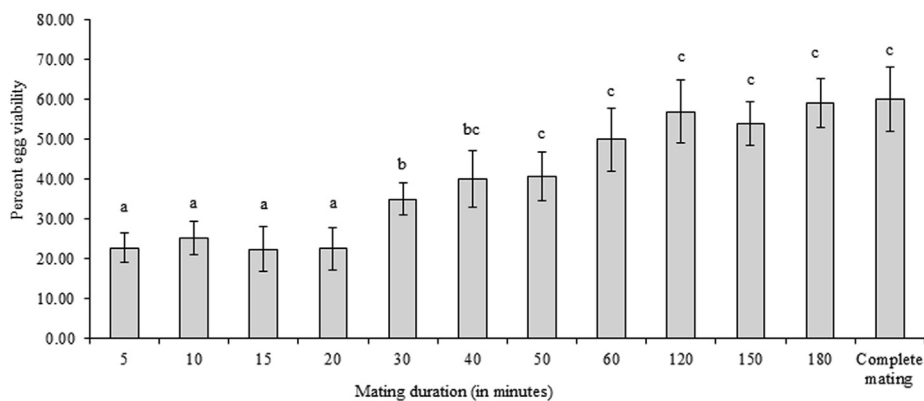


Fig. 2. Effect of mating duration on the percent egg viability of *Zygogramma bicolorata*.

and Beveridge, 2011) transferred during copulation might stimulate both fecundity and percent egg viability in *Z. bicolorata* females (Avila et al., 2011; Simmons and Beveridge, 2011; Yamane et al., 2015). In several species of insects, these seminal fluid proteins are found to be directly proportional to the copula duration (Omkar et al., 2006; Engqvist, 2007).

Both fecundity and percent egg viability increased with increase in copula duration and were maximum at 60 min but after that there was insignificant effect of copula duration on fecundity and egg viability till natural disengagement. This physical post insemination association may be for increasing paternity success by increasing seminal fluid and nutrients transfer. Correlation between copula duration with paternity success has been reported in many organisms by various mechanism (Schoffl and Toborsky, 2002; Linn et al., 2007). This increase in copula duration might be the mate guarding behaviour in this beetle which is one of the mechanism to increase paternity success (Linn et al., 2007; Chaudhary et al., 2015). The male benefited from mate guarding i.e. physical association of mating partners reduces the probability that female is physically available to another male (Mazzi et al., 2009). It also prevents female from removing spermatophore which again increase the chances of paternity success (Bateman and Mc Fadyen, 1999). Mate guarding and post insemination association may provide necessary proteins which are associated with seminal fluid that may continuously transfer during physical association which play vital role to stimulate fecundity and viability that ultimately increase paternity success (Riemann et al., 1967; Avila et al., 2011; Simmons and Beveridge, 2011; Yamane et al., 2015; Shahid et al., 2016). This increase in copula duration and mate guarding might be for increasing reproductive output in this beetle.

The reports of present investigation on determinants of paternity success and post insemination association of mating partners answer the question of benefits of prolonged mate guarding to increase reproductive success. Thus from the above observations, it can be concluded that: (1) mounting and mating attempts does exist in this beetle and number of mounting and mating attempts are required for establishment of successful mating, (2) the copula duration significantly affects the fecundity and percent egg viability and (3) *Zygogramma bicolorata* exhibits the mate guarding behaviour to increase reproductive output. (4) The results of the present study will elaborate the mating behaviour patterns and mate guarding behaviour in *Z. bicolorata*. However, still a lot of mating behaviour studies needs to be carried out to further strengthen and divulge the nature of interactions underplay in *Zygogramma bicolorata* which can be used as a tool for biocontrol strategies.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Adler, P.H., Adler, C.R.L., 1991. Mating behavior and the evolutionary significance of mate guarding in three species of crane flies (Diptera: Tipulidae). *J. Insect Behavior* 4, 619–632.
- Alcock, J., 1994. Postinsemination associations between males and females in insects: the mate guarding hypothesis. *Annu. Rev. Entomol.* 39, 1–21.
- Arnqvist, G., Danielsson, I., 1999a. Postmating sexual selection: the effects of male body size and recovery period on paternity and egg production rate in a water strider. *Behav. Ecol.* 10, 358–365.
- Arnqvist, G., Danielsson, I., 1999b. Copulatory behavior, genital morphology, and male fertilization success in water striders. *Evolution* 53, 147–156.
- Avila, F., Sirot, L.K., Lafamme, B.A., Rubinstein, C.D., Wolfner, M.F., 2011. Seminal fluid proteins: identification and function. *Annu. Rev. Entomol.* 56, 21–40.
- Bateman, P.W., MacFadyen, D.N., 1999. Mate guarding in the cricket *Grylodes sigillatus*: influence of multiple potential partners. *Ethology* 105, 949–957.
- Bath, E., Peters, C., Reddy, A., Tobias, J.A., Easton-Calabria, E., Seddon, N., Goodwin, S. F., Wigby, S., 2017. Sperm and sex peptide stimulate aggression in female *Drosophila*. *Nat. Ecol. Evol.* 1, 0154.
- Bishop, J.D., Jones, C.S., Noble, I.R., 1996. Female control of paternity in the internally fertilizing compound ascidian *Diplosoma listerianum*. 2. Investigation of male mating success using RAPD markers. *Proc. Royal Soc. London B: Biol. Sci.* 263, 401–407.
- Bissoondath, C.J., Wiklund, C., 1997. Effect of male body size on sperm precedence in the polyandrous butterfly *Pieris napi* L. (Lepidoptera: Pieridae). *Behav. Ecol.* 8, 518–523.
- Boorman, E., Parker, G.A., 1976. Sperm (ejaculate) competition in *Drosophila melanogaster*, and the reproductive value of females to males in relation to female age and mating status. *Ecol. Entomol.* 1, 145–155.
- Burdfield-Steel, E.R., Shuker, D.M., 2014. Mate-guarding in promiscuous insect: species discrimination influences context-dependent behaviour. *Evol. Ecol.* 28, 1031–1042.
- Carazo, P., Font, E., Alfthan, B., 2007. Chemosensory assessment of sperm competition levels and the evolution of internal spermatophore guarding. *Proc. Royal Soc. B: Biol. Sci.* 274, 261–267.
- Chaudhary, D.D., Mishra, G., Omkar, 2015. Prolonged matings in a ladybird, *Menochilus sexmaculatus*: a mate guarding mechanism?. *J. Asia-Pac. Entomol.* 18, 453–458.
- Chen, P.S., 1984. The functional morphological and biochemistry of insect male accessory glands and their secretions. *Annu. Rev. Entomol.* 29, 233–255.

- Chiver, I., Schlinger, B.A., 2017. Sex differences in androgen activation of complex courtship behaviour. *Anim. Behav.* 124, 109–117.
- Danielsson, I., Askenmo, C., 1999. Male genital traits and mating interval affect male fertilization success in the water strider *Gerris lacustris*. *Behav. Ecol. Sociobiol.* 46, 149–156.
- Dodson, G., Marshall, L., 1984. Mating Patterns in an Ambush Bug *Phymata fasciata* (Phymatidae). *JSTRO* 112, 50–57.
- Eberhard, W.G., 1985. Sexual selection and animal genitalia. Harvard University Press, Cambridge, MA, p. 244.
- Edvardsson, M., Canal, D., 2006. The effects of copulation duration in the bruchid beetle *Callosobruchus maculatus*. *Behav. Ecol.* 17, 430–434.
- Elgar, M.A., Bathgate, R., 1996. Female receptivity and male mate guarding in the jewel spider *Gasteracantha minax* thorell (Araneidae). *J. Insect Behavior* 9, 729–738.
- Elgar, M.A., Schneider, J.M., Herberstein, M.E., 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. *Proc. Royal Soc. London B: Biol. Sci.* 267, 2439–2443.
- Emily, R., Burdfield, S., Shuker, D.M., 2014. Mate-guarding in a promiscuous insect: species discrimination influences context-dependent behaviour. *Ecol. Ecol.* 28, 1031–1042.
- Engqvist, L., 2007. Male scorpionflies assess the amount of rival sperm transferred by females' previous mates. *Evolution* 61, 1489–1494.
- Gregory, P.G., Howard, D.J., 1994. A postinsemination barrier to fertilization isolated to closely related ground crickets. *Evolution* 48, 705–710.
- Han, H.S., Jablonski, P.G., 2018. Increased female resistance to mating promotes the effect of mechanical constraints on latency to pair. *Ecol. Evol.* 8, 9152–9157.
- Harmon, J.P., Hayden, A., Andow, W., 2008. Absence makes the heart grow fonder: Isolation enhances the frequency of mating in *Coleomegilla maculata* (Coleoptera: Coccinellidae). *J. Insect Behavior* 21, 495–504.
- Henar, A.P., Papaj, D.R., 1999. Resource presence and operational sex ratio as determinants of copulation duration in the fly *Rhagoletis juglandis*. *Anim. Behav.* 57, 1063–1069.
- Himuro, C., Fujisaki, K., 2015. Effect of mating duration on female reproductive traits of seed bug *Togo hemipterus* (Heteroptera: Lygaeidae). *Appl. Entomol. Zool.* 50, 491–496.
- Hockham, L.R., Vahed, K., 1997. The function of mate guarding in a field cricket (Orthoptera: Gryllidae; *Teleogryllus natalensis* otte and cade). *J. Insect Behavior* 10, 247–256.
- Hosken, D.J., Taylor, M.L., Hoyle, K., Higgins, S., Wedell, N., 2008. Attractive males have greater success in sperm competition. *Curr. Biol.* 18, R553–R554.
- Hsu, Y.H., Simons, M.J.P., Schroeder, J., Girndt, A., Winney, I.S., Burke, T., Nakagawa, S., 2017. Age-dependent trajectories differ between within-pair and extra-pair paternity success. *J. Evol. Biol.* 30, 951–959.
- Jayanth, K.P., Bali, G., 1993. Biological studies on *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae), a potential biological control agent of *Parthenium hysterophorus* L. (Asteraceae). *J. Biol. Control* 7, 93–98.
- Jormalainen, V., Merilaita, S., Riihimäki, J., 2001. Costs of intersexual conflict in the isopod *Idotea baltica*. *J. Evol. Biol.* 14, 763–772.
- Labine, P.A., 1964. Population biology of the butterfly, *Euphydryas editha*. *Int. J. Organic Evol.* 18, 335–336.
- LaMunyon, C.W., Ward, S., 1998. Larger sperm outcompete smaller sperm in the nematode *Caenorhabditis elegans*. *Proc. Royal Soc. London B: Biol. Sci.* 265, 1997–2002.
- Lewis, S.M., Austad, S.N., 1990. Sources of intraspecific variation in sperm precedence in red flour beetles. *Am. Nat.* 135, 351–359.
- Linn, C.D., Molina, Y., Difatta, J., Christenson, T.E., 2007. The adaptive advantage of prolonged mating: a test of alternative hypotheses. *Anim. Behav.* 74, 481–485.
- Mazzi, D., Kesaniemi, J., Hoikkala, A., Klappert, K., 2009. Sexual conflict over the duration of copulation in *Drosophila montana*: why is longer better? *BMC Evol. Biol.* 9, 132.
- McFadyen, R.E., McClay, A.S., 1981. Two new insects for the biological control of *Parthenium weed* in Queensland. *Proceedings of 6th Australian Weeds Conference* 1, 145–149.
- Omkar, Singh, K., Pervez, A., 2006. Influence of mating duration on fecundity and fertility in two aphidophagous ladybirds. *J. Appl. Entomol.* 130, 103–107.
- Otronen, M., Reguera, P., Ward, P.I., 1997. Sperm storage in the yellow dung fly *Scathophaga stercoraria*: identifying the sperm of competing males in separate female spermathecae. *Ethology* 103, 844–854.
- Otronen, M., 1997. Sperm numbers, their storage and usage in the fly *Dryomyza anilis*. *Proc. Royal Soc. London B: Biol. Sci.* 264, 777–782.
- Parker, G.A., 1970a. Sperm competition and its evolutionary consequences. *Biol. Rev.* 45, 525–567.
- Parker, G.A., 1970b. The reproductive behavior and the nature of sexual selection in *Scatophaga stercoraria* L. (Diptera: Scato-phagidae) VII. The origin and evolution of the passive phase. *Evolution* 24, 774–778.
- Perez-Staples, D., Martinez-Hernandez, M.G., Aluja, M., 2010. Male age and experience increases mating success but not female fitness in the Mexican fruit fly. *Ethology* 116, 778–786.
- Radwan, J., 1996. Intraspecific variation in sperm competition success in the bulb mite: a role for sperm size. *Proc. Royal Soc. London B: Biol. Sci.* 263, 855–859.
- Reimann, J.G., Moen, D.J., Thorson, B.J., 1967. Female monogamy and its control in the housefly, *Musca domestica* L. *J. Insect Physiol.* 13, 407–418.
- Robinson, B.W., Doyle, R.W., 1985. Trade-off between male reproduction (Amplexus) and growth in the amphipod *Gammarus lawrencianus*. *e: Biol. Bull.* 168, 482–488.
- Saeki, Y., Kruse, K.C., Switzer, P.V., 2005. Physiological costs of mate guarding in the Japanese beetle (*Popillia japonica* Newman). *Ethology* 111, 863–877.
- Sakaluk, S.K., Eggert, A.K., 1996. Female control of sperm transfer and intraspecific variation in sperm precedence: antecedents to the evolution of a courtship food gift. *Evolution* 50, 694–703.
- Sales, K., Trent, T., Gardner, J., Lumley, J.A., Vasudeva, R., Michalczyk, L., Martin, Y.O., Gage, G.J.M., 2018. Experimental evolution with an insect model reveals that male homosexual behaviour occurs due to inaccurate mate choice. *Anim. Behav.* 139, 51–59.
- Savalli, U.M., Fox, C.W., 1999. The effect of male mating history on paternal investment, fecundity and female re-mating in the seed beetle, *Callosobruchus maculatus*. *Funct. Ecol.* 13, 169–177.
- Schneider, J.M., Herberstein, M.E., DeCrespigny, F.C., Ramamurthy, S., Elgar, M.A., 2000. Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. *J. Evol. Biol.* 13, 939–946.
- Schofl, G., Taborsky, M., 2002. Prolonged tandem formation in firebugs (*Pyrrhocoris apterus*) serves mate-guarding. *Behav. Ecol. Sociobiol.* 52, 426–433.
- Seth, K.R., Kaur, J.J., Rao, D.K., Reynolds, S.E., 2002. Sperm transfer during mating, movement of sperm in the female reproductive tract, and sperm precedence in the common cutworm *Spodoptera litura*. *Physiol. Entomol.* 27, 1–14.
- Shahid, M., Siddiqui, A., Omkar, Mishra G., 2016. Mating alters the rate of development of ovarioles in the ladybird, *Propylea dissecta* (Copeoptera: Coccinellidae). *Eur. J. Entomol.* 113, 44–50.
- Shuker, D.M., Simmons, L.W., 2014. The Evolution of Insect Mating Systems. Oxford University Press, Oxford, p. 339.
- Simmons, L.W., Beveridge, M., 2011. Seminal fluid affects sperm viability in a cricket. *PLoS ONE* 6, e17975.
- Simmons, L.W., Parker, G.A., 1992. Individual variation in sperm competition success of yellow dung flies *Scatophaga stercoraria*. *Evolution* 46, 366–375.
- Simmons, L.W., Siva-Jothy, M.T., 1998. Sperm competition in insects: mechanisms and the potential for selection. In: Birkhead, T.R., Moller, A.P. (Eds.), *Sperm Competition and Sexual Selection*. London Academic Press, pp. 341–432.
- Simmons, L.W., 2001. *Sperm Competition and its Evolutionary Consequences in the Insects*. Princeton University Press, Princeton, New Jersey.
- South, A., Lewis, S.M., 2012. Determinants of reproductive success across sequential episodes of sexual selection in a firefly. *Proc. Royal Soc. B* 279, 3201–3208.
- Stoks, R., Luc, D.B., Matthysen, E., 1997. The adaptiveness of intense contact mate guarding by males of the emerald damselfly, *Lestes sponsa* (Odonata, Lestidae): The male's perspective. *J. Insect Behav.* 10, 289–298.
- Vahed, K., Parker, D.J., Gilbert, J.D., 2011. Larger testes are associated with a higher level of polyandry, but a smaller ejaculate volume, across bush cricket species (Tettigoniidae). *Biol. Lett.* 7, 261–264.
- Ward, P.I., Simmons, L.W., 1991. Copula duration and testes size in the yellow dung fly, *Scathophaga stercoraria* (L.): the effects of diet, body size, and mating history. *Behav. Ecol. Sociobiol.* 29, 77–85.
- Watson, P.J., 1991. Multiple paternity as genetic bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae). *Anim. Behav.* 41, 135–148.
- Yamane, T., Goenaga, J., Ronn, J.L., Arnqvist, G., 2015. Male seminal fluid substances affect sperm competition success and female reproductive behavior in a seed beetle. *PLoS ONE* 10, e0123770.
- Zeh, J.A., Zeh, D.W., 1994. Last-male sperm precedence breaks down when females mate with three males. *Proc. Royal Soc. London B: Biol. Sci.* 257, 287–292.
- Zeh, J.A., Zeh, D.W., 1996. The evolution of polyandry I: Intra-genomic conflict and genetic incompatibility. *Proc. Royal Soc. London B: Biol. Sci.* 263, 1711–1717.