



## OVERVIEW OF THE REPRODUCTIVE BEHAVIOUR AND DEVELOPMENT OF APHIDOPHAGOUS LADYBIRD BEETLES

Deepa Arya<sup>1\*</sup>, Ahmad Pervez<sup>2</sup>, Noorin Saifi<sup>1</sup> and Mamtesh Kumari<sup>2</sup>

<sup>1</sup>Department of Zoology, Radhey Hari Govt P.G. College, Kashipur, U.S. Nagar-244713 (Uttarakhand), India.

\*Corresponding Author E-mail: [deepa262402@gmail.com](mailto:deepa262402@gmail.com)

<sup>2</sup>Biocontrol Laboratory, Department of Zoology, Sri Dev Suman Uttarakhand University, Pt. L.M.S. Campus, Rishikesh, Uttarakhand, India.

(Received on November 10, 2023; Revised on December 12, 2023; Accepted on December 24, 2023).

### ABSTRACT

We reviewed the recent information on the reproductive behaviour and development of aphidophagous ladybird beetles. The effects of body size, age, morph and familiarity were determined based mate-choice in these ladybird beetles in terms of mating behaviour and the reproductive output. We inferred that the larger female ladybird beetles would probably carry more eggs and thereby should be more rigorous and active during mate-selection than the smaller ones. Similarly, these females prefer younger and unmated males as their potential mates, as the probability of producing high-quality sperm which in turn improves the quality of offspring is more in the younger males. In terms of morphs, females often select males with the most elaborate ornaments and displaying attributes. When females were provided with a choice towards familiar and unfamiliar males, the former prefer to mate with new males. During oviposition, as reproductive output, a series of behavioral steps are required, viz. habitat selection, approaching plant, landing decision on possible host or not, decision to oviposit or not, number of clutches and clutch size. The eggs hatch and develop into instars to adults, and their overall development period were longer on *L. erysimi* and shorter on *R. maidis*. The information obtained from the present study will be helpful in improving the methods for the mass-multiplication of these ladybirds, and aid successful biocontrol of aphid pests.

**Keywords:** mating behaviour, Coccinellidae, mate choice, oviposition, development, aphids

### INTRODUCTION

Ladybird beetles (Coleoptera: Coccinellidae) are commercially important predaceous insects with a wide prey range (Pervez and Omkar 2004; Hodek et al. 2012; Omkar and Pervez 2016). Their reproductive behaviour is well-studied because of their biocontrol potential. Mate choice or mate selection is described as the result of the individuals' inherent property to mate more readily with individual of certain traits (Kokko et al. 2006). Divergence of interest during mating might cause a preference for a specific trait. Several processes, including direct phenotypic impacts and genetic compatibility mechanisms, have been proposed to

explain the evolution of mate choice. The advantages of mate selection can be direct or indirect. Direct advantages include more fecund females and increased parental care, while indirect advantages include genetic advantages. Apart from these benefits, there are drawbacks, such as risks of rejecting mates, predation, and loss.

Female ladybirds use various indicators shown by males to make the best mate choice, including body size (Jiaqin Xie et al. 2015), phenotype (Wang et al. 2009), and age (Bista and Omkar 2015). These cues have long been recognized as the most important factors influencing mate selection. While studying these seemingly profligate qualities, Charles Darwin

developed and communicated his thoughts using the name sexual selection, because his theory of natural selection appeared insufficient to account for such non-survival adaptations. He concluded "Sexual selection depends, not on a struggle for existence, but on struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring" (Darwin 1871)

Egg-laying is the last stage of reproduction in ladybirds. Other than the female providing eggs and ovipositing in appropriate sites, there is no sign of parental care in the Coccinellidae. Many factors influence ladybird egg-laying tactics. Mating encourages oviposition (Sem'yanov 1970), while increasing female promiscuity promotes fertility (Haddrill 2001). The quantity of eggs laid at any given time is affected by female size, female condition, ovariole number, food consumption, and prey size. Food availability, the age and structure of prey colonies, the presence of other ladybirds and other predators in various phases of development, as well as the time of year and climatic circumstances, all influence where and when eggs are placed. This research article examines ladybird reproductive methods and the evolutionary causes that shaped them.

## MATING AND REPRODUCTION

Finding and selecting mates is an important stage in the reproductive success of sexually reproducing animals. Ladybird species exhibit a variety of reproductive behaviour, and chemical cues are frequently involved (Fassotte et al. 2016). Mating behaviour is defined as the physical and chemical interactions that occur between mates as a result of their behavioural and physiological reactions (Sahu 2012). Thus, mating behaviour is a series of activities that begin with attraction and progress through establishing genital contact, insemination, and genital contact termination.

### Courtship and copulation.

In the laboratory, male ladybirds often dominate and express their initiatives to mate in the form of courtship. Courtship in ladybirds usually occurs in six stages, namely approach, watch, examine, mount, embrace and attempt. However, as the male ladybird gets mature the events of courtship show a declining trend. Adult ladybird species, go through a pre-mating stage during which their gonads mature (Obata and

Hidaka 1987). Several behavioral data indicate that males are attracted from a long distance (e.g. Schaller and Nentwig 2000; Omkar and Pervez 2005; Monalisa et al. 2020), and *Harmonia axyridis* (Pallas) is the first known ladybird species with a female volatile sex pheromone (Fassotte et al. 2014). Virgin *H. axyridis* females exhibit typical calling behavior in the presence of prey, raising their elytra and squeezing their abdomen. The release of five compounds that attract males is related with this behavior:(-)- $\beta$ -caryophyllene (the major constituent),  $\beta$ -elemene, methyl-eugenol,  $\alpha$ -humulene and  $\alpha$ -bulnesene.

Traditional research in ladybirds suggested that pre-copulatory mate choice was the most important factor of reproductive success in both males and females (Srivastava and Omkar 2005; Omkar and Afaq 2013; Bista and Omkar 2015). However, molecular approaches have demonstrated that pre-copulatory selection does not guarantee paternity in ladybirds, particularly in the wild, where paternity is not fixed but imbalanced (Haddrill et al. 2008; Awad et al. 2015). Adult ladybird beetles use numerous post-copulatory sperm use strategies to maximize their odds of paternity in terms of both the number and quality of offspring (Thornhill and Alcock 1983). Apart from mate guarding (Chaudhary et al. 2015) and cryptic female choice (Ransford 1997; Awad et al. 2015), sperm precedence (Chaudhary et al. 2016) occurs *via* sperm displacement (de Jong et al. 1993, 1998) and sperm fushing (Ueno 1994). Females of various species have been observed removing sperm from their storage organs following copulatory male stimulation (Birkhead et al., 1990). Laugier et al. (2013) and Awad et al. (2015) found that females of *H. axyridis* are exceptionally polyandrous in natural conditions, not only mating several times but also fertilizing their eggs with sperm from multiple males.

### Mate selection

The selection of mating partners was influenced by both extrinsic as well as intrinsic factors (*viz.* age, mating history or genetic makeup) (Michaud et al. 2013). The sexual selection theory aims to explain how individuals enhance their fitness through reproduction (Darwin 1871). The mate selection is likely to be dependent on following factors:



**Body size dependent:** One of the most essential key factors for the evolution of sexual selection is body size. The function of body size in male-male competition and female fecundity is well known. In response to the extra cost of higher fertility, larger females would most likely carry more eggs and be more selective in partner selection than smaller females. Females are known to reject copulation efforts from large males more frequently than smaller male (Singh et al. 2018). When females of various sizes were grouped with large and small male, larger-sized females had more mating than small and medium-sized females (Omkar and Afaq 2012).

**Age dependent:** Evidences from mate choice experiments have shown that females are able to recognize male age and prefer to mate with older, younger, or middle-aged mates (Pandey and Omkar, 2013). Such selection allows females to get direct benefits related to sperm quantity or quality, as well as indirect benefits related to the progeny's viability or mating potential. However, male mate choice based on female age received less attention than female mate choice based on male age. It is widely assumed that males are less likely to pursue any mating opportunity because their fitness is determined by the number of offspring they produce. However, fertility is substantially related to the female's age at mating (Omkar et al. 2010). Mating strategy (Omkar and Pervez 2005), reproductive performance (Mishra and Omkar 2004; Pervez et al. 2004; Srivastava and Omkar 2004; Michaud et al. 2013), and offspring development and survival strategies (Singh and Omkar 2009; Omkar et al. 2010) are all influenced by mate age. Some models explain the importance of age in the selection of mating partners by both males and females. According to the viability indicator model or good genes model, females prefer older/experienced males over younger males (Michaud et al. 2013). *Coccinella septempunctata* L. and *Coccinella transversalis* (Fabricius) have shown a preference for experienced males (Michaud et al. 2013).

**Morph dependent:** Female mate-choice is a prime agent of sexual selection with females frequently

favoring males with the broadest ornamentation (Andersson 1994). *Propylea dissecta* (Mulsant) is a little size having three morphs: pale, intermediate, and typical, with pale and typical being the most prevalent. The male and female can be distinguished by the presence of patches on the head and pronotum (Omkar and Pervez 2000). These morphs are genetically defined (Majerus, 1994), but their incidence and occurrence in the field are thought to be regulated by seasonal conditions (Wang et al. 2009). Ladybirds have been reported to exhibit non-random mating in favor of certain morphs, mainly melanics (Majerus et al. 1982; Srivastava and Omkar 2005), with the degree of preference fluctuating with the season (Osawa and Nishida 1992; Wang et al. 2009). Several organisms have shown evidence of such non-random mating in favor of a specific morph. Preference for melanic partners has been reported to result in greater reproductive output in *C. septempunctata* (Srivastava and Omkar 2005). Seasonal changes in mate preference have been found in *H. axyridis* (Osawa and Nishida 1992; Wang et al., 2009), and it has been proposed to be related to size differences across morphs (Ueno et al. 1998). This preference variation was also seen in female *H. axyridis* in the form of rejection behavior and extended egg retention periods (Wang et al. 2009).

**Familiarity dependent:** Familiarity influences female mate selection, which can vary depending on the unfamiliarity of the mates (Singh et al. 2018). Both male and female mating tactics have played a significant role in determining mating outcomes throughout the evolution of mating behavior. These are important to understanding the relative importance of both sexes and the extent to which they can dominate through sexual conflict and sexually antagonistic evolution (Arnqvist and Rowe 2005), as well as a very interesting question for researchers to understand why females mate with specific males (Andersson 1994; Arnqvist and Nilsson 2000). The choice of a mating partner has the purpose to maximize the individual's own genetic benefit (Arnqvist and Rowe 2005), and variance in reproductive status within and between species has been widely recognized.

**Oviposition**

Following mate attraction and selection, the next essential behavioral stage for female ladybeetles is oviposition. The distribution of oviposition sites among female conspecifics is critical because it allows them to share resources by partitioning their niches (Sicsu et al. 2015). Oviposition-deterring pheromones (ODP) are chemicals generated by intruders that prevent the mother ladybird from ovipositing in such locations (Ruzicka 2006; Michaud and Jyoti 2007). A few laboratory and semi-field investigations suggest that *H. axyridis* is discouraged from ovipositing in the presence of conspecifics, whereas heterospecific competitors do not affect oviposition site selection (Yasuda et al., 2000; Almohamad et al., 2010). Females dropped their oviposition rates when exposed to the feces of conspecifics, but not when exposed to the faeces of heterospecific *Propylea japonica* (Thunberg) (Agarwala

et al. 2003). However, the inverse is true: *P. japonica* avoids areas contaminated with either heterospecific or conspecific excrement. *H. axyridis* females were not deterred from laying eggs by chemical markers left by syrphid and coccinellid larvae. Similar findings were found in other ladybeetle species, such as *C. septempunctata*, *Hippodamia convergens* Guérin-Méneville, and *A. bipunctata*, where oviposition was discouraged in the presence of conspecific larvae but not in the presence of heterospecific competitors (Ruzicka 1997; Doumbia et al. 1998; Michaud and Jyoti 2007). These findings suggest the presence of an oviposition-deterring pheromone in ladybeetles that must be discovered and explored across coccinellid taxa. Finally, studies of *H. axyridis* in the laboratory and in the field show that cluster size and distance from an aphid colony influence the fraction of cannibalized eggs (Osawa 2003).

**Table 1. larval and total development periods of ladybirds on different aphid species.**

Prey species	Larval period				Development period	References
	L1	L2	L3	L4		
<i>Aphis gossypii</i>	2.13±0.02 4.03±0.12 2.03±0.06	2.28±0.03 5.10±0.14 1.88±0.14	2.490±0.02 5.50±0.14 2.15±0.18	3.50±0.03 6.82±0.19 2.56±0.24	17.94±0.13 30.6±0.56 14.83±0.49	Omkar et al. 2003 Arshad et al 2020 Omkar et al. 2005
<i>Lipaphis erysimi</i>	1.72±0.03 3.80±0.37 2.55±0.08 1.45±0.18	1.64±0.04 4.20±0.5 2.61±0.09 1.30±0.13	1.84±0.05 5.80±0.50 2.32±0.07 1.20±0.09	2.75±0.04 6.00±0.7 3.81±0.13 2.80±0.15	13.93±0.12 16.19±1.26 36.4±0.50 -	Omkar et al. 2003 Sahito et al. 2019 Arshad et al. 2020 Abbas et al. 2020
<i>Myzus persicae</i>	1.79±0.04 2.05±0.18	1.84±0.07 1.00±00	2.00±0.05 1.05±0.05	2.99±0.03 2.30±0.18	15.24±0.08 -	Omkar et al. 2003 Abbas et al. 2020
<i>Aphis craccivora</i>	1.98±0.04 1.98±0.04	2.18±0.03 1.67±0.27	2.34±0.04 1.89±0.20	3.24±0.09 2.32±0.19	16.83±0.14 13.80±0.51	Omkar et al. 2003 Omkar et al. 2005
<i>Uroleucon compositae</i>	2.60±0.05	2.55±0.05	3.11±0.03	4.49±0.8	20.95±0.14	Omkar et al. 2003
<i>Aphis nerii</i>	2.96±0.02 2.25±0.12	2.75±0.03 1.10±0.10	3.34±0.03 1.00±0.00	5.08±0.03 2.10±0.10	22.85±0.10	Omkar et al. 2003 Abbas et al. 2020
<i>Rhopalosiphum maidis</i>	2.10±0.13	1.95±0.20	2.17±0.22	2.60±0.24	15.18±0.43	Omkar et al. 2005

**GROWTH AND DEVELOPMENT**

Coccinellids are important predators, and their food resources are determined by the abundance of prey



in their environment (Dixon 2000). They are polyphagous, preying on a wide range of economically important agricultural insect pests such as mealy bugs, thrips, aphids, leafhoppers, mites, scale insects, and other soft-bodied insects (Khan et al 2009). The diet of coccinellid beetles varies because they reproduce and develop best when fed varied aphid species (Omkar and Mishra 2005; Pervez et al. 2018). The findings are also comparable with those of Abbas et al. (2020), who observed that the coccinellid, *Menochilus sexmaculatus* (Fabricius), varied its incubation period when feeding on different aphid species. Similarly, when fed *L. erysimi* instead of *A. gossypii*, all four larval instars developed more quickly. The pupal duration was 4.47 days when the larvae were fed *L. erysimi*, which was less than when the larvae were fed *A. gossypii* (6.82 days). *H. convergens* performance was evaluated using the interaction effects of two aphid species. *L. erysimi* was chosen by *H. convergens* over *A. gossypii*. Coccinellid longevity, fertility, and survival may be influenced by prey quality (Ghafouri Moghaddam et al. 2016). The type of prey may affect coccinellid development; low-quality food inhibits development, whereas high-quality or nutritional food encourages development (Snyder et al. 2000). The findings are likewise compatible with those of Ali and Rizvi (2007), who discovered that coccinellid adult duration was longer on *L. erysimi* than on *Macrosiphum rosae* (Linnaeus).

## CONCLUSION

Sexual selection research is important not only for filling information gaps, but also for understanding the comparative evolutionary significance of various reproductive strategies, which can provide insight into differences and similarities between species by encouraging rigorous examination of adaptive problems and evolved solutions (Daly and Wilson 1998). It is a major evolutionary factor that increases offspring fitness by picking stronger and more attractive partners who have superior genes and higher levels of fitness. Mate selection was undertaken such as body-size, age, morph and familiarity. It was concluded from this overview that female mate preference with small body size, young age, mostly typical and melanic morphs and unfamiliar male choice. Female ladybirds are larger in body size than males. It helps them in quantitative egg production and a stronger reproductive numerical response in the biological program. ODPs (oviposition deterrent pheromones) of both conspecific and heterospecific invaders reflect the age and future of the victim colony. The conclusion was reached that prey specialization and availability influence the life table parameters of the ladybird beetle. Mustard crops were discovered to be the most vulnerable to sucking insect pests from planting to harvesting, with mustard aphids inflicting high-level damage that was decreased by its biological control agent, which was proven under laboratory circumstances.

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