AN OVERVIEW OF SEXUAL ACTIVITY AND MATING ISSUES IN PREDATORY LADYBIRD BEETLES (COLEOPTERA: COCCINELLIDAE)

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ABSTRACT

Sexual activity and mating issues in predaceous ladybird beetles have been reviewed. The sexual maturation largely depends upon resource consumption during the life stages and supports ovarian maturation in females. The male ladybirds court their females before mating and this courtship is skewed towards younger side of male age. Copulation can be either active involving body shaking or entirely quiescent. Mating refusals is conspicuous among female ladybirds, particularly during second mating. These refusals are highly age-dependent. Body size has a high impact on the mating behaviour and refusals and such behaviour is highly modulated by larger males and females. Food intake during the early stages could modulate the sexual development, adult phenotype, and reproduction of an individual, thereby shaping the reproductive success and providing a direction to sexual selection. Variation in parental age affects offspring phenotype and older parents produce offspring of lower quality and fitness. The mating status influences mate choice for attaining high reproductive success in an individual. Females prefer younger and inexperienced males for their quantitative fecundity and offspring quality. Familiarity influences mate selection and females prefer unfamiliar males over familiar ones. Similarly, females prefer unrelated males to avoid inbreeding depressions.

INTRODUCTION

adybirds or coccinellids belong to a monophyletic insect family, the Coccinellidae (of order Coleoptera), which comprise 360 genera and 42 tribes with 6,000 known species, and most of them are predaceous and can serve as biocontrol agents of numerous insect pests (Hodek et al. 2012; Omkar and Pervez 2016; Pervez et al. 2020). Their sexual activities are highly intricate and a key to their mass multiplication that may lead to augmentative biocontrol programme. Usually, mating system describes various dimensions of reproductive biology including the nature and type of gametes, the number and location of mate availability, selection of a novel mate, and behavioural strategies for mates who are not selected as a potential mate to attain reproductive success (Edward and Chapman 2011). Male ladybirds before undergoing sexual reproduction perform a courtship that results in copulation by convincing the females through satisfying their mate choice criteria (Omkar and Pervez

2005; Tatarnic et al., 2014). Before the formation of progeny, the mating partners undergo sexual maturity in which the development of their gonads takes place like ovaries in females and accessory glands in males. However, mating may even occur before attaining sexual maturity. The process of sexual maturity is correlated with the age of males and females, particularly in ladybirds the testicular and follicular development takes place in the pupal state before the emergence of adults (Hodek and Honek 1996).

The preeminent aspect of sexual reproduction involves the formation of fertile progeny by the fusion of male and female gametes that occurs through the finding of suitable mates (Nilsson 2004). Hence during mating, both sexes (male and female) through physical and chemical interaction work in harmony for offspring production (Eberhard 1996), and their behavioural and physical response toward the copulatory aspect is known as mating behaviour (Sahu 2012). The mating behaviour

is a sequential process in which through the courtship behaviour, the establishment of genital contact (mating commencement) takes place that leads to female insemination and the entire mating process terminates with the detachment of genital contact. Recently, Yadav and Pervez (2022) reviewed the pre-copulatory, copulatory and post-copulatory behaviour and responses of predaceous ladybirds. However, the issue of sexual activities and mating systems in predatory ladybirds needs to be further analysed. Hence, we are presenting a few aspects of mating and sexual activities, which are crucial and are associated with sexual selection and the success of biocontrol.

SEXUAL MATURATION

Sexual maturity is a phase in the individual life when males and females attain gonadal maturity and it correlates with the ages of both sexes (Brent 2010). In ladybirds, the testis (male) and follicular tissues (female) start their activity during the pupal stage before adult emergence. This is followed by colouring and hardening of elytra (Figure-1). The degree of sexual maturity directly depends upon resource consumption (food) during the life stages, where the rate of ovarian maturation in females could step up by nutrient uptake it could also be detained by the lack of protein (Papaj 2000).

(A)

(B)

(C)

(D)

Figure-1: Different adult phases of a ladybird, *Coccinella transversalis* under the process of attaining sexual maturity post-emergence. (A) right after emergence, (B) four hours post-emergence, (C) two days post-emergence, and (D) after attaining sexual maturity (four days older) [© Photographed by Mumtaj Jahan].

As a survival skill, the females rely on informational cues like male odour or sexual signals, which promote egg production by correlating with resource and mate availability (Aluja et al. 2000). The sexual maturity assessed by the mating incidents with successful offspring production varies with the age of mating commencement in adults. The mating may commence within 2-3 days after emergence, as in smaller species, *viz. Micraspis discolor* (Prodhan et al. 1995) and 5-days in *Menochilus sexmaculatus* (Fabr.) (Omkar 2004), or it may take 8-11 days in bigger species, *viz. Coccinella septempunctata* L. (Omkar and Srivastava 2002) and *Coccinella transversalis* Fabricius. However, copulation can spike upto 100% at the age of ten days, as in *Coelophora saucia* (Mulsant) (Omkar and Singh 2010).

COURTSHIP

Male ladybird courts the female before establishing genital contact and tries to convince a female to engage in copulation by satisfying the different set of the female choice criteria (Alexander et al. 1997) that eventually overcome female fear towards mating and results into copulation (Tatarnic et al. 2014). Cues like visual, tactile, and acoustic factors with chemical signals (sex pheromones) play a crucial role in courtship initiation (Omkar and Pervez 2005; Omkar et al. 2013). Under courtship behaviour, firstly proper watching and examination take place between both sexes that lead to female convincing and male mounting (embrace) over female thereafter, having a general entrust of both partners copulation takes place (Figure-2). However, copulation sometimes could occur during the initial disagreement also. In disagreement for grasping females to engage in copulation males chase females by taking sharp turns. Thereby, the male-oriented courtship behaviour includes the approach of mate with their watch and examination that after general intrust results into an embrace with male mounting and attempt to form genital contact that results into mating commencement (Obata 1987; Omkar and Pervez 2005; Omkar et al. 2013).

The male physical attractiveness with their persistent behaviour towards copulatory attempts makes them able to engage a female for longer under copulation which could result in influencing the reproductive output of both males and females. The longer copulatory duration could enhance the female mating success by giving rise to more eggs and males assure more paternity success by fertilizing a higher number of eggs for producing more offspring (South et al. 2012). If present nuptial feeding also takes place as a part of male courtship behaviour in which males provide edible stuff or as exception defence material for a female that engages female in eating and males utilize this opportunity for further female insemination as a paternal investment (Monalisa et al. 2020).

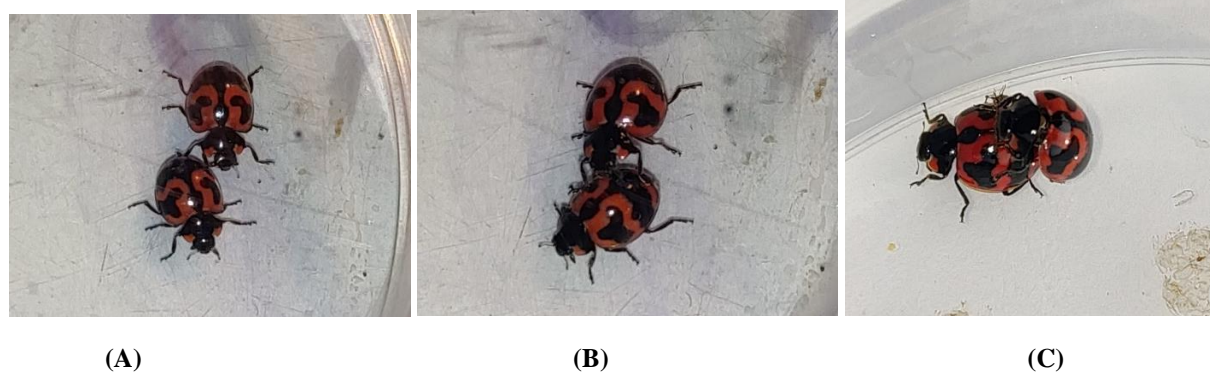|		
(A)	**(B)**	**(C)**

Figure-2: Different phases of courtship behaviour in a ladybird, *Coccinella transversalis* (A) examine, (B) approach, (C) mount and attempt [© Photographed by Mumtaj Jahan].

MATING and REFUSALS

Obata (1987) was a pioneer in describing the mating behaviour of a ladybird, *Harmonia axyridis* (Pallas). This was followed by a series of mating experimentations, coming up with two mating patterns, which include, (i) active process involving bouts

(vigorous body shaking), as in *C. septempunctata, C. transversalis* (Omkar 2004), and *C. saucia* (Omkar and Singh 2010). The mating pattern is quiescent (bereft of bouts), as in *M. sexmaculatus* (Omkar 2004)*, P. dissecta* (Omkar and Pervez 2005) and *A. cardoni* (Omkar et al. 2013). The transfer of sperm also occurs through two different modes and could be direct or indirect in a manner. Under indirect sperm transfer, no involvement of spermatophore occurs that is found in *M. sexmaculatus, P. dissecta,* and *C. saucia* (Omkar 2004; Omkar and Pervez 2005; Omkar and Singh 2010). However, indirect sperm transfer occurs by spermatophore in *H. axyridis, C. septempunctata, and C. transversalis* (Obata 1987; Omkar and Srivastava 2002; Omkar and James 2005). The duration of the copula is species-specific and depends upon the mating status of mates with their ecological conditions from food to rearing and reproductive environment. The increased copulatory duration could enhance female fecundity and egg viability and maximize the immature survival and growth index of the offspring (Omkar and Sahu 2012).

The male and female ladybird mate with the same or different mates in their lifetime for offspring production, and exhibit promiscuity (tendency to mate with multiple mates) which is favoured by sexual selection for enhancing genetic variations (Møller and Ninni 1998). Multiple mating enhances male fitness and increases paternity share through mating with various females of different mating statuses (Loose and Koene 2008). Females face both costs and benefits associated with multiple mating. The benefits can be direct (material) like elevated oviposition with associated accessory gland proteins (Jennions and Petrie 2000) and new sperm replenishment for enhancing offspring production (Vahed 1998). The indirect benefits include increased offspring survival by giving rise to offspring with more genetic compatibility (Xu and Wang 2009a) and enhanced genetic diversity (Xu and Wang 2009b). However, related costs of multiple mating are increased predation risk (Rowe 1994), increased physical damage (Wigby and Chapman 2005), and a hike in infection transmission (Hurst et al. 1995) downregulating the female immune system. Thereby females resist to re-mating avoid unfavourable outcomes of multi-mating.

Although females mate with the same or different partners and enhance their reproductive output, their mating refusals are very common, as they run away from the male approach. In addition, they bent their terminal abdominal segments to prevent mating and shake off mounted males to prevent genital contact (Obata 1988). Majerus (1994) suggested two hypotheses for female reluctance to re-mate, firstly females reject those copulations where the net gain from mating does not lead to any advantage. Secondly, the lack of good genes in a mating partner possibly does not result in the fittest offspring and hence cannot overcome the female resistance. However, the unsteadiness of cost and benefits for both sexes generates a sexual conflict that causes more female sexual harassment by males and results in coercive mating (Harano 2015) consequently to avoid the costs of male harassment the females avoid strong resisting behaviour (Hosken and Stockley 2003). However, sexual conflicts may have evolutionary and ecological effects on the species' abundance leading to sexual selection (Pervez et al. 2022). Females actively resist male mating attempts in ladybirds, *H. axyridis* (Obata 1988), *Adalia bipunctata* L. (Perry et al. 2009) and *C. transversalis* (Pervez et al. 2022). They are quite choosier, show higher mating biases, and choose large males over smaller ones as potential mates (Fukaya 2004). However, they mostly suffer from forced copulatory attempts from unwanted males (Vahed and Carron 2008). Females though try to resist forced copulation they are often compelled to accept it which generates a hike in the sexual conflict that leads to evolving the female mate choice and exerts strong evolutionary pressure on morphology and behaviour strategies of mating in both sexes (Burke et al. 2021).

The female reluctance toward male re-mating attempts is probably due to the costly and superfluous copulations (Perry et al. 2009), including reduced foraging opportunities with increased physical damage and increased risk of sexually transmitted fungus that results in elevated mortality (Fiedler and Nedved 2019). Sometimes females also show mating refusals to select potential mates of high quality for benefits (Perry et al. 2009; Pervez and Singh 2013). Females can modulate reproductive behaviour through mate discrimination by the administration of two hypotheses *(i) test hypothesis-*females reject male copulatory attempts till they overcome the female's resistance behaviour and *(ii) rape hypothesis-* males subdue the female resistance and though the female does not willing to mate she compelled to copulate (Majerus 1994). The unmated males force females to mate by increasing the likely cost of rejection (Pervez et al. 2004; Omkar and Pervez

2005). Coercive mating is more prominent in mature males when they copulate with immature females (Harano 2015). Under male continuous coercion, females try to fight off or escape from the male approach, show latency to mate with a shorter mating duration, and produce fewer eggs than females who have consensual mating (Seeley and Dukas 2011; Dukas and Jongsma 2012). However, males have more paternity share when they forcibly mate with mature females than immature ones (Biaggio et al. 2016).

Effect of body size on mating behaviour and refusals

The relation between reproductive success and the variable body sizes of males and females has been demonstrated by many researchers based on the clear distinction in the body sizes of both sexes. According to the *fecundity advantage hypothesis*, larger females have higher reproductive success and are more fecund. The maternal body sizes possibly correlate with lifetime fecundity under controlled conditions (Speight et al. 1999). Larger males have more probability of being chosen as the potential mate over the smaller males because they have better competitive abilities with large ejaculate with the fittest genes that provide more sperms with accessory gland proteins and elevate fecundity by re-mating incidents (Avila *et al.,* 2011). The greater body size may also take part in sexual coercion (Wallen et al. 2016) and could also favour it by influencing the pattern of gene flow and the level of genetic diversity (Zeh and Zeh 1997). There is a diversification in the mating strategies of males and females, where the females are profound towards mate choice and invest more resources in copulation compared to males. Males elevate their paternity success with increased mating incidents and try to coerce females to mate by overriding female resistance to mating through forced copulation which sometimes leads to an extreme sexual conflict between both sexes and intensifies the arms race (Trivers, 2017).

Effect of diets on mating behaviour and re-mating refusals.

Food intake during the early stages could modulate the sexual development, adult phenotype, and reproduction of an individual (Schultzhaus et al. 2017). Thereby, shaping their reproductive success and also providing a direction to sexual selection (Richardson and Smiseth 2019). Individuals who experienced adequate (good) nutritional conditions during earlier stages (juvenile) mature early with large body size and have an advantage in terms of higher fitness over the individuals who were reared in stressed conditions (Dmitriew 2011). However, *the environment-matching hypothesis* states that the fitness of an individual rather than alone depending on the juvenile condition also relies on the adult stage where the continuation of a favourable diet from the juvenile to adult stage produces individuals with higher fitness (Dmitriew and Rowe 2011). Adults reared in a food-stressed environment perform better under energy-limited conditions than the adults reared in an energy-rich environment (Bateson et al. 2004). The food-stressed conditions may adversely affect reproduction by influencing the male and female mating decisions leading to a sexual conflict (Duxbury and Chapman 2020). During the adult stage, the food-limited environment influences fecundity by reducing feeding potential resulting in reduced offspring (Auer et al. 2010) and influences the mating choice and mating frequency of mates (Gwynne 2008). These factors may further influence the individual aging process (Morley 2001), increase interactions between predators and pathogens (Garbutt and Little 2014), and decrease maternal investment. Hence the nutritional conditions affect the individual from the egg to adulthood by influencing its development, reproduction, aging, and immunity (Leftwich et al. 2017).

In ladybirds, both stages from larvae to adults survive prolonged food stress (Omkar and Pervez 2003) by reducing their energy requirements resulting in the development of adults with smaller body sizes (Agarwala et al. 2001). However, their reproductive performance gets hampered contrary to the beetles reared under an *ad libitum* diet (Dmitriew and Rowe 2011). Thereby, the food quality and quantity majorly influence the immature development, reproductive output, and fitness of ladybird beetles (Singh et al. 2016). It's been known from previous laboratory studies that female fitness reduces with body size and food availability because the adult and ovipositing females consume more food compared to the males (Ashraf et al. 2010). Under the deprived conditions females can curtail energy expenditure for either the maintenance or reproduction by ceasing oogenesis or by producing extra eggs (tropic) for nourishing themselves and their offspring under limited food conditions (Santi and Maini

2007). Hence, the variation in the food conditions leads to the alteration of reproduction and longevity (Bista and Omkar 2013).

Effect of Age on reproduction

Age creates permanent changes in an individual biological makeup and works as a natural and pre-programmed process with irreversibility in its nature that reduces the rate of survival and fertility with being old. The process of aging is also known as a conceptual hub that interlinks various systems from biological behaviour to ecology, evolution, molecular, and system biology (Promislow et al. 2022). The evolution of aging was explained by some theories those states, *(i) mutation accumulation theory*- an organism has the highest fitness at a young age that gradually decreases with time by the accumulation of deleterious mutations (Rose *et al.,* 2008), (ii) *antagonistic pleiotropy theory*- the genes which were beneficial at a younger age can cause a detrimental effect at the later life with individual becomes older (Williams and Day 2003), and (iii) *disposable soma theory*- maintains a balance between maintenance and repair with investment in growth and reproduction (Kirkwood 2017). Under life history theory, the reproductive output of individuals changes with the variation in their body size with the growth rate and age of an individual to a larger extent (Bonduriansky and Brassil, 2002). The process of aging itself increases individual longevity, which diminishes fertility by decreasing sperm content production in males and egg viability in females and by doing so reduces offspring survivorship (Johnson and Gemmell, 2012).

The mating incidents are affected by the age of mating partners and the age differences between mates affect their reproductive success and progeny development. The individuals follow their pattern of having higher reproductive potential by copulating with mates of different age groups. The age of females at the time of their first mating considerably influences maternal reproductive success and offspring fitness (Ivimey-Cook and Moorad, 2018). Variation in parental conditions affects offspring phenotype and generally, it is believed that older parents produce offspring of lower quality who have lower chances of survival and a slow rate of development. The influence of parental age on reproduction has been studied by a few researchers (Pervez et al. 2004; Trumbo 2009).

The age differences directly affect the individual reproductive parameters by affecting their mating success (Pervez et al. 2004; Bista and Omkar 2015; Vanpe et al. 2019). The mating of female insects with males of different ages is prevalent and females prefer mating with younger (Beck and Promislow, 2007) and middle-aged (Pandey and Omkar 2012) males. Mating with older males reduces fertilization success by producing lesser viable eggs and declines progeny output (Wylde et al. 2019). Overall creates a preference in females for younger and middle-aged males, who can be taken as suitable mates for attaining higher reproductive success (Lai et al. 2020).

The younger mothers upon copulation give rise to offspring that have higher survival skills with a rapid development rate, and enhanced longevity (Omkar and Mishra 2009). However, an increase in female age could result in a fecundity decline (Heinze and Schrempf, 2012). The age of fathers with their mating status also affects reproductive success (Scauzillo and Ferkin, 2019; Aich et al., 2020). The paternal age influence can be direct or indirect in a manner that further can positively affect progeny development with survival (Pervez et al. 2004; Krishna et al. 2012; Heinze et al. 2018). The male willingness towards mating works in an age-dependent manner and older males are fancier for mating than the younger males. However, their reproductive performance decreases gradually as they age. Their poor reproductive performance results in reduced egg viability as age reaches a certain level as observed in ladybirds that after becoming 30 days old the fecundity decreases, while the adults of younger age are more capable of giving rise to more offspring in *C. septempunctata*, *M. sexmaculatus*, and *P. dissecta* (Pervez et al. 2004; Srivastava and Omkar 2004; Omkar et al. 2006; Saxena et al. 2020). The offspring production and phenotype vary with the parental conditions where the age of parents plays a crucial role. The size of male ejaculate decreases with successive mating and once-mated males produce larger ejaculate than multi-mated males, upon mating with younger counterparts, females become more fecund and fertile, while they live longer when they mate with older males (Zhao et al. 2017).

Mate choice

The mate choice is a process of choosing a potential mate that may be attributed to the better competitive skills or attractive display of a partner

(Wong et al. 2011). The mate choice is influenced by the individual behaviour in between or within a population (Moore and Moore, 2001) and has been studied in many ladybirds, viz. *A. bipunctata, C. septempunctata, C. transversalis, H. variegata*, *P. dissecta*, and *M. sexmaculatus* (Hemptinne et al. 1998; Matsubayashi and Katakura 2007; Pervez and Maurice 2011; Mishra and Omkar 2014; Dubey et al. 2018; Saxena et al. 2018). Though the exhibition of mate choice occurs under both sexes, it is more prominent in females who traditionally have been regarded as much choosier compared to males. In females, mate choice either depends on phenotype matching where females prefer a mate of similar size (Conte and Schluter 2013) or preference depends on a particular trait (Hingle and Pomiankowski 2001). Apart from females, males can be choosier too by showing a cryptic male choice before precopulatory attempts (Edward and Chapman 2011). The choice criteria for both sexes can be the same or different and highly depend on the mate's sexual status and body size.

The mating status influences mate choice for attaining high reproductive success in an individual (Smith and Harper 2003). Because in both sexes there are some relevant costs associated with reproduction and neither ejaculate production in males for sperm transfer nor fertilization of eggs in females is cost-free (Trivers 2017). Thereby, before copulation, the copulatory history of a mate provides basic information about sperm allocation and utilization for the furthering of generation. When multiple mating is common in both sexes, sexual selection is likely to favour those traits which help in the identification of the reproductive status of mates to minimize or avoid sexual competition (Ridley 1983). Generally, males can detect the sexual status of females which helps in successful sperm allocating and maximizing paternity investment (Fitzpatrick and Servedio 2018). It is better known that either the production of ejaculate or the transfer of sperm could be costly for males (Dewsbury 1982). McCartney and Heller (2008) reported that upon mating with virgin or inexperienced females, males are likely to produce a larger ejaculate that contains more sperms with accessory gland protein and males try to mate for a longer duration (Dubey et al. 2018). The mating with virgin females ensures males no competition with the sperm of other males and increases fertilization success with a lesser risk of infection caused by sexually transmitted diseases until the female performs a re-mating (Simmons 2019). Mating with an already mated female costs more for males in terms of reduced ejaculate size lower paternity share and elevate sperm competition (Dowling and Simmons 2012).

Like males, females can also identify and discriminate against males based on their mating status (Harris and Moore 2005). Mating with an already-mated male leads to reduced sperm content and a prolonged copulatory duration that adversely affects reproductive output by decreasing fertilization success with reduced egg hatching, and a shorter female lifespan (Rincon and Garcia 2007). Females show fancy toward younger and inexperienced males, which elevate their fecundity and increases offspring quality (Jiao et al. 2011). The mate quality generates a hike in selective mating in both sexes (Byrne and Rice, 2006).

The body size of mating partners works as a primary mover in sexual selection by affecting the mate choice of an individual. Studies consider size as the criterion for mate discrimination that provides information about the interaction of male-male competition and female fecundity (Bowcock et al., 2013). Body size indicates the physiological state of mates and indirectly reflects good genes (Pech-May et al. 2012). Sexual selection of body size is a frequently selected trait because body size influences the assortative mating in individuals with their reproductive output and offspring fitness. Under mate choice, a preference is given to large individuals over smaller ones. The females of large body size have more internal space to accommodate more developing embryos resulting in higher fecundity with larger eggs and egg clutches (Omkar and Afaq 2013), giving rise to offspring that have higher fitness with fast development (Roff 2002), preferred by males as potential mates in comparison to small size females. Similarly, for large males, size confers advantages in terms of better fighting skills and competitive ability (Filin and Ovadia 2007), providing them more probability to be selected as the potential mate (Anjos-Duarte et al. 2011). Large males produce ejaculates with more sperm (Bissoondath and Wiklund 1996) and nutrients with accessory gland proteins (Avila et al. 2011), influence sperm uptake (Wedell 2005), increase their re-mating propensity, and elevate fecundity with higher offspring fitness and rapid progeny development (Vahed 1998).

Despite overwhelming evidence for selection for large body size, selection for small size also occurs and can take place in the same species (Blanckenhorn et al. 1995). Because the larger the better hypothesis does not always hold true and with advantages, costs are also associated with large size. Large individuals are more visible and less agile, can easily find out by predators (Blanckenhorn 2000), have longer developmental periods which makes them more susceptible to disproportionately increased risk of parasitism (Zuk and Kolluru 1998), require more food to support themselves and unable to efficiently utilize energy under food stress (Blanckenhorn 1998) which increases mortality risk under resource limitation (Dixon 2007). However, small individuals apply more resources to reproduction they have a short generation time with higher agility (Singer 1982) and they quickly adapt according to environmental conditions and can survive the food scarcity (Polet 2011).

Effect of familiarity and kinship on reproduction

Familiarity is the ability to recognize an individual based on their previous encounter. The ability to recognize familiar mates is present in both invertebrates and vertebrates (Hughes et al. 1999) and the discrimination between conspecific and heterospecific mates modifies individual behavioural interaction. The modified behavioural interactions due to familiarity include enhanced competitive behaviour, provides clear territorial discrimination for the avoidance of unwanted conflict, and visual plus chemical cues that help inmates recognize and influence sexual selection by reducing inbreeding depression (Fassotte et al., 2016).

The chemical cues (cuticular hydrocarbons) are volatile substances present on the body surface of animals and transmit signals between individuals for sexual communication and recognition of mates by the identification of familiarity with the degree of relatedness in mates before the copulation (Keeling et al. 2021). Besides being useful in sexual communication they also indicate the prey quality and quantity with habitat information (Pervez and Yadav 2018). In insects, the sex hormones are prominent in discriminating between males and females they can also discriminate between heterospecific and conspecific mates (Carazo et al. 2004). The novelty of mates can be identified by the chemical cues. In ladybirds, physical and chemical cues

are prominent (Durieux et al. 2010; Sloggett et al. 2011) and play an important role in courtship behaviour where the female sex pheromones attract the male for copulation (Fassotte et al. 2016). However, sometimes the chemical signals of one species work in a limiting manner for another species like the feces of *H. axyridis* have a deterrent effect on oviposition and feeding of *P. japonica* (Agarwala et al. 2003), larval tracts of *M. sexmaculatus*, *C. limbifer,* and *C. undecimnotata* works as the ovipositing deterrent for the females of *M. sexmaculatus* (Ruzicka 2006), and the larval life stages work as an ovipositing deterrent in a density-dependent manner in *C. septempunctata, C. transversalis, M. sexmaculatus, P. dissecta* and *A. cardoni* (Mishra et al. 2012). The ladybirds are polymorphic, the mate preference for different morphs is based on the different elytral hydrocarbon compositions (True 2003). The ladybirds have sex-specific volatile hydrocarbon profiles (Pattanayak et al. 2014). The chemical cues can locate a mate and odour of females work as male attractant (Omkar and Pervez 2005).

Familiarity plays an important role in mate selection, and females prefer unfamiliar males over familiar ones (Saxena et al. 2018) and the coexistence with mixed-sex groups relatively reduces the mating urge (Harmon et al. 2008). Mate selection by familiarity provides specific advantages, improves growth with fitness, leads to a hike in foraging efficiency, and elevates cooperative behaviour with better reproductive success (Fortin et al. 2018). Under familiarity, females control the male sperm storage and provide more sperm storage with higher sperm mobility to unrelated males for attaining higher paternity share and avoiding inbreeding depression (Gasparini and Pilastro 2011). In males, the sexual desire to mate is higher with new females relative to the previously mated females. When copulation occurs between a familiar male and a familiar female, the male produces an ejaculate that has a lesser number of sperm. However, sometimes females' relatedness with familiarity is preferred over the larger body size and unfamiliar males (Senar et al. 2013).

Kin recognition is an ability to recognize related individuals based on the familiarity of mates, their phenotype match, or allelic recognition and is well established in insects (Mateo 2010). Individuals recognize kinship by assessing the genetic relatedness and by doing so they preferentially provide benefits to the closely related mates like nest soil hydrocarbons in

ants which help in nestmate recognition (Bos et al. 2011) and ability in males and females of *P. dissecta* to recognize their eggs that refrain themselves from consuming them (Pervez and Khan 2020). The chemical cues are efficient and provide a helping hand in the recognition of conspecific and heterospecific kin across all the genera (Breed 2019). Multiple mating is common in insects which elevates the risk of copulation with close relatives and mating with relatives leads to reduced reproductive output with reduced offspring and results in inbreeding depression (Futuyma 2005). Kin recognition helps in preventing mating between close relatives which leads to the avoidance of inbreeding depression (Pitcher et al. 2007). By kin recognition, the discrimination between relatives and non-relatives could occur at pre and post-copulatory levels. While at the precopulatory level, the chemical cues help in discrimination, post-copulatory precautions occur in both sexes like the females bias their mating behaviour and try to copulate with the most compatible males (good quality) to assure high offspring fitness (Trivers 2017).

In females, the post-copulatory mechanisms include (i) favouring the sperm of unrelated males over the related ones that bias the fertilization process by preferencing one over another (Tuni et al. 2013), (ii) controlling sperm storage and provide more storage for sperms of unrelated males (Bretman et al. 2009). However, on the other hand, males transfer smaller ejaculations that contain a relatively lesser number of sperms to related females in comparison to unrelated females (Wedell et al. 2002). Parker (2006) stated that inbreeding avoidance occurs in organisms that have higher costs and are associated with reproduction and inbreeding depression. For instance, in *H. axyridis* and *M. sexmaculatus*, avoidance for related copulation observed for reducing the inbreeding depression (Saxena et al., 2016). In mate choice under sexual selection, a preference is given to unrelated and familiar mates rather than related ones (Fortin et al. 2018).

Multiple mating

The mating systems are mainly classified into two types monogamy and polygamy. Polygamy is further divided into monogyny and polygyny. Under monogamy, the same mating partners mate with each other throughout their entire life. However, in polygamy males and females could mate with different mating partners during a breeding season, when they mate repetitively with the same mating partner it is known as monogyny and called polygamy when mating partners are different. Multiple matings are quite common in insect taxa (Hodek and Ceryngier 2000), even when single copulation could provide sufficient sperm to fertilize all the eggs in females (Hodek et al. 2012).

Earlier, it was believed that monogamy was prominent, however, these thoughts had been changed after the studies done by Bateman (1948) and Trivers (2017) that concluded males have numerous smaller gametes while females have limited numbers of large gametes. This difference in the number and size of gametes in both sexes bias reproductive success. In which male mating success is enhanced by each further mating, fewer mating is sufficient for females. However, females show polyandrous nature to gain more benefits that can be direct or indirect (Tang et al. 2019). The females, if reared in laboratory conditions, cultivate the desire of re-mating to enhance their reproductive success and sometimes the tendency to re-mate could be heritable also (Shuker et al. 2007). Thus, the flexibility in the mating system is situation-specific and individuals modulate their mating behaviour according to conditions.

Multiple matings have their own cost and benefits for both sexes (Thornhill and Alcock 2013). Several hypotheses explain the female evolution toward multiple mating (Slatyer et al. 2012) and female benefits associated with multiple mating can be direct (non-genetic/material) or indirect (genetic) in nature. Under direct benefits, females re-mate to obtain male-controlled resources, such as nesting sites, food availability, protection from conspecific and heterospecific (Kaitala and Wiklund 1994), gaining nuptial feeding (Monalisa et al. 2020), reduce costs of male harassment (Thornhill and Alcock 2013), sperm replenishment with accessory gland protein those provide fertilization assurance by elevating depleted sperm storage (Worthington and Kelly 2016), and increased oviposition rate with a higher percentage of egg hatchability and offspring fitness owing to increased heterozygosity by reducing inbreeding depression (Nason and Kelly 2020). The indirect benefits are mainly postcopulatory mate selection and trans-generation effects of mating with multiple males (Jennions and Petrie 2000). Females can modify sperm use of previous

mates to attain superior offspring that have more attractiveness ('sexy-sons' hypotheses) with viability to be chosen as potential mates (Firman and Simmons 2012), and have higher genetic diversity (Barbosa and Magurran 2010). For males, each further mating results in elevated fitness by increasing paternity share (Loose and Koene 2008).

Besides above benefits to males and females, multiple mating has relevant costs. These include elevated risk of predation due to their lesser mobility at the time of mating (Rowe 1994), greater physical damage with increased sexual harassment (Boulton and Shuker 2015), increase risk of mating with related individuals that reduce reproductive output and increase genetic incompatibility or homozygosity (Tregenza and Wedell 2002), increased parasitic and pathogenic infection (Hurst et al. 1995), leads to decreased longevity due to associated energy allocation (Omkar and Mishra, 2005), and sometimes due to polyspermy reduction in fecundity (Rodrigues et al. 2020). In males, the ejaculate expenditure reduces with accessory gland proteins in repetitive matings (Dowling and Simmons 2012), which results in sperm depletion and reduced survival (Wedell et al. 2002) and frequent mating attempts result in reduction of their body size because mating associated with energy consumption (Shandiya et al. 2021). The ladybirds are known to be promiscuous, multiple mating is frequent and females undergo polyandry to receive qualitative and quantitative sperm for storage and egg-fertilization (Awad et al., 2015; Dubey et al., 2018). Simultaneously, repeated matings indirectly stimulate egg production in females and result in enhanced fecundity and an optimal number of mating is needed to maximize the fecundity (Pervez et al. 2022).

CONCLUSION

This overview highlights the key components in the reproductive ecology of predaceous ladybirds, *viz.* courtship, mating behaviour, mating refusals, mate-choice, multiple mating, and effect of age, familiarity and kin-recognition on mating behaviour. These mating issues need to be dealt separately, as they have direct and indirect influence on sexual selection, sexual conflicts, and biological control.

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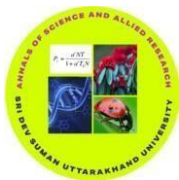
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