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Ecology of two-spotted ladybird, *Adalia bipunctata*: a review

Omkar and A. Pervez
Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow-226 007, India

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Abstract: *Adalia bipunctata* (Linnaeus) is a generalist aphidophagous ladybird having a wide prey range. It exhibits complex polymorphism. We reviewed the information on its general characteristics, polymorphism, sexual activity, foraging behaviour, food range and prey suitability, growth and development, heterospecific interactions including natural enemies, and its biocontrol potential. Although a poor biocontrol agent (only successful against aphid, *Dysaphis plantaginea* in Switzerland), it was used in the past as a good model to test various hypotheses and models facilitating ecological understanding in insects. In the present review, the empirical data are interpreted and inferences drawn and a checklist of its prey is provided.

Key words: *Adalia bipunctata*, aphids, Coccinellidae, ecology, polymorphism, reproduction

1 Introduction

Predaceous ladybirds (Col., Coccinellidae) have largely fascinated ecologists the world over, because of their biocontrol potential against aphids, diaspids, coccids, aleyrodids and other soft-bodied insects and mites. There are three books on their natural history, ecology and prey–predator interactions (Majerus, 1994a; Hodek and Honek, 1996; Dixon, 2000). The importance of certain ladybirds as biocontrol agents has been described in recent reviews, e.g. *Cheilomenes sexmaculata* (Fabricius) (Agarwala and Yasuda, 2000), *Coccinella septempunctata* Linnaeus (Omkar and Pervez, 2002), *Chilocorus nigritus* (Fabricius) (Omkar and Pervez, 2003) and *Harmonia axyridis* (Pallas) (Koch, 2003; Pervez and Omkar, 2005).

Adalia bipunctata (Linnaeus) is an aphidophagous ladybird endemic to Europe, Central Asia and North America (Majerus, 1994a). Mills (1979) described *A. bipunctata* as a generalist predator of aphids. Majerus (1994a) and Dixon (2000) discussed the natural history of ladybirds and their predator–prey interactions respectively. These authors largely discussed information on predaceous ladybirds, which also included *A. bipunctata*. Thus, there is no exclusive review on the ecology of *A. bipunctata*. Previously, we have reviewed the ecology of certain other ladybird species (Omkar and Pervez, 2002, 2003; Pervez and Omkar, 2005). The present review is an attempt to add a link to this chain of reviews by discussing the ecology of *A. bipunctata*. A checklist of its prey is also given.

2 General Characteristics and Polymorphism

Adalia bipunctata is a tree-dwelling species. It commonly feeds on more mobile prey with long legs than coccidophagous ladybirds. A glandular swelling at the posterior end, the pygopodium, of larvae possibly serves them to provide adhesion on smooth surfaces, thus preventing dislodgement (Dixon, 2000). The larvae are positively phototactic and are attracted towards blue-green light (480–522 nm wavelength) that enhances the positive visual orientation towards host plants containing aphid colonies (Dimetry and Mansour, 1976). Females prefer a red colour substratum and undersurface of leaves for oviposition and are seemingly negatively geotactic (Radwan and Lovei, 1982; Iperti and Prudent, 1986). Undersurfaces of leaves provide shady microenvironments and protect the eggs from predators. The leaf architecture influences the predation potential of *A. bipunctata* larvae (Shah, 1982) and ovipositional behaviour. The females laid more number of eggs on *Berberis vulgaris* than on other shrubs (Shah, 1983). Oviposition increases linearly, with prey density showing a numerical response (Wratten, 1973).

Adalia bipunctata is a polymorphic species with Palaearctic and Nearctic distribution. It occurs in many forms ranging from red to black in colour, and is controlled by multiple allelic series comprising of at least 11 alleles at a single locus. The most common melanic forms are *quadrimaculata* and *sexpustulata* (black with four and six red spots, respectively), and non-melanics are *typica* (red with two black spots) and *annulata* (red with two irregular black patches or with two large black spots, each having one or more small satellite spots). The other rare forms of non-melanics are *interpunctata*, *unifasciata* and *haneli* (Majerus et al., 1982a). There is also a 'wingless' form, which is weaker (Marples et al., 1993) and lacks all or part of the elytra and flight wings. European and North Asian populations of *A. bipunctata* contain

5–10% of melanics (black individuals) with high percentages (60–80%) in Rome (Italy), Marseilles (France), St Petersburg, Vologda (Russia), Yalta (Ukraine), and Yerevan (Armenia) (Zakharov, 2003). The possible factors responsible for the occurrence of numerous melanic forms are environmental pollution, ecodegradation and evolution.

The colour polymorphism, because of the expression of a super gene (Majerus, 1994a) was studied in the context of thermal melanism. The theory of thermal melanism proposes that the melanic morphs are benefitted under controlled conditions of low temperature and limited radiative regime, because a dark ectothermic insect will heat up faster and reach a higher equilibrium temperature when isolated, resulting in a higher level of activity and a reproductive advantage (Lusis, 1961). It is highly operational in *A. bipunctata.* First, relative frequencies of melanic morphs and levels of sunlight have a negative correlation (Muggleton et al., 1975; Scali and Creed, 1975). Secondly, differential reproductive activity between colour morphs was observed in the field, in accordance with prediction from the thermal melanism hypothesis (Brakefield, 1984a,b,c). In addition, laboratory data revealed a lower cuticular reflectance for melanic ladybirds resulting in higher body temperatures and higher activities under a limited range of conditions (Brakefield and Wilmer, 1985). A biophysical model coupled with empirical data conclusively proved high degree of thermal melanism in *A. bipunctata* (De Jong et al., 1996). Calculations from this model revealed that both the properties of *A. bipunctata* (i.e. reflection, transmission, body size, width of subelytral cavity) and climatic factors (radiation, intensity, ambient temperature, wind speed) are expected to influence equilibrium body temperature. All these factors are interrelated and may vary between ladybirds of different colour morphs.

3 Sexual Activity

3.1 Sexual maturation and mate recognition

Sexual activity has been more adequately studied in *A. bipunctata* than in other ladybird species (Hodek and Ceryngier, 2000). Usually, ladybirds are protandrous (Hodek and Honek, 1996); however, there is a slight tendency towards protogyny in *A. bipunctata*, possibly advantageous to females to indulge in mating and store sperm for a short period prior to sexual maturation (Hemptinne et al., 2001). As a result of overlapping generations, it will be advantageous for both sexes to have similar sexual maturation periods (Hemptinne, 1989). Moreover, if a species has overlapping generations, a constant population size and polygamous females, then there will be no advantage in males emerging and/or maturing sexually before females.

The elytral cues attract males towards females (Hemptinne et al., 1998). The elytra of both sexes of *A. bipunctata* have glands that secrete long strands of wax-like material (J. M. Pasteels and J. L. Hemptinne, unpubl. data). There are fewer glands in males. Their secretion appears to elicit sexual behaviour, as elytra washed in chloroform failed to trigger mating (Hemptinne et al., 1998). The waxy secretion is a blend of 46 hydrocarbons, consisting of branched molecules ranging from C_{22} to C_{23}. The secretion plays a major role in mate recognition (Hemptinne et al., 1998). The behavioural cues are also responsible in mate recognition and a female on encounter with a male, stops movements and elevates the tip of its abdomen indicating its willingness to mate, while young and immature ones run and dislodge the mounted male.

3.2 Mating behaviour

Both sexes of *A. bipunctata* are promiscuous. Promiscuity is not an exceptional behaviour in males because they produce a huge number of energetically cheap sperm to mate with multiple females (Majerus, 1994b). However, the females produce relatively few energy-rich eggs and protect them for mating with the potent males. There are certain costs of mating, such as energy lost in copulation, in carrying males on their back for hours, abstaining from feeding and oviposition and a risk of being infected with sexually transmitted diseases (STD) (Majerus, 1999). However, they should mate a sufficient number of times in order to fertilize their entire sets of eggs and to achieve this, they mate almost 10 times more than that required.

Males normally dominate during mating in laboratory conditions. They approach the females, climb over them and attempt to copulate. Females reject the males' advances, which is considered evolutionary, as the males which succeed in mating are considered to be good mates (Majerus, 1999). There are twisting and rocking phases in mating. In the twisting phase, the male makes bouts consisting of six units (rapid thrust against female) with 30s intervals and the rhythmicity is maintained for at least the first 45 min. This is followed by the rocking phase, where male repositions itself and makes a series of five to six rocking motions separated by a 30s interval. Sperm transfer takes place through the spermatophore, which occurs between the twisting and rocking phases. After completion of the cycle, the male may repeat this cycle two or three times and multiple ejaculations take place during a single mating. A spermatophore contains, on average, 14, 000 sperm and a female spermatheca can store around 18, 000 sperm (Majerus, 1999). The non-diapausing females of *A. bipunctata* store, on average, 13, 688 sperm in their spermatheca, while the majority of diapausing females had a sperm number of 250 (Arnaud et al., 2003). The mean length of spermatozoa stored by non-diapausing females was 2068.5 μm (Arnaud et al., 2003).

Smaller males are better mates than larger ones, supporting the eat-or-mate hypothesis, which predicts that during food scarcity, the smaller males will spend less time feeding and more time mating than the larger males (Yasuda and Dixon, 2002). Interspecific mating also occurs in *A. bipunctata*, where it usually mates with *Adalia decempunctata* (Linnaeus) (Majerus, 1997). Such matings appear to be a waste of reproductive resources, especially for females because they produce heavily resourced gametes. Some researchers reported oviposition after hybrid matings (P. M. Brakefield, per. comm. to Majerus, 1997); however, it is suspected that it may be a result of the female having previously mated with a conspecific male.

3.3 Preferential mating

Mating is non-random in *A. bipunctata* and females prefer certain types of males. This phenomenon was first observed by Lusis (1961). Mating preference is largely affected by the frequency of forms and rare morph is preferred over the common one (Muggleton, 1978, 1979). Majerus et al. (1982b) suggested that the preference of female *A. bipunctata* could be substantially increased in successive generations by artificial selection, revealing involvement of genetic component. Later on, it was demonstrated that a simple genetic basis of female mating preference implies that sexual selection by female choice is not only important for male sexual adornments but also for polymorphism that is not sex-limited (Majerus et al., 1986). In some populations, there was a significant mating advantage to heavier males irrespective of the morph (Tomlinson et al., 1995), albeit they neither produced more eggs nor showed higher activity rates. It was suggested that some forms of mate competition favour larger individuals.

4 Foraging Behaviour

4.1 Searching behaviour

Ferran and Dixon (1993) reviewed the foraging behaviour of ladybird larvae. Unlike others, *A. bipunctata* do not respond differentially to cues associated with the age of aphid colonies and the host plants, rather they appear to use cues associated with the presence of conspecifics (Hemptinne et al., 1992, 2000a). Its neonates are attracted to chemicals released by aphid victims on being attacked by conspecific larvae (Hemptinne et al., 2000b). These chemicals largely constitute the alarm pheromone, β-farnesene. The neonates then share the food with other larvae. This is known as social feeding (Hemptinne et al., 2000b). This greatly increases the probability of neonates to survive to the next instar.

The females of *A. bipunctata* switch over from extensive to intensive search after consuming one individual of suitable prey [*Phorodon humuli* (Schrank)], which makes them less susceptible to insecticides (Kalushkov, 1999). In the field, they exploit a series of nursery and patchy prey and reproduce a couple of generations on finding long patches of suitable prey (Pruszynski and Lipa, 1970). The prey consumption increased curvilinearly in response to increasing prey density supporting type II functional response (Mills, 1982a). On the contrary, the males did not show functional response and seemingly utilize the foraging time in mate search (Hemptinne et al., 1996). The functional response comes into existence in prey-rich habitat, where it is easier for ladybirds to find prey. Females of *A. bipunctata* eat a large number of aphids and increase in number when aphid populations increase (Mills, 1979). They have higher energy demands because they produce eggs which are energetically expensive. Therefore, females require and consume more aphids per day than males do (Hemptinne et al., 1996). Exceptionally poor functional response of the males could be ascribed to their lower energy requirements. It appears that the males might be focusing on a currency with an even more powerful influence on fitness than food that is mates. Roche (1998) argued that the male does exhibit functional response, as Hemptinne et al. (1996) did not observe this in the field and did not compare the performance of mated male with unmated ones. He believed that once a male ladybird mates and fulfils its sexual urge, it exhibits functional response too, as the males of other ladybird species did (Omkar and James, 2001; Omkar and Srivastava, 2003a; Pervez and Omkar, 2003; Omkar and Pervez, 2004).

4.2 Food range and prey suitability

Adalia bipunctata is a polyphagous species with a wide range of aphid prey (table 1). It uses coccids and diaspids as its alternative prey and also indulges in pollenvory, which supports survival in the absence of aphids (Hemptinne and Desprets, 1986). Its four successive instars consume aphids in the ratio of 1 : 2.4 : 3.7 : 6.6 (Semyanov, 1970). There is an inconsistency in the literature on the prey suitability of *A. bipunctata*. The aphid, *Hyalopterus pruni* (Geoffroy), previously claimed as rejected food (Hawkes, 1920), is now found to be an essential food (Pruszynski and Lipa, 1970), which can support development and reproduction. Certain aphids, viz. *Aphis fabae* Scopoli, *Aphis craccivora* Koch, *Aphis nerii* Boy., *Aphis sambuci* (Linnaeus), *Megoura viciae* Buckton and *Megoura albifrons* are sub-optimal foods, possibly because of their low nutritive value, non-palatability and difficulty in ingestion, and inefficiency in prey capture. The efficiency of prey capture depends on relative sizes of predator and prey along with the type of aphid structure and defence (Mills, 1979). Mobile, long-legged aphids (e.g. *Euceraphis betulae* Koch) escape more successfully than flat and sessile ones (*Betulaphis brevipilosa* Borner; Hajek and Dahlsten, 1987). Prey capture also depends upon the direction of attack. For instance, *Eucallipterus tiliae* can easily be hunted by *A. bipunctata* from its posterior end (Wratten, 1976).

Allelochemicals or secondary plant metabolites also affect prey suitability. Glucosinolates (GLS) induce deleterious effects on *A. bipunctata* (Francis et al., 2001a). A suitable aphid, *Brevicoryne brassicae* Linn. reared on plants with a high GLS content can be more toxic than the less suitable one, *Myzus persicae*. Prey suitability also depends on the duration of exposure of *A. bipunctata* generations to aphid prey. Previously considered poor-quality prey could become suitable and vice versa, if the ladybird is constantly reared on it for many generations (Rana et al., 2002). The gradual prey suitability and specialization on one aphid species

Table 1. *Prey checklist of* A. bipunctata

Prey	References
Acyrthosiphon ignotum Mordvilko	Kalushkov (1998)
Acyrthosiphon kondoi Shinji	Lamp et al. (1994)
Acyrthosiphon pisum (Harris)	Francis et al. (2000)
Adelges laricis (Linnaeus)	Mills (1981)
Aphis fabae Scopoli	Rana et al. (2002)
Aphis farinose Gmelin	Kalushkov (1998)
Aphis hederae (Linnaeus)	Mills (1981)
Aphis pomi (de Geer)	Iperti (1965)
Aphis sambuci (Linnaeus)	Mills (1981)
Aphis spiraephaga Muller	Kalushkov (1998)
Appelia tragopogonis (Kaltenbach)	Iperti (1965)
Aulacorthum circumflexum (Buckton)	Blackman (1967)
Aulacorthum solani (Kaltenbach)	Mills (1981)
Betulaphis quadrituberculata (Kaltenbach)	Mills (1981)
Brachycaudus helichrysi (Kaltenbach)	Mills (1981)
Brachycaudus subterranean (Walker)	Iperti (1965)
Brevicoryne brassicae Linnaeus	Francis et al. (2001b)
Cavariella konoi Takahashi	Kalushkov (1998)
Cavariella spp.	Mills (1981)
Chaitophorus capreae (Mosley)	Mills (1981)
Chaitophorus versicolor Koch	Mills (1981)
Chromaphis juglandicola (Kaltenbach)	Mills (1981)
Drepanosiphum platanoidis (Schrank)	Mills (1981)
Dysaphis plantaginea (Passerini)	Minarro and Dapena (2001)
Elatobium abietinum Walker	Leather and Owuor (1996)
Eucallipterus tiliae (Linnaeus)	Mills (1981)
Euceraphis betulae (Koch)	Kalushkov (1998)
Euceraphis punctipennis (Linnaeus)	Mills (1981)
Hyalopterus pruni (Geoffrey)	Semyanov (1970)
Hyperomyzus lactucae (Linnaeus)	Mills (1981)
Liosomaphis berberidis (Kaltenbach)	Kalushkov (1998)
Macrosiphoniella artemisiae (Boyer de Fonscolombe)	Kalushkov (1998)
Macrosiphum rosae (Linnaeus)	Brun and Iperti (1978)
Megoura viciae Buckton	Dixon and Agarwala (1999)
Microlophium carnosum (Linnaeus)	Mills (1981)
Microlophium evansi Theobald	Blackman (1967)
Monaphis antennata (Kaltenbach)	Hopkins and Dixon (1997)
Myzocallis boerneri Stroyan	Mills (1981)
Myzocallis carpini (Koch)	Mills (1981)
Myzocallis castanicola Baker	Mills (1981)
Myzocallis coryli (Goeze)	Mills (1981)
Myzus cerasi (Fabricius)	Mills (1981)
Myzus persicae (Sulzer)	Francis et al. (2001b)
Pentalonia nigronervosa Coquerel	Padmalatha and Singh (1998)
Periphyllus lyropictus (Kessler)	Mills (1981)
Periphyllus viridis	Sakuratani et al. (2000)
Phorodon humuli (Schrank)	Mills (1981)
Phyllaphis fagi (Linnaeus)	Mills (1981)
Pineus pini (Macquardt)	Mills (1981)
Ptercallis alni (Linnaeus)	Mills (1981)
Rhopalosiphum maidis (Fitch)	Mills (1981)
Rhopalosiphum padi (Linnaeus)	Semyanov (1970)
Rhopalosiphum insertum (Walker)	Olszak (1988)
Sitobion avenae (Fabricius)	Ozder and Saglam (2003)
Tuberculatus annulatus (Hartig)	Kalushkov (1998)
Tuberolachnus salignus (Gmellin)	Mills (1981)
Uroleucon cirsii (Linnaeus)	Mills (1981)

by *A. bipunctata* for generations has an evolutionary significance in its establishment in different zoogeographical habitats.

The low nutritional value or food limitation often expedites development, resulting in smaller adults (Francis et al., 2000). Female larvae consume more food and have a higher relative growth rate in the fourth instar than the male larvae (Yasuda and Dixon, 2002). Adults of *A. bipunctata* feed continuously compared with the coccidophagous ladybird, *Cryptolaemus montrouzieri* Mulsant which did not feed continuously and spent lesser time on feeding because of its smaller gut capacity (Magro et al., 2002). Their feeding time varied significantly, as *C. montrouzieri* ate many fold lesser and attained satiation soon after eating a smaller quantity of prey. However, this could not be attributed to gut capacity as the ratio of gut capacity was 22.3 : 37.7 and the amount eaten was 2 : 24 (*C. montrouzieri* : *A. bipunctata*).

5 Growth, Development and Reproduction

Like other ladybirds, *A. bipunctata* grows and develops optimally on suitable prey and abiotic conditions (table 2). The development rate is mainly dependent on food quality, food quantity and temperature (Wratten, 1973). Sub optimal quality prey slows down its developmental rate (Smith, 1965). *Aphis pisum* (Harris) (0.07/day) supports faster development than *Rhopalosiphum maidis* (0.05/day). Sub-optimal prey causes reduction in body weight to almost half the normal; for instance, feeding on *A. fabae* lead to a reduction in the weight of *A. bipunctata* to 50% of that on suitable prey, viz. *A. pisum*, *Dysaphis plantaginea* (Passerini) and *Rhopalosiphum insertum* (Walker) (Olszak, 1988). Starvation also decreases adult weight up to half of the original weight (Dimetry, 1976).

An increase in prey consumption increases the growth and development rates of *A. bipunctata* (Mills, 1981) with the amount of food required as a basal metabolism cost to maintain larval life with no growth increases with successive instars being 0.10, 0.29, 0.64 and 1.17 mg fresh food/larva/day (Mills, 1981). The bioconversion efficiency, i.e. ratio of adult weight to larval consumption in weight ranged between 0.1 and 0.3 (Blackman, 1967; Mills, 1979).

The body weight of adult males and females was insignificantly affected at varying temperatures (15–25°C) (Mills, 1981). The lower developmental threshold of *A. bipunctata* was 6.3°C, while the sum of effective temperatures was 322.6 Day-Degrees (Sakuratani et al., 2000). Increase in temperature from 15.6 to 29.4°C decreases the larval duration from 22.5 to 7.8 days. The relative duration for successive larval instars is 1.2 : 1.0 : 1.0 : 1.4 (Mills, 1981), which is not affected by the increase in temperature (Obrycki and Tauber, 1981).

Mills (1979) obtained a triangular relationship between body weight and temperature. The former increases with increase in temperature from 15°C, attained a peak at optimum temperature and decreased on further increase in temperature. The larvae that developed slowly are lighter than those that developed faster, supporting the finding on

***Table 2.** Development of* A. bipunctata *on some essential prey*

Aphid species	Host plant	Larval period (in days)	Total development period (in days)	% Mortality	Longevity females (in days)	Longevity males (in days)	Reference
P. humuli	*Humulus lupulus*	8.9	15.8	16.7	73.3	55.2	Kalushkov (1994)
A. fabae	*Vicia faba*	14.6	21.6	83.3	30.1	32.8	Kalushkov (1994)
A. fabae + *A. craccivora*	*Vicia faba*	15.1	20.8	90	24.1	20.4	Kalushkov (1994)
M. persicae	*Vicia faba*	13.5	23.4	*	*	*	Francis et al. (2001b)
M. persicae	*Brassica napus*	11.7	22	*	*	*	Francis et al. (2001b)
M. persicae	*Sinapis alba*	11.9	21.8	*	*	*	Francis et al. (2001b)
S. avenae	*Triticum aestivum*	13.17	20.67	33	*	*	Ozder and Saglam (2003)
R. padi	*Triticum aestivum*	10.29	16.71	22	*	*	Ozder and Saglam (2003)
M. cerasi	*Triticum aestivum*	11.13	17.93	18	*	*	Ozder and Saglam (2003)
H. pruni	cherry	13.4	19.8	50	*	*	Ozder and Saglam (2003)

*Data not available.

other ladybird species (Omkar and Srivastava, 2003b; Omkar and Bind, 2004; Omkar and James, 2004; Pervez and Omkar, 2004).

Males of *A. bipunctata* are smaller than females, albeit of similar developmental rates, which supports the gonadal constraint hypothesis (Dixon, 2000). This reveals that males are poor converters of aphid biomass into ladybird biomass and have a lower relative growth rate than females. There is also a possibility that gonads in males start competing with the soma for the resources earlier than in females, which reduces their growth. Males normally eat lesser (58.5% of female diet), which is also a reason for their lower growth rates (Ellingsen, 1969). The smaller males live longer than the larger ones (Yasuda and Dixon, 2002).

Females of *A. bipunctata* lay eggs in batches. The number of eggs per batch normally ranges between 11 and 30 (Stewart et al., 1991). Adults fed on a high-quality diet lay more eggs and survive for a shorter period than those fed on an excess of poor-quality food (Kariluoto, 1980). Dixon (2000) reported a fecundity–longevity trade-off, which reveals that females laying lesser eggs will live longer than those laying a greater number of eggs. This finding was supported in a ladybird, *Propylea dissecta* (Mulsant) (Mishra, 2004).

Differences in host plants affect the fecundity and development of *A. bipunctata* (table 3). For instance, rape (*Brassica napus*)-fed *M. persicae* enhanced egg production and larval hatching, whereas mustard (*Sinapis alba*)-fed *M. persicae* induced lower fecundity and egg viability (Francis et al., 2001b). This is largely because of the differences in allelochemicals and secondary plant metabolites. High GLS plant-fed *M. persicae* reduces the fitness of *A. bipunctata* than the other plants (Francis et al., 2001a). Changing high GLS-fed aphid to a suitable prey gradually improves the temporary negative effect of the former diet (Vanhaelen et al., 2002).

The net reproductive rate, intrinsic rate of increase and finite rate of increase of six cohorts of *A. bipunctata* under controlled conditions (24 ± 2°C) was 58.88 ± 21.58, 0.16 ± 0.01 and 1.17 ± 0.01 respectively (Pelicano and Folcia, 2003), which support the ease in mass-rearing of *A. bipunctata* in the laboratory.

6 Predator–Predator Interactions

6.1 Cannibalism

Cannibalism is common in ladybirds and largely prevalent in *A. bipunctata*. Hawkes (1920) recorded egg cannibalism by the neonates of *A. bipunctata*, which caused about a quarter of egg mortality. Sibling cannibalism by the neonates is favoured, as the larvae remained clustered on the empty eggshells for 12–24 h (Banks, 1956). Egg clustering, however, reduces non-sibling egg cannibalism and intraguild predation (IGP) (Agarwala and Dixon, 1993a). Eggs of *A. bipunctata* are suitable for conspecific larvae in development and the adult females, as they oviposited soon after feeding on an exclusive egg diet (Dimetry, 1974). Larvae survive longer by eating

***Table 3.** Reproductive attributes of* A. bipunctata *on some essential prey*

Aphid species	Host plant	Pre-oviposition period	Fecundity	Oviposition Rate	% Egg viability	Reference
P. humuli	*H. lupulus*	*	1011	*	*	Kalushkov (1994)
A. fabae	*V. faba*	*	63	*	*	Kalushkov (1994)
A. fabae + *A. craccivora*	*V. faba*	*	20.4	*	*	Kalushkov (1994)
M. persicae	*V. faba*	4.6	*	6.82	64.9	Francis et al. (2001b)
M. persicae	*B. napus*	5	*	10.35	57.6	Francis et al. (2001b)
M. persicae	*S. alba*	3.5	*	4.42	48.8	Francis et al. (2001b)

*Data not available.

conspecific eggs than aphids (Agarwala, 1991). Cannibalism in *A. bipunctata* is strongly density-dependent (Mills, 1982b). After hatching, competition between larvae could become severe and constitute the main risk. It is a self-regulatory mechanism that increases in intensity as egg density rises. Contrary to laboratory findings, cannibalism is less prevalent in the field (Mills, 1982b). Cannibalism is supposed to be the major reason for optimal foraging in ladybirds (Kindlmann and Dixon, 1993). There is an interesting mechanism of auto-regulation with oviposition and cannibalism occurring simultaneously. Adult females and early instars appear to be capable of kin recognition, as they avoid eating kins. Kin recognition is seemingly absent in adult males and higher instars (Agarwala and Dixon, 1993b).

6.2 IGP

Intraguild predation is a negative interaction occurring between heterospecific predators in a prey patch. This undoubtedly results in immediate energy to the starving predators and reduces the potential competitors to exploit and share a common prey resource (Polis and Holt, 1992; Omkar et al., 2002). In the field, *A. bipunctata* shares aphid prey resources with *C. septempunctata*, *H. axyridis* and *Coleomegilla maculata* (DeGeer). Its egg mortality was exceptionally higher than that of *C. maculata*, as it preferably oviposits on the upper portion of the plant, which enhances egg vulnerability (Schellhorn and Andow, 1999a). IGP by *C. maculata* increased at aphid population crash but *A. bipunctata* was escaped by leaving the plants having less or no aphids (Schellhorn and Andow, 1999b).

Both *A. bipunctata* and *C. septempunctata* avoid eating heterospecifics (Hemptinne et al., 2000c). Surface alkanes of eggs of *A. bipunctata* provide protection against IGP. In laboratory conditions, *A. bipunctata* larvae avoided eating both conspecific and heterospecific eggs, while *C. septempunctata* larvae only avoided eating *A. bipunctata* eggs (Hemptinne et al., 2000c). The species-specific alkaloids present in ladybirds are likely to protect the life stages against IGP, as these substances are toxic to heterospecific ladybirds (King and Meinwald, 1996). This could be a reason as to why cannibalism is normally preferred over IGP (Burgio et al., 2002; Omkar et al., 2004). Naïve, experienced and exotic adults of *A. bipunctata* ate conspecific eggs instead of those of *H. axyridis* (Burgio et al., 2002; Santi et al., 2003). Species-specific oviposition behaviour largely determined the relative strength of cannibalism and IGP. Although *A. bipunctata* larvae completed development on eggs of *C. septempunctata*, they took nearly two times longer than those fed aphids indicating that the costs of IGP might outweigh the benefits (Hemptinne et al., 2000d). When imported in Japan, *A. bipunctata* became the intraguild prey of indigenous *C. septempunctata* and *H. axyridis* (Kajita et al., 2000; Yasuda et al., 2004). The situation became even worse when all *A. bipunctata* larvae died after consuming eggs of *H. axyridis* (Sato and Dixon, 2004). This was a major reason for its inability to establish in tropical countries including India.

7 Natural Enemies and Defence

Adalia bipunctata is always at risk of attack by predators, especially birds (Majerus and Majerus, 1997). Some coleopterans, viz. *Carabus violaceus* Linnaeus, *Nebria brevicollis* (Fabricius), *Harpalus tardus* (Panzer), *Creophilus maxillosus* Rove, *Cantharis livida* Linnaeus and *Rhagonycha fulva* Scopoli are its potential natural enemies (Majerus, 1998). *Adalia bipunctata* uses its bright colouration for defence. Although *A. bipunctata* are regarded as Batesian mimics of chemically well-defended seven spot (*C. septempunctata*), they do not need to have an aposematic dependence on the latter, as they produce large quantities of reflex fluid rich in adaline, an alkaloid (De Jong et al., 1991). The adaline, oozing out as reflex blood, is malodorous and foul tasting to attackers. The amount of adaline in reflex blood varies in different individuals of different body sizes (Dixon, 2000).

Adults of *A. bipunctata* are always at risk of contracting a sexually transmitted disease (STD) because of their polygamous habits. They are prone to parasitism by a mite, *Coccipolipus hippodamiae* (Boots and Knell, 2002) attacking about 4.1% of Moscow's population (Zakharov and Eidel'berg, 1997). But parasitism has no adverse effect on its mating fitness, frequencies or vigour (Webberley et al., 2002, 2004). The pupae are vulnerable to parasitization by *Phalacrotophora delageae* Disney in Germany (Triltsch, 1999).

There was a high female-biased sex ratio in *A. bipunctata* in the fields, which could be exceptionally high (82 : 18; female : male) (Zakharov and Shaikevich, 2001). This bias is largely because of heavy mortality of male embryos during development by male-killing bacteria. Earlier, it was suggested that an unknown bacterium, transmitted through egg cytoplasm but not sperm, is responsible for the early mortality of male embryos (Hurst et al., 1992). This was supported by recent research on *A. bipunctata*, where its ovarioles were found to be infected with *Spiroplasma*, *Wolbachia* and *Rickettsia* (Sokolova et al., 2002). The four male-killing symbionts were reported (Werren et al., 1994; Hurst et al., 1999a,b), which can also coexist in a ladybird population.

8 Biocontrol

A series of attempts to establish *A. bipunctata* in new pest-prevalent habitats have failed in the past, which suggest that *A. bipunctata* is not a successful biocontrol agent, unlike some coccidophagous ladybirds and parasitoids (Omkar and Pervez, 2003). Some early releases in the form of eggs failed, as eggs did not hatch, probably because of poor weather conditions. However, recent field releases of larvae and eggs of *A. bipunctata* against the rosy apple aphid, *Dysaphis plantaginea* in Switzerland, were successful in predator establishment and aphid biocontrol (Wyss et al., 1999a). They were effective just before flowering at a time when growers normally have to spray their trees. Their effectiveness, however, decreased on encountering the indigenous ants.

A combined release of *A. bipunctata* with *Aphidoletes aphidimyza* and *Episyrphus balteatus* for the biocontrol of *D. plantaginea* was conducted in Switzerland (Wyss et al., 1999b; Kehrli and Wyss, 2001). Their additive effects significantly reduced the aphid densities (Wyss et al., 1999b). An integrated strategy of using *A. bipunctata* and honeydew has also been tested recently against *E. tiliae* infesting lime trees in France (Bardoux et al., 2003).

9 Conclusion

Protogyny and multiple ejaculations in *A. bipunctata* are two interesting aspects in its life history and could be advantageous, as the female can reproduce earlier than the male and more eggs could be fertilized because of multiple ejaculations. Little is known about the influence of age, temperature and food on its ecological attributes. Studies on demographic parameters may throw some light on the ease and difficulties in the laboratory rearing of this ladybird. Effective alternative diets are needed to support laboratory rearing under conditions of prey scarcity. *Adalia bipunctata* was used in the past as a good model to test various hypotheses and models facilitating ecological understanding in insects.

It may be concluded that except for a traceable record (*D. plantaginea* in Switzerland), *A. bipunctata* can be claimed as a poor biocontrol agent. The attempts to establish it were unsuccessful because of unfavourable abiotic and biotic factors, which limit the scope of its establishments in South Asia and other tropical countries. It was out-competed by indigenous *H. axyridis* in Japan and *C. septempunctata* in India and other South Asian countries. Although being a generalist having vast prey range, food cannot be a limiting factor for its survival. Although adaline-driven defence system initially provides some protection, they are victimized by birds and certain coleopteran predators. In addition, the male embryos are susceptible to male-killing symbionts, which checks its population.

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Author's address: Omkar (corresponding author), Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow – 226 007, India. E-mail: omkaar55@hotmail.com

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