

Ecology of Aphidophaga:
Biology, Ecology and Behaviour of
Aphidophagous Insects
Proceedings of the 8th International Symposium

Ponta Delgada 1-6 September 2002

António O. Soares, Maria A. Ventura,
Vasco Garcia & Jean-Louis Hemptinne (Eds)



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TABLE OF CONTENTS

	PAG.
PREFACE	v
LIST OF PARTICIPANTS	vi
GROUP PHOTO	ix
DIXON, A.F.G. & J.-L. HEMPTINNE Ladybirds and the biological control of aphid populations.	1
WIESSER, W.W. Additive effects of pea aphid natural enemies despite intraguild predation.	11
BUENO, V.H.P., A.B. CARNEVALE & M.V.SAMPAIO Host preference of <i>Lysiphlebus testaceipes</i> (Cresson) (Hymenoptera: Aphidiidae) for <i>Myzus persicae</i> (Sulzer) and <i>Aphis gossypii</i> Glover (Hemiptera: Aphididae).	17
SCHULT, J.-V. & F. WÄCKERS. The biological control of <i>Aulacorthum solani</i> (Kaltenbach) (Homoptera: Aphididae) in greenhouse grown pepper; research on a tri-trophic system.	21
MAGRO, A., J.-L. HEMPTINNE, A. NAVARRE & A.F.G.DIXON Comparison of the reproductive investment in Coccidophagous and Aphidophagous ladybirds (Coleoptera: Coccinellidae).	29
HEMPTINNE, J.-L., A.F.G. DIXON & E. WYSS Biological control of the rosy apple aphid, <i>Dysaphis plantaginea</i> (Passerini) (Homoptera: Aphididae): learning from the ecology of ladybird beetles.	33
SERPA, L., H. SCHANDERL, C. BRITO & A. O. SOARES Fitness of five phenotypes of <i>Harmonia axyridis</i> Pallas (Coleoptera: Coccinellidae).	43
SOARES, A.O., D. CODERRE & H. SCHANDERL Influence of prey quality on the reproductive capacity of two phenotypes of <i>Harmonia axyridis</i> Pallas (Coleoptera: Coccinellidae).	51
JAROŠÍK, V., J. POLECHOVÁ, A.F.G. DIXON & A. HONĚK Developmental isomorphy in ladybirds (Coleoptera: Coccinellidae).	55
KINDLMANN, P. & A.F.G. DIXON. Past and future models of predator-prey population dynamics: the importance of generation time ratio.	65
FRÉCHETTE, B., C. ALAUZET & J.-L. HEMPTINNE Oviposition behaviour of the two-spot ladybird beetle <i>Adalia bipunctata</i> (L.) (Coleoptera: Coccinellidae) on plants with conspecific larval tracks.	73
GODEAU, J.-F., J.-L. HEMPTINNE & J.-C. VERHAEGHE Ant trail: a highway for <i>Coccinella magnifica</i> Redtenbacher (Coleoptera: Coccinellidae).	79

8th International Symposium on Ecology of Aphidophaga
University of the Azores, Ponta Delgada, 1-6 September 2002

RŮŽIČKA, Z. & R. ZEMEK Effects of conspecific and heterospecific larval tracks on mobility and searching patterns of <i>Cycloneda limbifer</i> Say (Coleoptera: Coccinellidae) females.	85
BASKY, Z. Predators and parasitoids on different cereal aphid species under caged and no caged conditions in Hungary.	95
FÉLIX, S. & A. O. SOARES Intraguild predation among the aphidophagous ladybird beetles <i>Harmonia axyridis</i> Pallas and <i>Coccinella undecimpunctata</i> L. (Coleoptera: Coccinellidae): characterization of the direction and symmetry.	103
SOARES, A.O., R. B. ELIAS & A. RAIMUNDO Approach to the knowledge of Coccinellidae (Coleoptera) species diversity of Madeira and Porto Santo Islands.	107

PREFACE

Aphids and their natural enemies were central stage from 1st to 6th of September, 2002, at the University of the Azores in Ponta Delgada. Aphids were recorded as major pests early in the XXth Century (GAUMONT 1977) and continue to threaten field and greenhouse crops. As a consequence, pesticides are used regularly and intensively, which hampers the move towards sustainable agriculture. In theory, biological control of aphids is an alternative to chemical control but the record of biological control is not good (DIXON 2000). This does not mean that biological control should be abandoned. On the contrary, we should attempt to improve it, and this is the main objective of the IOBC Working Group "Ecology of aphidophaga".

Traditionally the majority of the communications presented at the meetings of this Working Group are on ladybird beetles. This was also the case at this meeting but the prominence of ladybirds was not a deliberate attempt to restrict the scientific scope of the meeting. History partly explains the domination of ladybirds. The outstanding success of *Rodolia cardinalis* in California many years ago still influences these conferences. This is not the only explanation. Ladybirds are a good model organism for improving our understanding of the role of natural enemies in regulating herbivore populations. Parasitoids have, and continue to be used as models for studying predator-prey dynamics. However, the biology of parasitoids differs fundamentally from that of predators (DIXON 2000) and it is therefore unlikely that studies on parasitoids will shed light on all the theoretical and practical aspects of the interactions between prey and natural enemies. Studies on ladybirds complement those on parasitoids and give a better understanding of why the biological control of aphids sometimes fails. This was central to the interesting communications on predator-prey models, guild structure, fundamental biology and applications presented at the meeting.

For practitioners confronted with aphid outbreaks, however, theoretical studies may seem a waste of time. In the face of heavy economic losses immediate action often appears to be the only solution. KAREIVA (1996) has highlighted the risks of a "hit and miss" approach to biological control. However, a "search and wait" strategy, in which all efforts are directed to research while farmers sit and wait for a solution, is not practical. The future is a trade-off between research and practice. In theory there is an infinity of possible trade-offs, but which is the best? In Ponta Delgada the Scientific Committee decided that the Working Group should provide opportunities for practitioners of biological control and scientists to meet and discuss mutual problems. Through exchange of ideas and discussion of field results the right trade off will be approached and the gap between academics and practitioners of biological control progressively reduced.

The meeting in Ponta Delgada was fruitful in both scientific and strategic terms. I thank the University of the Azores for hosting the congress and the Local Committee for all its efforts and dedication. Muito obrigado pela sua hospitalidade!

The next meeting will be held in Japan at Yamagata University in September 2005. The first announcement is already on our web site (<http://www.bf.jcu.cz/tix/strita/aphidophaga/main.html>).

REFERENCES

- DIXON, A.F.G. 2000. *Insect predator-prey dynamics. Ladybird beetles & biological control*. Cambridge University Press. 257 pp.
- GAUMONT, L. 1977. L'importance économique des aphides (Texte inédit publié à l'occasion du centenaire de sa naissance). *Annales de Zoologie-Ecologie animale* 9: 173-180.
- KAREIVA, P. 1996. Contribution of ecology to biocontrol. *Ecology* 77: 1964-1965.

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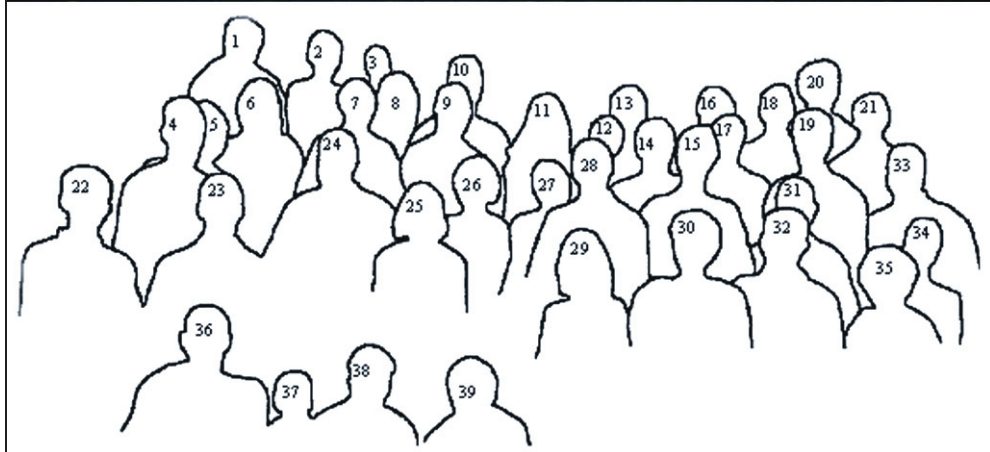
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Biology, Ecology and Behaviour of Aphidophagous Insects



- | | | |
|--------------------------|----------------------------|------------------------------|
| 1 - António Martins | 14 - Peter Duelli | 27 - Tessa Grasswitz |
| 2 - Vanda Bueno | 15 - Felix Bianchi | 28 - Bertin Boertjes |
| 3 - Paula Lourenço | 16 - Tadashi Takizawa | 29 - Salima Machkour M'Rabet |
| 4 - Jeroen van Schelt | 17 - Jean-François Godeau | 30 - Zsuzsa Basky |
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| 12 - Roberto Resendes | 25 - Alexandra Magro | 38 - Edward W. Evans |
| 13 - Zdenek Růžička | 26 - Sook Ming Ng | 39 - Pavel Kindlmann |

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University of the Azores, Ponta Delgada, 1-6 September 2002

LADYBIRDS AND THE BIOLOGICAL CONTROL OF APHID POPULATIONS

A.F.G. DIXON & J.-L. HEMPTINNE

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Although *Rodolia* and other ladybirds have been successfully used to control pest coccids they have not proved effective in classical biological control programmes against aphids. A better understanding of the foraging behaviour of ladybirds and a more realistic theory of insect predator- prey dynamics are beginning to reveal the reason for this.

Aphidophagous ladybirds exploit patches of aphid prey for feeding and reproduction. As suitable nurseries for their offspring patches of aphid prey generally only persist for about the same period of time as it takes the larvae of these ladybirds to complete their development. This is the case even in the absence of natural enemies. Thus aphids become scarce within a patch just when the food requirements of the ladybirds are greatest. Optimal foraging theory predicts that ladybirds should lay a few eggs early in the development of a patch and empirical data indicates that ladybirds appear to forage optimally.

There have been several studies on the cues used by ladybirds when selecting patches of prey for oviposition. This review will consider how the responses shown by ladybirds may have shaped what has become known as the "egg window", how cannibalism may regulate the number of ladybirds within a patch, and the consequences of this for classical biological control.

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THEORY

In classical insect predator-prey population dynamics organisms in two trophic levels interact; prey and predator (Fig. 1A).

A plant through its morphology and chemistry can directly affect the well being of herbivores, and they similarly can affect predators. That is, in addition to their effects on one another's abundance a plant can have a direct effect on a herbivore, which can have a direct effect on a predator, and *vice versa*. In addition to these direct effects there is a growing literature that claims predators and parasitoids are attracted by volatiles emitted by plants under attack by herbivores. This is regarded as a mutualism, in which the effectiveness of the searching behaviour of the natural enemy is enhanced and the herbivore pressure on the plant reduced

(PRICE et al. 1980; Fig 1B). Predators are considered to be part of a plant's defence. When attacked by herbivores some plants emit volatiles that are attractive to natural enemies, which has resulted in them being likened to "body guards" and the use of emotive phraseology like "the enemy of my enemy is my ally" (DICKE & SABELIS 1988; SABELIS et al. 2001). That ladybirds respond to these volatiles is supported by technically elegant studies in which gas chromatography of plant volatiles was directly coupled with recordings from the olfactory organs of a ladybird. Herbivore damaged plants emit (Z)-jasmone, which is attractive to adult *Coccinella septempunctata* (BIRKETT et al. 2000; NINKOVIC et al. 2001). The central tenet of the mutualism hypothesis is that herbivore-induced plant volatiles enable natural enemies to more easily find their prey and so reduce herbivore pressure.

Claims that such signals are so used by parasitoids was scrutinized by VINSON (1999) and VAN DER MEIJDEN & KLINKHAMMER (2000), who found no field evidence for this.

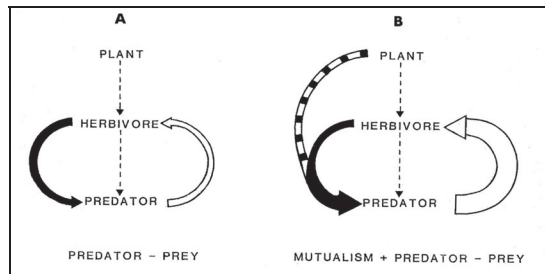


Fig. 1. The direct and indirect effects on one another of plants, herbivores and predators in classical insect population dynamics (A) and plant predator mutualisms (B).

Although there is no doubting that the volatiles (synomones - DICKE & SABELIS 1988) released by plants when attacked by herbivores are attractive to predators and parasitoids, the way in which they affect their searching behavior and the distance over which they operate still needs to be resolved. Discussions of this problem (e.g. JANSSEN et al. 2002) tend to follow PRICE et al. (1980) and only consider the adaptive significance of herbivore-induced plant volatiles in terms of plant fitness. It is generally assumed it is advantageous for natural enemies to respond to such signals. However, it is pertinent to ask - What advantages would a predator gain by responding to these signals? Here we consider only ladybird beetles, but the principles are likely to apply to all natural enemies.

It seems likely that the quantity of volatile material released by a plant depends on the intensity of herbivore attack, i.e., density-dependent. If this is true then aphid-infested plants are likely to be at their most attractive for ladybirds when aphids are most abundant. However, at this stage in the infestation it is highly likely that ladybird larvae will already be present. Therefore, responding to a strong cue that a plant is under attack by aphids is not necessarily advantageous. In addition, as not all aphids are equally suitable as prey for ladybirds (RANA et al. 2002) it is relevant to ask: - Is the synomone emanating from a plant specific for a particular species of aphid or a general response

to aphid infestation? Similarly, is the synomone produced by a plant in response to being eaten by lepidopterous larvae different from that produced when infested with aphids? Therefore, in addition to determining whether the odour originates directly from the prey (prey pheromone hypothesis) or indirectly - after feeding by the prey - from the plant (plant synomone hypothesis) there is an urgent need to determine whether the signals are prey specific and how they affect predators' searching behaviour. It is well documented that bark beetles aggregate in response to volatiles produced by trees and attractant pheromones produced by the beetles, and so overcome the host's defences by a mass attack, but avoid heavily attacked trees, when the beetles present produce deterrent pheromones (WOOD 1982; RAFFA 2001). That is, if chemical signaling by plants significantly influences ladybird foraging then it is likely the signal is complex, as in bark beetles.

Alternatively one can ignore plants when considering predator-prey interactions, which is the case in most mathematical models of population dynamics. These have been widely used to predict the behavior of predator-prey systems, in particular their stability and the outcome of introducing natural enemies on the abundance of pests (BEDDINGTON et al. 1976, 1978; HASSELL 1978; MURDOCH 1994). In spite of the great and long-standing interest in these models, there has been little success in using them to account for why insect predators, compared to parasitoids, have generally not been very effective in suppressing the numbers of their prey (DEBACH 1964).

Our studies on the way insect predators, and ladybirds in particular, forage, led to an appreciation of the ecological significance of the difference in mobility of juvenile and adult insects; the latter can fly while the former cannot (Fig. 2). That larvae generally stay within a prey patch while adults may not was incorporated into a model. Patch in this sense means the space that a larva can explore by walking, usually one or only a few adjacent plants, or even only part of an individual plant as in the case of trees. Three factors are likely to determine the reproductive strategy of ladybirds to a much greater extent than availability of food, which is the usual

assumption of models of predator-prey systems: (1) Ladybird developmental time is much longer than that of its aphid prey and comparable with the average duration of a patch of prey (Fig. 3; HEMPTINNE et al. 1990; HEMPTINNE & DIXON 1991). Thus it is maladaptive for a ladybird to lay eggs in an old prey patch, as they are unlikely to complete their development before the aphids disappear. (2) As shown by KINDLMANN & DIXON (1993), there should be a selective advantage in optimizing the number of eggs laid in a patch. This is because - as stated above - ladybird developmental time is similar to the duration of a patch of aphids. If many eggs are laid, the ladybird larvae may reduce the rate of increase of the aphids, cause an earlier decline in aphid abundance, and thus food may become scarce well before the larvae complete their development (Fig. 3). (3) Cannibalism is common in aphidophagous ladybirds and in nature often reduces juvenile survival dramatically, as only

about 1% of the eggs laid in a patch survive (DIXON 2000). Cannibalism may be selected for (see below) and even sibling cannibalism may have a selective advantage, if prey becomes scarce (OSAWA 1992). To avoid cannibalism, adults should avoid patches of aphids where ladybird larvae are already present.

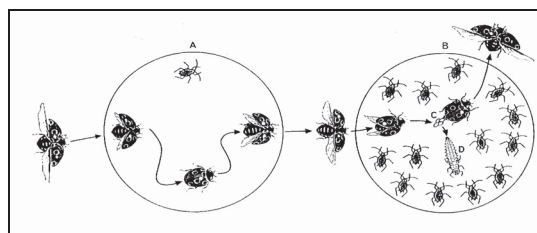


Fig. 2. Aphidophagous ladybirds quickly leave patches where aphids are scarce (A) but oviposit in patches where prey is abundant (B). The larvae (D) that hatch from the eggs (C) are confined to the patch, and have to pursue and subdue the aphids they need for their development.

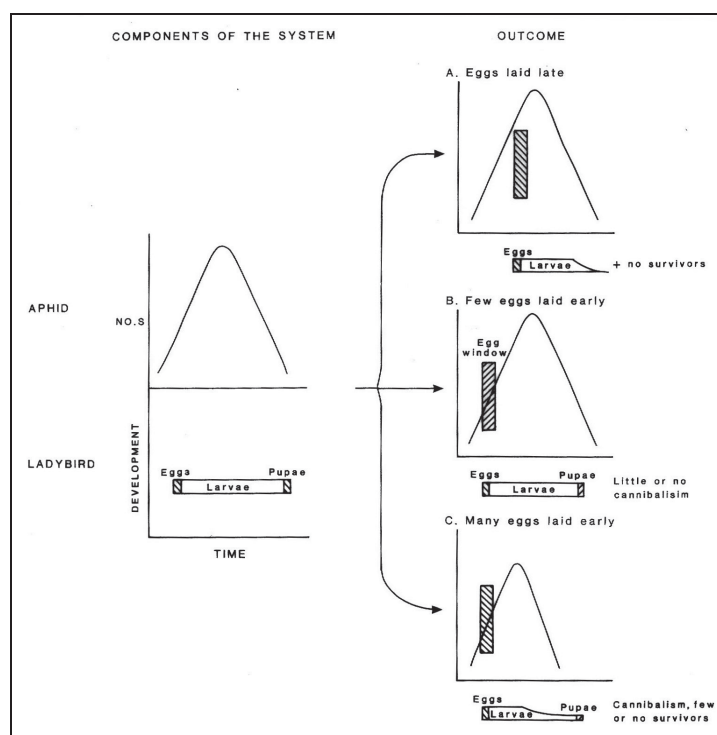


Fig. 3. Graphical presentation of the components of the ladybird-aphid interaction: temporal changes in the abundance of aphids and relative developmental time of the ladybird, and the outcome if (A) the eggs are laid late, (B) a few eggs are laid early, or (C) many eggs are laid early.

Assuming that the proportion of conspecifics in the diet of ladybirds is proportional to their relative abundance then if prey abundance is kept constant the incidence of cannibalism increases with increase in predator abundance. That is, cannibalism is likely to act as a density dependent mortality factor. Alternatively if the number of predators is kept constant and that of their prey is varied the incidence of cannibalism decreases with increase in the abundance of prey (Fig. 4).

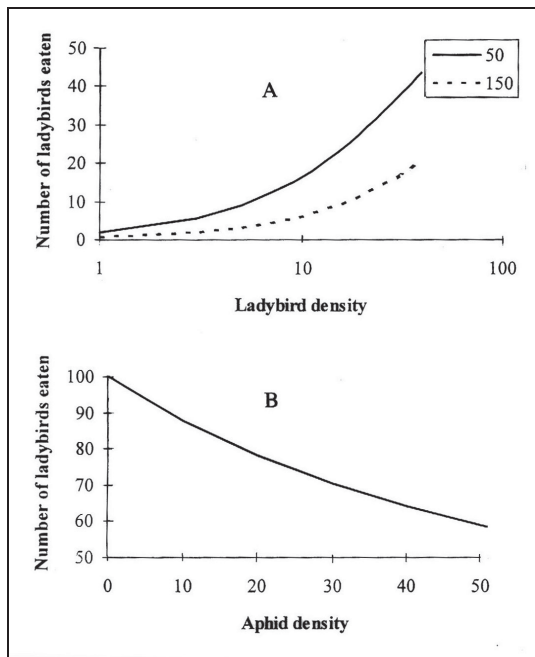


Fig. 4. The predicted (A) increase in cannibalism with increase in predator density, 50 and 150, and (B) the decrease in cannibalism with increase in aphid density when predator density is kept constant assuming that: $f(x, y) = ay/(x+y)$, where x is the number of prey, y is the number of ladybirds and a is a scaling constant.

This is referred to as the "meet and eat" hypothesis and accounts for the incidence of cannibalism in time (DIXON 2000). However, it is just as plausible that the latter is due to the occurrence in time of certain vulnerable stages - eggs/hatchling larvae and pre-pupae/pupae, which are unable to avoid or defend themselves against active larvae. Whatever the reason for the temporal incidence of cannibalism the outcome is the same: cannibalism is proportional to the

relative abundance of the predator and therefore likely to be density dependent.

Consideration of the above leads to the prediction that there should be a strong selection for ladybirds to lay eggs only in patches in the early stages of development and avoid those containing conspecific larvae (KINDLMANN & DIXON 1993; DOSTALKOVA et al. 2002). Thus in assessing the potential effectiveness of a predator for biological control one should take into account that selection maximizes predator fitness, not its effectiveness as a biocontrol agent (KINDLMANN & DIXON 1999a). In aphidophagous ladybirds the major determinant of their reproductive strategy is that their prey develops much faster than they do (DIXON et al. 1995; DIXON & KINDLMANN 1998; KINDLMANN & DIXON 1999b). Therefore, the potential fitness of an adult depends mainly on the future trends in resource availability for its larvae, which unlike the adult are confined to a patch (Fig. 2). This leads to the following predictions. In arthropod predator-prey systems in which the predator has a long generation time relative to that of its prey (ladybird/aphid systems), predator reproduction should be correlated with the age of a prey patch rather than the numbers of prey present, and top-down regulation is unlikely. However, in ladybird/ coccid systems, where both prey and predator have similar developmental times, ladybird reproduction is likely to be correlated with prey abundance and top-down regulation is possible (KINDLMANN & DIXON 2001). In addition there is evidence that specificity may also be an important attribute of a biological control agent. The coccidophagous ladybirds that feed on Margarodidae, the group of coccids that includes *Icerya*, are generally more specific than those that feed on other groups of coccids. In terms of successful control ladybirds have been used 20 times more successfully to control Margarodidae than other groups of coccids (DIXON 2000).

EXPERIMENTAL EVIDENCE FOR OPTIMAL FORAGING IN LADYBIRDS

What evidence is there that selection maximizes predator fitness? Below is presented the results of

studies undertaken to assess this in the case of aphidophagous ladybirds. In particular, this will be done by examining the evidence for an egg window, mechanisms for avoiding cannibalism and the proposed consequences for aphid abundance.

Egg Window

Experimental and field studies indicate there is a density below which ladybirds are unlikely to lay eggs (DIXON 1959; WRATTEN 1973; HONĚK 1978). In addition, in the field ladybirds tend to lay their eggs well before aphid populations peak in abundance (Fig. 5; HEMPTINNE et al. 1992). That is, there is a window in the development of a patch of aphids when ladybirds are most likely to lay their eggs. The opening of the window is possibly determined by the minimum density of aphids required for the survival of the first instar larvae (DIXON 1959). The closing of the window appears to be initiated by adults responding to the presence of conspecific larvae (HEMPTINNE et al. 1992).

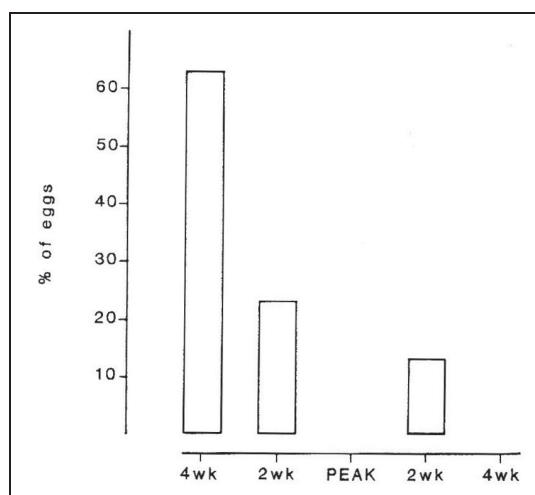


Fig. 5. Distribution in time, relative to peak aphid abundance of the laying of eggs by *Adalia bipunctata* on lime trees. Development of aphid populations expressed in weeks before and after the recorded peak in aphid abundance in each year. (After HEMPTINNE et al. 1992)

In the presence of conspecific larvae and/or their tracks gravid females of *Adalia bipunctata*, *Coccinella septempunctata*, *Cycloneda limbifer*, *Harmonia axyridis*, and *Semiadalia undecimnotata* become very active and if prevented from leaving the area refrain from laying eggs for a few hours (HEMPTINNE et al. 1992; DOUMBIA et al. 1998; YASUDA et al. 2000; RŮŽIČKA 2001b). Similar responses are observed when females of *A. bipunctata* are placed on plants in the field experimentally infested with aphids and contaminated with larval tracks. (Fréchette, unpublished). Although some species of ladybird respond to the tracks left by larvae of other species the response is generally statistically insignificant and much weaker than that to conspecific larvae or their tracks (HEMPTINNE et al. 1992; YASUDA et al. 2000; RŮŽIČKA 1997b, 2001a, b). This is expected because the greatest threat to the survival of a ladybird in its preferred habitat, where it is likely to be the most abundant ladybird, are individuals of the same species. In addition, ladybirds appear to be well defended chemically against intraguild predation (AGARWALA & DIXON 1992; HEMPTINNE et al. 2000). The deterrent effect of larval tracks is density dependent and mediated via a pheromone present in the tracks. In the case of *A. bipunctata* the cue consists of a cocktail of alkanes, which spread easily on the hydrophilic cuticle of plants and so leave a large signal. In addition the oviposition-detering pheromone is very stable lasting for at least 10 days (DOUMBIA et al. 1998; HEMPTINNE et al. 2001).

In summary, there is good field evidence that aphidophagous ladybirds, as predicted by theory, lay their eggs early in the development of patches of aphids, and laboratory and field experiments reveal the possible mechanisms by which this is achieved.

Cannibalism

Cannibalism is widely recorded for aphidophagous ladybirds, but rarely mentioned in the literature on coccidophagous species. Theory predicts that it should occur when the relative abundance of ladybirds is high and/or is

associated with an asymmetry between cannibal and victim. The victim is usually at a vulnerable stage in its development (AGARWALA & DIXON 1992), i.e., in the egg or pupal stage, or is smaller or about to moult or pupate. That is, cannibalism should be highest in the egg and pupal stages, and in the fourth instar larval stage when prey is likely to be scarce, and decrease with increase in aphid abundance (Fig. 4). Life table studies done on field populations and laboratory studies (Fig. 6) support these predictions (AGARWALA & DIXON 1992; YASUDA & SHINYA 1997).

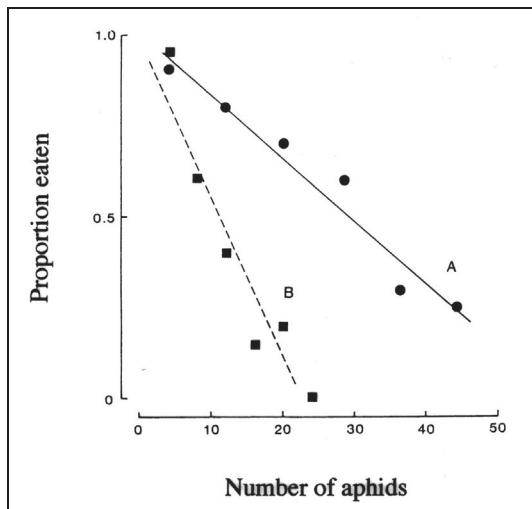


Fig. 6. The incidence of cannibalism in the laboratory of clutches of eggs (A) and larvae (B) of *Adalia bipunctata* in relation to aphid abundance (After AGARWALA & DIXON 1992)

In the grain beetle *Tribolium* there are strains that show either a high or a low level of cannibalism, which is genetically determined (STEVENS 1992). This has also been shown for *H. axyridis* (WAGNER et al. 1999). Thus, selection should favour an optimum level of cannibalism in a given environment. That is, a species may be more or less cannibalistic than one would expect on the basis of the predicted frequency of encounters between conspecifics outlined above. Is there any evidence for this? Clearly some species are more difficult to rear collectively because they show higher levels of cannibalism than other species (unpublished results). A recent study of cannibalism in the aphidophagous

ladybird *H. axyridis* indicates it prefers to eat conspecifics (GAGNÉ et al. 2002). Thus cannibalism would appear to have been selected for in the individuals of *H. axyridis* used in this study.

Not only does the high probability of egg cannibalism make it advantageous for ladybirds to avoid ovipositing in patches of prey already occupied by conspecific larvae field, but evidence indicates that cannibalism, as predicted by theory, serves subsequently to regulate the numbers of ladybird larvae within a patch (Fig. 7).

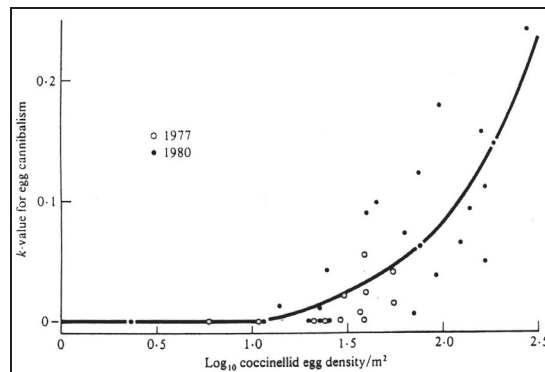


Fig. 7. The relationship between egg cannibalism and the number of eggs of *Adalia bipunctata* per unit area of lime foliage in relation to aphid abundance in the field (After MILLS 1982)

That is, cannibalism is strongly density dependent and capable of regulating the abundance of ladybird larvae within patches (KINDLMANN & DIXON 2001).

In summary, there is good field evidence that cannibalism is widespread and an important mortality factor potentially capable of regulating the abundance of aphidophagous ladybird larvae in a patch.

Aphid abundance

The prediction that ladybirds that forage optimally have little affect on aphid abundance (KINDLMANN & DIXON 1993) is the most contentious. The implied altruism on the part of the ladybirds and criticism of biological control practice has greatly impeded the general acceptance of this supposedly counterintuitive

idea. There is good evidence that ladybirds forage in a way similar to that predicted by optimal foraging theory and they achieve this by behaviour that is clearly adaptive at the individual level. The fact that cannibalism is adaptive and strongly density dependent indicates that ladybird numbers are likely to be strongly auto-regulated. Therefore, the prediction that ladybirds should have little effect on aphid abundance is in reality also not counterintuitive.

This prediction was tested by monitoring the numbers of the aphid, *Aphis gossypii*, on 34 two metre high shrubs of *Hibiscus syriacus* in the field. All the eggs of *Coccinella septempunctata brucki* were removed from 8 of the shrubs, all those of *Harmonia axyridis* from another 8, all the eggs of both ladybirds from another 12 and no eggs were removed from the remaining 6 shrubs (control). Sticky bands were placed around the base of the stem of each shrub to prevent the immigration of larvae on to the shrubs from surrounding plants. The results were very variable but clearly indicate that the presence of aphidophagous predators on the shrubs did not significantly affect the peak number of aphids (Fig. 8).

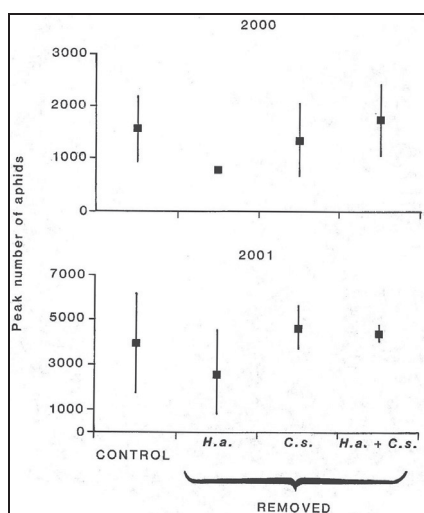


Fig. 8. The peak number of *Aphis gossypii* on *Hibiscus* shrubs in the field when aphid numbers were monitored in the presence of all the naturally occurring natural enemies (control), and when all the *Harmonia axyridis* (H.a) or *Coccinella septempunctata brucki* (C.s.) or both species of ladybird (H.a. + C.s.) were removed at the egg stage.

Unlike in other studies (e.g. ELLIOT & KIECKHEFER 2000) the shrubs were not caged, so the patches in effect were open to both immigration and emigration of both aphids and ladybirds as in natural ecosystems. That is, as predicted by theory these predators do not have a negative effect on the peak numbers of aphids in nature.

In summary, although well based theoretically and supported by a rigorous field experiment, the prediction that aphidophagous ladybirds have little effect on aphid abundance is likely to be subject to further critical experimentation before it is generally accepted.

CONCLUSIONS

Although the idea of a mutualism between plants and ladybirds is an attractive one there are no compelling theoretical reasons for, or field evidence of, such a relationship. Classical predator-prey models do not account for why insect predators are generally less effective in suppressing the abundance of pests than parasitoids. A model that includes the essential features of the foraging behavior of larvae and adults and the reproductive behavior of adult ladybirds predicts the patterns observed in the field. The major determinant of abundance in this system is the relative developmental times of the predator and prey - generation time ratio (GTR) hypothesis. If that of the predator is considerably longer than that of the prey, as in aphid/ladybird systems, then top down regulation of prey abundance is unlikely, whereas when it is of similar length, as in coccid/ladybird systems, then top down regulation is possible. The cues used by aphidophagous ladybirds to assess the quality of patches of prey have been identified and rigorously assessed. That is, in the last ten years there has been a great advance in our understanding of the patterns and processes in ladybird-prey interactions.

The GTR model should apply to all insect predators. However, as far as aphidophaga are concerned it makes a prediction: those that have longer generation times than aphids should behave similarly to ladybirds. Although this has not been studied intensively many are known to

be cannibalistic and show similar reproductive behaviour. For example, the adults of some cecidomyids, chrysopids and syrphids are deterred from ovipositing by the presence of conspecific larvae or their tracks (HEMPTINNE et al. 1993; RŮŽIČKA 1994, 1996, 1997a, 1998; RŮŽIČKA & HAVELKA 1998). Thus, it is likely that the GTR hypothesis holds for all insect predators. At present the best support for this comes from studies on aphidophagous insects.

REFERENCES

- AGARWALA, B.K. & A.F.G. DIXON 1992. Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecological Entomology* 17: 303-309.
- BEDDINGTON, J.R., C.A. FREE & J.H. LAWTON 1976. Concepts of stability and resilience in predator-prey models. *Journal of Animal Ecology* 45: 791-816.
- BEDDINGTON, J.R., C.A. FREE & J.H. LAWTON 1978. Characteristics of successful natural enemies in models of biological control of insect pests. *Nature* 273: 513-519.
- BIRKETT, M.A., C.A.M. CAMPBELL, K. CHAMBERLAIN, E. GUERRIERI, A.J. HICK, J.L. MARTIN, M. MATTHES, J.A. NAPIER, J. PETERSSON, J.A. PICKETT, G.M. POPPY, E.M. POW, B.J. PYE, L.E. SMART, G.H. WADHAMS, L.J. WADHAMS & C.M. WOODCOCK 2000. New roles for cis-jasmone as an insect semiochemical and in plant defense. *Proceedings National Academy of Science, USA* 97: 9329-9334.
- DEBACH, P. 1964. *Biological Control of Insect Pests and Weeds*. Chapman & Hall, London.
- DICKE, M. & M.W. SABELIS 1988. How plants obtain predatory mites as body guards. *Netherlands Journal of Zoology* 38: 131-138.
- DIXON, A.F.G. 1959. An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *Journal of Animal Ecology* 28: 259-281.
- DIXON, A.F.G. 2000. *Insect Predator-Prey Dynamics: Ladybirds & Biological Control*. Cambridge University Press, Cambridge.
- DIXON, A.F.G., J.-L. HEMPTINNE & P. KINDLMANN 1995. The ladybird fatasy - prospects and limits to their use in biocontrol of aphids. *Züchtungsforschung* 1: 395-397.
- DIXON, A.F.G., J.-L. HEMPTINNE & P. KINDLMANN 1997. Effectiveness of ladybirds as biological control agents: patterns and processes. *Entomophaga* 42: 71-83.
- DIXON, A.F.G. & P. KINDLMANN 1998. Generation ratio and the effectiveness of ladybirds as classical biological control agents. Pp. 315-320 in M.P. ZALUCKI, R.A.I. DREW & G.G. WHITE (Eds.) *Pest Management - Future Challenges* 1. University of Queensland Printery.
- DOSTÁLKOVÁ, I., P. KINDLMANN & A.F.G. DIXON 2002. Are classical predator-prey models relevant to the real world? *Journal of Theoretical Biology* 218: 328-330.
- DOUMBIA, M., J.-L. HEMPTINNE & A.F.G. DIXON 1998. Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia* 113: 197-202.
- ELLIOT, N.C. & R.W. KIECKHEFER 2000. Response of coccinellids to spatial variation in cereal aphid density. *Population Ecology* 42: 81-90.
- GAGNÉ, I., D. CODERRE & Y. MAUFFETTE 2002. Egg cannibalism by *Coleomegilla maculata lengi* neonates: preference even in the presence of essential prey. *Ecological Entomology* 27: 285-291.
- HASSELL, M.P. 1978. *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton.
- HEMPTINNE, J.-L., A.F.G. DIXON & A. MACKENZIE 1990. Adaptations du cycle biologique des prédateurs aphidiphages aux fluctuations démographiques de leurs proies. Pp. 101-104 in Ed. INRA. *Régulation des cycles saisonniers chez les Invertébrés*. Les Colloques de L'INRA 52.
- HEMPTINNE, J.-L. & A.F.G. DIXON 1991. Why ladybirds have generally been so ineffective in biological control. Pp. 149-157 in L. POLGAR, R.J. CHAMBERS, A.F.G. DIXON & I. HODEK (Eds.) *Behaviour and Impact of Aphidophaga*.
- HEMPTINNE, J.-L., A.F.G. DIXON & J. GOFFIN 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* 90: 238-245.
- HEMPTINNE, J.-L., A.F.G. DIXON, J.-L. DOUCET & J.-E. PETERSEN 1993. Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): Mechanisms. *European Journal of Entomology* 90: 451-455.
- HEMPTINNE, J.-L., A.F.G. DIXON & C. GAUTHIER 2000. Nutritive cost of intraguild predation on eggs of *Coccinella septempunctata* and *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* 97: 559-562.
- Hemptinne, J.-L., G. Lognay, M. Doumbia & A.F.G. Dixon 2001. Chemical nature and persistence of the oviposition deterring pheromone in the tracks of the larvae of the two spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). *Chemoecology* 11: 43-47.

- HONĚK, A. 1978. Trophic regulation of post diapause ovariole maturation in *Coccinella septempunctata* [Col.: Coccinellidae]. *Entomophaga* 23: 213-216.
- JANSSEN, A., M.W. SABELIS & J. BRUIN 2002. Evolution of herbivore-induced plant volatiles. *Oikos* 97: 134-138.
- KINDLMANN, P. & A.F.G. DIXON 1993. Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. *European Journal of Entomology* 90: 443-450.
- KINDLMANN, P. & A.F.G. DIXON 1999a. Strategies of aphidophagous predators: lessons for modelling insect predator-prey dynamics. *Journal of Applied Entomology* 123: 397-399.
- KINDLMANN, P. & A.F.G. DIXON 1999b. Generation Time Ratios - Determinants of prey abundance in insect predator-prey interactions. *Biological Control* 16: 133-138.
- KINDLMANN, P. & A.F.G. DIXON 2001. When and why top-down regulation fails in arthropod predator-prey systems. *Basic and Applied Ecology* 2: 333-340.
- MILLS, N.J. 1979. *Adalia bipunctata* (L.) as a generalist predator of aphids. Ph.D. Thesis, University of East Anglia, UK
- MILLS, N.J. 1982. Voracity, cannibalism and coccinellid predation. *Annals of Applied Biology* 101: 144-148.
- MURDOCH, W.W. 1994. Population regulation in theory and practice. *Ecology* 75: 271-287.
- NINKOVIC, V., S. AL ABASSI & J. PETTERSON 2001. The influence of aphid-induced plant volatiles on ladybird beetle searching behavior. *Biological Control* 21: 191-195.
- OSAWA, N. 1992. Sibling cannibalism in the lady beetle *Harmonia axyridis*: fitness consequences for mother and offspring. *Researches in Population Ecology* 34: 45-55.
- PRICE, P.W., C.E. BOUTON, P. GROSS, B.A. MCPHERON J.N. THOMSON & A.E. WEIS 1980. Interaction among three trophic levels: Influence of plants on interaction between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11: 41-65.
- RAFFA, K.F. 2001. Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. *Chemoecology* 11: 49-65.
- RANA, J.S., A.F.G. DIXON & V. JAROSIK 2002. Costs and benefits of prey specialization in a generalist insect predator. *Journal of Animal Ecology* 71: 15-22.
- RŮŽIČKA, Z. 1994. Oviposition-detering pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae). *European Journal of Entomology* 91: 361-370.
- RŮŽIČKA, Z. 1996. Oviposition-detering pheromone in chrysopids: Intra- and interspecific effects. *European Journal of Entomology* 93: 161-166.
- RŮŽIČKA, Z. 1997a. Persistence of the oviposition-detering pheromone in *Chrysopa oculata* (Neur.: Chrysopidae). *Entomophaga* 42: 109-114.
- RŮŽIČKA, Z. 1997b. Recognition of oviposition-detering allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae). *European Journal of Entomology* 94: 431-434.
- RŮŽIČKA, Z. 1998. Further evidence of oviposition-detering allomone in chrysopids (Neuroptera; Chrysopidae). *European Journal of Entomology* 95: 35-39.
- RŮŽIČKA, Z. 2001a. Response of chrysopids (Neuroptera) to larval tracks of aphidophagous coccinellids (Coleoptera). *European Journal of Entomology* 98: 283-285.
- RŮŽIČKA, Z. 2001b. Oviposition responses of aphidophagous coccinellids to tracks of ladybirds (Coleoptera: Coccinellidae) and lacewings (Neuroptera: Chrysopidae) larvae. *European Journal of Entomology* 98: 183-188.
- RŮŽIČKA, Z. & J. HAVELKA 1998. Effects of oviposition-detering pheromone and allomone on *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *European Journal of Entomology* 95: 211-216.
- SABELIS, M.W., A. JANSSEN & M.K. KANT 2001. Perspective: The enemy of my enemy is my ally. *Science* 291: 2104-2105.
- STEVENS, L. 1992. Cannibalism in beetles. Pp. 156-175 in ELGAR, M.A. & B. J. CRESPI (Eds). *Cannibalism, Ecology and Evolution among Divers Taxa*. Oxford: Oxford University Press.
- VAN DER MEIJDEN, E. & P.G.L. KLINKHAMMER 2000. Conflicting interests of plants and natural enemies of herbivores. *Oikos* 89: 202-208.
- VINSON, S.B. 1999. Parasitoid manipulation as a plant defense strategy. *Annals of Entomological Society of America* 92: 812-828.
- WAGNER, J.D., M.D. GLOVER, J.B. MOSELEY & A.J. MOORE 1999. Heritability and fitness consequences of cannibalism in *Harmonia axyridis*. *Evolutionary Ecology Research* 1: 375-388.
- WOOD, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection behaviour of bark beetles. *Annual Review of Entomology* 27: 411-446.
- WRATTEN, S.D. 1973. The effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the lime aphid, *Eucallipterus tiliae* (L.). *Journal of Animal Ecology* 42: 785-802.
- YASUDA, H. & K. SHINYA 1997. Cannibalism and

8th International Symposium on Ecology of Aphidophaga
University of the Azores, Ponta Delgada, 1-6 September 2002

- interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42: 155-165.
- YASUDA, H., T. TAKAGI & K. KOGI, K. 2000. Effect of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology* 97: 551-553.
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ADDITIVE EFFECTS OF PEA APHID NATURAL ENEMIES DESPITE INTRAGUILD PREDATION

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Intra-guild predation (IGP) has been shown for many arthropod pest - natural enemy systems but the importance of IGP for biological control is still unclear. While theoretical results and some experiments suggest that IGP can disrupt long-term control of pest populations, few studies have investigated short-term consequences of IGP. An experiment was performed in which up to two larvae of the predatory ladybird *Coccinella septempunctata* and up to two females of the parasitoid *Aphidius ervi* were released in colonies of pea aphids, *Acyrtosiphon pisum*. Ladybirds kill parasitoid larvae when they consume parasitized aphids. After one week, aphid population size in the control treatment was higher than in treatments with natural enemies. The effect of predators and parasitoids on aphid population size was additive, and the greatest effect on aphid population size was found with two predator larvae and two parasitoid females. Thus, in this experiment, a release of multiple natural enemies was beneficial and IGP did not interfere with the short-term control of the pest. It is suggested that the effects of IGP on biological control will depend on the desired aims of the control program. If short-term control is desired, the disadvantages of IGP for long-term control may not be important.

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INTRODUCTION

Most herbivorous arthropods are attacked by a variety of natural enemies. In the case of generalist predators, these predators may not only feed on the herbivore but also on other natural enemies. Predation on other natural enemies, an interaction referred to as intraguild predation (IGP), appears to be common among generalist predators, in both natural (POLIS et al. 1989; YASUDA & KIMURA 2001) and agricultural (ROSENHEIM et al. 1993, 1995; ROSENHEIM 1998) systems. For biological control, IGP is important as it may interfere with the efficient control of pest species (ROSENHEIM et al. 1995). Specialist natural enemies, in particular parasitoids, are most often the victims of IGP by generalist predators (SNYDER & IVES 2001; LUCAS et al. 1998). A number of studies have shown that the

presence of generalist predators can reduce the number of herbivores parasitized by parasitoid Hymenoptera and Diptera (references in SNYDER & IVES 2001). However, the occurrence of IGP does not necessarily imply that biological control of a pest species is interrupted. Only a few studies have tested whether IGP has a measurable effect on the population growth of the pest species, as predicted by theory (POLIS et al. 1987). For example, SNYDER & IVES (2001) found that control of pea aphids by the parasitoid *Aphidius ervi* Haliday was disrupted when predatory carabid beetles were present in field cages. This effect, however, only appeared after more than one parasitoid generation, presumably because the IGP Predator mostly consumed prey in the first generation after introduction. On short plants that could be climbed by carabids, the immediate effect of predators was a strong

reduction in aphid densities (SNYDER & IVES 2001). Thus, while long-term control of the pest was hindered by the presence of generalist predators, IGP did not appear to have hindered short-term reduction of pest densities. For biological control of insect pests, in particular in glasshouse situations, a short-term reduction of pest densities may often be more desirable than a long-term control of the herbivore. If short-term reduction of pest densities is the aim, a joint release of natural enemies might be useful despite the occurrence of IGP.

Pea aphids, *Acyrtosiphon pisum* Harris, are pests of legumes (BLACKMAN & EASTOP 2001). Among the many natural enemies that attack the pea aphid are the aphid parasitoid *A. ervi* and the predatory coccinellid, *Coccinella decempunctata* L. In pea aphid-ladybird-parasitoid systems, IGP occurs when ladybirds feed on parasitized aphids, killing both the aphid and the developing parasitoid larvae (e.g. SNYDER & IVES 2001). Both natural enemies are regularly used as biological control agents. The experiment reported here was designed to test whether the effects of the parasitoid and the predator are additive in reducing aphid population growth over a short time scale of one week. Specifically, I was interested in testing the hypothesis that a joint release of both natural enemies leads to a more efficient control of pea aphids in a situation when colonies of *A. pisum* are still small and a swift reduction of pest density is desired.

MATERIAL & METHODS

For all experiments, the pea aphid clone RG2 was used. This clone was collected in Riehen, Switzerland, in 1998 and reared in the laboratory in low densities on a dwarf form of broad bean, *Vicia faba* L. (variety The Sutton, Nickerson-Zwaan Ltd, Roswell, Lincolnshire LN7 6DT, UK), potted in 10cm (Ø) pots. Aphids and plants were kept in constant temperature chambers under long-day conditions (L:D 16:8) at 20±1°C. Ladybird larvae, *C. septempunctata*, were collected around Jena in 1999 and bred in the

laboratory. For the experiment, 2nd and 3rd-instar larvae were used. Mummies of the parasitoid *A. ervi* were obtained from Katz Biotech Services, Industriestr. 38, 73642 Welzheim. Females were fed for 1-3 days with honey and allowed to mate before use in the experiment.

For the experiment, aphid colonies of a fixed age-structure were obtained by placing on each plant nine 1st or 2nd instar, eight 3rd instar, six 4th instar and seven adults, in total 30 aphids. Clone RG2 has an intrinsic growth rate of about $r=0.4$ (Braendle, unpubl.) and the age composition of the colony mimicked its stable age distribution.

All aphid colonies were assembled on the same day. To start the experiment, zero, one or two females of *A. ervi* and zero, one or two larvae of *C. septempunctata* were introduced into the colony. The treatment with no predators and no parasitoids served as a control. In total, there were three (parasitoid treatments) x three (ladybird treatments) x 15 replicates = 135 replicates. To prevent the escape of aphids and natural enemies, plants were caged using micro-perforated polypropylen bags (230x420mm). Replicates were blocked in groups of nine (one replicate for each treatment) to control for the effects of microclimatic differences within the climate chamber on aphid population growth.

After one week, all aphids were carefully brushed from the plant into Petri dishes and frozen for counting. Parasitoid mummies found on plants were counted separately.

Data was analysed using three-way ANOVAs using the software package SPSS (SPSS 1993). Data was tested for normality prior to the analysis and transformed as necessary. Block was treated as a random effect.

RESULTS

Both ladybirds and parasitoids significantly reduced the number of aphids counted after one week (Table 1). The interaction between predators and parasitoids was not significant. The block effect was not significant (Table 1).

Table 1.

Results of a 3-way ANOVA on aphid population size (ln-transformed). SS-sum of squares, df - degrees of freedom, MS - mean square. Error terms were calculated by SPSS.

Source		SS	df	MS	F	Significance
Intercept	Hypothesis	2108.2	1	2108.2	507.1	<0.001
	Error	16.6	4	4.2		
Ladybirds	Hypothesis	390.8	2	195.4	74.3	<0.001
	Error	21.0	8	2.6		
Parasitoids	Hypothesis	103.7	2	51.8	31.1	<0.001
	Error	13.4	8	1.7		
Block	Hypothesis	16.6	4	4.2	1.6	0.307
	Error	11.4	4.5	2.5		
Ladybirds*Parasitoids	Hypothesis	13.9	4	3.5	2.0	0.151
	Error	28.4	16	1.8		
Ladybirds*Block	Hypothesis	21.0	8	2.6	1.5	0.239
	Error	28.4	16	1.8		
Parasitoids*Block	Hypothesis	13.4	8	1.7	0.9	0.511
	Error	28.4	16	1.8		
Ladybirds*Parasitoids*Block	Hypothesis	28.4	16	1.8	0.9	0.535
	Error	171.0	90	1.9		

Only few parasitoid mummies were found on the plants (Fig. 1). While the parasitoid effect was significant, the ladybird effect was marginally not significant. None of the interactions or the block effect were significant (Table 2 next page).

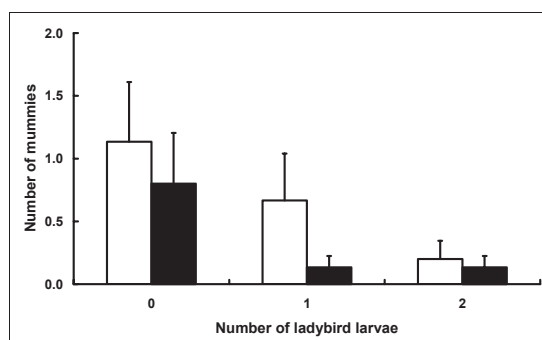


Fig. 1. The effect of the numbers of predators and parasitoids on the number of parasitoid mummies. No mummies were counted in the absence of parasitoids. Open bars: one parasitoid female, black bars: two parasitoid females.

DISCUSSION

The main result of the experiment was that the effects of the parasitoid and the predator on aphid

population size were additive. The interaction term was far from being significant, emphasising that IGP was not strong enough to interfere with the control of aphids by the natural enemies. The same results were obtained when data were not log-transformed (data not shown). Thus, for any given number of ladybird larvae, the addition of parasitoid females led to a better control of the aphid population. Over the time scale of one week, therefore, the control was better the more natural enemies were used. The control was dramatic: instead of on average more than 600 aphids on the control plant, aphid population size was often reduced to zero when two ladybird larvae and two parasitoids were released on the plants. A mean aphid population size smaller than 30, the initial size of the aphid populations, was only obtained when at least two ladybird larvae and at least one parasitoid female were released in the aphid colony. Densities of aphids as high as observed in the control lead to a fast death of the host plant (Weisser, unpublished). A fast reduction of pea aphid populations is therefore necessary to limit the damaging effects on the host plant. Thus, in this experiment, efficient pest control was possible when both natural enemies were used.

Table 2.

Results of a 3-way ANOVA on the number of parasitoid mummies (ln-transformed). SS-sum of squares, df - degrees of freedom, MS - mean square. Error terms were calculated by SPSS.

Source		SS	df	MS	F	Significance
<i>Intercept</i>	<i>Hypothesis</i>	3.7	1	3.7	12.1	0.025
	<i>Error</i>	1.2	4	0.3		
<i>Ladybirds</i>	<i>Hypothesis</i>	1.2	2	0.6	4.1	0.060
	<i>Error</i>	1.2	8	0.1		
<i>Parasitoids</i>	<i>Hypothesis</i>	2.2	2	1.1	11.4	0.005
	<i>Error</i>	0.8	8	0.1		
<i>Block</i>	<i>Hypothesis</i>	1.2	4	0.3	2.8	0.244
	<i>Error</i>	0.3	2.5	0.1		
<i>Ladybirds*Parasitoids</i>	<i>Hypothesis</i>	0.7	4	0.2	1.4	0.282
	<i>Error</i>	2.1	16	0.1		
<i>Ladybirds*Block</i>	<i>Hypothesis</i>	1.2	8	0.1	1.1	0.402
	<i>Error</i>	2.1	16	0.1		
<i>Parasitoids*Block</i>	<i>Hypothesis</i>	0.8	8	0.1	0.7	0.673
	<i>Error</i>	2.1	16	0.1		
<i>Ladybirds*Parasitoids*Block</i>	<i>Hypothesis</i>	2.1	16	0.1	0.8	0.635
	<i>Error</i>	14.0	90	0.2		

The number of parasitoid mummies found after one week was very low because of the duration of parasitoid development (SEQUEIRA & MACKAUER 1992). As a consequence, the effect of ladybird presence on the number of mummies was marginally non-significant. It is likely that a later sampling date would have resulted in a significant ladybird effect. Similarly, the apparent decrease in mummy number when two rather than one parasitoid females were released is likely due to chance effects given the very low numbers of mummies.

The experimental situation was artificial in the sense that natural enemies and aphids were not able to emigrate from the host plant. Nevertheless, it would be premature to conclude that the results do not apply to a greenhouse or field situation. SNYDER & IVES (2001) also found a strong reduction in aphid numbers by generally less effective carabid beetles in large field enclosures. Thus, it is well possible that the results reported here also hold in a greenhouse scenario. Because of the high rates of increase of aphid populations, control has to be fast to limit the impact on the host plants. The results presented in this paper suggest that the joint release of parasitoids and ladybirds can be

effective in preventing the outbreak of an aphid population despite the adverse effects of the predator on parasitoid reproduction.

More generally, the results presented here suggest that the presence of IGP does not necessarily interfere with biological pest control. In the past years, an increasing number of studies have found that IGP commonly occurs in pest-natural enemy systems. The implicit assumption in many of the studies is that if IGP can be documented in feeding trials in the laboratory or in the field, it must have negative consequences for biological control. Theoretical studies that focus on long-term equilibrium conditions support this view (e.g. POLIS et al. 1989). However, as shown in this study, it depends not only on the biology of the system but also on the aims of a biological control program whether or not IGP prevents efficient pest control. If a short term reduction of pest densities is desired because a harvest in the immediate future is endangered, long-term negative effects of IGP may not be important. Similarly, if the aim is to quickly reduce pest density populations to prevent an outbreak, then a release of multiple natural enemies may still be advisable despite the occurrence of IGP. To assess the importance of

IGP for a biological control program, experiments should be performed that are closely linked to the aims of this program.

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REFERENCES

- BLACKMAN, R. L. & V.G. EASTOP 2001. *Aphids on the world's crops: an identification and information guide*. John Wiley & Sons, New York, USA. 476 pp.
- LUCAS, E., D. CODERRE & J. BRODEUR 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* 79: 1084-1092.
- POLIS G.A., C. MYERS & R. HOLT 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20: 297- 330.
- ROSENHEIM, J.A. 1998. Higher-order predators and the regulation of insect herbivore populations. *Ann. Rev. Entomol.* 43: 421-447.
- ROSENHEIM, J.A., H.K. KAYA, L.E. EHLER, J.J. MAROIS & B.A. JAFFEE 1995. Intraguild predation among biological control agents: Theory and evidence. *Biological Control* 5: 303-335.
- ROSENHEIM, J. A., L.R. WILHOIT & C.A. ARMER 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96: 439-449.
- SEQUEIRA, R. & M. MACKAUER 1992. Nutritional ecology of an insect host-parasitoid association: the pea aphid-Aphidius ervi system. *Ecology* 73: 183-189.
- SPSS for Windows: Base System User's Guide, Release 6.0, 1993. SPSS Inc. Headquarters, 233 S. Wacker Drive, 11th floor, Chicago, Illinois 60606.
- YASUDA, H. & T. KIMURA 2001. Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. *Entomologia Experimentalis et Applicata* 98: 17-25.

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HOST PREFERENCE OF *Lysiphlebus testaceipes* (CRESSON) (HYMENOPTERA: APHIDIIDAE) FOR *Myzus persicae* (SULZER) AND *Aphis gossypii* GLOVER (HEMIPTERA: APHIDIDAE).

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BUENO, V.H.P., A.B. CARNEVALE & M.V. SAMPAIO. 2003. Host preference of *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Aphidiidae) for *Myzus persicae* (Sulzer) and *Aphis gossypii* Glover (Hemiptera: Aphididae). Pp. 17-20 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

The acceptance of a host by a parasitoid should indicate that the host must have appropriate characteristics for oviposition. The majority of Aphidiid parasitoids attack a range of host species, but these hosts may differ in visual and gustatory cues and/or in the quality for parasitoid progeny. Such differences may lead to evolution of host preference. We studied the host preference of *L. testaceipes* for *A. gossypii* and *M. persicae* in choice and non-choice tests. The searching behavior of *L. testaceipes* in a non-choice test and in a choice test with *A. gossypii* and *M. persicae* as hosts showed that the numbers of encountered hosts, probes with the ovipositor, ovipositions, and the parasitoid larvae found after host dissection were higher in *A. gossypii* than in *M. persicae*. Based on the number of hosts accepted for oviposition we conclude that the parasitoid *L. testaceipes* preferred *A. gossypii* both in the non-choice and in choice tests.

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INTRODUCTION

Whether an immature parasitoid will successfully develop in its host, depends on the host choice by the adult parasitoid female. Host acceptance by parasitoids is composed of three steps: host habitat finding, host finding, and host acceptance (VINSON & IWANTSCH 1980). Success of development of the parasitoid is determined by the suitability of the host. After host finding, the parasitoid begins its evaluation of the host by antennal tapping and ovipositor probing (MACKAUER et al. 1996). Physiological and nutritional conditions of the host are inspected by the parasitoid during its evaluation (VINSON 1997), but behavioral responses are also important in host acceptance/rejection (CHAU & MACKAUER 2001). The understanding of parasitoid behavior is accomplished by studying the steps in the host selection process and helps

explain the final parasitization rates of the host population.

Aphidiidae are solitary parasitoids of aphids (HAGEN & BOSCH 1968). *Lysiphlebus testaceipes* together with *Aphidius colemani* stand out as the dominant species in South America with several host species (STARÝ & CERMELI 1989) including *Myzus persicae* (Sulzer) and *Aphis gossypii* Glover (STARÝ et al. 1993). Parasitism of *L. testaceipes* is low in *M. persicae* (CARVER 1984; STEENIS 1993; CARNEVALE 2002) when compared to other parasitoids species such as *Aphidius colemani* (STEENIS 1993; SAMPAIO et al. 2001a, b), or to *L. testaceipes* parasitism on *A. gossypii* (RODRIGUES & Bueno 2001; CARNEVALE 2002) in laboratory conditions.

We studied the host preference of *L. testaceipes* for *M. persicae* and *A. gossypii* through comparison of the searching and host acceptance behavior of the parasitoid.

MATERIAL & METHODS

Insect rearing: Rearing and experiments were carried out at $25\pm 1^\circ\text{C}$, $70\pm 10\%$ RH and 12 hr photophase. *M. persicae* and *A. gossypii* were reared on sweet pepper and cotton seedlings, respectively. Twenty apterous females of each aphid species were placed in Petri dishes (15 cm Ø) with a 1 cm layer of 1% agar-water medium and leaves of sweet pepper and cotton according to the aphid species to be studied. These dishes were placed in climatic chambers and adult females removed after two days, with nymphs of 2nd and 3rd instars left for the studies with the parasitoids.

L. testaceipes was kept on *Schizaphis graminum* (Rondani) on sorghum leaves. Only 24 hr old mated females without previous oviposition experience were used in this study.

Preference in non-choice and choice tests: Petri dishes (5 cm Ø) with a 1 cm layer of agar-water medium and 4 cm Ø sweet pepper leaf disks with 20 *M. persicae* nymphs and/or *A. gossypii* were used. A single female of *L. testaceipes* was released in each dish and observations were performed under a stereoscopic microscope during 15 minutes. The number of encounters of the parasitoid with hosts, the number of ovipositor probings and the number of accepted hosts were recorded. *A. gossypii* was transferred to cotton leaves in a new Petri dish after the experiment while *M. persicae* was kept on sweet pepper leaves. The number of larvae of the parasitoid in the hosts was determined by dissecting of aphids three days after parasitism.

In the non-choice test, 20 aphids of one of a

species were placed in a Petri dish, and 15 *L. testaceipes* females were tested per treatment (N= $2\times 15= 30$ replicates). In the choice test each female of *L. testaceipes* was exposed to 10 aphids of each species; 28 females were tested (N= 28 replicates). In the non-choice test the counts were transformed as $\sqrt{x+0.5}$, and a t-test at 5% of probability was used to test for differences between aphid species. To test for differences between aphid species in the choice test, the χ^2 test was used.

RESULTS & DISCUSSION

In the non-choice tests, the mean number of encounters ($t = 3.49$; $p < 0.05$), ovipositor probes ($t = 2.97$; $p < 0.05$), and ovipositions ($t = 8.57$; $p < 0.05$) in the 15min period and the number of parasitoid larvae ($t = 6.32$; $p < 0.05$) of *L. testaceipes* found after host dissection were all significantly higher in *A. gossypii* (mean \pm SD, 37.7 ± 3.60 , 18.7 ± 1.83 , 18.0 ± 1.28 , and 10.5 ± 1.44 respectively) than in *M. persicae* (mean \pm SD, 21.2 ± 3.78 , 10.7 ± 2.28 , 5.1 ± 0.79 , and 2.0 ± 0.83 respectively) (Fig. 1). In the choice test we found the same differences as in the non-choice test: the number of encounters of *L. testaceipes* was significantly higher in *A. gossypii* (537) than in *M. persicae* (457) ($\chi^2 = 6.44$; $p < 0.05$), as well as ovipositor probing (286 and 168, respectively) ($\chi^2 = 30.67$; $p < 0.01$), the number of ovipositions (277 and 65, respectively) ($\chi^2 = 131.41$; $p < 0.01$), and the total number of parasitoid larvae found at dissection (132 and 29, respectively) ($\chi = 65.89$; $p < 0.01$) (Table 1).

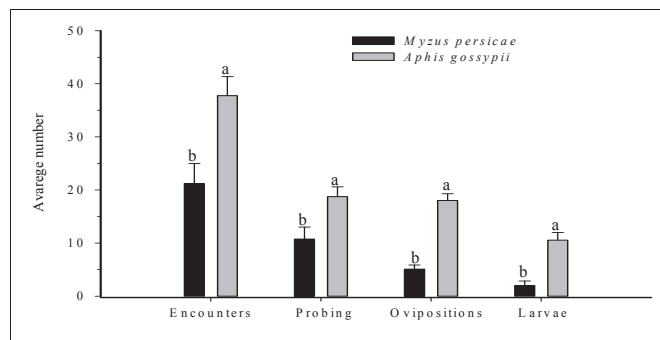


Fig. 1. Average number of antennal tapping (encounters), ovipositor probing, oviposition and total of parasitoid larvae (mean \pm standard error) of *Lysiphlebus testaceipes* on *Myzus persicae* and *Aphis gossypii* in non-choice test.

Table 1.

Number of encounters, ovipositor probes, ovipositions and parasitoid larvae of *Lysiphlebus testaceipes* on *Aphis gossypii* and *Myzus persicae* in choice test. Significant at 5% (*) and 1% (**) probability, χ^2 test.

Hosts		Total number			
Species	Number	Encounters	Probes	Ovipositions	Larvae
<i>A. gossypii</i>	280	537*	286**	277**	132**
<i>M. persicae</i>	280	457*	168**	65**	29**

Olfactory and visual stimuli may have great importance in the mechanism of locating and recognition of hosts at short distances, besides offering information of direction and distance of the hosts (MACKAUER et al. 1996). Observations of the number of encounters in the choice and non-choice test differed statistically between the two host species. Thus, it was demonstrated that the host preference of *L. testaceipes* was apparently determined before antennal contact.

For host preference of other species of aphidiids in choice tests, CHOW & MACKAUER (1991) and SAMPAIO et al. (2001b) found differences only in the number of accepted hosts, demonstrating that the preference is defined only after the touch with the ovipositor. On the contrary, *L. testaceipes* preferred *A. gossypii* in this study without need of host touching with the ovipositor.

In this study, *L. testaceipes* clearly preferred *A. gossypii* over *M. persicae*. Surprisingly, it seems that both hosts are suitable for development of *L. testaceipes*. The only difference we found was that parasitoids reared on *A. gossypii* had a higher longevity (5 days) than the ones reared on *M. persicae* (4 days) (CARNEVALE 2002). It is generally proposed that parasitoids prefer hosts that guarantee optimum conditions for development and growth in immature stages (GODFRAY 1994). In some cases, however, the opposite was found: MESSING & RABASSE (1995) showed that *Aphis citricola* van der Goot (unsuitable) was preferred by *Aphidius colemani* instead of *M. persicae* (suitable). In other cases the preferred host is the one more easily attacked by the parasitoid female, even if it is less suitable (CHAU & MACKAUER 2001).

The parasitoid *L. testaceipes* preferred the species *A. gossypii* in all tests we carried out, although this host does not seem to be more suitable than *M. persicae*. In the choice and in the non-choice test the preference was defined

without need of physical contact with the host. The low number of *M. persicae* hosts accepted by *L. testaceipes* directly influences the low percentage parasitism of this host.

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REFERENCES

- CARNEVALE, A.B. 2002. *Adequabilidade de Myzus persicae (Sulzer) e Aphis gossypii Glover (Hemiptera: Aphididae) como hospedeiros de Lysiphlebus testaceipes (Cresson) (Hymenoptera: Aphidiidae)*. (MS Thesis). UFLA, Lavras, 47 pp.
- CARVER, M. 1984. The potential host ranges in Australia of some imported aphid parasites (Hym.: Ichneumonidae: Aphidiidae). *Entomophaga* 38: 351-359.
- CHAU, A. & M. MACKAUER 2001. Host-instar selection in the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae): assessing costs and benefits. *Canadian Entomologist* 133: 549-564.
- CHOW, A. & M. MACKAUER 1991. Patterns of host selection by four species of aphidiid (Hymenoptera) parasitoids: influence of host switching. *Ecological Entomology* 4: 403-410.
- GODFRAY, H.C.J. 1994. *Parasitoids, behavioral and evolutionary ecology*. Princeton, New Jersey: Princeton University Press. 473 pp.
- HAGEN, K.S. & R. VAN DEN BOSCH 1968. Impact of pathogens, parasites, and predators on aphids. *Annual Review of Entomology* 13: 325-384.
- MACKAUER, M., J.P. MICHAUD, & W. WÖLKL 1966. Host choice by aphidiid parasitoid (Hymenoptera: Aphidiidae): host recognition, host quality, and host value. *Canadian Entomologist* 6: 959-980.

8th International Symposium on Ecology of Aphidophaga
University of the Azores, Ponta Delgada, 1-6 September 2002

- MESSING, R.H., & J.M. RABASSE 1995. Oviposition behavior of the polyphagous aphid parasitoid *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae). *Agriculture, Ecosystems and Environment* 52:13-17.
- RODRIGUES, S.M.M., & V.H.P. BUENO 2001. Parasitism rate of *Lysiphlebus testaceipes* (Cresson) (Hym.: Aphidiidae) on *Schizaphis graminum* (Rond.) and *Aphis gossypii* Glover (Hem.: Aphididae). *Neotropical Entomology* 30: 625-629.
- SAMPAIO, M.V., V.H.P. BUENO, & R. PÉREZ-MALUF 2001a. Parasitismo de *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae) em diferentes densidades de *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). *Neotropical Entomology* 30: 81-87.
- SAMPAIO, M.V., V.H.P. BUENO, & J.C. VAN LENTEREN 2001b. Preferência de *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae) por *Myzus persicae* (Sulzer) e *Aphis gossypii* Glover (Hemiptera: Aphididae). *Neotropical Entomology* 30: 655-660.
- STARÝ, P., M. GERDING, H. NORAMBUENA, & G. REMAUDIÈRE 1993. Environmental research on aphid parasitoid biocontrol agents in Chile (Hym., Aphidiidae; Hom., Aphidoidea). *Journal of Applied Entomology* 115: 292-306.
- STARÝ, P., & M. CERMELI 1989. Parasitoides de áfidos en plantas cultivadas de Venezuela. *Boletín de Entomología venezolana* 5: 77-80.
- STEENIS, M.J. VAN 1993. Suitability of *Aphis gossypii* Glov., *Macrosiphum euphorbiae* (Thom.) and *Myzus persicae* Sulz. (Hom.: Aphididae) as host for several aphid species (Hym.: Braconidae). *IOBC/WPRS* 26: 157-160. (Bulletin).
- VINSON, S.B. 1997. Comportamento de seleção hospedeira de parasitoides de ovos, com ênfase na família Trichogrammatidae. Pp. 67-119 in J.R.P. PARRA, & R.A. ZUCHI (Eds.). *Trichogramma e o controle biológico aplicado*. Piracicaba, FEALQ. 324 pp.
- VINSON, S.B., & G.F. IWANTSCH 1980. Host suitability for insect parasitoids. *Annual Review of Entomology* 25: 397-419.

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THE BIOLOGICAL CONTROL OF *Aulacorthum solani* (KALTENBACH) (HOMOPTERA: APHIDIDAE) IN GREENHOUSE GROWN PEPPER; RESEARCH ON A TRI-TROPHIC SYSTEM

J.V. SCHELT & F. WÄCKERS

SCHELT, J.V. & F. WÄCKERS 2003. The biological control of *Aulacorthum solani* (Kaltenbach) (Homoptera: Aphididae) in greenhouse grown pepper; research on a tri-trophic system. Pp. 21-27 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

To improve the control of the foxglove aphid (*Aulacorthum solani*) in greenhouse sweet pepper, several trials on three trophic levels have been conducted. Two different lines of *Aphelinus abdominalis* were compared on flight capacity, parasitism and predation. One line was significantly better in parasitism of *A. solani* (6.3 vs 0.2 mummies/female/day). This line performed also better at lower temperatures (15-18° C.) in flight capacity. Predation was the same for both lines (2 aphids/female/day).

The honeydew of *A. solani* was tested as a food source on *Aphidius* spp. The life span of *Aphidius* on this honeydew was 4 days which was equal to water and half of sucrose. On 100 ha. of commercially grown sweet pepper a banker plant system (wheat, *Sitobion avena*, *A. abdominalis*) was used. In general growers were able to reduce the number of chemical corrections from 7 to around 3.

In sweet peppers grown under glass there is a natural oscillation of 4-5 weeks in flowering and fruit set. We observed large differences in aphid growth depending on this vegetative or fruiting phase. The practical considerations how to adjust the biological control still has to be investigated.

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INTRODUCTION

The integrated control of aphids in glasshouses has become common practice in tomatoes, peppers, cucumbers, and aubergines. (VAN SCHELT 1999; KLAPWIJK 1999; MULDER et al. 1999). *Aphis gossypii* and *Myzus* spp. are controlled with *Aphidius colemani*; *Macrosiphum euphorbiae* with *Aphidius ervi*. Often generalist predators like *Aphidoletes aphidimyza* and lady beetles are used in conjunction with the parasitoids to control high aphid numbers. However the control of *Aulacorthum solani* in peppers is still very problematic.

A. solani has become a very common pest in sweet pepper in greenhouses over the last three

years. Because *A. solani* is a very polyphagous and a cosmopolitan species, it has become a problem in most pepper growing regions in North West Europe and Canada. The aphids are generally found in the lower parts of the plant and are easily overlooked at the beginning of an infestation. Already at low densities the plants can react very strongly to the saliva of the aphid. On the leaves yellow necrotic spots can be found and often the top is showing malformations. In the period 1997-2000 biological control with *A. ervi* and the gall midge *A. aphidimyza* was practised on several hundreds of hectares by commercial growers in the Netherlands. Results were unsatisfactory because too often chemical corrections with Pirimicarb had to be applied.

The low percentage parasitism may be explained by the foraging behaviour of this parasite (SCHWORER & VÖLKL 2001). If within a certain time no aphids are found than *A. ervi* has the tendency to disperse over large distances.

The potential use of another parasite, *Aphelinus abdominalis*, was explored. Two lines were compared on their dispersal capacity and fecundity. The use of banker plant systems (winter wheat with *Sitobion avenae*) was developed to enhance the numbers of *A. abdominalis* before aphid growth in the crop.

Research on the aphid itself was carried out by NIOO-CTE. We speculated that the aphid's honeydew could be toxic or unsuitable as a food source for the beneficials used. Finally we looked more in detail at the physiological status of the plant and its influence on aphid growth.

SELECTING LINES OF *A. abdominalis*

Introduction

Selecting of lines within a species can be an option to improve the control capacity of beneficials.

Aphelinus abdominalis is normally associated with *Macrosiphum euphorbiae* and cereal aphids as *Sitobion avenae*. HÖLLER & HAARDT (1993) compared a uniparental German line and a biparental French line. Both lines showed a high fecundity on *S. avenae* in the laboratory but failed in the field. Both lines however had similar biological characteristics, but were only tested on *S. avenae*.

In this study we compared two lines of *A. abdominalis*. One line came from a German producer, the other line was provided by INRA/Antibes (France). Both lines were reared separately on *Macrosiphum euphorbiae*.

They were compared with respect to their host feeding behaviour and their fecundity with *A. solani* as a host.

Because there is a tendency to save energy in greenhouse systems by reducing temperature in the winter, the dispersal capacity of beneficials under cool conditions (15-18 °C) is important. Moreover if the leaves of the plants are not touching each other in the beginning of the season

the beneficials have to fly for an optimal dispersal in the greenhouse. Flight propensity was assessed at different temperatures for both lines.

Material and Methods

The parasitism and predation rate was determined by introducing individual females of *A. abdominalis* (n=30) for 24 hours on a sweet pepper leaf disc on agar with 20 first and second instar *A. solani*. After 24 hours the female was removed and the number of aphids that were fed upon by the female, was determined. Because of slow deterioration of the leaf, the aphids were transferred to a fresh leaf after 8 days. After fourteen days the number of parasitized aphids (mummies) was assessed.

The French line was tested again on *A. solani* after being reared for one generation on this host.

The experiments were conducted in a climate cell at 21 ± 1°C, 70% RH, 16L:8D.

Flight propensity was determined by putting 100 adult wasps, less than 24 hrs old, in an open 50 ml. plastic bottle. The bottle was placed on a small concrete platform in the middle of a bowl (Ø 25 cm.) with water containing a drop of detergent.

This set up was put in a cage of 30 by 30 cm. and 50 cm. in height. The opening of the bottle was 6.5 cm. above the surface of the water. The cage was put in a climate box with fluorescent tubes at all sides. Experiments were done at 15, 18, 21, 24 and 27 °C and 75% RH. After 24 hours the number of parasitic wasps that remained in the bottle, that had drowned, and that had crossed the water were counted. Before releasing the parasitic wasps, they were acclimatised for one hour to the ambient temperature. All tests were done twice.

Results

Parasitism and Predation

Amount of host feeding was 2.33 aphid/day for the French line, 2.03 for the German line (n.s. MWU-test).

Parasitization was significantly different: 6.3 mummie/female for the French line, 0.23 for the German line (MWU, P<0.001)

No differences could be seen between the parasitisation capacity of the French line that had been reared on *M. euphorbiae* (6.3 mummie/female) and parasites of the same line that had been reared for one generation on *A.solani* (7.7 mummie/female) (n.s. MWU).

Flight capacity

The lines also differed clearly with respect to their flight capacity. The number of wasps from the German line that left the bottle was significantly lower at 15 and 18°C. (MWU-test) (Fig. 1) In the numbers that actually flew across the water the same pattern was visible (Fig. 2).

The flight-pattern could be well observed in this set-up. When *A. abdominalis* are taking off, they jump up a little, and subsequently lose altitude very quickly before regaining height again. Only when they did not hit the water at the lowest point, could they reach the other side of the barrier.

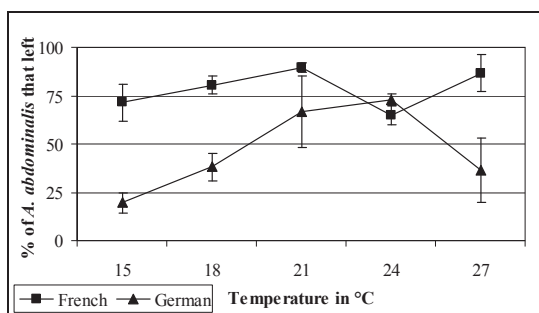


Fig. 1. Percentage adult *A. abdominalis* that left the bottle at different temperatures.

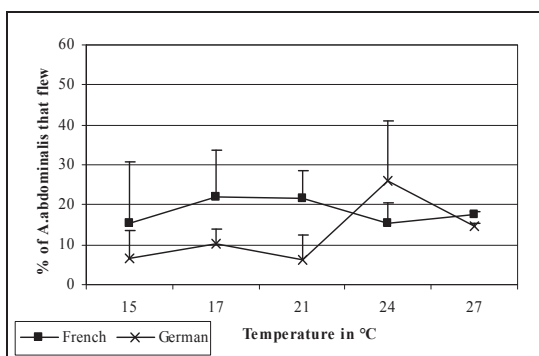


Fig. 2. Percentage adult *A. abdominalis* that flew across the waterbarrier.

Discussion

From these results it was concluded to use the French strain of *A. abdominalis* in the mass rearing and for commercial use. In theory the German line could be improved by rearing them for several generations on *A. solani*, but the offspring of the first experiment was so low, that further efforts in this direction were stopped. Also *M. euphorbiae* and not *A.solani* is the preferred aphid for a mass rearing system.

It can be speculated that a further exploration of *A. abdominalis* coming from other parts of its distribution area can be interesting.

THE SUITABILITY OF *A. solani* HONEYDEW AS A FOOD SOURCE FOR *Aphidius* spp.

Introduction

The great majority of parasitoids and many arthropod predators depend on sugar sources to cover their energetic needs. There is strong theoretical as well as empirical evidence that the availability of suitable sugar sources can be a key factor determining the population dynamics of predator-prey and parasitoid-host systems (KRIVAN & SIROT 1997; WÄCKERS 2003). Besides (extra) floral nectar, honeydew is the most prevalent source of exogenous sugars in nature. Due to the fact that agricultural ecosystems often lack flowering plants, honeydew is likely of particular importance in agriculture. A recent study by Wäckers and Steppuhn (unpublished) demonstrated that 80% of the larval parasitoid *Cotesia glomerata* collected in a cabbage field contained honeydew specific sugars, indicating a high incidence of honeydew feeding by this parasitoid. Parasitoids of honeydew-producing insects are believed to be even more intimately linked to this food source.

Despite this intimate link, honeydew can vary considerably with respect to its nutritional quality. Whilst certain types of honeydew can be equally suitable as nectar or sugar solutions, others are clearly inferior or even toxic (WÄCKERS 2000). To test the suitability of *A. solani* honeydew from various *A. solani*-plant

combinations for aphid parasitoids, we compared the longevity of honeydew-fed *A. colemani*, to parasitoids fed with a sucrose solution. Though *A. colemani* is not a natural parasite of *A. solani* it served as a model for aphid parasitoids in general and *Aphidius* spp. in particular.

Materials and method

Aulacorthum solani honeydew was collected from aphid colonies feeding on the following plant species: *Brassica nigra*, *Capsicum frutescens*, *Gossypium herbaceum*, and *Vicia sativa*. The plants had been grown in 1l. potting soil in greenhouses at the Dutch Institute for Ecology (NIOO-CTE) in Heteren. Growing conditions were T=20°C, RH=50-80%, 16L8D.

The homopteran-plant combinations were kept in fine-mesh screen cages to prevent contamination. To collect the honeydew, a glass plate was placed underneath the plant. After 24 hours the honeydew was collected using a glass micropipette and subsequently stored in a freezer at -15°C.

Newly emerged parasitoids were placed in a petridish and provided with a piece of water-soaked cotton wool as well as a 1µl droplet of one of the honeydew types placed on the lid. As

controls, separate *A. colemani* cohorts were subjected to water only and a 1µl droplet of a 1M sucrose solution respectively. The petridishes were kept at T=20°C, RH=95-100%, 16L8D. The high humidity prevented the honeydew and sucrose solution from becoming too viscuous.

Survival of wasps was scored daily. Every second day the food droplets were renewed. For each treatment we tested 50-60 individuals. Parasitoids that were found dead in the honeydew droplets were discarded.

We used HPLC (High Performance Liquid Chromatography) to analyse the sugar composition of the honeydew types used in the longevity experiment

Results

Longevity

Parasitoids provided with water only (control) lived 4.0 days on average. Access to the sucrose solution increased parasitoid lifespan more than twofold (8.4 days). The honeydew, on the other hand, had only a marginal effect on parasitoid longevity (Fig 3). Only honeydew from *A. solani* on *V. sativa* raised parasitoid longevity relative to the water control (Mann-Whitney U-test).

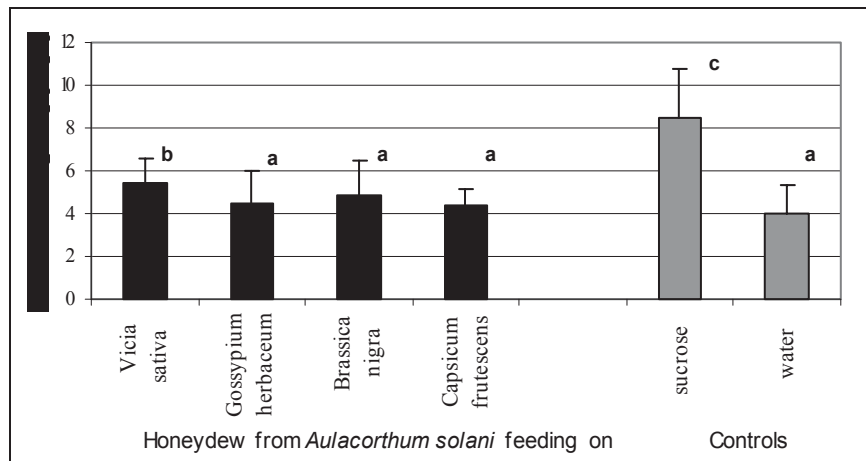


Fig. 3. Longevity of *A. colemani* when provided with various sugar sources, or water only (control). Different letters indicate significant differences among treatments (MWU-test).

Honeydew Sugar Composition

The HPLC sugar analysis showed that the composition of *A. solani* honeydew depends on

the aphid's host plant (Table 1). Most notably, the aphid synthesized sugar erlose was absent in honeydew from *G. herbaceum*, while occurring in

substantial amounts in honeydew collected from the other three plants. Maltose was only found in the honeydew collected from *Vicia faba*. Overall,

however, the honeydew was dominated by sucrose and its hexose components glucose and fructose.

Table 1
Sugar composition of honeydew collected from various *Aulacorthum solani*-plant combinations. Numbers represent percentage of total sugar content (weight/weight).

	Sucrose	Glucose	Fructose	Unidentified	Erlöse	Trehalose	Maltose	Sorbitol	Mannitol
<i>Capsicum frutescens</i>	46.9	12.0	22.5	1.4	15.6	1.1	0.0	0.0	0.4
<i>Gossypium herbaceum</i>	35.5	19.4	39.5	2.0	0.0	0.0	0.0	1.3	2.3
<i>Brassica nigra</i>	35.0	15.2	27.7	3.3	16.7	0.8	0.0	0.0	1.4
<i>Vicia sativa</i>	26.8	19.7	30.5	2.1	11.5	0.0	7.7	0.8	0.9

Discussion

Based on the fact that honeydew is primarily a sugar solution, it is often assumed that it makes for a suitable insect food source. However, the data presented here, as well as previous reported studies show that there can be a considerable variation in honeydew suitability. It is yet unclear which honeydew components are responsible for this variation, but two possibilities have been proposed: (i) secondary plant compounds and (ii) sap-feeder synthesized sugars. It has been reported that secondary plant compounds appear in honeydew (e.g. MALCOLM 1990). However, little is known about the effects of these compounds on honeydew-feeding insects. While secondary plant compounds in the honeydew might have been responsible for the poor suitability of *A. solani* honeydew, it would be remarkable that the effect on the parasitoid would be similar in the four plants tested, as they represent a wide variation in plant secondary chemistry.

The few studies addressing the effect of sap-feeder synthesized sugars indicate that these specific sugars might have a negative effect on insect longevity (WÄCKERS 2000). ZOEBELEIN (1956) reported that melezitose feeding reduced the life span of the parasitoid *Microplectron uscipennis* in comparison to food-deprived individuals, while sucrose, glucose or fructose increased *M. uscipennis* longevity by a factor of more than 2. In studies with *C. glomerata*, melezitose prolonged the parasitoid's life span relative to control individuals provided with water only, but reduced longevity by 44-47% in comparison to sucrose, fructose and glucose. Of

the other honeydew oligosaccharides studied, erlose was moderately suitable as a food source, while trehalose and raffinose were unsuitable (WÄCKERS 2001). Similar results were obtained in sugar longevity studies for *A. colemani* (Wäckers, unpublished). However, given the relatively low concentration of these sugars in the honeydew tested here, it is unlikely that the sugar composition is responsible for the poor survival of *A. colemani* in this study.

Irrespective of the underlying mechanism, the poor quality of *A. solani* honeydew may have considerable ecological and applied implications. The poor performance of *A. ervi* in controlling *A. solani* in the glasshouse may be partly due to the limited survival of *Aphidius* spp. on *A. solani* honeydew.

THE USE OF *A. abdominalis* ON BANKER PLANTS

In order to obtain large numbers of *A. abdominalis* in the greenhouse at the right time, a banker plant system was developed. Winter wheat (cv. "Vivant") was sown in hanging baskets (Ø 20 cm.) and infected with the cereal aphid *Sitobion avenae*. Small numbers of parasitoids (20-30 /banker) were introduced on the bankers. It took two generations before a large number of mummies (2-3000/banker) could be found. Most bankers were started in February (20/ha.) and peaked in parasite production at the beginning of April when first infections with *A. solani* could be expected.

By putting yellow sticky traps in the greenhouse it was possible to monitor the

production and dispersal of adult *A. abdominalis* over time. Peak production of the bankers occurred in week 15 (around 8-10 weeks after their introduction); bankers were removed at week 20, because all aphids were parasitised and all mummies were emerged. Until week 29 *A. abdominalis* was trapped on yellow sticky traps. The impact of *A. abdominalis* on the population of *A. solani* was hard to quantify. Marked colonies of *A. solani* often had disappeared when inspected again after one week. This can be partly explained by host feeding of the parasites. Black mummies however were found not only on leaves, but also at the base of the stem, on ropes, plastic of the rock wool pot, and even on the ground.

In 2002 the banker plant system was used on approximately 100 ha. One grower (10 ha.) did not need to use any chemicals for aphid control, though several infections with *A. solani* were observed. Most other growers were able to reduce the number of Pirimicarb applications from around 7 to 2-3.

THE INFLUENCE OF TIMING OF FRUIT SET ON APHID CONTROL

An aspect which is easily overlooked is the influence of the physiology of the plant on aphid

growth and subsequently aphid control. We observed large differences in aphid growth between different greenhouses and we concluded that this could only be explained by differences in plant physiology. As an example in figure 4 the number of newly formed pepper fruits per week is plotted for the same greenhouse in two consecutive years. In 2001 fruit set occurred continuously during the year. In 2002 however, oscillations with a period of 4 weeks occurred. Especially in peppers fluctuations in fruit set is a "natural" phenomenon, though plant breeders are selecting for varieties with a more even fruit set. Also abiotic factors (like day/night temperature and feeding regime) can influence fruit set. Finally growers know that if fruit set is unequal at the beginning of the season it is almost impossible to go back to a more even fruit set later on. As a consequence it is observed that the aphid population growth is reflected in the fruit set pattern. In the vegetative phase the aphid population will grow much faster than in the fruiting phase. Small infections with *A. solani* will explode very fast in this period. Until now practical consequences for the release of beneficial insects have not been considered. However if the biological control is already poorly established and the crop is in a vegetative phase, an advice to use a chemical correction will be given sooner.

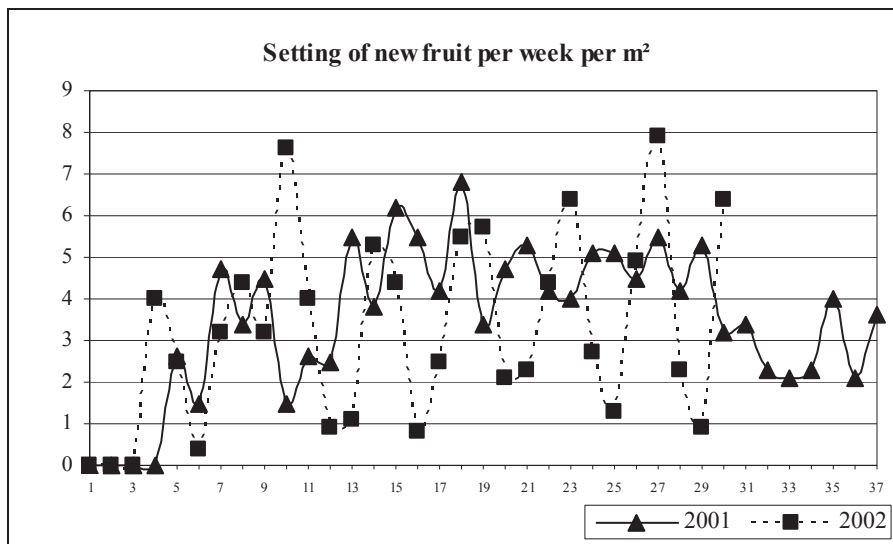


Fig. 4. Setting of new peppers per week/m² for 2 consecutive years.

OVERALL CONCLUSIONS

The biological control of the foxglove aphid *A.solani* in peppers has been improved by several measurements. By comparing two lines of *A. abdominalis*, a line was chosen which performs better at lower temperatures. This is important because there is a tendency to lower the temperatures in greenhouses during winter and spring. Because the rate of increase of *A. abdominalis* is rather low, a banker plant system was developed to rear high numbers of parasites before *A. solani* can be expected in the greenhouse. With an average of 20 bankers per hectare and 3000 mummies per banker, around 6 parasites/m² were reared in the greenhouse. Numbers were sometimes that high that the number of predated aphids was even higher than the number of mummies found.

The hypothesis that the honeydew of the aphids was toxic for *Aphidius* spp. could not be confirmed. However the result that this honeydew had the same nutritional value as water was remarkable.

Future research will focus on further improvement of the banker plant system (optimal timing, quality of the banker plant), the screening of new parasites and predators. The influence of the plant physiology on the aphids and subsequently on biological control is challenging but can only be solved in cooperation with other partners.

REFERENCES

- HÖLLER, C. & H. HAARDT 1993. Low field performance of an aphid parasitoid, *Aphelinus abdominalis*, efficient in the laboratory (Hym., Aphelinidae). *Entomophaga* 38: 115-124
- KLAPWIJK, J.N. 1999. Biological control of tomato pests in the Netherlands. *IOBC Bulletin* 22(1): 125-128
- KRIVAN, V. & E. SIROT 1997. Searching for food or hosts: the influence of parasitoids behavior on host-parasitoid dynamics. *Theoretical Population Biology* 51: 201-209.
- MALCOLM, S.B. 1990. Chemical defences in chewing and sucking insect herbivores: plant-derived cardenolides in the monarch butterfly and oleander aphid. *Chemoecology* 1: 12-21.
- MULDER, S., H. HOOGERBRUGGE, K. ALTENA & K. BOLCKMANS 1999. Biological pest control in cucumbers in the Netherlands. *IOBC Bulletin* 22(1): 177-180
- SCHULT, J.VAN 1994. The selection and utilisation of parasitoids for aphid control in glasshouses. *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society* 5: 151-157
- SCHULT, J.VAN 1999. Biological control of sweet pepper pests in the Netherlands. *IOBC Bulletin* 22(1): 217-220
- SCHWORER, U. & W. VÖLKL 2001. Foraging behavior of *Aphidius ervi* (Haliday) (Hymenoptera: Braconidae: Aphidiinae) at different spatial scales: Resource utilization and suboptimal weather conditions. *Biological Control* 21(2): 111-119
- WÄCKERS, F.L. 2000. Do oligosaccharides reduce the suitability of honeydew for predators and parasitoids? A further facet to the function of insect-synthesized honeydew sugars. *Oikos* 90: 197-201.
- WÄCKERS, F.L. 2001. A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *Journal of Insect Physiology* 47: 1077-1084.
- WÄCKERS, F.L. 2003. The effect of food supplements on parasitoid-host dynamics. Pp. 226-231 in R. VAN DRIESCHE (Ed). *International symposium on biological control of arthropods*. USDA Forest Service, publication FHTET-03-05
- ZOEBELEIN, G. 1956. Der Honigtau als Nahrung der Insekten. *Zeitschrift für angewandte Entomologie* 38: 369-416.

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COMPARISON OF THE REPRODUCTIVE INVESTMENT IN COCCIDOPHAGOUS AND APHIDOPHAGOUS LADYBIRDS (COLEOPTERA: COCCINELLIDAE).

A. MAGRO, J-L. HEMPTINNE, A. NAVARRE & A.F.G. DIXON

MAGRO, A., J-L. HEMPTINNE, A. NAVARRE & A.F.G. DIXON 2003. Comparison of the reproductive investment in Coccidophagous and Aphidophagous ladybirds (Coleoptera: Coccinellidae). Pp. 29-31 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

The prey of coccidophagous ladybird beetles has a slower rate of development and is less mobile than that of aphidophagous ladybirds. These differences are paralleled by a suite of characters suggesting that coccidophagous species live at a slower pace than aphidophagous species. Data in the literature tend to indicate that coccidophagous ladybirds live longer and have a lower fecundity than aphidophagous species. Thus the expectation is that coccidophagous species allocate proportionally less resources to their gonads than aphidophagous species. The reproductive investment in *C. montrouzieri* and *A. bipunctata* support this prediction. The fat in gonads represents 27.4 % of the total body fat in *C. montrouzieri* and 37.1 % in *A. bipunctata*.

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INTRODUCTION

Worldwide there have been 155 attempts to control aphids by introducing ladybirds, and only one was supposedly substantially successful, whereas of the 613 such attempts to control coccids resulted in 53 complete or substantial successes (DIXON 2000). Coccidophagous ladybirds are therefore very successful biocontrol agents compared to aphidophagous species. DIXON (2000) suggested, therefore, that the study of ladybird successes and failures in biological control programmes might enable us to identify the specific attributes of successful biological control agents.

Reproductive potential is generally regarded as an important attribute of natural enemies (e.g., DEBACH 1973; MESSENGER et al. 1976; VAN DRIESCHE & BELLOWS JR. 1996). STEWART et al. (1991) measured reproductive investment as the

egg weight multiplied by the ovariole number and related this to adult weight for 8 aphidophagous ladybirds. There is a very strong positive correlation between reproductive investment and adult weight. Gonads make up a fixed proportion of the body weight, and there is a trade-off in the number of eggs a species can lay per day and egg size. MAGRO (1997) performed the same kind of study on 3 coccidophagous ladybirds, where the reproductive biomass is again a fixed proportion of the total body mass. However, the reproductive biomass in coccidophagous ladybirds makes up a smaller percentage of the total body mass than in aphidophagous species. That is, coccidophagous ladybirds invest proportionally less in reproduction than aphidophagous ladybirds.

DIXON (2000) states that there is a slow-fast continuum in the life history characteristics of ladybirds. When the reproductive investment of coccinellids is considered along with other

parameters such as rate of development, relative growth rate, the rate of metabolism, speed of movement, reproductive rate and rate of ageing, coccidophagous species appear to have a slow pace of life and aphidophagous species a fast pace of life. These different paces of life reflect those of their prey.

As fat is the chief form in which energy is stored (WIGGLESWORTH 1972), we decided to verify the above conclusions by comparing the allocation of fat to gonads and soma in an aphidophagous and a coccidophagous ladybird. This paper reports the preliminary results of this study.

MATERIAL & METHODS

Biological material

Two similar-sized ladybird species were studied. *Cryptolaemus montrouzieri* Mulsant is a well-known Australian coccid predator, which has been introduced all around the world to control mealybugs. Adults weigh on average 11.1 mg (MAGRO 1997). *Adalia bipunctata* (L.) is a European aphidophagous ladybird. Adult weight is on average 15.8 mg (STEWART et al. 1991).

Both species came from our laboratory stock cultures: *C. montrouzieri* was reared on potato sprouts infested with *Planococcus citri* Risso and *A. bipunctata* on *Acyrtosiphon pisum* Harris reared from bean plants.

Measure of reproductive investment

The reproductive investment was measured in terms of mg of fat.

The analyses were made on 15 females of *C. montrouzieri* and 14 of *A. bipunctata*. Females were between 15 and 30 days old and were laying eggs regularly.

Each female was weighed (Sartorius Supermicro SC2 balance), dissected and its body cut in three parts: head and thorax, ovaries and abdomen without ovaries. Each part was dried at 35°C until it reached a constant weight. The dried tissues was put in Petroleum spirit (boiling range 40–60 °C) for 9 hours and then the solvent was

replaced and the extraction continued for another 9 hours. The tissues were then removed and the solvent evaporated off overnight, after which the tissues were weighed.

Fat contents were estimated as indicated by equations 1 and 2:

$$Ovfat = Ovdw - Ovdws \quad (1)$$

$$Tfat = Tdw - Tdws \quad (2)$$

where *Ovfat* is the fat content of gonads, *Ovdw* is the dry weight of the gonads and *Ovdws* is the dry weight of the gonads after fat extraction. *Tfat* is the total fat content of the body, *Tdw* is the total dry weight of the body and *Tdws* is the total dry weight of the body after fat extraction.

Mean values for both species were compared using a t test.

RESULTS & DISCUSSION

Figure 1 presents the results of this study in terms of the mean percentage as well as the standard deviation of fat invested in the gonads of the two ladybirds.

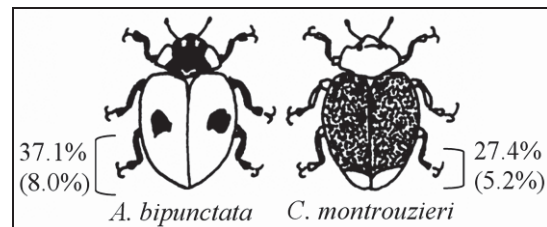


Fig. 1. Mean reproductive investment in an aphidophagous ladybird - *Adalia bipunctata* - and a coccidophagous ladybird - *Cryptolaemus montrouzieri*. Results presented in terms of fat in gonads as a percentage of total body fat. Standard deviation values are between parentheses.

Figure 1 indicates that *A. bipunctata* invests more of its energy reserves in reproduction than *C. montrouzieri*: the percentage of fat in the gonads of the aphidophagous species is greater than in the coccidophagous species (aphidophagous: 37.1%; coccidophagous: 27.4%; $P < 0.05$). This supports the idea that

aphidophagous species invest proportionally more of their fat reserves in reproduction than coccidophagous species of ladybirds.

CONCLUSIONS

The present work strengthens the conclusions of STEWART et al (1991) and MAGRO (1997) as the aphidophagous ladybird allocated proportionally more of its energy reserves to reproduction than the coccidophagous ladybird.

This conclusion is important from two points of view:

The evolutionary point of view: Organism are energy limited (KREBS 1994). Limited resources should be allocated in a way that maximises fitness. That is, reproduction is maximised within the constraints of other energy requirements. Therefore it is relevant to ask: Why do coccidophagous species invest proportionally more of their fat reserves in soma than aphidophagous species? DIXON (2000) argues that coccids in nature are generally much less abundant than the aphid prey of aphidophagous ladybirds and therefore it would appear to be advantageous for coccidophagous ladybirds to allocate more of their energy reserves to searching for prey.

In terms of biological control: A high reproductive investment, although important, does not seem to be an essential characteristic of a successful biological control agent.

REFERENCES

- DIXON, A.F.G. 2000. Insect predator-prey dynamics. Ladybird beetles and biological control. Cambridge: Cambridge University Press. 257 pp.
- DOUTT, R.L. & P. DEBACH 1973. Some Biological Control Concepts and Questions. Pp.118-142 in P. DEBACH (Ed.) Biological Control of Insect Pests and Weeds. London: Chapman and Hall Ltd. 844 pp.
- KREBS, C.J. 1994. Ecology. The experimental analysis of distribution and abundance (4th ed.). New York: Harper Collins College Publishers. 801 pp.
- MAGRO, A. 1997. *Os Coccinélideos dos Citrinos: estudo comparativo do seu interesse em luta biológica*. Unpublished doctoral dissertation, University of Évora, Portugal. 177 pp.
- MESSINGER, P.S., F. WILSON & M.J. Whitten 1976. Variation, Fitness and Adaptability of Natural Enemies. Pp. 209-231 in C.B. Huffaker & P.S. Messenger (Eds). Theory and Practice of Biological Control. New York: Academic Press, Inc. 788 pp.
- STEWART L.A., J.-L. Hemptinne & A.F.G. Dixon 1991. Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Functional Ecology* 5: 380-385.
- VAN DRIESCHE, R.G. & T.S. BELLOWS Jr. 1996. Biological Control. New York: Chapman and Hall. 539 pp.
- WIGGLESWORTH, V.B. 1972. The principles of Insect Physiology (7th ed.). London: Chapman and Hall. 827 pp.

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BIOLOGICAL CONTROL OF THE ROSY APPLE APHID, *Dysaphis plantaginea* (PASSERINI) (HOMOPTERA: APHIDIDAE): LEARNING FROM THE ECOLOGY OF LADYBIRD BEETLES.

J.-L. HEMPTINNE, A.F.G. DIXON & E. WYSS

HEMPTINNE, J.-L., A.F.G. DIXON & E. WYSS 2003. Biological control of the rosy apple aphid, *Dysaphis plantaginea* (Passerini) (Homoptera: Aphididae): learning from the ecology of ladybird beetles. Pp. 33-41 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

D. plantaginea is one of the major pests of apple. Technical advisers use empirically derived action thresholds, which depending on the geographic area, vary from 1 to 10 aphids per 100 fruit clusters. Not surprisingly the majority of orchards are sprayed every year. As a consequence, clones of this aphid are now resistant or tolerant to insecticides. There is therefore a need to develop other strategies for controlling this pest. Conservation and enhancement of natural enemies in apple orchards is one of the possible strategies but this technique does not produce consistent results. Releases of larvae of aphidophagous predators are promising but they are still expensive. In the near future, significant improvements in the biological control of *D. plantaginea* require of a threshold of economic damage, a better understanding of the ecology of this aphid and of its natural enemies, and the utilization of more resistant varieties of apple.

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INTRODUCTION

Dysaphis plantaginea (Passerini) is one of the major pests of apple in Western Europe and North America (BONNEMAISON 1959; BASSINO 1982; PASQUALINI & BRIOLINI 1982; WHALON & CROFT 1984; CRUZ DE BOELPAEPE et al. 1987; BARONIO et al. 1988; GENDRIER et al. 1989; TOURNEUR et al. 1992; BLOMMERS 1994; SAVINI 2000). It causes the leaves to curl and distorts current year shoots. Heavy infestations, particularly just after flowering, reduce the growth of the fruit and yield by 20 to 30 % (GRAF et al. 1999). However, the aphid is rarely abundant several years running, but tends to reach outbreak levels approximately every 5 to 6 years. Farmers and technical advisers do not seem to be aware of these fluctuations and spray or recommend spraying of orchards every year. The

pest status of this aphid has increased over the last decade. Spring infestations have become more severe and last longer. In addition, *D. plantaginea* has become more tolerant and in some cases resistant to the commonly used insecticides (DELORME et al. 1998). Reflecting these trends, the average number of insecticide treatments per growing season in Swiss orchards increased from 1.2 in 1990 to 1.8 in 1995 (HOEHN et al. 1996; GRAF et al. 1999). In South-western France, in 1998 the majority of farmers sprayed 3 to 4 times against *D. plantaginea* (DEDIEU 1998).

Although *D. plantaginea* severely affects apple production (DE BERARDINIS et al. 1994) the threshold of economic damage, surprisingly, has not been determined (WHALON & CROFT 1984). Technical advisers use empirically derived action thresholds, which depending on the geographic area, vary from 1 to 10 aphids per 100 fruit

clusters (WHALON & CROFT 1984). In Europe the action threshold is 1 aphid (BLOMMERS 1994). Thus not surprisingly, the majority of orchards are sprayed every year in early spring. This frequent use of insecticides probably accounts for the existence of resistant clones of *D. plantaginea*. This threshold hampers any change in the control of apple aphids. It indicates that *D. plantaginea* is extremely harmful and as a consequence technical advisers and farmers are reluctant to reconsider the methods used to control this aphid. The widespread and frequent use of insecticides in apple orchards is contrary to the political desire for the development of sustainable agriculture in Europe. Therefore, there is an urgent need to develop other strategies for controlling *D. plantaginea*.

The guilds of natural enemies associated with apple aphids have been extensively recorded (HODEK 1973; TOURNEUR et al. 1992; HODEK & HONĚK 1996). They generally consist of a minimum of 50 species of insects belonging to several families. Coccinellidae is one of the three most important families contributing 4 to 6 species to these guilds. This diversity of beneficial insects encourages the view that biological control is feasible. Thus the exploitation of the entire guild as a biological control agent is an attractive strategy. The objective is to keep the beneficial insects in the orchards and increase their abundance. To encourage them overwintering sites are provided and/or additional sources of food such as cover crops, strips of flowers or hedgerows are sown or planted. Alternatively the guilds can be used as a catalogue of potential biological control agents. Those selected can be reared in factories and released in the orchards. This paper considers these two approaches to the biological control of apple aphids with special emphasis on ladybird beetles.

CONSERVATION AND ENHANCEMENT OF NATURAL ENEMIES IN APPLE ORCHARDS

Since at least the beginning of the XXth Century circumstantial evidence was thought to favour the concept that simple communities on cultivated land were more prone to insect outbreaks than

more natural communities (ELTON 1958). As the later harbour more species than the former, the stability of these communities was seen as a consequence of their greater biological diversity. The structure of food webs was often invoked as an explanation. In complex communities, there are not only more species of herbivore but also of carnivore. That is, there are more pathways to channel the energy from one trophic level to the next. If one or few carnivore species are temporarily absent, there are still enough consumers to exploit the herbivore productivity. As a consequence, populations show slight fluctuations in abundance around an equilibrium (KREBS 1994). This ecological concept probably inspired the use of biological control based on natural enemy conservation and enhancement by making fields more hospitable to natural enemies by cultivating hedgerows, cover crops or weed strips.

This idea is not new and was already practised in the first decade of the XXth Century in attempts at controlling aphids (DIXON 2000). Later it received some theoretical support from ROOT (1973) who proposed two hypotheses to account for the fact that herbivorous insects are less abundant in complex agroecosystems than in simple ones (Fig. 1).

a)

	Simple	Complex
Diversity of prey/hosts species	Low	High
Fluctuations of natural enemies	Large	Small
Availability of pollen and nectar	Low	High
Functional response of natural enemies	Low	High

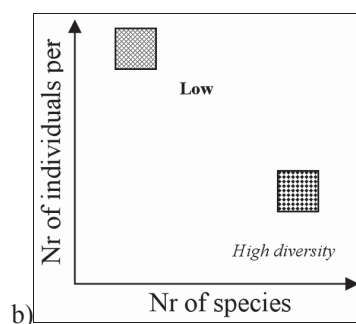


Fig. 1. Summary of Root's two hypotheses: a) the four main characteristics of the enemies hypothesis and b) the relationship between the number of species and the number of individuals per species in a community according to the resource concentration hypothesis.

Firstly, the enemies hypothesis postulates that predators and parasitoids are more efficient in diverse than simple communities of plants. RUSSELL (1989) reviewed the literature for evidence in favour of this hypothesis. Secondly, the resource-concentration hypothesis stipulates that specialist herbivores more easily find, stay in, and reproduce in monocultures of their host plants. Modern apple orchards typically are simplified communities: the soil below the trees is kept bare and grass between the rows of trees is mown regularly. Thus it is not surprising that attempts have been made to control aphids by increasing plant diversity in European and North American orchards (BROWN & WELKER 1992; WYSS 1995; BROWN & SCHMITT 1996; BROWN et al. 1997; KIENZLE et al. 1997; SOLOMON et al. 1999; VOGT & WEIGEL 1999). WYSS' seminal study (1995) lasted for 3 years during which *D. plantaginea* infestation and aphidophagous predators were monitored in two parts of an organic orchard. In the first year aphid infestation and predator abundance were identical in the two zones. In the second year a mixture of species of indigenous dicotyledons was sown in six one-meter wide strips located in one of the two zones. These plants flowered successively from early spring to late autumn. Some of them also host aphids when they are rare on apple. Therefore, pollen, nectar and aphids were available to the aphidophagous predators throughout the year. Later in the second and in the third year, aphidophagous predators appeared to be more abundant on the trees in the zone with the strip planting and there were fewer trees with large *D. plantaginea* colonies in this zone than in the control area (Fig. 2). Unfortunately, when VOGT & WEIGEL (1999) repeated WYSS' experiment in a much smaller orchard, they recorded more *D. plantaginea* on the trees in the zone with the strip planting than in the control zone.

These cases studies show that a greater abundance and/or diversity of natural enemies achieved by manipulating plant diversity does not automatically translate into aphid control (ANDOW 1986, 1988; VAN EMDEN 1990; VAN DRIESCHE & BELOW 1996; OBRYCKI & KRING 1998; DIXON 2000; LANDIS et al. 2000). This forces a reconsideration of the link between diversity and stability and the role of

aphidophagous predators in determining aphid abundance.

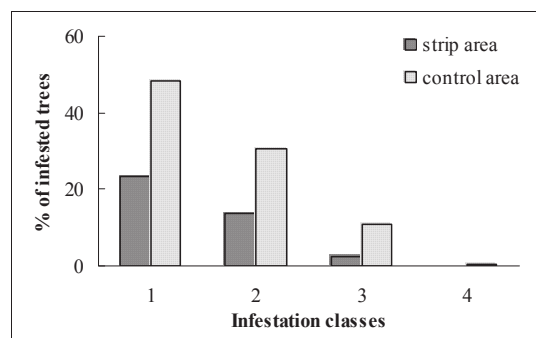


Fig. 2. Percentage of infested trees in the strip sown area and the control area in an experimental organic orchard in May 1993 (After WYSS 1995). Infestation classes: 1, 1 to 3, 2, 4 to 10, 3, 11 to 50 and 4, 51 to 200 aphid colonies.

Diversity and Stability

It is surprising that the enhancement of plant diversity in or near fields in attempts to control pests attracted such wide support, especially as it was not founded on sound scientific principles or experiments (PIMM 1984). As early as 1968, HAIRSTON et al. failed to increase the stability of experimental communities of bacteria and ciliates by increasing the number of species in his microcosms. Mathematical models of food webs showed that complex networks of consumers were not more stable than simple ones (MAY 1973). Finally, ROOT (1973) and RUSSELL (1989) based their hypotheses on circumstantial evidence. Currently, the link between diversity and stability in communities is still a highly controversial issue (KREBS 1994; DIAZ & CABIDO 2001). However, properties of communities such as resistance and/or resilience to perturbations are thought to depend on plant functional diversity rather than number of species. Plant functional types are sets of species showing similar responses to the environment and similar effects on ecosystem functioning (DIAZ & CABIDO 2001). It should be noted, however, that the impact of plant functional diversity has been studied in relatively few cases (DIAZ & CABIDO 2001). Recently, field trials in Sweden and

Switzerland yielded a positive correlation between plant functional richness and composition, and the number of aphids, and a negative one with the number of parasitoids (KORICHEVA et al. 2000). Although an interesting result the mechanism linking plant functional diversity and the abundance of these insects is unknown. Finally, in the absence of a well founded theoretical understanding it is not surprising that the results of studies on the conservation and enhancement of natural enemies in apple orchards are contradictory.

The role of aphidophagous predators

The two spot ladybird beetle *Adalia bipunctata* is one of the most abundant predators of *D. plantaginea* in European apple orchards. Its reproductive behaviour provides an explanation of why it is unable to regulate aphid abundance (HEMPTINNE et al. 1992; DOUMBIA et al. 1998). Aphids are smaller and grow much faster than two spot ladybirds (DIXON 1998, 2000). In the field, the developmental time, from egg to adult, of *A. bipunctata* is slightly shorter than the duration of an aphid colony. If a female ladybird is to maximize its fitness it has to carefully select its oviposition sites. If its larvae hatch in a very young colony, the probability of finding and catching prey is extremely low so they are likely to die of starvation. An old colony is not better because the number of prey is more likely to become scarce before the larvae can complete their development and they then have to compete for a dwindling resource and most if not all of them will die, mainly as a result of cannibalism. Between these two extremes, there is a narrow reproductive window, oviposition during which results in maximum larval survival. However, laying too many eggs in an aphid colony or in colonies where there are already ladybird larvae is likely to result in poor survival. In both cases the many predators hasten the decline in aphid abundance and increases competition for food. In addition, the youngest larvae will be the first to be eaten by older larvae (AGARWALA & DIXON 1992). Natural selection is likely to have favoured ladybird females that are able to assess the quality

of aphid colonies and lay a few eggs during the reproductive window (KINDLMANN & DIXON 1993). This is more fully discussed by DIXON & HEMPTINNE (2003).

RELEASE OF APHIDOPHAGOUS PREDATORS TO CONTROL APPLE APHIDS

There have been few releases of natural enemies in apple orchards (BOUCHARD et al. 1988; HAGLEY 1989; GRASSWITZ & BURTS 1995; WYSS et al. 1999a, b).

In Europe, Wyss experimentally assessed the ability of predators to keep the numbers of *D. plantaginea* below the action threshold. As producers routinely spray against this aphid early in spring, because of the low value of the action threshold, the study was aimed at determining the effectiveness of predators to reduce the numbers of fundatrices of the aphid. According to the literature and field observations, *A. bipunctata*, *Episyrphus balteatus* (De Geer) and *Aphidoletes aphidimyza* (Rondani) are the most abundant enemies of *D. plantaginea*. In Northern Europe, climatic conditions are often harsh when aphids hatch from overwintering eggs. Therefore, preliminary trials were made in 1995 to evaluate the searching ability of these predators in the field. Apple seedlings kept in 1 m³ cages were infested with fundatrices of *D. plantaginea*. Eggs or larvae of the three predators were then introduced in the cages. Larvae of *A. bipunctata* were the most resistant to frost and efficient at finding and killing the fundatrices (WYSS et al. 1999a). The effectiveness of this ladybird was further studied on 3-year-old apple trees and on apple branches in a commercial orchard.

On 3 year old apple trees, each infested with 5 fundatrices, were placed ladybird eggs or larvae to give four predator-prey ratios: 0:5, 1:5, 1:1 and 5:1. The treatments with eggs were unsuccessful because all the batches of eggs were either destroyed by rain or frost. Larvae at the two highest predator-prey ratios prevented the increase in aphid abundance (Fig. 3; WYSS et al. 1999b). These results were confirmed using naturally infested branches of apple trees (Wyss, unpublished results).

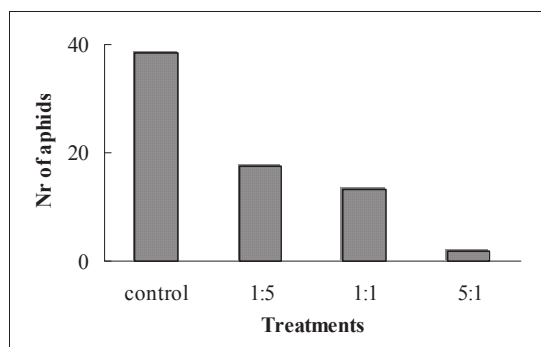


Fig. 3. The average number of aphids per tree on control trees and on trees on which larvae of *A. bipunctata* were released at one of the three predator-prey ratios: 1:5, 1:1 and 5:1 (After WYSS et al. 1999b).

INTEGRATED PEST MANAGEMENT

At a time when sustainable agriculture appears more and more frequently at the top of political agendas, it is important to convince farmers that the biological control of *D. plantaginea* is as reliable and efficient as the current methods of control. To reach this objective, research has to be developed in three directions.

Firstly, a real economic threshold of damage is needed. In conjunction with forecasts of aphid abundance, it will enable technical advisers and farmers to make more effective decisions- and is the corner stone of IPM in apple orchards.

Secondly, we have to learn more about the weak points in the *D. plantaginea* life cycle and how to use this knowledge to control the abundance of this aphid. For example, field observations (BONNEMAISON 1959) and time series analysis of the suction trap catches (HEMPTINNE et al. *in press*) indicate that mortality in autumn is important and influences the number of aphids next spring. Would it be possible to increase autumn mortality? According to two recent studies the answer to this question might be positive. WYSS et al. (1995) showed that spider webs caught many migrants. The more spider webs the more aphids caught and the fewer fundatrices next year. Release of predators seems also to be efficient in autumn. The impact of larvae of *A. bipunctata*, released before mid-October, on sexuparae and gynoparae

significantly affects the number of fundatrices next spring (KEHRLI & WYSS 2001). So there is a potential for biological control in autumn, which needs to be further explored. At first sight, autumn is probably more favourable for biological control than spring: producers are less busy and the risk of bad weather interfering with natural enemies is less.

Thirdly, the protection of apple has to be thought of in terms of IPM. More attention has to be paid to planting more aphid resistant varieties of apple. They continue to be an effective means of reducing the population growth rate of *D. plantaginea* and so maximizing the impact of natural enemies. Florina, Delorina, FloRub, Goldrush, Red Devil are resistant to *D. plantaginea* (WÜRTH et al. 1999, 2002). In addition, Ariwa, Renora, Rewena, Rubinola, Saturn are less susceptible to this aphid. All these varieties are hardly planted in Europe and the US. The major problem is to introduce them onto the market and to convince consumers to buy them. A lower productivity or a poor ability to sustain conservation might create additional problems for some of these apples. However, one should learn how to use this genetic potential in commercial orchards.

The cost of ladybird larvae is high so their use for aphid control is expensive. One way of reducing the cost is to target the fundatrices because fewer larvae are required to achieve an efficient predator-prey ratio. Time series analyses of suction trap catches show a cyclical pattern in the variation in abundance of *D. plantaginea* in France. Years with the lowest catches of aphids are separated by 6 to 4 years of higher catches (HEMPTINNE et al. *in press*; Fig. 4). If one could predict aphid outbreak years the cost of releasing natural enemies could be spread over more than one year. Currently analysis of suction trap catches has revealed that the abundance of *D. plantaginea* is regulated by density-dependence with weather acting as a disturbing factor (HEMPTINNE et al. *in press*). We do not know what regulates its abundance and cannot therefore devise a reliable forecasting system. However, the results provide working hypotheses for field and laboratory experiments, the objective of which is to identify the regulating mechanism.

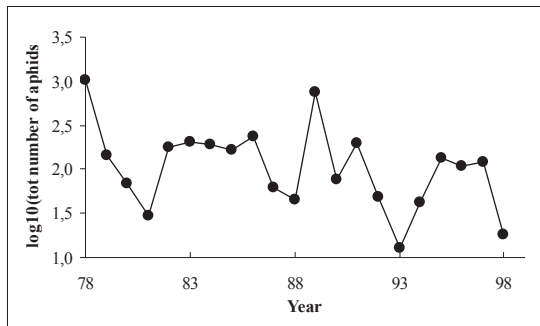


Fig. 4. The logarithm of the numbers of *Dysaphis plantaginea* caught every year from 1978 to 1999 in the suction trap at Rennes (Brittany, France).

CONCLUSION

Conservation and enhancement of natural enemies is an attractive strategy for controlling aphids, which has been tested in apple orchards. However, the results are not consistent. The problem is twofold. Firstly, it rests on the idea that diversity creates stability. Undoubtedly accumulating evidence indicate that diverse systems have interesting properties that are already visible when organic fields are compared with conventionally managed fields (MÄDER et al. 2002). Unfortunately we still do not know how these properties are generated and it is therefore difficult to engineer a system to achieve desirable properties (HINDMARCH & PIENKOWSKI 2000). Secondly, stability does not necessarily mean regulation of a population in the sense of keeping its abundance under a threshold of economic damage. The main weakness of conserving and enhancing natural enemies in order to control pests was pointed out by RUSSELL in 1989: the almost complete lack of field studies "on the behavior of individual arthropod enemies". If we do not correct this, techniques of biological control conceived from theory built on speculation will continue to yield inconsistent results.

From a purely technical point of view, it is possible to control *D. plantaginea* using natural enemies. Experiments have revealed that larvae of *A. bipunctata* can locate and kill fundatrices of this aphid early in spring even when the weather is cold and humid. They are also active and

efficient in autumn when *D. plantaginea* returns to the apple. If it is decided to release predators, then it should be larvae rather than adults because they tend to stay in or in the vicinity of patches of prey where they are released. A farmer that introduces ladybird larvae in his orchard behaves like a gravid ladybird female, carefully selecting prey colonies where its larvae will later develop. However, this method of biological control is expensive because the price per predator larva is high and large numbers are required to treat an orchard.

Like Janus biological control by natural enemies has two faces. Schematically and in the evolutionary framework, natural enemies tend to aggregate where prey or hosts are abundant, that is in the more profitable patches. As their abundance gradually increases there they compete for the resource and they interfere with each other. Good patches gradually lose their value and natural enemies begin to leave and search for better patches. Two opposing forces are at work: attraction to resources and repulsion (BEGON et al. 1996). The first force is emphasized in biological control strategies, while the second is neglected. Intercrops, cover crops or hedgerows provide more resources and support more consumers. But how do consumers distribute themselves between patches of resource and what is their impact on resource abundance?

To answer such a question, one needs to focus on the ecology of the protagonists, which in this case are aphids and ladybird beetles. Aphids are particularly adapted to exploit transient and ephemeral resources, the sap flow rich in nitrogen, which only occurs in spring and in autumn (DIXON 1998). Their life history is summarized by a short motto: "going fast". Ladybird beetles evolved the ability of exploiting such prey. Their reproductive behaviour, as described for *A. bipunctata*, is an expression of their adaptation. It clearly shows the two forces mentioned above in action. Ladybird females are attracted to aphid colonies but they also avoid those colonies that are marked by the tracks left by conspecific larvae. As a result, female *A. bipunctata* tend to distribute their eggs in many colonies of prey and show a weak numerical response to aphid abundance (HEMPTINNE et al. 1992). Field work aimed at understanding how

ladybird beetles behave in strip managed orchards and at assessing their impact on more diverse food sources is needed.

REFERENCES

- AGARWALA, B.K. & A.F.G. DIXON 1992. Laboratory study of cannibalism and interspecific predation in ladybird. *Ecological Entomology* 17: 303-309.
- ANDOW, D.A. 1986. Plant diversification and insect population control in agroecosystems. Pp. 277-386 in D. PIMENTEL (Ed.) *Some aspects of integrated pest management*. Ithaca: Cornell University Press.
- ANDOW, D.A. 1988. Management of weeds for insect manipulation in agroecosystems. Pp. 265-301 in M. A. ALTIERI & M. LIEBMAN (Eds). *Weed management in agroecosystems: ecological approaches*. Boca Raton, CRC Press.
- BARONIO, P., G. BRIOLINI, A. BUTTURINI & G. FACCIOLI 1988. Dinamica di popolazioni dell'afide grigio del melo (*Dysaphis plantaginea* Pass.). 1. Ricerche etologiche su ospite secondario. *Bolletín Istituto Entomologico « G. Grandi » Università di Bologna*. 43: 9-16.
- BASSINO, J.P. 1982. Les pucerons des arbres fruitiers. Travaux récents et perspectives. Pp. 237-242 in *Les Pucerons des cultures. Journée d'Etudes et d'Information*. ACTA: Le Carroussel.
- BEGON, M., J.L. HARPER, C.R. TOWNSEND 1996. *Ecology, populations and communities* (3rd edition). Oxford: Blackwell Science. 1068 pp.
- BLOMMERS, L.H.M. 1994. Integrated pest management in European apple orchards. *Annual Review of Entomology* 39: 213-241.
- BONNEMAISON, L., 1959. Le puceron cendré du pommier (*Dysaphis plantaginea* Pass.). Morphologie et biologie - Méthodes de lutte. *Annales des Epiphyties* 10: 257-320.
- BOUCHARD, D., S.B. HILL & J.G. PILON 1988. Control of green apple aphid populations in an orchard achieved by releasing adults of *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). Pp. 257-260 in E. NIEMCZYK & A.F.G. DIXON (Eds). *Ecology and Effectiveness of Aphidophaga*. The Hague: SPB Academic Publishing. 341 pp.
- BROWN, M.W. & W.V. WELKER 1992. Development of the phytophagous arthropod community on apple as affected by orchard management. *Environmental Entomology* 21: 485-492.
- BROWN, M.W. & J.J. SCHMITT 1996. Impact of ground cover plants on beneficial arthropods in an apple orchard in West Virginia, USA. *IOBC/WPRS Bulletin* 19: 332-333.
- BROWN, M.W., E. NIEMCZYK, T. BAICU, K. BALAZS, V. JAROSIK, G. JENSER, F. KOCUREK, R. OLSZAK, A. SERBOIU, & T. VAN DER ZWET 1997. Enhanced biological control in apple orchards using ground covers and selective insecticides: an international study. *Zahradnictví - Horticultural Sciences* 24: 35-37.
- CRUZ DE BOELPAEPE, M.O., N.M. FILIPE & V.C. AFONSO 1987. Dynamique des populations aphidiennes en verger de pommiers. Leurs fluctuations saisonnières dans la province de Beira-Baixa (Portugal) en fonction des facteurs de l'environnement. *La Défense des Végétaux* 246: 5-16.
- DE BERARDINIS, E., P. BARONIO & J. BAUMGÄRTNER 1994. The effect of aphid (*Dysaphis plantaginea* Pass., Hom., Aphididae) feeding on apple fruit growth. *Ecological Modelling* 72: 115-127.
- DEDIEU, J.-L. 1998. Les pucerons cendrés en 1998 : année atypique ou nouvelle situation. *La Lettre du Cercle Arbo* 11: 1.
- DELORME, R., D. AUGE, P. TOUTON, C. VERGNET & F. VILLATTE 1998. La résistance des pucerons aux insecticides. Enquête 1997. Pp. 375-384 in 1^{er} Colloque transnational sur les luttes biologiques, intégrée et raisonnée. Bilan et perspectives au regard d'expériences régionales et européennes. Lille. 576 pp.
- DIAZ, S. & M. CABIDO 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *TRENDS in Ecology & Evolution*, 16: 646-655.
- DIXON, A.F.G. 1998. *Aphid ecology. An optimization approach*. London: Chapman & Hall. 300 pp.
- DIXON, A.F.G. 2000. *Insect predator-prey dynamics. Ladybird beetles & biological control*. Cambridge: Cambridge University Press. 257 pp.
- DIXON, A.F.G. & J.-L. HEMPTINNE 2003. Ladybirds and the biological control of aphid populations. Pp. 1-10 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.
- DOUMBIA, M., J.-L. HEMPTINNE & A.F.G. DIXON 1998. Assessment of patch quality by ladybird: role of larval tracks. *Oecologia* 113: 197-202.
- ELTON, C.S. 1958. *The ecology of invasions by Animals and Plants*. London: Methuen.
- GENDRIER, J.P., Y. MONNET, C. MAILLET & H. AUDEMARD 1989. Les arthropodes ravageurs : situation et lutte. *L'Arboriculture fruitière* 420: 33-40.
- GRAF, B., H. HOEHN & H.U. HOEPLI 1999. Optimizing

- the control of rosy apple aphid *Dysaphis plantaginea* (Pass.) (homoptera: Aphididae). in F. POLESNY & B. GRAF (Eds). *IOBC workshop on Arthropod Pest Problems in Pome fruits. Bulletin IOBC/WPRS* 22(5): 71-76
- GRASSWITZ, T. & E.C. BURTS 1995. Effect of native natural enemies and augmentative releases of *Chrysoperla rufilabris* Burmeister and *Aphidoletes aphidimyza* (Rondani) on the population dynamics of the green apple aphid, *Aphis pomi* DeGeer. *International Journal of Pest Management* 41: 176-183.
- HAGLEY, E.A.C. 1989. Release of *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae) for control of the green apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae). *The Canadian Entomologist* 121: 309-314.
- HAIRSTON, N.G., J.D. ALLEN, D. COLWELL, D.J. FUTUYMA, J. HOWELL, M.D. JUBIN, J. MATHIAS & J.H. VANDERMEER 1968. The relationship between species diversity and stability: An experimental approach with protozoa and bacteria. *Ecology* 49: 1091-1101.
- HEMPINNE, J-L., A.F.G. DIXON & J. COFFIN 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* 90: 238-245.
- HEMPINNE, J-L., A. MAGRO, A. MAUREAU, M. HULLÉ & A.F.G. DIXON *in press*. Development of a forecasting system for the integrated pest management of *Dysaphis plantaginea*. *Proceeding of the symposium Aphids in the New millennium*. Rennes: INRA Editions.
- HINDMARCH, C., & M. PIENKOWSKI 2000. *Land management: the hidden costs*. The British Ecological Society, Ecological Issues Series. Oxford: Blackwell Publishing. 60 pp.
- HODEK, I. 1973. *Biology of coccinellidae*. The Hague: Dr. W. Junk Editor and Praha: Academia. 260 pp.
- HODEK, I. & A. HONÉK 1996. *Ecology of Coccinellidae*. Dordrecht: Kluwer Academic Publishers. 464 pp.
- HOEHN, H., H.U. HOEPLI & B. GRAF 1996. Mehliges Apfelblattlaus: Befallsentwicklung und Bekämpfung. *Schweizerisch Zeitschrift Obst- und Weinbau* 132: 60-62.
- KEHRLI, P. & E. WYSS 2001. Effects of augmentative releases of the coccinellid, *Adalia bipunctata*, and of insecticide treatments in autumn on the spring population of aphids of the genus *Dysaphis* in apple orchards. *Entomologia Experimentalis et Applicata* 99: 245-252.
- KIENZLE, J., C.P.W. ZEBITZ & S. BRASS 1997. Floral and faunal species diversity and abundance of aphid predators in ecological apple orchards. *Biological Agriculture and Horticulture* 15: 233-240.
- KINDLMANN, P. & A.F.G. DIXON 1993. Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. *European Journal of Entomology* 90: 443-450.
- KORICHEVA, J., C.P.H. MULDER, B. SCHMID, J. JOSHI & K. HUSS-DANELL 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grassland. *Oecologia* 125: 271-282.
- KREBS, C.J. 1994. *Ecology. The experimental analysis of distribution and abundance* (4th edition). Menlo Park: HarperCollins College Publishers. 801 pp.
- LANDIS, D.A., S.D. WRATTEN & G.M. GURR 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45: 175-201.
- MÄDER, P., A. FLIEBBACH, D. DUBOIS, L. GUNST, F. PADRUOT & U. NIGGLI 2002. Soil fertility and biodiversity in organic farming. *Science* 296: 1694-1697.
- MAY, R.M. 1973. *Stability and complexity in model ecosystems*. Princeton: Princeton University Press. 265 pp.
- OBRYCKI, J.J. & T.J. KRING 1998. Predaceous coccinellidae in biological control. *Annual Review of Entomology* 43: 295-321.
- PASQUALINI, E. & G. BRIOLINI 1982. Stratégies de lutte contre les pucerons du pommier. Pp. 251-252 in *Les Pucerons des cultures. Journée d'Etudes et d'Information*. ACTA: Le Carroussel.
- PIMM, S.L. 1984. The complexity and stability of ecosystems. *Nature* 307: 321-326.
- ROOT, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43: 95-124.
- RUSSEL, E.P. 1989. Enemies hypothesis: A review of the effect of vegetational diversity on predatory insect and parasitoids. *Environmental Entomology* 18: 590-599.
- SAVINI, J.R. 2000. Problématique puceron cendré. *Réussir Fruits & Légumes* 182: 52-54.
- SOLOMON, M., J. FITZGERALD & R. JOLLY 1999. Artificial refuges and flowering plants to enhance predator populations in orchards. *IOBC/WPRS Bulletin* 22: 31-38.
- TOURNEUR, J.C., D. BOUCHARD & J.-G. PILON 1992. Le complexe des ennemis naturels des pucerons en pommeraie au Québec. Pp. 179-193 in C. VINCENT & D. CODERRE (Eds). *La lutte biologique*. Québec: G. Morin éditeur. 671 pp.

- VAN DRIESCHE, R.G., & T.S. BELLOWS JR. 1996. *Biological control*. New York: Chapman & Hall. 539 pp.
- VAN EMDEN, H.F. 1990. Plant diversity and natural enemy efficiency in agroecosystems. Pp 63-80 in M. MACKAUER, L.E. EHLER & J. ROLAND (Eds). *Critical issues in Biological Control*. Andover: Intercept. 330 pp.
- VOGT, H. & A. WEIGEL 1999. Is it possible to enhance biological control of aphids in an apple orchard with flowering strips? *IOBC/WPRS Bulletin* 22: 39-46.
- WHALON, M.E., & B.A. CROFT 1984. Apple IPM implementation in North America. *Annual Review of Entomology* 29: 435-470.
- WÜRTH, M., H. BENTZ, J. GUIOT, F. WEIBEL & M. LITTERST 1999. *Abschlussbericht zum ITADA-Projekt A3.3: Obstbau*. Institut Transfrontalier d'Application et de Développement Agronomique. 42 pp.
- WÜRTH, M., J. GUIOT, H. BENTZ, R. KEIM & F. WEIBEL 2002. *Abschlussbericht des Arbeitsprogramm ITADA II^{bis} Projekt 2-1-4: Prüfung krankheitsresistenter neuer Apfelsorten für Tafel- und Industrieobst mit dem Ziel der Reduzierung des Einsatzes von Pflanzenbehandlungsmitteln*. Institut Transfrontalier d'Application et de Développement Agronomique. 23 pp.
- WYSS, E. 1995. The effects of weed strips on aphids and aphidophagous predators in an apple orchard. *Entomologia Experimentalis et Applicata* 75: 43-49.
- WYSS, E., U. NIGGLI & W. NENTWIG 1995. The impact of spiders on aphid populations in a strip-managed apple orchard. *Journal of Applied Entomology* 119: 473-478.
- WYSS, E., M. VILLIGER J.-L. HEMPTINNE & H. MÜLLER-SCHÄRER 1999a. Effects of augmentative releases of eggs and larvae of the ladybird beetle, *Adalia bipunctata*, on the abundance of the rosy apple aphid, *Dysaphis plantaginea*, in organic apple orchards. *Entomologia Experimentalis et Applicata* 90: 167-173.
- WYSS, E., M. VILLIGER & H. MÜLLER-SCHÄRER 1999b. The potential of three native insect predators to control the rosy apple aphid, *Dysaphis plantaginea*. *BioControl* 44: 171-182.

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FITNESS OF FIVE PHENOTYPES OF *Harmonia axyridis* PALLAS
(COLEOPTERA: COCCINELLIDAE).

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SERPA, L., H. SCHANDERL, C. BRITO & A.O. SOARES 2003. Fitness of five phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Pp. 43-49 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

H. axyridis is a highly polymorphic ladybird beetle with phenotypes that vary in their elytral patterns. In natural populations the relative frequency of phenotypes is not constant, but is subject to a strong geographic and temporal variation. The selective forces that are the basis for those variation are diverse and difficult to determine. In this work we suggest that fitness of phenotypes could contribute to these variations. That is, a specific genotype could also confer a specific reproductive capacity. We compare the reproductive capacity of adults of five phenotypes [*succinea* (h) or s0, *succinea*-3 (h³) or s9, *conspicua* -1 (h^{C1}) or c1, *aulica*-1 (h^{A1}) or au and *nigra* [?(h[?])] or ni]. Our results show that under the same biotic and abiotic conditions, there are differences in biological parameters of the phenotypes that affect their fitness. The rare phenotype *nigra*, and the relatively uncommon *aulica* have lower reproductive capacity than the most frequent phenotypes *succinea* and *conspicua*.

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INTRODUCTION

Fitness is defined as a measure of the reproductive success of a genotype relative to another in the same environment. It measures the capacity of a genotype to transmit its genes to the next generation (BEGON et al. 1990). The direct evaluation of fitness has rarely been performed (HOFFMAN 1994). Generally, researchers measure fitness indirectly by using biological parameters such as viability (survival, fecundity and fertility). If genotypes differ in their viability then the relative frequency of genotypes will differ in the next generation. For this reason, one simple measure of fitness is considered to be the number of offspring produced by a specific genotype relative to another (FUTUYMA 1998).

Various natural populations of insects are made up of individuals of different phenotypes, more or less similar, whose relative frequency

remains fairly constant. The relative frequency of phenotypes is genetically determined as the result of mating between individuals of the same populations. The phenotypes will persist as long as different genotypes are favorably selected in different parts of the ecosystem or at different times (BUSKIRK et al. 1997; RICKLEFS 1990). This phenomenon is called genetic polymorphism (MAJERUS 1994; FUTUYMA 1998). The genetic polymorphism determines the existence of geographical races, subspecies, seasonal variation in the relative frequency of phenotypes, and the occurrence of rare phenotypes, which otherwise would be eliminated from populations (MAJERUS 1994).

Harmonia axyridis Pallas, like other ladybird beetle species, shows a highly polymorphic elytral pattern. Some of its phenotypes were previously considered different species and/or different genera (KOMAI 1956). The phenotypes

are classified in two main groups; (i) the *succinea* group, or light forms, characterized by the presence of elytras with color varying between shiny red and brown, and by the presence of a variable number of spots between 0 and 19, and (ii) the dark or melanic group, characterized by the presence of red spots on a dark background. The melanic group includes the phenotypes *conspicua*, *spectabilis* and *aulica* (TAN 1946, 1949; KOMAI 1956).

Different populations of *H. axyridis* show considerable geographic variation in the relative frequency of phenotypes (so called micro-geographic variation). In China and Manchuria, the phenotypes *succinea*, *conspicua* and *spectabilis* are very frequent (TAN 1946, 1949; KOMAI 1956). In Japan, *conspicua* and *spectabilis* phenotypes are the most frequent while in Korea the *succinea* phenotype predominates (DOBZHANSKY 1933; KOMAI 1956; OSAWA & NISHIDA 1992). On the other hand the phenotype *aulica* is at low frequency or is even absent in certain regions (DOBZHANSKY 1933). Very rare phenotypes such as *corvine* may also occur in natural populations (MADER 1932 in TAN 1946).

Some attempts have been made to relate elytral phenotypes in *H. axyridis* with geographical and seasonal factors (KRYLTSOV 1956; ABBAS & NAKAMURA 1985; ABBAS et al. 1988; OSAWA & NISHIDA 1992; HODEK & HONĚK 1996). However, the precise selective forces associated with the phenomenon are still very difficult to determine (MUGGLETON 1978). Macro-geographical variation of Asian populations of *H. axyridis* is apparently related to climatic factors, whereas micro-geographical variation, that is, differences in the relative frequency of elytral phenotypes between host plants in the same habitat, appear mostly related to food availability (KOMAI & HOSINO 1951; KOMAI 1956). Seasonal variation in the proportion of dark and light forms in Japanese populations has also been observed (TAN 1949; OSAWA & NISHIDA 1992). OSAWA & NISHIDA (1992) demonstrated a significant increase in the relative frequency of light phenotypes during spring and early summer. This result, supported by laboratory experiments, suggest the occurrence of assortative mating between different phenotypes. KOMAI (1956) reported long-term

changes in the relative frequency of elytral phenotypes in a population at Suwa, Japan. This author suggested that these change was due to natural selection, probably in relation to the milder winters in Suwa in more recent years.

Those observations suggest that polymorphism in *H. axyridis* can be adaptive and that the relative frequency of phenotypes in different populations could be related to their differing fitnesses in different environments. Recently, we showed that the *nigra* and *aulica* phenotypes of *H. axyridis* differ in their fitness (SOARES et al. 2001). Nevertheless remained to be tested the possibility that the most common phenotypes have highest fitnesses. We hypothesized that (i) a particular genotype that confers specific coloration pattern could also confer other specific attributes, as stated by LAMANA & MILLER (1995) and (ii) the most abundant phenotypes in Asian populations should show a higher fitness than the less abundant and rare phenotypes. We therefore predicted that the rare phenotype *nigra* [h^2], should show a lower performance than the less frequent, *aulica*-1 (h^{A1}), or the most abundant *succinea* (h), *succinea*-3 (h^3) and *conspicua*-1 (h^{C1}).

MATERIAL AND METHODS

Biological material

The phenotypes of *H. axyridis* individuals came from mass rearing at 25 ± 1 °C, 75 ± 5 % RH and photoperiod of 16L:8D. Coccinellids were fed on a diet of *Aphis fabae* Scopoli and eggs of *Ephestia kuehniella* Zeller. Field collected individuals of *H. axyridis* were added regularly to minimize inbreeding.

We used two phenotypes classified in the *succinea* group, *succinea* (h) or s0 and *succinea*-3 (h^3) or s9 and three classified in the melanic group, *conspicua*-1 (h^{C1}) or c1, *aulica*-1 (h^{A1}) or au and *nigra* [h^2] or ni. These forms occurred naturally in our mass rearing.

Biology of adults: longevity, body-weight and reproductive parameters

In order to evaluate the biology of adults of different phenotypes we sexed and paired 200 individuals of five phenotypes, thereby creating

20 couples for each phenotype. Each couple was isolated in a 60 ml Petri dish Mino-Gaillard (Ø: 5 cm, height: 3 cm). A daily surplus of apterous *A. fabae* females was provided. Egg clusters were removed from Petri dishes every day. All individuals were monitored until they death. The experiment was performed at 25 ± 1 °C, 75 ± 5 % RH and a photoperiod of 16L:8D, under fluorescent lamps (Sanyo FL 40 SS W/37). Different biological features were evaluated: longevity, percentage of fertile couples, number of egg clusters, number of days of oviposition, total and daily fecundity, daily fertility (including sibling cannibalism), percentage of hatching, sterile and embrionate eggs (3 days after the last hatched eggs), sex ratio and body-weight. Body-weight was determined for the parental generation (P), in the first day after emergence and in the first day of sexual maturation, and also for a pool including both parental and progeny of the same elytra, in the first day after emergence. Adults were weighed to an accuracy of 10^{-4} mg on a Mettler AM 50 analytical balance. Longevity, fecundity, fertility (including sibling cannibalism) and percentage of hatching were compared. Proportions were arcsin $\sqrt{\%}$ transformed (ZAR 1984). One-factor ANOVA was used to compare longevity, fecundity, fertility (including sibling cannibalism), percentage of hatching and body weight. All statistical tests were done using JMP (SALL et al. 2001). The χ^2 test was used to compare the sex ratio in each phenotype.

Raw multivariate data were arranged in a square matrix, assigning individuals to rows and biological features (variables) to columns, and standardised (ROHLF 1994; FIELD et al. 1982). Individuals were compared using euclidean distances arranged in a symmetrical matrix of association (ROHLF 1994; LEGENDRE & LEGENDRE 1984; CLIFFORD et al. 1975), followed by a cluster analysis, using Unweighted Pair-Group Arithmetic Average (UPGMA). Principal component analysis (PCA) was used, in order to reduce the dimensionality of the data, to a few artificial variables (principal components), linearly uncorrelated and arranged in order of importance, in terms of the variance accounted for. The final plot of both phenotypes and biological parameters permitted us to visualize

the contribution of the latter to the statistical separation of phenotypes based on their biological characteristics.

RESULTS

Biological attributes of the elytral phenotypes, including longevity and reproductive capacity of adults, are summarized in Table 1. The longevity of *nigra* females and males was significantly less than the other phenotypes. Longevity did not differ between *aulica* and *succinea* (s0 e s9) males, which lived longer on average than *conspicua* males. No significant differences were found among longevities of *conspicua*, *succinea* (s0) and *aulica* females. The lowest percentage of fertile couples was observed in the *nigra* phenotype. The *nigra* and *succinea* (s9) couples showed a significant lower fecundity than the other phenotypes (Table 1). The *nigra* couples showed the lowest value for daily fertility (including sibling cannibalism). That is, females of this phenotype produced fewest larvae per day, followed by females of *aulica* phenotypes. No significant differences in daily fertility were observed between *succinea* s0 and *succinea* s9. The highest fertility values were observed in *conspicua* couples (Table 1). *Nigra* and *aulica* females showed the lowest hatching percentage of eggs. The highest hatching percentage was observed in *conspicua* couples. *Aulica*, *nigra* and *succinea* s9 showed no significant differences in terms of percentage of embrionate eggs, nor were there differences between *conspicua* and *succinea* s0. We observed the highest percentage of sterile eggs for the *nigra* couples, followed by the *aulica* and *succinea* s9 couples. No significant differences were observed between *succinea* s0 and *conspicua* (Table 1). The proportion of females obtained from *conspicua* ($\chi^2=0.093$, df=1, p=0.76) and *aulica* ($\chi^2=39.68$, df=1, p<0.0001) couples was significantly higher a 50:50 sex ratio. However, no significantly differences from a 50:50 sex ratio were obtained in *nigra* ($\chi^2=0.093$, df=1, p=0.76), *succinea* (s0) ($\chi^2=0.477$, df=1, p<0.489) and *succinea* s9 ($\chi^2=0.253$, df=1, p<0.614) (Table 1).

Table 1
 Comparisons of longevity, body-weight and reproductive attributes of five phenotypes of *H. axyridis* [conspicua (c1), aulica (au), nigra (ni) and succinea (s9 and s0)]. Means and standard errors followed by different letters indicate post-hoc significantly differences. Last column indicate F values, degrees of freedom and p value of ANOVA.

Biological parameters	Phenotypes					F values, df, P
	<i>conspicua</i> (c1)	<i>aulica</i> (au)	<i>nigra</i> (ni)	<i>succinea</i> (s9)	<i>succinea</i> (s0)	
Longevity (days)						
Males (LM)	66.6±6.3c	76.3±5.4b	43.6±3.4a	75.3±7.4b	79.7±6.8b	F=5.89, df=4, 94, P=0.0003
Females (LF)	62.2±6.5b	60.3±4.2b	30.7±3.1a	52.2±5.5c	64.8±4.5b	F=8.04, df=4, 94, P<0.0001
Percentage of fertile couples (FrC)	95.0	85.0	55.0	85.0	90.0	
Number of batches (Bt)	33.5±4.1b	31.1±2.7b	11.4±1.4a	24.0±2.4c	34.9±3.4b	F=10.8, df=4, 94, P<0.0001
Number of day of oviposition (Ov)	26.8±3.1b	25.4±2.0b	10.7±1.3a	18.7±1.8c	27.7±2.6b	F=10.3, df=4, 94, P<0.0001
Total fecundity (TFc)	885.3±96.6b	808.3±85.1b	311.8±47.7a	579.5±72.9c	815.8±90.8b	F=8.58, df=4, 94, P<0.0001
Daily fecundity (DFc)	34.4±2.0a	31.1±1.8a	27.3±2.1a	31.0±2.3a	28.0±1.8a	F=2.06, df=4, 94, P=0.0925
Daily fertility (DFr)	12.8±2.1d	4.0±1.0b	0.56±0.3a	7.1±2.0c	8.1±1.3c	F=9.35, df=4, 94, P<0.0001
Percentage of hatching (Ha)	47.2±2.7c	22.8±2.7b	2.3±0.5a	26.3±2.9b	39.4±2.7c	F=72.7, df=4, 74, P<0.0001
Percentage of embryonates (Em)	7.6±0.7b	5.8±0.7a	5.6±0.7a	5.6±0.9a	7.4±0.7b	F=6.02, df=4, 74, P<0.0001
Percentage of sterile (St)	45.1±2.9a	71.2±3.4b	94.1±0.9c	68.2±3.3b	53.2±9.9a	F=39.9, df=4, 74, P<0.0001
Sex ratio (females/males) (Sr)	1.11	1.62	1.09	0.96	1.03	
Body-weight after emergence (mg)						
Males (W1M)	25.8±0.7a	27.4±0.6a	26.2±0.6a	25.2±0.6a	26.3±0.3a	F=2.07, df=4, 99, P=0.091
Females (W1F)	32.1±1.2a	32.3±0.6a	31.3±0.6a	34.5±0.7a	32.2±0.4a	F=2.77, df=4, 99, P=0.310
Body-weight in the first day of sexual maturation						
Males (W2M)	31.7±0.8a	33.7±0.7a	31.8±0.6a	31.3±0.8a	32.3±0.3a	F=1.97, df=4, 99, P=0.105
Females (W2F)	44.3±1.6a	44.2±1.4a	44.6±0.9a	43.5±1.1a	43.9±0.6a	F=0.21, df=4, 99, P=0.935
Body-weight after emergence (P+F)						
Males (W3M)	26.2±0.4a	33.2±0.4b	25.8±0.4a	26.9±0.3a	26.6±0.3a	F=62.65, df=4, 458, P<0.0001
Females (W3F)	32.8±0.5a	38.2±0.5b	31.5±0.6a	32.3±0.4a	33.7±0.4a	F=31.11, df=4, 468, P<0.0001

Among the three estimates of body weight, significant differences are evident between males and females. Only the pooled estimate, included weights of both parents and progeny of the same elytral genotype, showed a significant difference among phenotypes: both females and males were heavier for *aulica* than for other phenotypes.

The UPGMA dendrogram using of euclidean distances, based on standardized biological data, cluster C1, S0 and S9, apart from both *aulica* and *nigra* phenotypes (Fig. 1).

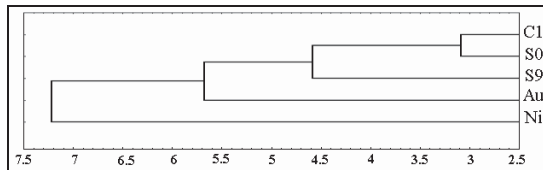


Fig. 1. UPGMA cluster of elytral phenotypes, based on euclidean distances using standardized biological parameters. Symbols are those presented in the text (Material and methods).

This grouping is also supported by the results of principal component analysis (PCA) that reduced the multidimensional data set to two principal axes, which explained 81.7% of the variance. The main contributions for the first axis

correspond to parameters related to longevity, fecundity and fertility, which could be associated to a general fitness dimension. On the other hand, the main contributions to axis 2 correspond to sex ratio of the offspring and body weight, with special importance of both sexes for W3, and males W1 and W2. While the first axis clearly separates the phenotype *nigra* from the other phenotypes, axis 2, discriminates phenotype *aulica*, and to lesser extent, phenotype s9, from the core group made by c1 and s0 (Fig. 2).

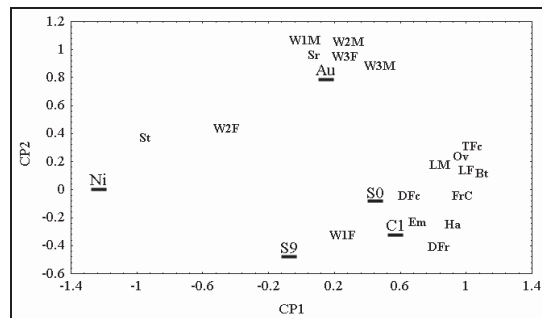


Fig. 2. PCA ordination was based on biological data of *H. axyridis*. PC1 and PC2 refer to the first principal components that explain, respectively, 52.5 % and 29.2 % of the variance. Elytral morphotypes are underlined. Symbols correspond with those in Table 1.

DISCUSSION

Stability of genetic polymorphism in a population is a consequence of the balance of diverse selective forces (SHEPPARD 1975). Most of the published studies focus on one selective factor thought to be responsible for the success of a particular phenotype relative to another. Direct or indirect fitness evaluation of phenotypes, under diverse ambient conditions, has rarely been done.

Biological control programs generally focus on the selection of the best parasitoid or predator species to be introduced based on criteria related to their capacity to have substantial impact on a pest population (WAAGE & MILLS 1992). However, selection of the most fit phenotypes of a selected species is rarely attempted (SOARES et al. 2001). Selection of the best phenotype will depend on the biological control strategy used. Certain biological parameters, such as reproductive capacity, will favor population establishment and predator-prey stabilization and may be most desirable in classical biological control programs, whereas short-term efficacy may be favored in inundative biological control programs. Our study showed that, under our experimental conditions, phenotypes of *H. axyridis* apparently differed in fitness. The most abundant phenotypes in nature, *succinea* and *conspicua*, were also the phenotypes with higher longevity, fertility, fecundity and percentage of hatching, in a clear contrast with the rare/less abundant phenotypes of *nigra* and *aulica*, which confirm our hypotheses that is the most abundant phenotypes in Asian populations should show a higher fitness than the less abundant and rare phenotypes. Our results suggest, also, that *conspicua* and *succinea* (s0 and s9) individuals should be used in classical biological control programs because they have a greater longevity and higher reproductive capacity. These characteristics favor population adaptation and stabilization.

Temperature determines longevity in ectothermic species. In coccinellids longevity generally decreases with the increase of temperature. This effect was reported for *C. novemnotata* Herbst (MCMULLEN 1967), *Coleomegilla maculata lengi* (WRIGHT & LAING

1978) and *Olla v-nigrum* (Mulsant) (KREITER & IPERTI 1984). Despite the fact that experimental temperature was fixed at 25 °C, *nigra* phenotype was found to have a relatively short adult lifespan. This could be a disadvantage in biological control programs, from a practical point of view, since the decrease in time spent in foraging activity and ovipositing may reduce its fitness.

For polymorphic species, such as *H. axyridis*, the degree of melanization can also be an important factor affecting longevity. Melanic forms can reach a higher body temperature than non-melanic forms (DE JONG et al. 1996), and consequently they can reach higher metabolic rate and biological activity (DIGBY 1955; LUSIS 1961; DIXON 1972; BENHAM et al. 1974; MUGGLETON et al. 1975; WILLMER & UNWIN 1981; BRAKEFIELD & WILLMER 1985; STEWART & DIXON 1989; DE JONG et al. 1996). Our experiment was performed using low radiation fluorescent lamps. We therefore doubt that melanism decreased longevity of *nigra* through elevated body temperature. Instead, we suggest that longevity may be directly determined genetically, and the short lifespan of *nigra* may be adaptive when the environment is characterized by low temperature.

Indeed macro-geographic variation in Asiatic populations of *H. axyridis* is associated with climatic factors, such as temperature, as the result of physiological adaptations. In cold regions the dark phenotypes are, generally, more frequent than the light forms (KOMAI 1956).

Every species of coccinellid has genetically fixed rates of fecundity and egg sizes that are also affected by food availability and environmental conditions. If food supply is limited, coccinellids decrease their fecundity but will maintain egg size (HODEK & HONĚK 1996). More voracious and heavier coccinellid females have more resources to invest in egg production (FERRAN et al. 1984; HODEK 1993; STEWART et al. 1991a, b; SOARES et al. 2001). Observed differences in body weight of *aulica* adults versus adults of other phenotypes may reflect the particular dietary condition of our experiment. It remains to be investigated whether the same differences will occur in mass rearing programs. Nevertheless, given (1) the absence of significant differences in

female body weight among the parental generations of the different phenotypes and (2) the significant differences between fecundity and fertility, among the various phenotypes, our results suggest that reproductive capacity of phenotypes could be correlated with environmental conditions and prey quality. Thus additional experiments using other temperatures and prey should be performed.

REFERENCES

- ABBAS, I. & K. NAKAMURA 1985. Variation of elytral spot patterns in a field population of lady beetle *Epilachna aff. sparsa* (Coleoptera, Coccinellidae) feeding on bitter cucumber in Sumatra. *Scientific Report Kanazawa University* 30: 27-32.
- ABBAS, I., K. NAKAMURA, H. KATAKURA & H. SASAJI 1988. Geographical variation of elytral spot patterns in the ladybird *Epilachna vigintiduopunctata* (Coleoptera, Coccinellidae) in the province of Sumatra Barat, Indonesia. *Research of Population Ecology* 30: 43-56.
- BEGON, M., J.L. HARPER & C.R. TOWNSEND 1990. *Ecology: Individuals, population and communities* (2nd ed.). Blackwell Scientific Publications, London. 945 pp.
- BENHAM, B.R., D. LONSDALE & J. MUGGLETON 1974. Is polymorphism in two-spot ladybird an example of non-industrial melanism? *Nature London* 249: 179-180.
- BRAKEFIELD, P.M. & P.G. WILLMER 1985. The basis of thermal-melanism in the ladybird *Adalia bipunctata*: differences in reflectance and thermal properties between the morphs. *Heredity* 54: 9-14.
- BUSKIRK, J.V., S.A. MCCOLLUM & E.E. WERNER 1997. Natural selection for environmentally induced phenotypes in tadpoles. *Evolution* 51: 1983-1992.
- CLIFFORD, H.T. & W. STEPHENSON 1975. *An Introduction to Numerical Classification*. Academic Press. New Press. 229 pp.
- DE JONG, P.W., S.W.S. GUSSEKLOO & P.M. BRAKEFIELD 1996. Differences in thermal balance, body temperature and activity between non-melanic and melanic two-spot ladybird beetles (*Adalia bipunctata*) under controlled conditions. *Journal Experimental Biologie* 199: 2655-2666.
- DIGBY, P.S.B. 1955. Factors affecting the temperature excess of insects in sunshine. *Journal Experimental Biologie* 32: 279-298.
- DIXON, A.F.G. 1972. Control and significance of the seasonal development of colour forms in the sycamore aphid, *Drepanosiphum platanoides* (Schr.). *Journal of Animal Ecology* 41: 689-697.
- DOBZHANSKY, TH.G. 1933. Geographical variations in lady-beetles. *American Naturalist* 709: 97-126.
- FERRAN, A., M.O. CRUZ DE BOELPAEPE, H. SCHANDERL & M.-M. LARROQUE 1984. Les aptitudes trophiques et reproductrices des femelles de *Semiadalia undecimnotata* (Col.: Coccinellidae). *Entomophaga* 29: 157-170.
- FIELD, J.C., K.R. CLARKE & R.M. WARWICK 1982. A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology-Progress Series* 8: 37-52.
- FUTUYMA, D.J. 1998. *Evolutionary Biology* (3rd ed.). Sinauer Associates, Inc., Massachusetts. 763 pp.
- HODEK, I. & A. HONĚK 1996. *Ecology of Coccinellidae*. Kluwer Academic Publishers, Netherlands. 260 pp.
- HOFFMAN, A.A. 1994. Genetic analysis of territoriality of *Drosophila melanogaster*. Pp. 188-205 in: C. BOAKE (Ed) *Quantitative genetic studies of behavioral evolution*. Chicago University Press, Chicago. 390 pp.
- HODEK, I. 1993. Habitat and food specificity in aphidophagous predators. *Biocontrol Science and Technology* 3: 91-100.
- KOMAI, T. 1956. Genetics of ladybeetles. *Advances in Genetics* 8: 155-189.
- KOMAI, T. & Y. HOSINO 1951. Contributions to the Evolutionary Genetics of the Lady-beetle, *Harmonia*. II. Microgeographic Variations. *Genetics* 36: 382-390.
- KREITER S. & G. IPERTI 1984. Étude des potentialités biologiques et écologiques d'un prédateur aphidiphage *Olla-v-nigrum* Muls. (Coleoptera; Coccinellidae) en vue de son introduction en France. *109^e Congrès National des Sociétés. Savantes, fasc. II: 275-282.*
- KRYLTSOV, A.I. 1956. Geographical variability of ladybirds (Coleoptera, Coccinellidae) in north Kirghisia. *Entomological Obozr* 35: 771-781.
- LAMANA, M.L. & J.F. MILLER 1995. Temperature-dependent development in polymorphic lady beetle, *Calvia quatuordecimguttata* (Coleoptera, Coccinellidae). *Annals of the Entomological Society of America* 88: 785-790.
- LEGENDRE, L. & P. LEGENDRE 1984. *Écologie numérique 2: La structure des données écologiques* (2nd ed.). Masson Presse Université du Québec. 254 pp.
- LUSIS, J.J. 1961. On the biological meaning of colour polymorphism of ladybeetle *Adalia bipunctata* L. *Latvijas Entomologs* 4: 3-29.
- MAJERUS, M.E.N. 1994. *Ladybirds*. The New Naturalist Library, Harper Collins, London. 367 pp.
- MCMULLEN, R.D. 1967. The effects of photoperiod, temperature, and food supply on rate of development and diapause in *Coccinella*

- novemnotata*. *The Canadian Entomologist* 99: 578-586.
- MUGGLETON, J. 1978. Selection against the melanic morphs of *Adalia bipunctata* L. (two-spot ladybird): a review and some new data. *Heredity* 40: 269-280.
- MUGGLETON, J., D. Lonsdale & B.R. Benham 1975. Melanism in *Adalia bipunctata* L. (Col., Coccinellidae) and its relationship to atmospheric pollution. *Journal Applied Ecology* 12: 451-464.
- OSAWA N. & T. NISHIDA 1992. Seasonal variation in elytral colour polymorphism in *Harmonia axyridis* (the ladybird beetle): the role of non-random mating. *Heredity* 69: 297-307.
- RICKLEFS, R.E. 1990. *Ecology*. (3rd ed.). W.H. Freeman and Company, New York. 896 pp.
- ROHLF, F.J. 1994. NTSYS-pc *Numerical Taxonomy System & Multivariate Analysis System Exeter Software*. New York.
- SALL, J., A. LEHMAN & L. CREIGHTON 2001. JMP start statistics: a guide to statistical and data analysis using JMP® and JMP IN software. Duxbury Press, Toronto. 656 pp.
- SHEPPARD, P.M. 1975. *Natural Selection and Heredity* (5th ed.). Hutchinson, London. 239 pp.
- SOARES, A.O., D. CODERRE & H. SCHANDERL 2001. Fitness of two phenotypes of *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology* 98: 287-293.
- SPSS Production Facility 2001. SPSS, version 11th ed. LEAD Technologies Inc., Chicago, IL.
- STEWART, L.A. & A.F.G. DIXON 1989. Why big species of ladybird beetles are not melanics. *Functional Ecology* 3: 165-177.
- STEWART, L.A., A.F.G. Dixon, Z. Růžička & I. Iperfi 1991a. Clutch and egg size in ladybird beetles. *Entomophaga* 36: 329-333.
- STEWART, L.A., J.-L. HEMPTINNE & A.F.G. DIXON 1991b. Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Functional Ecology* 5: 380-385.
- TAN, C.C. 1946. Mosaic Dominance in the inheritance of colour patterns in the Lady-birds Beetle, *Harmonia axyridis*. *Genetics* 31:195-210.
- TAN, C.C. 1949. Seasonal variations of color patterns in *Harmonia axyridis*. *Proceedings of the 8th International Congress of Genetics*: 669-670.
- WAAGE, J.K. & N.J. MILLS 1992. Biological control. Pp. 421-430 in M.J. CRAWLEY (Ed) *Natural enemies*. Blackwell Scientific Publications, Oxford. 592 pp.
- WILLMER, P.G. & D.M. UNWIN 1981. Field analysis of insect heat budget: reflectance, size and heating rates. *Oecologia* 50: 250-255.
- WRIGHT, E.J. & J.E. Laing 1978. The effects of temperature on development, adult longevity and fecundity of *Coleomegilla maculata lengi* and its parasite *Perilitus coccinellae*. *Proceedings of Entomological Society of Ontario* 109: 33-48.
- ZAR, J.H. 1984. *Biostatistical analysis* (2nd ed.). Prentice-Hall, New Jersey. 718 pp.

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INFLUENCE OF PREY QUALITY ON THE REPRODUCTIVE CAPACITY OF TWO PHENOTYPES OF *Harmonia axyridis* PALLAS (COLEOPTERA: COCCINELLIDAE).

A.O. SOARES, D. CODERRE & H. SCHANDERL

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H. axyridis is a highly polymorphic ladybird beetle with a wide geographical distribution in the palearctic region. Genetic polymorphism seems to be the strategy adopted in order to face different habitats at different times. In this paper we suggest that a genotype that confers a specific elytral pattern may also confer a particular reproductive capacity when fed on single diets of essential preys such as *A. fabae* or *M. persicae*. We discuss KOMAI & HOSINO (1951) hypothesis, which predicts that the differences in the relative frequency of elytral pattern phenotypes in relation to the host plants in a same habitat could be related with specific composition of aphid populations. Our results revealed that *A. fabae* significantly increased reproductive capacity of *nigra* phenotype without affecting reproductive capacity of *aulica* phenotype.

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INTRODUCTION

Asian populations of *Harmonia axyridis* Pallas show a highly level of genetically polymorphic, with more than one genotype occurring in a population. To identify precisely selective forces that act to maintain different phenotypes of *H. axyridis* in the same population is a very difficult task. Genetic polymorphism should persist only when different genotypes are selectively favoured in varying parts of the environment or at different times. Thus a single phenotype cannot be equally fit in all environmental conditions. This fact challenges our understanding of adaptation. One of the important issues raised concerns how environmental heterogeneity facilitates the coexistence of more than one genotype within a population (RICKLEFS 1991).

H. axyridis is a euriphagous predator that prefers aphids (HUKUSIMA & KAMEI 1970; HUKUSIMA & OHWAKI 1972; OSAWA 1992; IABLOKOFF-KHNZORIAN 1982; SCHANDERL et al. 1988). It also feeds on psillids (FYE 1981), coccids (MCLURE 1987; HODEK & HONĚK 1996), spider mites (LUCAS et al. 1997) and lepidopteran eggs (SCHANDERL et al. 1988).

A particular phenotype of *H. axyridis* may confer different specific morphological, physiological and behavioural attributes (TAN 1946, 1949; KOMAI 1956; FUTUYMA 1998). If so, then the differences in nutritive demands of phenotypes, or in nutritive value of different prey, could affect relative fitnesses of different phenotypes, when fed different prey. In Japan, KOMAI & HOSINO (1951) reported differences in the relative frequency of elytral pattern phenotypes between host plants in the same

habitat (so called micro-geographic variation). They suggested that such differences could be correlated somehow with differences in the composition of the aphid populations, and the feeding preferences of the phenotypes. However, the hypothesis was not addressed further until this study.

We have shown recently that the *nigra* and *aulica* phenotypes of *H. axyridis* differ in their fitness fed on the same prey (SOARES et al. 2001, 2003), but we do not know if the differences would remain consistent on other diets. Despite the well-documented polyphagy in *H. axyridis*, we hypothesise that *aulica* and *nigra* phenotypes will display different reproductive capacity fed on *Aphis fabae* Scopoli or *Myzus persicae* (Sulzer). In this study, we evaluate the reproductive capacity of *aulica* and *nigra* fed diets of either *A. fabae* or *M. persicae*.

MATERIAL & METHODS

Biological material

H. axyridis individuals of the *aulica* and *nigra* phenotypes came from mass cultures reared at $22 \pm 1^\circ\text{C}$, $75 \pm 5\%$ RH and a photoperiod of 16L:8D, using fluorescent lamps (Philips ref.: TDL 23W/54 and TDL 18W/54). Coccinellids were fed a mixed diet of the aphids, *A. fabae* and *M. persicae*, and eggs of *Ephesttia kuehniella* Zeller. Prey were provided on bean plants (*Vicia fabae* L. Major) placed in the rearing cages. Individuals of *M. persicae* and *A. fabae* strongly differed in size. The average weight of a wingless female of *M. persicae* was 0.48 mg and of *A. fabae* 1.09 mg. Field collected ladybirds were added to the mass culture at regular intervals in order to minimize inbreeding. The *aulica* and *nigra* phenotypes occurred naturally in our cultures. The different phenotypes were reared separately.

Measure of reproductive capacity

To evaluate reproductive capacity, we sexed and paired 40 individuals of each phenotype. Each of the twenty pairs was isolated in a 60 ml Petri dish (\varnothing : 5 cm, height: 3 cm). One of two diets was provided to 10 couples of each phenotype. The *A. fabae* and *M. persicae* were supplied daily in excess. Abiotic conditions were $20 \pm 1^\circ\text{C}$, $75 \pm 5\%$ RH and a photoperiod of 16L:8D, using fluorescent lamps (Philips ref.: TDL 23W/54 and TDL 18W/54). Egg clusters were removed from Petri dishes twice daily. Fecundity, fertility and percentage hatch were compared over the first fifteen days of a females' reproductive life. Percentages were arcsin $\sqrt{\%}$ transformed (ZAR 1984). One-factor ANOVA was used to compare fecundity, fertility and percentage hatch of the eggs of the phenotypes fed on the different diets. All statistical tests were done using JMP[®] (SALL et al. 2001).

RESULTS

Comparative reproductive capacity of *aulica* and *nigra* phenotypes fed *A. fabae* or *M. persicae*

Independent of the prey offered, fecundity, fertility and percentage hatch of the eggs of *aulica* females of *H. axyridis* were significantly higher than for *nigra* females (Table 1).

Influence of prey quality on the reproductive capacity of *aulica* and *nigra* phenotypes

There was no significant difference in the fecundity, fertility and percentage hatch of the eggs in the *aulica* phenotype of *H. axyridis* fed either *M. persicae* or *A. fabae* (Table 2). However, the reproductive capacity of *nigra* females was significantly higher than that of *aulica* females when fed on *A. fabae* (Table 2).

Table 1

Fecundity (average number of eggs / female / day \pm s.e.), fertility (average number of embrionate eggs / female / day \pm s.e.) and hatching (percentage of hatching \pm s.e.) of *aulica* and *nigra* phenotypes of *H. axyridis* fed on *A. fabae* and *M. persicae*. Different letters indicate significant differences at $p < 0.05$

	<i>A. fabae</i>			<i>M. persicae</i>		
	<i>aulica</i>	<i>nigra</i>		<i>aulica</i>	<i>nigra</i>	
Fecundity	22.8 \pm 1.6a*	17.2 \pm 1.1b	F=7.88, df=1, 298, P \leq 0.005	20.9 \pm 1.4a	12.6 \pm 0.9b	F=23.57, df=1, 297, P \leq 0.0001
Fertility	20.6 \pm 1.5a	6.2 \pm 0.7b	F=76.75, df=1, 298, P \leq 0.0001	19.3 \pm 1.4a	2.6 \pm 0.6b	F=124.7, df=1, 298, P \leq 0.0001
Percentage of hatching	63.8 \pm 2.7a	25.1 \pm 2.8b	F=100.8, df=1, 229, P \leq 0.0001	63.2 \pm 2.7a	13.7 \pm 2.8b	F=209.4, df=1, 227, P \leq 0.0001

Table 2

Fecundity (average number of eggs / female / day \pm s.e.), fertility (average number of embrionate eggs / female / day \pm s.e.) and hatching (percentage of hatching \pm s.e.) of *aulica* and *nigra* phenotypes of *H. axyridis* fed on *A. fabae* and *M. persicae*. Different letters indicate significant differences at $p < 0.05$

	<i>aulica</i>			<i>nigra</i>		
	<i>A. fabae</i>	<i>M. persicae</i>		<i>A. fabae</i>	<i>M. persicae</i>	
Fecundity	22.8 \pm 1.6a*	20.9 \pm 1.4a	F=0.74, df=1, 298, P=0.39	17.2 \pm 1.1a	12.6 \pm 0.9b	F=9.78, df=1, 297, P=0.001
Fertility	20.6 \pm 1.5a	19.3 \pm 1.4a	F=0.42, df=1, 298, P=0.515	6.2 \pm 0.7a	2.6 \pm 0.6b	F=13.2 df=1, 297, P=0.0003
Percentage of hatching	63.8 \pm 2.7a	63.2 \pm 2.7a	F=0.171, df=1, 298, P=0.679	25.1 \pm 2.8a	13.7 \pm 2.8b	F=19.1, df=1, 234, P \leq 0.0001

DISCUSSION

Generalist predators attack a variety of prey, which differ in energy content and cost of capture and ingestion (ROGER et al. 2000). Food availability (KAWAUCHI 1981; FERRAN et al. 1984; STEWART et al. 1991; DIXON & GUO 1993; DIXON 2000) and prey quality (BLACKMAN 1967; NIJIMA & TAKAHASHI 1980; NIJIMA et al. 1986) affect the fecundity of ladybird beetles, which is an important determinant of their fitness (HEMPTINNE et al. 1993; EVANS et al. 1999). Significant differences in the reproductive capacity of *nigra* and *aulica* females, and a significant increase in the reproductive capacity of *nigra* females when fed on *A. fabae* versus *M. persicae* suggest the quality of *A. fabae* and *M. persicae* as prey differs for the two phenotypes.

As predicted by optimal foraging theory, predators utilize the different prey types available so as to maximize their rate of gain of energy (STEPHENS & KREBS 1986; CRAWLEY & KREBS 1992) or maximize the ingestion of nutrients (WALDBAUER et al. 1984). Such results support the hypothesis of KOMAI & HOSINO (1951), that micro-geographic variation in the relative frequency of elytral patterns within *H. axyridis* populations could be correlated somehow with differences in the composition of aphid populations. The key may lie in intra-specific differences in the food preferences of phenotypes in order to increase their fitness. Requirements for high-energy resources for metabolism and reproduction could determine prey choice by females of ladybird beetles (HOUCK 1991). As demonstrated in the laboratory by our experimental results, different phenotypes of *H. axyridis* may thrive on different preys species in nature. This may provide some selective basis for maintenance of genetic polymorphism in this species.

REFERENCES

- BLACKMAN, R.L. 1967. The effects of different prey on *Adalia bipunctata* L. and *Coccinella 7-punctata* L. *Annual Applied Biology* 59: 207-219.
- CRAWLEY, M.J. & J.R. KREBS 1992. Foraging theory. Pp. 90-114 in M.J. CRAWLEY (Ed.). *Natural Enemies*. Blackwell Scientific Publications, Oxford. 592 pp.
- DIXON, A.F.G. 2000. *Insect Predator-Prey Dynamics: Ladybirds Beetles & Biological Control*. Cambridge University Press, Cambridge. 257 pp.
- DIXON, A.F.G. & Y. GUO 1993. Eggs and cluster size in ladybird beetles (Coleoptera: Coccinellidae): the direct and indirect effects of aphid abundance. *European Journal of Entomology* 90: 457-463.
- EVANS, E.W., A.T. STEVENSON & D.R. RICHARDS 1999. Essential versus foods of insect predators: benefits of a mixed diet. *Oecologie* 121: 107-112.
- FERRAN, A., M.O. CRUZ DE BOELPAEPE, H. SCHANDERL & M.M. LARROQUE 1984. Les aptitudes trophiques et reproductrices des femelles de *Semiadalia undecimnotata* (Col.: Coccinellidae). *Entomophaga* 29: 157-170.
- FYE, R.E. 1981. Rearing and release of coccinellids for potential control of pear Psylla. *Agricultural Research Service (Western Region)* 20: 1-9.
- FUTUYMA, D.J. 1998. *Evolutionary Biology* (3rd ed.). Sinauer Associates Inc., Massachusetts. 763 pp.
- HEMPTINNE, J.-L., A.F.G. DIXON, J.L. DOUCET & J.E. PETERSEN 1993. Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): Mechanisms. *European Journal of Entomology* 90: 141-150.
- HODEK, I. & A. HONĚK 1996. *Ecology of Coccinellidae*. Dordrecht: Kluwer Academic Publishers. 260 pp.
- HOUCK, M.A. 1991. Time and resource partitioning in *Stethorus punctum* (Coleoptera: Coccinellidae). *Environmental Entomology* 20: 479-497.
- HUKUSIMA, S. & M. KAMEI 1970. Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Research Bulletin. Faculty Agriculture. Gifu University* 29: 53-66

8th International Symposium on Ecology of Aphidophaga
University of the Azores, Ponta Delgada, 1-6 September 2002

- HUKUSIMA, S. & T. OHWAKI 1972. Further notes on feeding biology of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Research Bulletin. Faculty Agriculture. Gifu University* 33: 75-82.
- IABLOKOFF-KHNZORIAN, S.M. 1982. *Les coccinelles; Coléoptères-Coccinellidae*. Société Nouvelle des Éditions Boubée, Paris. 569 pp.
- KAWAUCHI, S. 1981. The number of oviposition, hatchability and the term of oviposition of *Propylea japonica* Thunberg (Coleoptera, Coccinellidae) under different food condition. *Kontyu* 49: 183-191.
- KOMAI, T. 1956. Genetics of ladybeetles. *Advances in Genetics* 8: 155-189.
- KOMAI, T. & Y. HOSINO 1951. Contributions to the Evolutionary Genetics of the Lady-beetle, *Harmonia*. II. Microgeographic Variations. *Genetics* 36: 382-390.
- LUCAS, E., D. CODERRE & C. VINCENT 1997. Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. *Entomologia Experimentalis et Applicata* 85: 151-159.
- MCLURE, M.S. 1987. Potential of the asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* Bean & Godwin (Homoptera: Margarodidae) in the United States. *Environmental Entomology* 16: 224-230.
- NIJIMA, K. & H. TAKAHASHI 1980. Nutritional studies of an aphidophagous coccinellid, *Harmonia axyridis* (IV). Effects of chemically defined diet and some fractions of drone honeybee on the reproduction. *Bulletin Faculty Agriculture. Tamagawa University* 20: 47-55.
- NIJIMA, K., M. MATSUKA & I. Okada 1986. Artificial diets for an aphidophagous coccinellid, *Harmonia axyridis*, and its nutrition (Minireview). Pp: 37-50 in I. HODEK (Ed). *Ecology of Aphidophaga*. Academia, Prague. 562 pp.
- OSAWA, N. 1992. A life table of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in relation to the aphid abundance. *Japan Journal of Entomology* 60: 575-579.
- RICKLEFS, R.E. 1990. *Ecology*. (3rd ed.). W.H. Freeman and Company. New York. 896 pp.
- ROGER, C., D. CODERRE & G. BOIVIN 2000. Differential prey utilization by generalist predator *Coleomegilla maculata* lengi according to prey size and species. *Entomologia Experimentalis et Applicata* 94: 3-13.
- SALL, J., A. LEHMAN & L. CREIGHTON 2001. JMP start statistics: a guide to statistical and data analysis using JMP® and JMP IN software. Duxbury Press, Toronto. 656 pp.
- SCHANDERL, H., A. FERRAN & M.M. LARROQUE 1985. Les besoins trophiques et thermiques des larves de la coccinelle *Harmonia axyridis* Pallas. *Agronomie* 5: 417-421.
- SCHANDERL, H., A. FERRAN & V. GARCIA 1988. L' élevage de deux coccinelles *Harmonia axyridis* et *Semiadalia undecomnotata* à l' aide d' oeufs d' *Anagasta kuehniella* tués aux rayons ultraviolets. *Entomologia Experimentalis et Applicata* 49: 417-421.
- SOARES, A.O., D. CODERRE & H. SCHANDERL 2001. Fitness of two phenotypes of *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology* 98: 287-293.
- SOARES, A.O., D. CODERRE & H. SCHANDERL 2003. Effect of temperature and intraspecific allometry on predation activity of two phenotypes of *Harmonia axyridis* (Coleoptera: Coccinellidae). *Environmental Entomology* 32: 939-944.
- STEPHENS, D.W. & J.R. KREBS 1986. *Foraging theory*. Princeton University Press, Princeton. 237 pp.
- STEWART, L.A., A.F.G. DIXON, Z. RŮŽIČKA & I. IPERTI 1991. Clutch and egg size in ladybird beetles. *Entomophaga* 36: 329-333.
- TAN, C.C. 1946. Mosaic Dominance in the inheritance of color patterns in the Lady-birds Beetle, *Harmonia axyridis*. *Genetics* 31:195-210.
- TAN, C.C. 1949. Seasonal Variations of color patterns in *Harmonia axyridis*. *Proceedings of the 8th International Congress of Genetics*: 669-670.
- WALDBAUER, G.P., R.W. COHEN & S. FRIEDMAN 1984. Self-selection of an optimal nutrient mix from defined diets by larvae of the corn earworm, *Heliothis zae* (Boddie). *Physiological Zoology* 57: 590-597.

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DEVELOPMENTAL ISOMORPHY IN LADYBIRDS (COLEOPTERA: COCCINELLIDAE)

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Analysis of the time spent in the egg, larval and pupal stages by insects reveal a distinct pattern. Although, well fed individuals kept at high temperatures complete their development much faster than poorly fed individuals kept at low temperatures, nevertheless, they all spend the same proportion of the total time required for development in each developmental stage. Data will be presented that indicate that ladybirds conform to this pattern. All stages of development appear to have the same lower developmental threshold. If this is true than it will greatly facilitate practical studies on the development of ladybirds and improve our understanding of how selection has shaped their life history strategies and those of insects in general.

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INTRODUCTION

That the developmental rate of insects increases with temperature is described by many models. To the best of our knowledge, the most appropriate model is that of SHARPE & DE MICHELLE (1977), which predicts a linear relationship between the developmental rate and temperature in the middle of the temperature range. The linear part of the relationship corresponds to temperatures that are ecologically relevant for insect development, and gives the most reliable approximation of developmental rate (J. Polechová personal communication). Here we show that the linear approximation is the most appropriate for ladybirds (Coleoptera: Coccinellidae), and introduce the notion of developmental isomorphy.

When data on duration of development are converted into its reciprocal, the developmental rate, the linear approximation of the relationship

between the rate of development and temperature enables us to calculate two virtual constants: the sum of effective temperatures, *SET*, i.e. the amount of heat needed to complete a developmental stage, and the lower developmental threshold, *LDT*, i.e. the temperature below which development ceases (e.g., HODEK & HONĚK 1996, pag. 65-71). The thermal constants *SET* and *LDT* can be used for the timing of life-history events, the determination of pre-adult thermal requirements when forecasting and monitoring agricultural and forestry pests, assessing natural enemies suitable for biological control, comparing populations, and determining the effect of phylogeny, geography, body size, food and other constraints on the duration of development. Since LUDWIG (1928) introduced this method it has been widely used, and there are several reviews of the results, including those for ladybirds (HONĚK & KOCOUREK 1990; HONĚK 1996; HODEK &

HONĚK 1996; KIRITANI 1997; DIXON 2000).

If the proportion of total developmental time spent in a particular developmental stage does not change with temperature, then the *LDT* is the same for all developmental stages of a species, and it shows developmental isomorphy. Developmental isomorphy is known for 7 species of mites and 342 species from 11 insect orders (JAROŠÍK et al. 2002). Here developmental isomorphy is demonstrated in non-dormant ladybirds. We discuss how developmental isomorphy can greatly facilitate practical studies on the development of ladybirds.

MATERIAL & METHODS

The linear model

The linear approximation of the relationship between the developmental rate, *DR* (i.e. proportion of development occurring per unit time) and temperature, *t*, can be described as $DR = a + b.t$, where *a* is the intercept with the *y*-axis, and *b* the slope of the linear function. From this equation, the lower developmental threshold, *LDT*, i.e. the temperature when development ceases ($DR = 0$, $t = LDT$) can be estimated as $LDT = -a/b$. Graphically, *LDT* is the value at which the relationship intercepts the temperature axis. Using the relationship between *DR* and *t*, the sum of effective temperatures, *SET*, i.e. number of day degrees above the *LDT* necessary for the completion of a particular developmental stage, can also be estimated. At the moment of completion of a development stage, $DR = 1$ and $t = SET$. Then, shifting *y*-axis so that $a = 0$, $SET = 1/b$.

Reliability of linear vs. exponential models of developmental rates

To assess the suitability of a simple linear model

for predicting thermal requirements, the accuracy of linear and exponential approximations of developmental rates were compared. Because the developmental rates at the very low and high temperatures for a species, where mortality sharply increases, are of little practical importance, only data for those temperatures where the mortality was lower than 10% of the maximum survivorship were included in the analysis. Then, the residuals of the linear and exponential approximations were compared using a paired T-test. The data used for this was that for *Hyperapsis notata* (DREYER et al. 1997), *Harmonia axyridis* (LAMANA & MILLER 1998), *Scymnus levaillanti* and *Cycloneda sanguinea* (ISIKBER 1999). These data sets are exceptional as they include the mortality experienced by the species at each temperature.

Testing of developmental isomorphy

The ratios of the times spent in each developmental stage at different constant temperatures (°C) were recalculated from the data on duration of non-dormant development. In most cases, it was calculated as a ratio of time spent in a particular stage divided by the total pre-imaginal development, i.e., $(egg)/(egg+larva+pupa)$. However, data on a particular stage and an uncompleted total development, e.g., $(larva)/(larva+ pupa)$ were also analysed. The calculations used data for three or more temperatures. The data was obtained from the studies listed in Table 1. All the 66 populations of 48 species and subspecies were analysed to avoid bias in favour of the hypothesis being tested. All the data for each particular stage evaluated fell within the range of the linear relationship between the rate of development and temperature.

Table 1
The species and source of the data used for determining developmental isomorphy.

Species	Reference	Temp. (°C)	
		# ¹	Range
<i>Adalia bipunctata</i> (L.)	OBRYCKI & TAUBER (1981)	4	18.3-26.7
<i>Adalia bipunctata</i> (L.)	HONĚK & KOCOUREK (1988)	4	15-24
<i>Adalia bipunctata</i> (L.)	GURNEY & HUSSEY (1970)	3	16-24
<i>Adalia flavomaculata</i> DeGeer	MICHELS & BATEMAN (1986)	3	25-29
<i>Brumus suturalis</i> F.	DE FLUITER (1939)	5	23.1-32.2
<i>Calvia quattuordecimguttata</i> (L.)	LAMANA & MILLER (1995)	3	14-26
<i>Calvia quattuordecimguttata</i> (L.)	SEMYANOV (1980)	4	15-30
<i>Cheilomenes sulphurea</i> (Olivier)	OKROUHLÁ et al. (1983)	3	20-28
<i>Chilocorus stigma</i> (Say)	MUMA (1955)	3	16.7-26.7
<i>Hyperaspis notata</i> (Mulsant)	CORREJO et al. (1991)	3	22-30
<i>Coccinella novemnotata</i> Herbst	MCMULLEN (1967)	3	15.6-26.7
<i>Coccinella quinquepunctata</i> L.	HONĚK & KOCOUREK (1988)	4	15-24
<i>Coccinella septempunctata</i> (L.)	HONĚK & KOCOUREK (1988)	4	15-24
<i>Coccinella septempunctata</i> (L.)	HODEK (1958)	3	15-25
<i>Coccinella septempunctata</i> (L.)	BUTLER (1982)	4	17-25
<i>Coccinella septempunctata</i> (L.)	OBRYCKI & TAUBER (1981)	4	18.3-26.7
<i>Coccinella septempunctata</i> (L.)	XIA et al. (1999)	3	15-25
<i>Coccinella septempunctata</i> (L.)	TRITISCH (1997)	3	17-25
<i>Coccinella septempunctata brucki</i> Mulsant	KAWAUCHI (1983)	4	15-25
<i>Coccinella septempunctata brucki</i> Mulsant	KAWAUCHI (1979)	3	20-30
<i>Coccinella septempunctata brucki</i> Mulsant	SAKURAI et al. (1991)	3	22-30
<i>Coccinella transversalis</i> F.	VEERAVEL & BASKARAN (1996)	3	18-30
<i>Coccinella transversoguttata</i> Brown	OBRYCKI & TAUBER (1981)	4	18.3-26.7
<i>Coccinella trifasciata</i> L.	MILLER & LAMANA (1995)	5	18-34
<i>Coccinella undecimpunctata</i> L.	ERAKY & NASSER (1993)	4	14-26
<i>Coelophora quadrivittata</i> Fauvel	CHAZEAU (1981)	3	20-30
<i>Coleomegilla maculata</i> (DeGeer)	OBRYCKI & TAUBER (1978)	4	18.3-26.7
<i>Coleomegilla maculata</i> (DeGeer)	GURNEY & HUSSEY (1970)	3	16-24
<i>Coleomegilla maculata lengi</i> Timberlake	WRIGHT & LAING (1978)	4	19-25
<i>Curinus coeruleus</i> Mulsant	DIRAVIAM & VIRAKTAMATH (1991)	4	22.8-25.8
<i>Cycloneda sanguinea</i> (L.)	ISIKBER (1999)	4	20-27.5
<i>Cycloneda sanguinea</i> (L.)	GURNEY & HUSSEY (1970)	3	16-24
<i>Delphastus catalinae</i> (Horn)	HEMACHANDRA (1994)	3	20-26
<i>Eriopis connexa</i> (Germar)	MILLER & PAUSTIAN (1992)	4	14-26
<i>Harmonia axyridis</i> (Pallas)	KAWAUCHI (1979)	3	20-30
<i>Harmonia axyridis</i> (Pallas)	LAMANA & MILLER (1998)	5	14-30
<i>Hippodamia convergens</i> Guerin	BUTLER & DICKERSON (1972)	4	20-28.9
<i>Hippodamia convergens</i> Guerin	OBRYCKI & TAUBER (1982)	5	15.6-26.7
<i>Hippodamia parenthesis</i> (Say)	ORR & OBRYCKI (1990)	4	14-26
<i>Hippodamia quinquesignata</i> (Kirby)	KADDOU (1960)	3	15.6-30
<i>Hippodamia sinuata</i> Mulsant	MICHELS & BEHLE (1991)	4	15-30
<i>Hippodamia variegata</i> Goetz	MICHELS & BATEMAN (1986)	3	25-29
<i>Hyperaspis notata</i> Mulsant	DREYER ET AL. (1997)	5	18-32
<i>Lemnia biplagiata</i> (Swartz)	SEMYANOV & BEREZNAYA (1988)	3	20-30
<i>Lioadalia flavomaculata</i> (DeGeer)	BROWN (1972)	6	13-27
<i>Menochilus sexmaculatus</i> (F.)	KAWAUCHI (1979)	3	20-30
<i>Menochilus sexmaculatus</i> (F.)	VEERAVEL & BASKARAN (1996)	3	18-30

¹Number of temperatures

Table 1 (continued)

The species and source of the data used for determining developmental isomorphy.

Species	Reference	Temp. (°C)	
		# ¹	Range
<i>Olla v-nigrum</i> (Mulsant)	KREITER (1985)	5	15-30
<i>Pharoscyrnus flexibilis</i> (Mulsant)	SHARMA et al. (1990)	3	24-32
<i>Pharoscyrnus numidicus</i> (Mulsant)	KEHAT (1967)	3	24-31
<i>Propylea japonica</i> (Thunberg)	KAWAUCHI (1979)	3	20-30
<i>Propylea japonica</i> (Thunberg)	KAWAUCHI (1983)	4	15-25
<i>Propylea quatuordecimpunctata</i> (L.)	HONĚK & KOCOUREK (1988)	3	15-24
<i>Propylea quatuordecimpunctata</i> (L.)	BAUMGAERTNER et al. (1987)	3	15.3-25.3
<i>Scymnus apiciflavus</i> Motschulsky	DE FLUITER (1939)	6	19.1-32.2
<i>Scymnus frontalis</i> (F.)	NARANJO et al. (1990)	3	15-26.2
<i>Scymnus hoffmani</i> Weise	ZHAO & WANG (1987)	4	18-30
<i>Scymnus hoffmani</i> Weise	KAWAUCHI (1983)	4	15-25
<i>Scymnus interruptus</i> (Goeze)	TAWFIK et al. (1973)	3	15.5-27.9
<i>Scymnus levaillanti</i> Mulsant	ISIKBER (1999)	5	17.5-27.5
<i>Scymnus roepkei</i> de Fluiter	DE FLUITER (1939)	6	19.1-32.2
<i>Semiadalia undecimnotata</i> (Schneider)	HONĚK & KOCOUREK (1988)	4	15-24
<i>Stethorus bifidus</i> Kapur	PETERSON (1993)	5	12.5-27.5
<i>Stethorus punctillum</i> Weise	BERKER (1958)	3	19-35.6
<i>Stethorus japonicus</i> H.Kamiya	TANAKA (1966)	13	17-29
<i>Subcoccinella vigintiquatuor punctata</i> (L.)	ALI (1971)	3	18-28

¹Number of temperatures

Angular transformed proportion of total developmental time spent in a particular stage was plotted against temperature, and the existence of developmental isomorphy inferred from a zero change in proportion. Temperature was first regressed with a different intercept and a different slope for each stage (using average proportion for replicated data due to origin or photoperiod), and the significance was then evaluated by simultaneous deletion test. Individual studies on populations of the same species were analysed separately because the results varied due to differences in experimental design. The calculations were performed using general linear modelling in GLIM v. 4 (FRANCIS et al. 1994).

To reach a general conclusion, all the data was then tested using meta-analysis, a statistical synthesis of the results of separate, independent experiments (HEDGES & OLKIN 1985; GUREWITCH & HEDGES 1993; COOPER & HEDGES 1994). The outcome of each analysis was represented by a quantitative index (the effect

size), which is independent of sample size, and the null hypothesis that the overall effect size indicates a zero slope was tested. The assumption that the individual analyses share a common population effect size was tested by the homogeneity statistic Q (SHADISH & HADDOCK 1994). Details of the statistical procedure are described in JAROŠÍK et al. (2002).

RESULTS

Linear vs. exponential models of developmental rate

For the four ladybird species for which there is sufficient data on developmental rate and mortality, the linear model gave a better fit ($R^2 = 0.991 \pm 0.0102$) than the exponential ($R^2 = 0.973 \pm 0.0194$) ($t = 2.62$; $df = 3$; $P < 0.05$) (Table 2). That is, the simple linear model is the best for practical purposes.

Table 2
Comparison of explained variance (R^2) obtained by fitting exponential (exp) and linear (lin) approximations to the relationships between developmental rate and temperature in 4 species of ladybirds.

Species	Stage	R^2 lin	R^2 exp
<i>Cycloneda sanguinea</i>	Pupa	0.990	0.960
<i>Harmonia axyridis</i>	Pupa	0.999	0.976
<i>Hyperaspis notata</i>	Egg - Adult	0.998	0.999
<i>Scymnus levaillanti</i>	Pupa	0.977	0.957
Average		0.991	0.973
Standard error		0.0102	0.0194

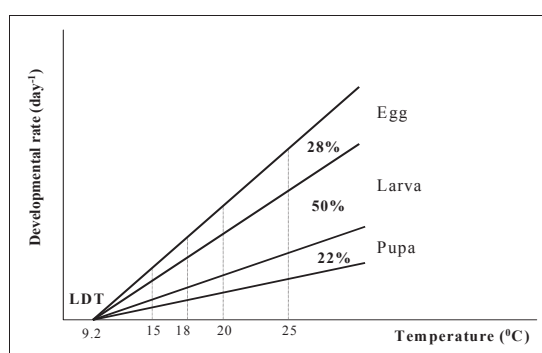


Fig. 1. Effect of temperature (t) on rate of development (RD) within the linear range of the relationship for *Propylea japonica*. Data from Kawauchi (1983). The population is isomorphic and spent 28% of total development in egg, 50% in larva, and 22% in pupa at temperatures 15, 18, 20 and 25 °C. All developmental stages have a common lower developmental threshold ($LDT = 9.2$) and for assessment of the number of day-degrees above the LDT necessary for completion of a particular development stage the sum of effective temperatures can be determined at any temperature within the linear range.

Developmental isomorphy

Combining statistically the results of the 68 studies in a meta-analysis indicated the overall prevalence of developmental isomorphy in ladybirds (the overall weighted average effect size: $7.10E-04$ with 95% confidence interval from $-2.94E-03$ to $4.36E-03$; homogeneity statistic $Q = 0.64$, $df = 65$, $p = 1$). That is, all the populations and species showed developmental isomorphy.

Developmental isomorphy in ladybirds implies no change in the proportion of time spent

in a particular developmental stage with change in temperature. It is illustrated for *Propylea japonica* in Fig. 1. Therefore, within the temperature ranges with a linear relationship between RD and t , for each species there is (1) a proportional SET for completion of each developmental stage at each temperature and (2) a common LDT for all developmental stages.

DISCUSSION

Linear vs. non-linear models of developmental rate

There are three categories of models of the relationship between temperature and duration of development in insects and other ectotherms (HONĚK 1999): (i) *Non-linear*. The objective of this kind of data fitting is the description of the developmental rate over a wide range of temperatures (e.g. STINNER et al. 1974; HAGSTRUM & MILLIKEN 1991). This type of model gives a good fit to the data, but the parameters have little biological meaning. (ii) *Non-linear incorporating physiological and biochemical constants*. These not only describe but also attempt to explain the relationship in terms of physiological mechanisms (e.g. LOGAN et al. 1976; SHARPE & DEMICHELLE 1977; SCHOOLFIELD et al. 1981; WAGNER et al. 1984, 1991). (iii) *A linear approximation*.

Models of type (ii) are often theoretically correct, but not tractable for most ecologists. In addition, only relatively recent models of this type (e.g. LACTIN et al. 1995) enable one to calculate lower developmental threshold. On the other hand, the type (iii) linear approximation within the range of temperatures ecologically relevant to where an insect lives, is a reliable model, and can be easily used to calculate two virtual constants: the lower developmental threshold, LDT (the temperature below which development ceases), and the sum of effective temperatures, SET (the amount of heat needed for completing a developmental stage). This greatly simplifies modelling. Therefore, we argue against non-linear models for practical purposes, and advocate the simple linear model. We believe that the simple linear model of the relationship

between developmental rate and temperature gives the best approximation of *LDT* and *SET* in insects.

The existence of a common *LDT* for all the developmental stages of a species

When the data for ladybirds were plotted against temperature, the developmental isomorphy hypothesis was supported by a zero change in the proportion of the total developmental time spent in a particular stage of a development. Developmental isomorphy in the overall pattern of the data thus indicates that all the developmental stages of each ladybird species have a common *LDT*. If so, there should be little variation in the *LDT* between stages and instars within a species, and within populations of individual species. This is not supported by the literature on ladybird development (HONĚK & KOCOUREK 1990; HONĚK 1996; HODEK & HONĚK 1996). Therefore, if developmental isomorphy is a common feature of ladybirds, then a significant proportion of the variation in *LDTs* within species is illusory and possibly a consequence of how it is estimated from experimental data.

What are the sources of error in estimating *LDT*? First, the values of developmental rate obtained at extreme (high or low) temperatures may violate developmental isomorphy (JAROŠÍK et al. 2002). At low temperatures there may be differential mortality. The individuals with the fastest development complete their development but the rest are more likely to succumb to adverse conditions, because their development is prolonged. Second, imprecise measurement of developmental time, particularly at high temperatures. As developmental rate increases with temperature, the number of observations per stage should also increase. To measure the rate of development with the same precision at low and high temperatures, the time interval must be proportional to the length of the development stage at each temperature. This is not the case in most studies (SHAFFER 1983; VAN RIJN et al. 1995). A constant monitoring is the most probable source of bias in data collected at high temperatures.

Even if *LDTs* are calculated from data collected over a range of ecologically relevant temperatures, and the regression of development rate on temperature is linear, the accuracy of the estimates is affected by errors in the estimates of the developmental rate (CAMPBELL et al. 1974). The low precision of *LDTs* is obvious from their standard errors (CAMPBELL et al. 1974), which are typically between 1-3 °C (J. JANÁČEK & A. HONĚK, unpublished data). Crucial from a statistical point of view is any bias in the measurements made at extreme temperatures. Important determinants of the slopes of the linear regressions, from which the *LDTs* are inferred, are the extreme values (see CRAWLEY 1993, p. 78-82). Therefore, a relatively small bias in the developmental rates measured at extreme temperatures will cause a large shift in the *LDT*. Poor estimates of developmental rate are most likely at high temperatures because the precision with which the duration of development is measured is poor and the error large (development rate is the reciprocal of duration of development).

CONCLUSIONS

The existence of rate isomorphy in ladybirds has important practical implications for the timing of life-history events. The experimental procedure for determining the thermal development constants, *LDT* and *SET*, can be simplified. The lower developmental threshold can be determined based on data for one stage, preferably the pupa, which is little affected by factors other than temperature, and has a duration usually longer than that of the egg stage. *SET* may also be calculated from the duration of development at one temperature (Fig. 1). Thus more effort can be invested in greater precision in determining the length of development.

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REFERENCES

- ALI, M. 1971. The effect of temperature and photoperiod on the behaviour and development of *Subcoccinella vigintiquatuor punctata* L. (Col., Coccinellidae). *Acta Phytopathologica Academiae Scientiarum Hungaricae* 6: 185-189.
- BAUMGAERTNER, J., M. BIERI & V. DELUCCHI 1987. Growth and development of immature life stages of *Propylaea 14-punctata* L. and *Coccinella 7-punctata* L. (Col.: Coccinellidae) simulated by the metabolic pool model. *Entomophaga* 32: 415-423.
- BERKER, J. 1958. Die natürlichen Feinde der Tetranychiden. *Zeitschrift für angewandte Entomologie* 43: 115-172.
- BROWN, H.D. 1972. On the biology of *Lioadalia flavomaculata* (Deg.) (Col., Coccinellidae), a predator of the wheat aphid (*Schizaphis graminum* (Rond.)) in South Africa. *Bulletin of Entomological Research* 61: 673-679.
- BUTLER, G.D. 1982. Development time of *Coccinella septempunctata* in relation to constant temperatures (Col.: Coccinellidae). *Entomophaga* 27: 349-353.
- BUTLER, G.D. & U.A. DICKERSON 1972. Life cycle of the convergent lady beetle in relation to temperature. *Journal of Economic Entomology* 65: 1508-1509.
- CAMPBELL, A., B.D. FRAZER, N. GILBERT, A.P. GUTIERREZ & M. MACKAUER 1974. Temperature requirements of some aphids and their parasites. *Journal of Applied Ecology* 11: 431-438.
- CORREJO, N.S., A.C. BELLOTTI & R. GONZÁLEZ 1991. Evaluación de algunos factores determinantes de la eficiencia de *Cleothora notata* (Col.: Coccinellidae) como depredador del piojo harinoso de la Yuca *Phenacoccus herreni* (Hom.: Pseudococcidae). *Revista Colombiana de Entomología* 17: 21-27.
- CHAZEAU, J. 1981. Données sur la biologie de *Coelophora quadrivittata* (Col.: Coccinellidae), prédateur de *Coccus viridis* (Hem: Coccidae) en Nouvelle-Calédonie. *Entomophaga* 26: 301-312.
- COOPER, H. & L.V. HEDGES (Eds). 1994. *The handbook of research synthesis*. Russell Sage Foundation, New York.
- CRAWLEY, M.J. 1993. *GLIM for ecologists*. Blackwell, London.
- DE FLUITER, H.J. 1939. Beitrag zur Kenntnis der Biologie und Ökologie einiger Coccinelliden von Java. *7th International Congress of Entomology, Berlin, 1939*: 1106-1119.
- DIRAVIAM, J. & C.A. VIRAKTAMATH 1991. Biology of the introduced ladybird beetle, *Curinus coeruleus* (Coleoptera: Coccinellidae). *Journal of Biological Control* 5: 14-17.
- DIXON, A.F.G. 2000. *Insect predator-prey dynamics: ladybird beetles and biological control*. Cambridge University Press, Cambridge.
- DIXON, A.F.G., J.-L. HEMPTINE & P. KINDLMANN 1997. Effectiveness of ladybirds as biological control agents: patterns and processes. *Entomophaga* 42: 71-83.
- DREYER, B.S., P. NEUENSCHWANDER, B. BOUYJOU, J. BAUMGÄRTNER & S. DORN 1997. The influence of temperature on the life table of *Hyperaspis notata*. *Entomologia Experimentalis et Applicata* 84: 85-92.
- ERAKY, S.A. & M.A.K. NASSER 1993. Effect of constant temperatures on the development and predation prey efficiency of the ladybird beetle, *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae). *Assiut Journal of Agricultural Sciences* 24: 223-230.
- FRANCIS, B., M. GREEN & C. PAYNE (Eds). 1994. *The GLIM system. Release 4 manual*. Clarendon Press, Oxford.
- FRAZER, B.D. & R.R. MCGREGOR 1992. Temperature-dependent survival and hatching rate of eggs of seven species of Coccinellidae. *Canadian Entomologist* 124: 305-312.
- GILBERT, N. & D.A. RAWORTH 1996. Insects and temperature - a general theory. *Canadian Entomologist* 128: 1-13.
- GUREVITCH, J. & L.V. HEDGES 1993. Meta-analysis: Combining the results of independent experiments. Pp. 378-398 in S.M. SCHEINER & J. GUREVITCH (Eds). *Design and analysis of ecological experiments*. Chapman & Hall, New York.
- GURNEY, B. & N.W. HUSSEY 1970. Evaluation of some coccinellid species for the biological control of aphids in protected cropping. *Annals of Applied Biology* 65: 451-458.
- HAGSTRUM, D.W. & G.A. MILLIKEN 1991. Modelling differences in insect developmental times between constant and fluctuating temperatures. *Annals of the Entomological Society of America* 84: 369-379.
- HAMALAINEN, M. & M. MARKKULA 1977. Cool storage of *Coccinella septempunctata* and *Adalia bipunctata* (Col., Coccinellidae) eggs for use in the biological control in greenhouses. *Annales Agricolae Fennicae* 16: 132-136.
- HEDGES, L.V. & I. OLKIN 1985. *Statistical methods for meta-analysis*. Academic Press, New York.
- HEMACHANDRA, K.S. 1994. Development, reproduction and feeding behaviour of *Delphastus catalinae*, a coccinellid predator of glasshouse whitefly,

- Trialeurodes vaporariorum*. M.Sc. Thesis, University of London.
- HONĚK, I. 1958. Influence of temperature, rel. humidity and photoperiodicity on the speed of development of *Coccinella septempunctata* L. *Časopis Československé Společnosti Entomologické* 55: 121-141.
- HONĚK, I. & A. HONĚK 1996. *Ecology of Coccinellidae*. Kluwer, Dordrecht.
- HONĚK, A. 1996. The relationship between thermal constants for insect development: a verification. *Acta Societatis Zoologicae Bohemoslovaca* 60: 115-152.
- HONĚK, A. 1997. Incidence of protogynous and protandrous development in the pre-imaginal stage of insect development: an overview. *Acta Societatis Zoologicae Bohemoslovaca* 61: 113-128.
- HONĚK, A. 1999. Constraints on thermal requirements for insect development. *Entomological Science* 2: 615-621.
- HONĚK, A., V. JAROŠÍK, Z. MARTINKOVÁ & I. NOVÁK 2002. Food induced variation of thermal constants of development and growth of *Autographa gamma* (Lepidoptera: Noctuidae) larvae. *European Journal of Entomology* 99: 241-252.
- HONĚK, A. & F. KOCOUREK 1988. Thermal requirements for development of aphidophagous Coccinellidae (Coleoptera), Chrysopidae, Hemerobiidae (Neuroptera), and Syrphidae (Diptera): some general trends. *Oecologia* 76: 455-460.
- HONĚK, A. & F. KOCOUREK 1990. Temperature and development time in insects: a general relationship between thermal constants. *Zoologische Jahrbücher Abteilung für Systematik und Ökologie der Tiere* 117: 401-439.
- ISIKBER, A.A. 1999. *Evaluation of two predatory coccinellid beetles, Scymnus levaillanthi and Cycloneda sanguinea (Coleoptera: Coccinellidae) for the biocontrol of cotton aphid, Aphis gossypii (Homoptera: Aphididae)*. Ph.D. Thesis, University of London.
- JAROŠÍK V., A. HONĚK & A.F.G. DIXON 2002. Developmental rate isomorphy in insects and mites. *American Naturalist* 160: 497-510.
- KADDOU, I.K. 1960. The fleeing behavior of *Hippodamia quinquesignata* (Kirby) larvae. *University of California Publications in Entomology* 16: 181-232.
- KAWAUCHI, S. 1979. Effect of temperatures on the aphidophagous coccinellids. *Kurume University Journal* 28: 47-51.
- KAWAUCHI, S. 1983. The threshold temperature and thermal constant for development from the egg to the adult form of *Coccinella septempunctata* brucki, *Propylea japonica* and *Scymnus (Pullus) hoffmani* (Coleoptera, Coccinellidae). *Kurume University Journal* 32: 45-51.
- KEHAT, M. 1967. Studies on the biology and ecology of *Pharoscyrmus numidicus* [Coccinellidae] an important predator of the date palm scale *Parlatoria blanchardi*. *Annales de la Société Entomologique de France (N.S.)* 3: 1053-1065.
- KIRITANI, K. 1997. The low development threshold temperature and the thermal constant in insects, mites and nematodes in Japan. *The Miscellaneous Publications of the National Institute of Agro-Environmental Sciences* 21: 1-72.
- KREITER, S. 1985. *Etude bioécologique d'Olla v-nigrum et essai de quantification de l'efficacité prédatrice d'Adalia bipunctata (L.) contre les aphides en verger de pechers (Coleoptera: Coccinellidae)*. Ph.D. Thesis, Université de Droit, d'Aix, Marseille.
- LACTIN, D.J., N.J. HOLLIDAY, D.L. JOHNSON & R. CRAIGEN 1995. Improved rate model of temperature-dependent development by arthropods. *Environmental Entomology* 24: 68-75.
- LAMANA, M.L. & S.C. MILLER 1995. Temperature-dependent development in a polymorphic lady beetle, *Calvia quatuordecimguttata* (Coleoptera: Coccinellidae). *Annals of Entomological Society of America* 88: 785-790.
- LAMANA, M.L. & S.C. MILLER 1998. Temperature-dependent development in an Oregon population of *Harmonia axyridis* (Coleoptera: Coccinellidae). *Environmental Entomology* 27: 1001-1005.
- LAMB, R.J. 1998. Insects and temperature - some comments on a general theory. *Canadian Entomologist* 130: 111-114.
- LOGAN, J.A., D.J. WOLLKIND, S.C. HOYT & L.K. TANIGOSHI 1976. An analytic model for description of temperature dependent rate phenomena in arthropods. *Environmental Entomology* 5: 1133-1140.
- LUDWIG, D. 1928. The effects of temperature on the development of an insect (*Poppilia japonica* Newman). *Physiological Zoology* 1: 358-389.
- MCMULLEN, R.D. 1967. The effects of photoperiod, temperature, and food supply on rate of development and diapause in *Coccinella novemnotata*. *Canadian Entomologist* 99: 578-586.
- MICHELS, G.J. & A.C. BATEMAN 1986. Larval biology of two imported predators of the greenbug, *Hippodamia variegata* Goetz and *Adalia flavomaculata* DeGeer, under constant temperatures. *Southwestern Entomologist* 11: 23-30.

- MICHEL, G.J. & R.E. BEHLE 1991. Effects of two prey species on the development of *Hippodamia sinuata* (Coleoptera: Coccinellidae) larvae at constant temperatures. *The Journal of Economic Entomology* 84: 1480-1484.
- MILLER, J.C. 1992. Temperature-dependent development of the convergent lady beetle (Coleoptera: Coccinellidae). *Environmental Entomology* 21: 197-201.
- MILLER, J.C. & M.L. LAMANA 1995. Assessment of temperature-dependent development in the general population and among isofemale lines of *Coccinella trifasciata* (Col.: Coccinellidae). *Entomophaga* 40: 183-192.
- MILLER, J.C. & J.W. PAUSTIAN 1992. Temperature-dependent development of *Eriopis connexa* (Coleoptera: Coccinellidae). *Environmental Entomology* 21: 1138-1142.
- MUMA, M.H. 1955. Some ecological studies on the twice-stabbed lady beetle *Chilocorus stigma* (Say). *Annals of the Entomological Society of America* 48: 493-498.
- NARANJO, S.E., T.L. GIBSON & D.D. WALGENBACH 1990. Development, survival, and reproduction of *Scymnus frontalis* (Coleoptera: Coccinellidae), on imported predator of Russian wheat aphid, at four fluctuating temperatures. *Annals of the Entomological Society of America* 83: 527-531.
- NYLIN S., C. WIKLUND, P.O. WICKMAN & E. GARCIA-BARROS 1993. Absence of trade-offs between sexual size dimorphism and early male emergence in a butterfly. *Ecology* 74: 1414-1427.
- OBRYCKI, J.J. & M.J. TAUBER 1978. Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasite *Perilitus coccinellae* (Hymenoptera: Braconidae). *Canadian Entomologist* 110: 407-412.
- OBRYCKI, J.J. & M.J. TAUBER 1981. Phenology of three coccinellid species: thermal requirements for development. *Annals of the Entomological Society of America* 74: 31-36.
- OBRYCKI, J.J. & M.J. TAUBER 1982. Thermal requirements for development of *Hippodamia convergens* (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* 75: 678-683.
- OKROUHLÁ, M., S. CHAKRABARTI & I. HODEK 1983. Developmental rate and feeding capacity in *Cheilomenes sulphurea* (Coleoptera: Coccinellidae). *Věstník Československé Společnosti Zoologické* 47: 105-117.
- OLSZAK, R.W. 1987. The occurrence of *Adalia bipunctata* (L.) (Coleoptera, Coccinellidae) in apple orchards and the effect of different factors on its development. *Polish Journal of Ecology* 35: 755-765.
- ORR, C.J. & J.J. OBRYCKI 1990. Thermal and dietary requirements for development of *Hippodamia parenthesis* (Coleoptera: Coccinellidae). *Environmental Entomology* 19: 1523-1527.
- PETERSON, P.G. 1993. *The potential ability of Stethorus bifidus* (Kapur) to regulate populations of *Tetranychus lintearius* (Dufour). M.Sc. Thesis, Massey University, New Zealand.
- ROSENTHAL, R. 1994. Parametric measures of effect size. Pp. 231-244 in H. COOPER & L.V. HEDGES (Eds). *The handbook of research synthesis*. Russell Sage Foundation, New York.
- SAKURAI, H., N. YOSHIDA, C. KOBAYASHI & S. TAKEDA 1991. Effects of temperature and day length on oviposition and growth of lady beetle, *Coccinella septempunctata bruckii*. *Research Bulletin of Faculty of Agriculture Gifu University* 56: 45-50.
- SEMYANOV, V.P. 1980. Biology of *Calvia quatuordecimguttata* L. (Coleoptera: Coccinellidae). *Revue d'Entomologie de l'URSS* 59: 757-763.
- SEMYANOV, V.P. & E.B. BEREZNAJA 1988. Biology and prospects of using Vietnam's lady beetle *Lemnia biplagiata* (Swartz) for control of aphids in greenhouses. Pp. 267-269 in E. Niemczyk & A.F.G. Dixon (Eds). *Ecology and effectiveness of aphidophaga*. Academic Publishers, The Hague.
- SHADISH, V.R. & C.K. HADDOCK 1994. Combining estimates of effect size. Pp. 261-281 in H. COOPER & L.V. HEDGES (Eds). *The handbook of research synthesis*. Russell Sage Foundation, New York.
- SHARMA, D.C., U.S. RAWAT & A.D. PAWAR 1990. Effect of temperature and humidity on the development, longevity and predatory potential of *Pharoscyms flexibilis* Muls. on San Jossé scale. *Journal of Biological Control* 4: 11-14.
- SHAFFER, P.L. 1983. Prediction of variation in development period of insects and mites reared at constant temperatures. *Environmental Entomology* 12: 1012-1019.
- SHARPE, P.J.H. & W. DE MICHELE 1977. Reaction kinetics of poikilotherm development. *Journal of Theoretical Biology* 64: 649-670.
- SHARPE, P.J.H., G.L. CURRY, D.W. DEMICHELE & C.L. COLE 1977. Distribution model of organism development times. *Journal of Theoretical Biology* 66: 21-38.
- SCHOOLFIELD, R.M., P.J.H. SHARPE & C.E. MAGNUSON 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. *Journal of Theoretical Biology* 88: 719-731.

8th International Symposium on Ecology of Aphidophaga
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- SLANSKY, F. 1993. Nutritional ecology: the fundamental quest for nutrients. Pp. 29-91 in N.E. STAMP & T.M. CASEY (Eds). *Caterpillars*. Chapman and Hall, New York.
- SLANSKY, F. & J.M. SCRIBER 1985. Food consumption and utilization. Pp. 87-163 in G.A. Kerkuth & L.I. Gilbert (Eds). *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, Vol. 4. Pergamon, Oxford.
- STINNER, R.E., A.P. GUTIERREZ & G.D. BUTLER 1974. An algorithm for temperature-dependent growth rate simulation. *Canadian Entomologist* 106: 519-524.
- TANAKA, M. 1966. Fundamental studies on the utilization of natural enemies in the citrus grove in Japan I. The bionomics of natural enemies of the most serious pests II. *Stethorus japonicus* H. Kamiya (Coccinellidae), a predator of the citrus red mites, *Panonychus citri* McG. *Bulletin Horticultural Research Japan Station Series D* 4: 22-42.
- TAWFIK, M.F.S., S. ABDUL-NASR & B.M. SAAD 1973. The biology of *Scymnus interruptus* Goeze (Coleoptera: Coccinellidae). *Bulletin de la Societe Entomologique d'Egypte* 57: 9-26.
- TRITISCH, H. 1997. Der Marienkäfer *Coccinella septempunctata* L. im Komplex Winterweizen-Getriedeblattläusen Antagonist. *Agrarökologie*, Vol. 24. Verlag Agrarökologie Berne, Hannover.
- TRUDGILL, D.L. 1995. Why do tropical poikilothermic organisms tend to have higher threshold temperature for development than temperate ones. *Functional Ecology* 9: 136-137.
- TRUDGILL D.L. & J.N. PERRY 1994. Thermal time and ecological strategies - a unifying hypothesis. *Annals of Applied Biology* 125: 521-532.
- VAN RIJN, C.J., C. MOLLEMA & G. STEENHUIS-BROERS 1995. Comparative life-history studies of *Frankliniella occidentalis* and *Thrips tabaci* (Thysanoptera: Thripidae) on cucumber. *Bulletin of Entomological Research* 85: 285-297.
- VEERAVEL, R., & P. BASKARAN 1996. Temperature-dependent development, adult longevity, fecundity and feeding potential of two coccinellid predators under laboratory conditions. *Entomon* 21: 13-18.
- WAGNER, T.L., R.L. OLSON & J.L. WILLERS 1991. Modeling arthropod development time. *Journal of Agricultural Entomology* 8: 251-270.
- WAGNER, T.L., H.I. WU, P.J.H. SHARPE, R.M. SCHOOLFIELD & R.N. COULSON 1984. Modeling insect development rates: a literature review and application of a biophysical model. *Annals of the Entomological Society of America* 77: 208-225.
- WRIGHT, E.J. & J.E. LAING 1978. The effects of temperature on development, adult longevity and fecundity of *Coleomegilla maculata lengi* and its parasite, *Perilitus coccinellae*. *Proceedings of the Entomological Society of Ontario* 109: 33-47.
- XIA, J.Y., W. VAN DER WERF & R. RABBINGE 1999. Temperature and prey density on bionomics of *Coccinella septempunctata* (Coleoptera: Coccinellidae) feeding on *Aphis gossypii* (Homoptera: Aphididae) on cotton. *Environmental Entomology* 28: 307-314.
- ZHAO, D.X. & Z.W. WANG 1987. Influence of temperature on the development of the coccinellid beetle, *Scymnus hoffmani* Weise. *Acta Entomologica Sinica* 30: 47-53.

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PAST AND FUTURE MODELS OF PREDATOR-PREY POPULATION DYNAMICS: THE IMPORTANCE OF GENERATION TIME RATIO

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Mathematical models of predator-prey population dynamics are widely used for predicting the effect of predators as biological control agents, but the assumptions of the models are more relevant to parasite-host systems. Predator-prey systems, at least in insects, substantially differ from what is assumed by these models. The main differences are: (i) Juveniles and adults have to be considered as two different entities, as the former stay within a patch and do not reproduce, while the latter move between patches of prey where they reproduce. (ii) Because of their high mobility, food availability is likely to be less restrictive for adults than juveniles, which are confined to one patch. Therefore, a functional response to prey abundance may not be important for adults. (iii) Egg and larval cannibalism are common in insect predators. Therefore, the quality of patches of prey for their larvae determines the reproductive strategy of adult predators more than the availability of food for the adults. Here we develop a new model, based on the above considerations, which is suitable for modelling these interactions. We show that selection should favour mechanisms that enable predators to avoid reproducing in patches with insufficient prey and those already occupied by predators.

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INTRODUCTION – THE PAST

Since the sixties, mathematical models have been widely used to describe the population dynamics of predator-prey systems. The main emphasis was put on calculating stability of their equilibrium points (BEDDINGTON et al. 1976, 1978; HASSELL 1978; GODFRAY & HASSELL 1987; MURDOCH 1994). These models have a lot in common. Stability and oscillatory behaviour of these models follow from the negative feedback between prey density and predator fecundity, which in turn is a function of predator voracity. Thus this feedback, which is dependent mainly on prey density (functional response), is the crucial factor determining the population dynamics of predator-prey systems (HASSELL 1978). The individual developmental stages of the predator

are treated similarly and a stable age distribution assumed. Similarly, all predators and prey are assumed to interact with each other and migration between patches ignored in the hope that the resulting population dynamics will be similar everywhere.

CLASSICAL MODELS VS. EVOLUTION OF LIFE HISTORIES

In insect predator-prey systems, however, the above assumptions are not satisfied. While juvenile predators (larvae) are confined to the patch of prey¹ where they were born, as they can

¹ Patch in this sense means the space that a larva of a predator can reach by walking, usually one or only a few adjacent plants, or even only a part of an individual plant as in the case of plants like trees.

only walk, adult predators can fly, which enables them to move between patches and therefore to find patches where food is abundant. Thus food availability is much less limiting for adult insect predators than for their larvae. In addition, the fitness of a female predator is determined by the number of her offspring that survive to reproductive age. Probability that an egg will survive and develop into a reproductive individual strongly depends on the quality (measured as food availability and risk of being killed during the period of larval development) of the patch where the egg is laid. Therefore, there are two life history traits that determine fitness of a female predator: number of eggs laid and quality of the patches where these eggs are laid. Which of these is likely to be the stronger selection force?

Before dealing with this question, it is necessary to accept that the fecundity of insect predators is enormous and can be a thousand eggs per female under laboratory conditions (DIXON 2000). Their realised fecundity in nature is most likely lower because of the harsher conditions prevailing there, but assuming that several hundreds of eggs are laid on average per female does not seem to be unrealistic. Although the numbers of insect predators may fluctuate from year to year, their numbers over the long term are stable, i.e., they neither approach infinity nor zero. Thus an average individual produces one offspring that survives to reproductive age. Assuming the sex ratio is close to 1:1, then a female predator produces on average two offspring that survive to reproductive age over the long-term (several decades). Combining the above, i.e., assuming that an average mother produces several hundreds of eggs, but only two survive to reproductive age then the mortality during development from egg to adult must be enormous: reaching values close to 99%. This theoretical prediction is strongly supported by empirical data: in nature mortality often reduces juvenile survival dramatically, as only about 1% of the eggs laid in a patch may survive (OSAWA 1989; AGARWALA & DIXON 1993; HIRONORI & KASUHIRO 1997; KINDLMANN et al. 2000).

The relative strength of selection acting on an increase in fecundity and better survival can be

illustrated by a simple mental exercise: Assume a univoltine population (genotype) P of predators, each female of which produces 200 eggs and that mortality during development from egg to adult is 99%. Fitness of a female in this population is the number of her offspring that survive to reproductive age and equals $200 \times 0.01 = 2$. Assume a mutant, genotype A, selected for better survival, the fecundity of which is the same as that of P, i.e., 200 eggs, but has a marginally lower mortality: 98%. Its fitness is $200 \times 0.02 = 4$. Genotype P would be out-competed by genotype A. For P to have the same fitness as A, its fecundity would have to be 400. Thus, in terms of fitness, a decline in mortality from 99% to 98% is equivalent to increasing fecundity from 200 to 400 eggs. Assuming the same scenario but a lower mortality, e.g., 50% for P and 49% for A, would yield a different result: fitness of P is then $200 \times 0.5 = 100$, and of A $200 \times 0.51 = 102$. For P in this case to have the same fitness its fecundity would have to be 204, i.e., a very small increase. This simple exercise illustrates a general phenomenon: in organisms suffering high mortality, very small improvements in survival can be very important in terms of fitness. In order to achieve the same result fecundity would have to be increased considerably. Such a change is likely to be more severely constrained than a small change in oviposition behaviour resulting in improved offspring survival. Assumption of univoltinism is convenient, as it simplifies the calculation of fitness, but is not crucial to the outcome.

The finding that selection for survival could be much more important for insect predators than selection for fecundity also changes our view of the nature of the models needed for insect predator-prey systems. Selection for voracity is still important, as a large voracity implies large adult size. However, in adults, voracity is positively correlated with fecundity (HEMPTINNE et al. 1992; DIXON 2000), but probably not survival – adults can fly and therefore are less likely to die from starvation, compared to their much less mobile larvae. An adult can, however, strongly influence the survival of its offspring by carefully selecting oviposition sites. The best sites are those, which contain enough food for their

larvae and in which the risk of their being killed is low.

Existence of patches of prey is time limited in many species. Aphids are one example: their colonies last only for a few months (DIXON 1997). By definition, the same is true for many other insect pests: they often severely damage their host plant. If this is true, then it does not make much sense to stay on a dead plant and it is advantageous for them to migrate somewhere else, which means that the existence of patches is time limited. In addition, the developmental time of many insect predators is comparable with the duration of the patches of their prey (DIXON 2000; KINDLMANN & DIXON 1993, 1999, 2001). For example, developmental time of aphidophagous ladybirds spans more than 1 month (about 6 weeks, depending mainly on temperature), which is comparable to the duration of an aphid colony. In such circumstances it is selectively advantageous to oviposit only during a short period, “*egg window*”, early in the existence of a patch of prey, as late laid eggs are unable to complete their development before prey becomes scarce. Therefore genotypes that are able to use cues that enable them to estimate the age of a patch of prey, and lay eggs only in patches in the early stages of development will be strongly selected for.

Another trait that increases the likelihood of survival of a juvenile predator is its ability to avoid being killed. This can be partially achieved via a large voracity as by eating a lot larvae become strong and better able to defend themselves, but is most likely more determined by adults avoiding ovipositing in “*dangerous*” patches. Which patches are “*dangerous*”? Most insect predators are cannibalistic (FOX 1975; OSAWA 1989, 1992a, 1992b, 1993; DIXON 2000). This is a strong selective force: on meeting another predator that is edible, belongs to a different genotype and is weaker than the potential cannibal, it is advantageous to eat it, as it is a source of energy and a potential competitor for food. Thus non-sibling cannibalism is undoubtedly advantageous. Even sibling cannibalism may have a selective advantage, if prey becomes scarce (OSAWA 1989, 1992b). If cannibalism is an important cause of mortality in insect predators, then genotypes that are able to

use cues that enable them to avoid being eaten by other conspecific predators will be strongly selected for. This prediction is empirically supported by the discovery of a pheromone that deters adults of many different groups of predatory insects from ovipositing in patches of prey contaminated with conspecific larval tracks (HEMPTINNE et al. 1992; DOUMBIA et al. 1998).

Avoiding oviposition in patches that are being attacked by larvae of predators could be important for another reason: presence of larvae is an indicator of the age of a patch of prey. Predators need some time to find a patch and the existence of larvae in a patch means that the patch must have existed for at least E time units ago, where E is the developmental time of the egg. In contrast the probability that a patch is not found by a predator clearly declines with the age of the patch. Therefore, a patch that has not yet been found by a predator is not likely to exist for long. Existence of predatory larvae in a patch of prey may indicate there is insufficient time for offspring, to complete their development because the patch is in a relatively advanced stage of development.

Thus the reason why adults migrate between prey patches so frequently is that it enables them to optimise the distribution of their eggs (numerical response), rather than optimise foraging in the terms of maximising food consumption per unit time (functional response). This numerical response, however, differs from that normally used as it reflects the ages of patches of a prey, rather than the amount of food they contain. It is surprising that this was completely ignored in the models of predator-prey population dynamics.

GENERATION TIME RATIO

Ovipositing during the short egg window early in the existence of a patch of prey is advantageous, only if developmental time of the predator is comparable with the average duration of patches of prey. If the generation time of the organism consuming the prey is short, then this advantage disappears, as there is no penalty for reproducing late. This is the case, e.g., of insect parasites, the developmental time of which is comparable with

that of their host and which are therefore able to complete several generations during the existence of a patch of prey. Adults of each generation redistribute themselves: they can either oviposit in the patch where they were born, if there are not many competitors and a lot of prey. However, they can also fly away and reproduce in another patch of prey. Therefore, short lived predators (like parasites) have several opportunities during the existence of a patch of prey to “adjust their strategy”: by ovipositing or flying away they can respond to changes in prey abundance and therefore deplete the patch more effectively – a possibility not available to predators that complete only one generation in a patch.

The situation is similar to an aircraft trying to follow the terrain: a slow flying aircraft (short-lived predator) can adjust its trajectory to the changes in the terrain much better than a fast flying one (long-lived predator). Thus in long-lived predators selection favours those individuals that are able to select patches for oviposition that contain sufficient prey and which will remain abundant for long enough to sustain its larvae (which results in egg windows etc.). These predators are unlikely to reduce prey abundance to the same extent as short-lived predators. In other words, if the ratio of the developmental time of the predator to that of its prey (“*generation time ratio*”, GTR – KINDLMANN & DIXON 1999) is large, then from an evolutionary perspective the predator has to “project” far into the future. If the existence of a patch of prey is limited in time, then it is advantageous for predators to lay eggs early in the existence of a patch, as future prey availability is uncertain. This uncertainty also makes cannibalism advantageous. Because of the risk of cannibalism, predators tend to lay fewer eggs in a patch, but continue to oviposit until cues indicate that it is highly likely that their eggs will be eaten by conspecific larvae. This is when the “egg window” closes and ovipositing predators abandon a prey patch. Cannibalism thus acts to regulate the numbers of predators per patch (MILLS 1982).

THE PREDATOR – PREY MODEL

Biological Assumptions

Insect herbivores have frequently been observed to first increase and then decline in abundance, even in the absence of natural enemies (DIXON 1997, 2000). As explained above, such declines are not likely to be due to regulation by predators. It was shown that prey individuals respond negatively to either lowering the carrying capacity of their host plant (deterioration of food quality during the season) or to their cumulative density, or to both by emigrating from patches and colonizing empty patches (KINDLMANN & DIXON 1996, 1997). Here we assume that the regulatory term for prey, when alone, is its cumulative density, h , instead of some function of its instantaneous density. In contrast to the logistic or exponential growth models, this function allows prey to decline in abundance with increasing time even in the absence of natural enemies. Analysis of other alternatives can be found in KINDLMANN et al. (2003).

We assume that predators only oviposit during the egg window early in the development of patches of prey. We follow the dynamics within a patch of prey from the instant when the egg window closes. Thus the initial density of a predator in a patch is defined by the number of eggs laid there by adults that developed in other patches of prey and oviposited there during the “egg window”. Changes over time in the number of predators within a patch are assumed to be due to larval cannibalism and not reproduction.

We assume the predator is cannibalistic but has a preference, p , for eating prey, as opposed to conspecifics. If they prefer prey, then $p > 1$, but p may also be smaller than one, as for example when the larvae of a predator prefer to eat conspecific eggs, which cannot defend themselves. If $p = 1$, the predator shows no preference for either prey or conspecifics (the “*meet and eat*” hypothesis).

Between-season dynamics are determined by

iterating the within-season dynamics. In this illustrative example we assume that the predator is univoltine, its prey achieves only one peak in abundance during a season and that both predator and prey redistribute themselves uniformly between seasons, so that the initial numbers of both predator and prey are the same for all patches. The numbers of prey next spring is calculated by multiplying its autumn numbers by winter mortality, and that of the predator by multiplying its autumn numbers by winter mortality and its fecundity. Between seasons both prey and predators redistribute themselves among the many patches that make up the population.

Within-Season Dynamics

Within-season, the dynamics of insect predator - prey system can be described by (KINDLMANN & DIXON 1993, 2002):

$$\frac{dh}{dt} = ax, \quad h(0) = 0 \quad (1a)$$

$$\frac{dx}{dt} = (r - h)x - \frac{vpxy}{b + px + y}, \quad x(0) = x_0 \quad (1b)$$

$$\frac{dy}{dt} = -\frac{vy^2}{b + px + y}, \quad y(0) = y_0 \quad (1c)$$

where:

- $h(t)$ - cumulative density of the prey at time t
- $x(t)$ - density of prey at time t
- a - scaling constant relating prey cumulative density to its own dynamics
- r - maximum potential growth rate of the prey
- $y(t)$ - density of predator at time t
- v - predator voracity
- b - parameter of the functional response of the predator
- p - predator's preference for prey
- T - time when predator matures; coincides with the duration of a patch of prey, yielding initial values $x(T)$ and $y(T)$ for the next season.

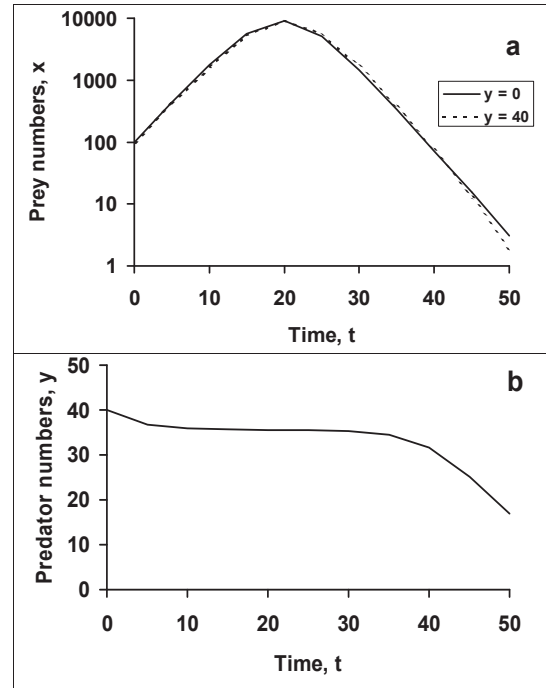


Fig. 1. Trends in time in prey (a) and predator (b) abundance predicted by the model when $a = .000005$, $r = .3$, $v = 1$, $b = 0$, $p = 1$, $x_0 = 100$, $y_0 = 0$ and $y_0 = 40$. In (a) prey density in the absence of predators and the presence of 40 predators (see inset) is also presented.

Equation (1a) describes changes in cumulative density of prey, (1b) describes changes in prey density, and (1c) describes the decrease in predator density due to cannibalism. A typical trend in numbers in a patch predicted by model (1) is shown in Fig. 1. There is no further predator reproduction in a patch; therefore, predator numbers monotonously decline. As a consequence, if prey abundance (x) increases at the beginning (i.e., if y_0 is sufficiently small, so that $\lim_{t \rightarrow 0^+} \frac{dx}{dt} < 0$), then as time proceeds the dynamics of the prey is less and less influenced by the declining numbers of the predator. Because of the way the diet of the predator is defined (the terms containing v in [1b] and [1c]), the decline in predator numbers is more pronounced when there are few prey individuals relative to predator individuals. That is, when the ratio x/y is small at the beginning and when prey numbers have

passed their peak and become small again due to the negative effect of cumulative density. Predators have almost no influence on the prey dynamics in this system (KINDLMANN & DIXON 1993). Not surprisingly, the number of predators that survive is positively influenced by the initial number of prey and negatively influenced by the initial number of predators (KINDLMANN et al. unpub.).

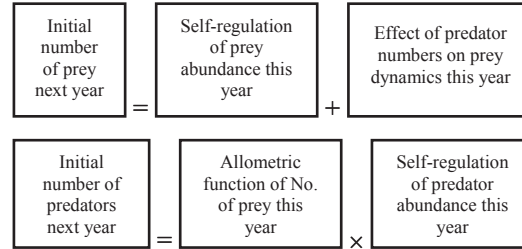
The predicted trends in abundance (Fig. 1) closely match those observed in nature in aphids (DIXON et al. 1996; KINDLMANN & DIXON 1996, 1997; DIXON & KINDLMANN 1998; KINDLMANN et al. 2003) and ladybird beetles (OSAWA 1993; HIRONORI & KATSUHIRO 1997; YASUDA & OHNUMA 1999; KINDLMANN et al. 2000; YASUDA et al. 2004).

Between-Season Dynamics

The above equations (1) translate the initial prey and predator numbers ($x[0]$ and $y[0]$) into their final numbers ($x[T]$ and $y[T]$) at the end of the season. Between-season dynamics of this system can then be obtained iteratively: If we denote the total number of prey and the total number of predators in a population consisting of n patches at the beginning of the year t , by x_t and y_t , respectively, and if $x_t = n \cdot x(0)$ and $y_t = n \cdot y(0)$, then $x_{t+1} = n \cdot d_x \cdot x(T)$ and $y_{t+1} = n \cdot d_y \cdot f \cdot y(T)$, where d_x and d_y are the probabilities of prey and predators, respectively, surviving from the end of one season to the beginning of the next and f is predator fecundity. It is not possible to derive the exact relations between x_t and y_t and x_{t+1} and y_{t+1} from model (1), but approximate relations were obtained by KINDLMANN & DIXON (2002), who linearised the dependence by making $X_t = \ln(x_t)$ and $Y_t = \ln(y_t)$. This results in the following system of difference equations:

$$\begin{aligned} X_{t+1} &= a_1 - b_1 X_t + (c_1 - d_1 X_t) \cdot Y_t \\ Y_{t+1} &= a_2 X_t^{b_2} \cdot (c_2 Y_t - d_2 Y_t^2) \end{aligned} \quad (2)$$

Biologically:



In this system when predators are absent, the number of prey next year increases when the number of prey this year is low, but is strongly regulated by itself ($X_{t+1} = a_1 - b_1 X_t$). Influence of the predator on prey dynamics is expressed by the term $(c_1 - d_1 X_t) \cdot Y_t$. The number of predators next year is positively, but less than linearly, influenced by the number of prey this year (see the term $a_2 X_t^{b_2}$). The shape of the between-season relation in the number of predators is parabolic, indicating that predators do best at intermediate densities - when there are few predators, few of them survive, and because of cannibalism, few survive even when they are initially numerous.

CONCLUSIONS

To conclude, in situations where the developmental time of the predator is long relative to its prey, predators are unlikely to be effective classical biological control agents. This is because the predator abundance is strongly regulated by cannibalism (KINDLMANN & DIXON 2001). This is well illustrated by the aphidophagous ladybird - aphid system.

REFERENCES

- AGARWALA, B.K. & A.F.G. DIXON 1992. Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecoogical Entomology* 17: 303-309.
 BEDDINGTON, J.R., C.A. FREE & J.H. LAWTON 1976. Concepts of stability and resilience in predator-prey models. *Jornal of Animal Ecology* 45: 791-816.

- BEDDINGTON, J.R., C.A. FREE & J.H. LAWTON 1978. Characteristics of successful natural enemies in models of biological control of insect pests. *Nature* 273: 513-519.
- DIXON, A.F.G. 1997. *Aphid ecology: an optimization approach*. London, UK: Chapman and Hall. 312 pp.
- DIXON, A.F.G. 2000. *Insect predator-prey dynamics ladybird beetles and biological control*. Cambridge, UK: Cambridge University Press. 257 pp.
- DIXON A.F.G. & P. KINDLMANN 1998. Population dynamics of aphids. Pp. 207-230 in J.P. DEMPSTER & I.F.G. MACLEAN (Eds). *Insect populations*. Dordrecht, The Netherlands: Kluwer Academic Publishers. 512 pp.
- DIXON, A.F.G., P. KINDLMANN & R. SEQUEIRA 1996. Population regulation in aphids. Pp. 77-88 in R.B. FLOYD, A.W. SHEPPARD & P.J. DEBARRO (Eds). *Frontiers of population ecology*. Melbourne, Australia: CSIRO Publishing. 639 pp.
- DOUMBIA, M., J.L. HEMPTINNE & A.F.G. DIXON 1998. Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia* 113: 197-202.
- FOX, L.R. 1975. Cannibalism in natural populations. *Annual Review of Ecology and Systematics* 6: 87-106.
- GODFRAY, H.C.J. & M.P. HASSELL 1987. Natural enemies may be a cause of discrete generations in tropical insects. *Nature* 327: 144-147.
- HASSELL, M.P. 1978. *The dynamics of arthropod predator-prey systems*. Princeton, NJ: Princeton University Press. 237 pp.
- HEMPTINNE, J.L., A.F.G. DIXON & J. COFFIN 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* 90: 238-245.
- HIRONORI, Y. & S. KATSUHIRO 1997. Cannibalism and interspecific predation in two predatory ladybird beetles in relation to prey abundance in the field. *Entomophaga* 42: 153-163.
- KINDLMANN, P. & A.F.G. DIXON 1993. Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. *European Journal of Entomology* 90: 443-450.
- KINDLMANN, P. & A.F.G. DIXON 1996. Population dynamics of tree-dwelling aphids: from individuals to populations. *Ecological Modelling* 89: 23-30.
- KINDLMANN, P. & A.F.G. DIXON 1997. Patterns in the population dynamics of the Turkey-oak aphid. Pp. 219-225 in J.M. NIETO NAFRIA & A.F.G. DIXON (Eds). *Aphids in natural and managed ecosystems*. Leon, Spain: Universidad de Leon. 688 pp.
- KINDLMANN, P. & A.F.G. DIXON 1999. Generation time ratios - determinants of prey abundance in insect predator - prey interactions. *Biological Control* 16: 133-138.
- KINDLMANN, P. & A.F.G. DIXON 2001. When and why top-down regulation fails in arthropod predator-prey systems. *Basic and Applied Ecology* 2: 333-340.
- KINDLMANN, P. & A.F.G. DIXON 2003. Insect predator-prey dynamics and the biological control of aphids by ladybirds. pp. 118-124 in R. VAN DRIESCHE (Ed). *International symposium on biological control of arthropods*. USDA Forest Service, publication FHTET-03-05.
- KINDLMANN, P., A.F.G. DIXON & V. JAROSIK *in press*. Population dynamics. in H. VAN EMDEN & R. HARRINGTON (Eds). *Aphids as insect pests*.
- KINDLMANN, P., H. YASUDA S. SATO & K. SHINYA 2000. Key life stages of two predatory ladybird species. *European Journal of Entomology* 97: 495-499.
- MILLS, N.J. 1982. Voracity, cannibalism and coccinellid predation. *Annals of Applied Biology* 101: 14-148.
- MURDOCH, W.W. 1994. Population regulation in theory and practice. *Ecology* 75: 271-287.
- OSAWA, N. 1989. Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in the field. *Research in Population Ecology* 31: 153-160.
- OSAWA, N. 1992a. Sibling cannibalism in the lady beetle *Harmonia axyridis*: fitness consequences for mother and offspring. *Research in Population Ecology* 34: 45-55.
- OSAWA, N. 1992b. Effect of pupation site on pupa; cannibalism and parasitism in the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Japanese Journal of Entomology* 60: 131-135.
- OSAWA, N. 1993. Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life tables and key factor analysis. *Research in Population Ecology* 35: 335-348.
- YASUDA, H. & N. OHNUMA 1999. Effect of cannibalism and predation on the larval performance of two ladybirds. *Entomologia Experimentalis et Applicata* 93: 63-67.
- YASUDA H., P. KINDLMANN, K. SHINYA & S. SATO *in press*. Intra- and interspecific interactions on survival of two predatory ladybirds in relation to prey abundance: competition or predation. *Applied Entomology and Zoology*.

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OVIPOSITION BEHAVIOUR OF THE TWO-SPOT LADYBIRD BEETLE *Adalia bipunctata* (L.) (COLEOPTERA: COCCINELLIDAE) ON PLANTS WITH CONSPECIFIC LARVAL TRACKS.

B. FRÉCHETTE, C. ALAUZET & J.-L. HEMPTINNE

FRÉCHETTE, B., C. ALAUZET & J.-L. HEMPTINNE 2003. Oviposition behaviour of the two-spot ladybird beetle *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) on plants with conspecific larval tracks. Pp. 73-77 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

There are many laboratory studies on the oviposition-deterring effect of conspecific larval tracks on the two-spot ladybird beetle, *Adalia bipunctata* (L.). However, this phenomenon has not been studied in the field. In near natural field conditions *A. bipunctata* foraging on aphid infested plants, with or without conspecific larval tracks, were reluctant to lay eggs on and quickly left the plants with conspecific larval tracks compared to the control plants. The results of this study indicate that *A. bipunctata* reacts to conspecific larval tracks on plants in near natural conditions, as they do in the laboratory.

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INTRODUCTION

Aphidophagous ladybird beetles seeking oviposition sites have to move between patches of aphids, evaluate patch quality and decide whether to feed and/or lay eggs. Patch quality is important since it determines the probability of survival of their progeny (KINDLMANN & DIXON 1993, 1999).

Ladybirds should avoid ovipositing in patches of aphids that are already exploited by conspecific larvae. Laying eggs in such patches will greatly increase the risk of cannibalism (MILLS 1982), which is an important mortality factor in natural population of several species of ladybird beetles (OSAWA 1989, 1993; HIRONORI & KATSUHIRO 1997).

Many field observations indicate that ladybird eggs are often laid near aphid colonies that are in an early phase of development (BANKS 1955; HEMPTINNE et al. 1992). These and other

observations led KINDLMANN & DIXON (1993, 1999) to propose that there is in the development of aphid patches a time, "egg window", when it is most advantageous for ladybirds to lay their eggs. This stresses the importance of the age of an aphid colony in determining its suitability for oviposition. Since ladybird larvae and aphid colonies have similar development times, the theory stipulates that ladybird should lay a limited number of eggs early in the development of aphid colonies. If eggs are laid later the aphid colony might disperse and disappear before the ladybird larvae complete their development. In the absence of food the risk of cannibalism greatly increases (AGARWALA & DIXON 1992).

Females of the two-spot ladybird beetle, *Adalia bipunctata* (L.), do not use the age structure of aphid colonies to assess their quality as oviposition sites (HEMPTINNE et al. 2000). However, in Petri dishes they refrain from ovipositing when confined with conspecific

larvae or adults (HEMPTINNE et al. 1992), or on substrates contaminated with conspecific larval tracks (DOUMBIA et al. 1998).

The oviposition-detering effect of larvae on the reproductive behaviour of aphidophagous was first described for *Adalia bipunctata* L. by HEMPTINNE et al. (1992) and that it was their larval tracks for *Chrysopa oculata* Say by RŮŽIČKA (1994). Subsequently the same phenomenon was recorded for many species of chrysopids (RŮŽIČKA 1996, 1997a, 1997b, 1998), ladybirds (RŮŽIČKA 1997b, 2001; YASUDA et al. 2000; HEMPTINNE et al. 2001) and the cecidomyiid fly *Aphidoletes aphidimyza* (Rondani) (RŮŽIČKA & HAVELKA 1998).

The experiments on the reproductive behaviour of the two-spot ladybird beetle *A. bipunctata* were done in the laboratory. The goal of this study was to determine the oviposition response of *A. bipunctata* in near natural conditions on broad bean plants contaminated with larval tracks.

YASUDA et al. (2000) counted the number of eggs laid by *Harmonia axyridis* Pallas on plants previously walked on by larvae of *H. axyridis* and *Coccinella septempunctata* L. This study was done in cages and the behaviour of the females was not observed. HEMPTINNE et al. (1992) observed that *A. bipunctata* confined in Petri dishes with conspecific larvae were more active than control beetles. Therefore, we also recorded the behaviour of the females.

MATERIALS & METHODS

Ladybirds

The eggs of the two-spot ladybird, *A. bipunctata*, were obtained from a stock culture. Larvae were reared at $20 \pm 1^\circ\text{C}$, LD 16:8, and fed an excess of pea aphids, *Acyrtosiphon pisum* Harris. Adults were isolated within 24 hours of their emergence from pupa. When their integuments had hardened, their sex was determined and they were kept in male female pairs. Every day, these pairs of adults were put in clean Petri dishes with a piece of corrugated paper and an excess of pea aphids;

any eggs laid were counted and removed daily. Ladybirds selected for the experiment were between 10-20 days old and had laid at least one egg batch in the last 5 consecutive days.

Bean plants

Broad-bean plants, *Vicia faba* L., used in the experiment were about 15 cm high and had 6 leaves. Experimental plants were those on which 5 fourth instar larvae had walked for 45 minutes 16 hours before the beginning of the experiment. Both control and experimental plants were then infested with about 100 aphids and left for 15 hours for the aphids to settle.

Experiments

Experiments were performed outdoors in the shade between 10:00 am and 1:00 pm in June and July 2001 and 2002. One female was released at the base of a bean plant and (1) whether or not it laid eggs, (2) the time spent *Walking*, *Resting*, *Eating* and *Ovipositing* and (3) its residence time were recorded. Whether the beetles walked or flew off the plants was also recorded. Mean temperature at the beginning of the experiment was $22.3 \pm 0.3^\circ\text{C}$. There were 40 replicates for each treatment.

Statistical analysis

Differences in proportions were compared using Pearson tests. Percentages were arcsin transformed before analysis and then compared using a t-test or a Wilcoxon test if the distribution of the results was not normal according to the Shapiro-Wilk test. All analysis were made using Jmp In® (SALL et al. 2001). For the residence times, the values for experimental and control beans were sorted into three categories: *short* (0-60 min), *medium* (60-120 min) or *long residence times* (more than 120 min). The distributions of frequencies were compared using a Log Likelihood Ratio test computed by hand following ZAR (1996).

RESULTS

Oviposition

A significantly greater proportion of females laid eggs on control than on experimental plants (Fig. 1; Pearson: $\chi^2=11.114$; $df=1$; $p=0.0009$). Only one female (2.5%) laid eggs on an experimental plant.

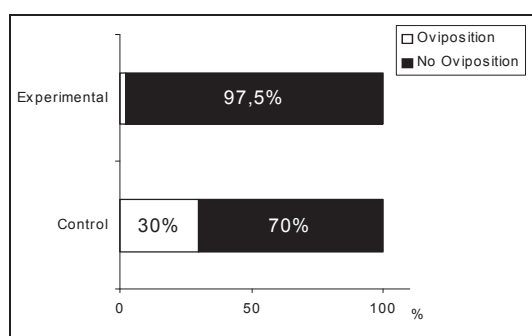


Fig. 1. The percentage of *A. bipunctata* females that laid eggs on control and experimental plants.

Residence time

Ladybirds tended to stay for a shorter period of time (0-60 min) on experimental plants than on control plants (Figure 2; Log Likelihood Ratio: $G=8.48$; $df=2$; $p<0.05$).

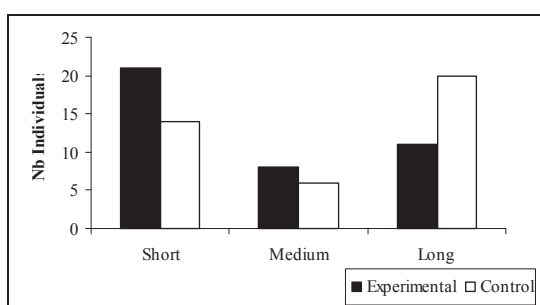


Fig. 2. The number of *A. bipunctata* females that had short, medium, and long residence times on control and experimental plants.

Behaviour

Only the behaviour of beetles that stayed at least 30min on the plants ($n=30$ for control, $n=26$ for experimental) was analysed. Other than in the

percentage of the time allocated to *Oviposition* (Wilcoxon: $\chi^2=7.9929$; $df=1$; $p=0.0047$), there were no significant differences in that allocated to *Walking* (t-test: $F=0.9087$; $df=1$; $p=0.3447$), *Resting* (t-test: $F=0.0060$; $df=1$; $p=0.9387$) or *Eating* (t-test: $F=0.0991$; $df=1$; $p=0.7541$) (Fig. 3). In both treatments, a similar percentage of beetles (12.5%) left the plants without eating, while 87.5% ate at least one aphid. Of the females that laid eggs and completed oviposition before the experiment ended, 80% (8 out of 10) ate at least 1 aphid before leaving the plant.

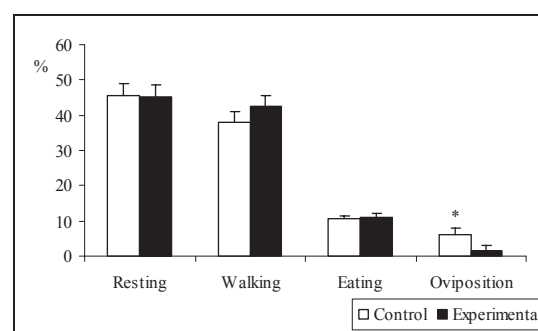


Fig. 3. The percentage of time spent in different activities by *A. bipunctata* females on control and experimental plants. Significant difference ($p<0.05$) is indicated by an asterisk (*).

Way of leaving the plants

Of the ladybirds that left plants before the end of 3 hours ($n=24$ for control plants, $n=31$ for experimental plants) most left by flying (70.8% for control plants, 77.4% for experimental plants), and the rest by walking (29.2% for control plants, 22.6% for experimental plants). The differences in percentages between treatments were not significant (Pearson: $\chi^2=0.309$; $df=1$; $p=0.5782$).

However, temperature had a significant effect on the tendency to fly (Pearson: $\chi^2=8.744$; $df=1$; $p=0.0031$). For both treatments combined, the percentage flying was significantly higher at $\geq 21^\circ\text{C}$ (83.7%, $n=43$) than at $< 21^\circ\text{C}$ (41.7%, $n=12$).

DISCUSSION

This study provides strong evidence that the effects of the pheromone in larval tracks on the

oviposition behaviour of *A. bipunctata* observed in the laboratory are also relevant to natural conditions. *A. bipunctata* females leave earlier and are reluctant to lay eggs on plants on which conspecific larvae have previously walked, even if food is abundant.

However, the agitated behaviour observed by HEMPTINNE et al. (1992) was not observed in this study. Females spend the same percentage of time walking, resting and eating on both control and experimental plants. Moreover, even though females tended to leave experimental plants earlier than control plants, the same percentage (87.5%) ate at least one aphid before leaving in both treatments. This indicates that females may refrain from ovipositing on aphid infested bean plants with larval tracks, but will stay on these plants and feed when hungry. That is, the only difference in behaviour was the acceptance or rejection of the plant as an oviposition site.

Even though the results clearly demonstrate that larval tracks deter oviposition, the low percentage of females that laid eggs on control plants (30%) is worrying. The reason may be that the ladybirds used in the experiment were not all equally 'ready' to oviposit within the 3 hour observation period. It is possible that female foraging behaviour depends on some intrinsic conditions, such as their egg load (MIKENBERG et al. 1992). A female that is not ready to oviposit may respond differently to environmental cues than one that is about to lay eggs. In addition, a female that takes a long time to find a 'suitable' site for oviposition may accept a site that she would have normally rejected as in HEMPTINNE et al. (1992). There is need for a better understanding of the physiological ecology of ladybirds.

A better knowledge of a ladybird's oviposition cycle could lead an improvement in experimental design and clearer results. Working only with beetles ready to, but not desperate to oviposit may result in a greater percentage ovipositing.

The response of adult ladybirds to larval tracks could help to explain how ladybirds distribute themselves in the environment. It may account for why even in patches of high aphid density there are often few ladybird eggs. For example, there is not a density dependent increase in oviposition by *A. bipunctata* in response to an

increase in abundance of its aphid prey on lime trees in the field (WRATTEN 1973). When cereal aphid density is augmented in wheat fields there is an augmentation in the adult numbers of both *Hippodamia convergens* Guérin-Méneville and *C. septempunctata*, but egg density is very low and about the same in both augmented and control patches of prey (ELLIOTT & KIECKHEFER 2000).

The effect of larval tracks on the distribution of aphidophagous ladybirds could affect their potential as biological control agents. By only laying a few eggs early in the development of an aphid colony (KINDLMANN & DIXON 1993), ladybirds are unable to marked aggregative response to patches of prey, a characteristic feature of effective biological control agent (BEDDINGTON et al. 1978).

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REFERENCES

- AGARWALA, B.K. & A.F.G. DIXON 1992. Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecological Entomology* 17: 303-309.
- BANKS, C.J. 1955. An ecological study of Coccinellidae (Col.) associated with *Aphis fabae* Scop. on *Vicia faba*. *Bulletin of Entomological Research* 46: 561-587.
- BEDDINGTON, J.R., C.A. FREE & J.H. LAWTON 1978. Characteristics of successful natural enemies in models of biological control of insect pests. *Nature* 273: 513-519.
- DOUMBIA, M., J.-L. HEMPTINNE & A.F.G. DIXON 1998. Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia* 113: 197-202.
- ELLIOTT, N.C. & R.W. KIECKHEFER 2000. Response by coccinellids to spatial variation in cereal aphid density. *Population Ecology* 42: 81-90.
- HEMPTINNE, J.-L., A.F.G. DIXON & J. COFFIN 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* 90: 238-245.

- HEMPTINNE, J.-L., M. DOUMBIA & A.F.G. DIXON 2000. Assessment of patch quality by ladybirds: role of aphid and plant phenology. *Journal of Insect Behavior* 13: 353-359.
- HEMPTINNE, J.-L., G. LOGNAY, M. DOUMBIA & A.F.G. DIXON 2001. Chemical nature and persistence of the oviposition deterring pheromone in the tracks of the larvae of the two spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). *Chemoecology* 11: 43-47.
- HIRONORI, Y. & S. KATSUHIRO 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42: 153-163.
- KINDLMANN, P. & A.F.G. DIXON 1993. Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. *European Journal of Entomology* 90: 443-450.
- KINDLMANN, P. & A.F.G. DIXON 1999. Strategies of aphidophagous predators: lesson for modelling insect predator-prey dynamics. *Journal of Applied Entomology* 123: 397-399.
- MIKENBERG, O.P.J.M., M. TATAR & J.A. ROSENHEIM 1992. Egg load as a major source of variability in insect foraging and oviposition behavior. *Oikos* 65: 134-142.
- MILLS, N.J. 1982. Voracity, cannibalism and coccinellid predation. *Annals of Applied Biology* 101: 144-148.
- OSAWA, N. 1989. Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in the field. *Researches on Population Ecology* 31: 153-160.
- OSAWA, N. 1993. Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life tables and key factor analysis. *Researches on Population Ecology* 35: 335-348.
- RŮŽIČKA, Z. 1994. Oviposition-deterring pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae). *European Journal of Entomology* 91: 361-370.
- RŮŽIČKA, Z. 1996. Oviposition-deterring pheromone in chrysopid: intra- and interspecific effects. *European Journal of Entomology* 93: 161-166.
- RŮŽIČKA, Z. 1997a. Persistence of the oviposition-deterring pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae). *Entomophaga* 42: 109-114.
- RŮŽIČKA, Z. 1997b. Recognition of oviposition deterring allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae). *European Journal of Entomology* 94: 431-434.
- RŮŽIČKA, Z. 1998. Further evidence of oviposition-deterring allomone in chrysopids (Neuroptera: Chrysopidae). *European Journal of Entomology* 95: 35-39.
- RŮŽIČKA, Z. 2001. Oviposition responses of aphidophagous coccinellids to tracks of coccinellid (Coccinellidae) and chrysopid (Chrysopidae) larvae. *European Journal of Entomology* 98: 183-188.
- RŮŽIČKA, Z. & J. HAVELKA 1998. Effects of oviposition-deterring pheromone and allomones on *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *European Journal of Entomology* 95: 211-216.
- SALL, J., A. LEHMAN & L. CREIGHTON 2001. *JMP® start statistics* (2nd ed.). Pacific Grove (CA): Duxbury. 656 pp.
- WRATTEN, S.D. 1973. The effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the lime aphid, *Eucallipterus tiliacae* L. *Journal of Animal Ecology* 42: 785-802.
- YASUDA, H., T. TAKAGI & K. KOGI 2000. Effect of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology* 97: 551-553.
- ZAR, J.H. 1996. *Biostatistical analysis*. (3rd ed.). Upper Saddle River (NJ): Prentice-Hall International Inc. 718 pp.

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ANT TRAIL: A HIGHWAY FOR *Coccinella magnifica* REDTENBACHER (COLEOPTERA: COCCINELLIDAE)

J.-F. GODEAU, J.-L. HEMPTINNE & J.-C. VERHAEGHE

GODEAU, J.-F., J.-L. HEMPTINNE & J.-C. VERHAEGHE 2003. Ant trail: a highway for *Coccinella magnifica* Redtenbacher (Coleoptera: Coccinellidae). Pp. 79-83 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

Red Wood Ant species chemically mark trails connecting their nest to aphid colonies. The trail pheromones are produced in the ant's hindgut. The large trails are maintained thanks to visual clue and because new pheromone marks are regularly laid down. As a consequence, Red Wood Ant's workers create a network of trails equivalent to hundreds of meters around every nest mound. *Coccinella magnifica* is an aphidophagous ladybird species living only in the vicinity of Red Wood ant's nests. It preys upon aphid colonies regardless of ant's presence. We show here that, in the laboratory, *C. magnifica* can follow a recruitment trail laid down by *Formica polyctena* under artificial conditions with its hindgut's pheromone. This is confirmed by field observations of ladybirds walking along natural Red Wood Ant's trails. As *C. magnifica* appears to be a specialist, this behaviour is adaptive to efficiently locate prey.

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INTRODUCTION

In most temperate forests, lives a well-known ant species: the red wood ant (*Formica rufa sensu lato*) which is a taxonomical complex including some ecological species separated by their habitat preferences (YARROW 1955; SEIFERT 1996). It lives in large colonies whose nests are built as a hillock of dead plant fragments. This mound can reach 1.5 to 2 meters high and shelter hundreds of thousands ant individuals (HÖLLDOBLER & WILSON 1990). The other striking aspect of that ant are their wide foraging trails, linking the nest to food resources scattered in the surrounding (SKINNER 1980). Trails are marked by workers which use chemical pheromones probably produced in the hindgut and in other glands (GABBA & PAVAN 1970; PARRY & MORGAN 1979; ATTYGALE & MORGAN 1984). Moreover, visual cues have been demonstrated to play an

important role in red wood ants orientation.

Ants are largely known as invertebrate predators but they also gather honeydew and occasionally prey upon aphids dwelling in trees and shrubs (e.g. WAY 1963; SKINNER 1980).

What are the relationships between ants, aphids and aphid predators?

Since more than half a century, it is largely admitted that ants increase attended aphid populations by cleaning the honeydew droplets glued on the colony and by protecting them against intruders, especially ladybirds, lacewings, bugs and syrphids (e.g. BANKS 1962; WAY 1963; HÖLLDOBLER & WILSON 1990).

Ladybirds found in red wood ant's habitat are mainly woodland-specialised species whose adults and larvae feed on tree aphids. In comparison with open areas, aphid resources are more dispersed vertically in the forest vegetation stages. All these hotspots of attended aphids are

where N_c = number of marked squares crossed by the ladybird, N_a = total number of marked squares and N_b = total number of squares crossed by the ladybird.

Occupation time of each square was also measured as an estimation of walk speed.

Each adult was firstly tested with a marked cardboard and then presented with an unmarked cardboard. There were 9 replicates with the ant trails and 8 with a clean cardboard.

Tests with an artificial circular trail

In the second experiment, we aimed at confirming our first results and obtaining more precise information about the nature of the observed ant-trail. We made an artificial circular trail, by dissecting ants, extracting the gland which produces the trail pheromones. Ant workers were collected on the foraging trails from the laboratory nest and dissected one by one under water, with ophthalmologic dissection tools. When one hindgut was isolated, it was transferred to 75 ml water and crushed. The results of five dissections were gathered and deposited on a strong filter paper with a Stadler® metallic pen. This method, described by Pasteels and VERHAEGHE (1974), has already been used in numerous trail-following experiments with ants and other invertebrates (CAMMAERTS et al. 1990; LENOIR et al. 1991; QUINET & PASTEELS 1995).

The 12-cm diameter circular trail on a filter paper was put in a circular arena of 25-cm in diameter and left for 10 minutes before the beginning of the tests. Two identical sequences of tests have been performed with the same trail: (1) four ants observed during two minutes; (2) four ladybirds (*C. magnifica* or *C. septempunctata*) during four minutes; (3) four ladybirds of the second species (*C. septempunctata* or *C. magnifica*) during four minutes; (4) four ants observed again during two minutes to check out whether the trail is still active. The first sequence took place 10 min after the trail has been laid down and the second 70 min later.

The artificial trail was compared to a control trail obtained with pure water. The sequence of tests was replicated 5 times with the trail and 4 times with the control.

All these observations were filmed and analysed afterward. For each sequence, the detection rate was measured and the “following score” was noted. The detection rate is the number of times an animal crossed the trail, stopped and eventually followed it. The “following score” is the number of 10° arcs consecutively followed by an insect. This score was log-transformed. Both the detection rates and the “following scores” are presented by their mean. The statistical difference between detection rates is obtained by comparing the proportion of defectives (detection of trail or not) during all tests. The result is a binomial distribution on which we calculated a value for z (NIST/SEMATECH 2003), representing the significance level for the difference between the two proportions (test vs. control). The differences between following scores were tested with a Median test.

RESULTS

Tests with a naturally-laid trail

As the trail is deposited by ants, we assume that the right pheromones are present on the cardboard sheet. In comparison with the control, *C. magnifica* walked more often ($S.I._{Test} = 0.4219$; $S.I._{Control} = 0.0417$; Mann-Whitney $U = 109.0$; $P < 0.01$, Fig. 2) and slower (Median occupation time: marked squares: 2.313 sec; covered squares: 1.259 sec; Mann-Whitney $U = 126.0$, $P < 0.001$ Fig. 3) on trail-marked squares. These results are consistent with an olfactory detection and orientation of *C. magnifica* thanks to *F. polyctena* trail pheromones.

Tests with an artificial circular trail

Over the course of the experiments the quality of the trails deteriorated so that the detection rate of ant F5 was not different in the presence or absence of the pheromone (Table 1). *C. magnifica* show a strong tendency to respond positively to the pheromone and not to the control. On the contrary, the detection rate of *C. septempunctata* is not modified by ant trails.

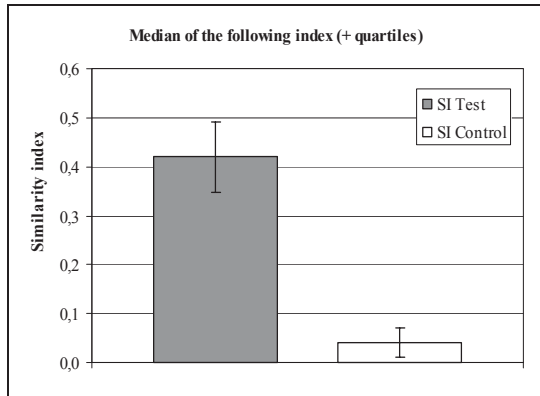


Fig. 2. Following index performed by *C. magnifica* on a marked sheet (in grey) and on control (in white).

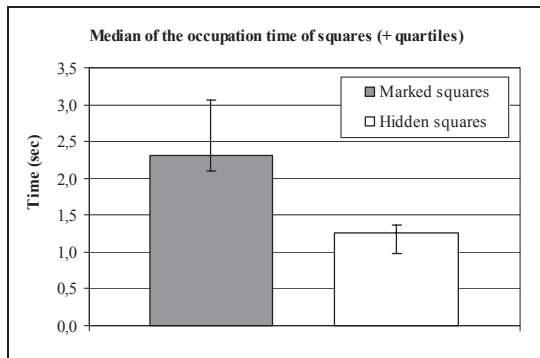


Fig. 3. Occupation time of squares, used as an estimation of walk speed on marked (in grey) and non-marked (in white) squares.

Table 1.

The detection rates of *F. polycytena* (F2, F3, F4 and F5), *C. magnifica* (CM_1 and CM_2) and *C. septempunctata* (C7_1 and C7_2) measured in two sequential experiments

Sequence	Detection rate (%)			
	Test (N=)	Control (N=)	z=	
Nr. 1	F2	60 (225)	45.99 (137)	4.28 (***)
	CM_1	45.78 (166)	36.14 (166)	2.58 (*)
	C7_1	56.25 (64)	51.19 (84)	0.81 (N.S.)
Nr. 2	F3	62.11 (190)	28.26 (92)	2.74 (**)
	F4	57.22 (180)	48.62 (181)	2.31 (*)
	CM_2	41.38 (145)	27.52 (109)	3.74 (***)
	C7_2	35.58 (104)	37.93 (58)	-0.61 (N.S.)
	F5	50.48 (198)	51.48 (154)	-0.61 (N.S.)

For all the insects tested, there was no difference between the “following scores” measured with and without pheromone.

DISCUSSION

In the laboratory, *C. magnifica*, is able to follow a natural foraging trail delineated by pheromone spots.

Artificial trails made up of hindgut extracts are less efficient than natural trails. They, however, trigger detection and trail-following by ants and *C. magnifica*.

Our preliminary results might be confirmed by testing an extract of 10-hindguts instead of 5, expecting a response twice bigger with ants and *C. magnifica*.

Knowledge about pheromones produced by Dufour, poison and mandibular glands are quiet scant in the literature, so that we do not know their respective role in the formation of *F. rufa* foraging trails. Additional tests must be performed to check whether one or more of these glands could be used to enhance trail-following efficiency.

The fact that *C. magnifica* is able to follow ants trails is adaptive because these ladybirds are able to discover and exploit large aphid colonies attended by ants.

This study leads to another question: does the trail pheromone intervenes in mate encountering, selection of oviposition sites and egg laying?

REFERENCES

- ATTYGALE, A. & E.D. MORGAN 1984. Chemicals from the glands of ants. *Chemical Society Reviews* 13: 245-278.
- BANKS, C.J. 1962. Effects of the ant *Lasius niger* (L.) on insects preying on small population of *Aphis fabae* Scop. on bean plants. *Annals of Applied Biology* 50: 669-679.
- CAMMAERTS, R., C. DETRAIN & M.-C. CAMMAERTS 1990. Host trail following by the myrmecophilous beetle *Edaphopausus favieri* (Fairmaire) (Carabidae Paussinae). *Insectes Sociaux* 37 (3): 200-211.
- DONISTHORPE, H.St.J.K. 1920a. The Myrmecophilous Lady-Bird, *Coccinella distincta*, Fald., its Life History and Association with Ants. *The Entomologist's Record* XXXI (12): 214-222.
- DONISTHORPE, H.St.J.K. 1920b. The Myrmecophilous Lady-Bird, *Coccinella distincta*, Fald., its Life History and Association with Ants. *The Entomologist's Record* XXXII (1): 1-3 + II

- GABBA, A & M. PAVAN 1970. Researches on trail and alarm substances in ants. Pp. 161-194 in JOHNSTON, J. W., D. G. MOULTON, AND A. TURK. (Eds). *Advances in chemoreception, Vol. 1. Communication by chemical signals*.
- HÖLDOBLER, B. & E.O. Wilson 1990. *The Ants*. Springer Verlag, Berlin and Heidelberg. 732 pp.
- MAJERUS, M.E.N. 1989. *Coccinella magnifica* (redtenbacher): a myrmecophilous ladybird. *British Journal of Entomological Natural History* 2: 97-106.
- MAJERUS, M.E.N. & P.W.E. KEARNS 1994. Ladybirds. *Naturalist's Handbook* 10: 339pp.
- NIST/SEMATECH *e-Handbook of Statistical Methods*, <http://www.itl.nist.gov/div898/handbook/>, 2003
- PARRY, K. & E.D. MORGAN 1979. Pheromones of ants: a review. *Physiological Entomology* 4: 161-189.
- PASTEELS, J.M. & J.-C. VERHAEGHE 1974. Dosage biologique de la phéromone de piste chez les fourrageuses et les reines de *Myrmica rubra*. *Insectes Sociaux* 21: 167-180.
- QUINET, Y. & J.M. PASTEELS 1995. Trail following and stowaway behaviour of the myrmecophilous staphylinid beetle, *Homoeusa acuminata*, during foraging trips of its host *Lasius fuliginosus* (Hymenoptera: Formicidae). *Insectes Sociaux* 42: 31-44.
- ROSENGREN, R. 1971. Route fidelity, visual memory and recruitment behaviour in foraging Wood ants of the genus *Formica* (Hymenoptera, Formicidae). *Acta Zoologica Fennica* 133: 1-106
- SEIFERT, B. 1996. *Ameisen: beobachten, bestimmen*. Naturbuch. Verlag. 352 pp.
- SKINNER, G.J. 1980. The feeding habits of the Wood-Ant, *Formica rufa* (Hymenoptera: Formicidae) in Limestone woodland in north-west England. *Journal of Animal Ecology* 49: 417-433.
- SLOGGETT, J.J., R.A. WOOD & M.E.N. MAJERUS 1998. Adaptations of *Coccinella magnifica* Redtenbacher, a Myrmecophilous Coccinellid, to Aggression by Wood Ants (*Formica rufa* Group). I. Adult Behavioral Adaptation, Its Ecological Context and Evolution. *Journal of Insect Behavior* 11(6): 889-904.
- SLOGGETT, J.J., A. MANICA, M.J. Day & M.E.N. MAJERUS 1999. Predation of ladybirds (Coleoptera: Coccinellidae) by wood ants, *Formica rufa* L. (Hymenoptera: Formicidae). *Entomologist's Gazette* 50: 217-221.
- VERHAEGHE, J.-C. 1982. Food recruitment in *Tertramorium impurum* (Hymenoptera: Formicidae). *Insectes Sociaux* 29 (1): 67-85.
- WAY, M.J. 1963. Mutualism between ants and honey-producing homoptera. *Annual Review of Entomology* 8: 307-344.
- YARROW, I.H.H. 1955. The british ants allied to *Formica rufa* L. (Hym. Formicidae). *Transaction of the Society for British Entomology* 12 (1): 1-48.

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EFFECTS OF CONSPECIFIC AND HETEROSPECIFIC LARVAL TRACKS ON MOBILITY AND SEARCHING PATTERNS OF *Cycloneda limbifer* SAY (COLEOPTERA: COCCINELLIDAE) FEMALES

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RŮŽIČKA, Z. & R. ZEMEK 2003. Effects of conspecific and heterospecific larval tracks on mobility and searching patterns of *Cycloneda limbifer* Say (Coleoptera: Coccinellidae) females. Pp. 85-93 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

EthoVision, a computerised video tracking system was used to monitor the behaviour of females of an aphidophagous coccinellid *Cycloneda limbifer* Say. Time spent on, and distance walked within 30 minutes, were recorded on simultaneously provided clean substrates and substrates with fresh tracks of conspecific or heterospecific first instar larvae. Females spent longer and walked a greater distance on substrates with fresh tracks of conspecific larvae than on clean substrates. In contrast, females of *C. limbifer* spent less time and walked a shorter distance on substrates with fresh tracks of larvae of the coccinellid *Ceratomegilla (Semiadalia) undecimnotata* (Schneider) than on clean substrates. During the middle period (10-20 minutes) of the tests, the speed of movement of *C. limbifer* females was significantly lower on substrates with conspecific larval tracks, and significantly higher on substrates with tracks of *C. undecimnotata* larvae than on clean substrates. Previous results show a strong intra- and interspecific oviposition-detering effect of fresh larval tracks of these coccinellid species on *C. limbifer*. Results presented paradoxically indicate that the tracks of conspecific larvae significantly increase the time *C. limbifer* spent on a substrate, while those of *C. undecimnotata* larvae decrease it.

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INTRODUCTION

Mechanisms regulating complex behaviour in insects are often found after laborious and time consuming experiments. The incidental discovery of the oviposition-detering effect of the tracks of an aphidophagous insect (RŮŽIČKA 1994) is an exception. It came after a lot of effort had been devoted to investigating spacing in different predators (SOLOMON 1949, 1964; KUCHLEIN 1966; MARKS 1977; HEMPTINNE & DIXON 1991; FERRAN & DIXON 1993).

Tracks of conspecific larvae deter females of many aphidophagous coccinellids from ovipositing (RŮŽIČKA 1997b; DOUMBIA et al. 1998; YASUDA et al. 2000; RŮŽIČKA 2001). Interspecific oviposition-detering effects of larval tracks in coccinellids (RŮŽIČKA 2001) are less frequently recorded than in chrysopids (RŮŽIČKA 1998). Intra- and interspecific oviposition-detering effects of the tracks of first instar larvae were especially strong between the

coccinellids *C. limbifer* and *C. undecimnotata*. The intensity of the oviposition-detering effects of fresh conspecific tracks and tracks of *C. undecimnotata* larvae on *C. limbifer* were similar, but the density of faecal spots on substrates with tracks of *C. undecimnotata* larvae was significantly lower than on clean substrates, that on substrates with fresh conspecific tracks was slightly higher, though not significantly so, than on clean substrates (RŮŽIČKA 2001). This indicates that fresh conspecific tracks only deter *C. limbifer* females from ovipositing, but heterospecific tracks deter them from ovipositing and searching.

In contrast, females of the coccinellid *Harmonia axyridis* Pallas laid fewer eggs and were observed less frequently on plants with tracks of conspecific larvae than with tracks of *Coccinella septempunctata* larvae (YASUDA et al. 2000). The authors suggested that the less time spent on plants contaminated with conspecific than on those with heterospecific tracks may

account for why fewer eggs were laid on plants with conspecific tracks.

Advanced technologies offer reliable ways of monitoring searching behaviour in insects. The new modes of digital data collection provide highly accurate information on insect mobility, which is less dependent on the skill and or time available to researchers. In this study, computerised video monitoring of coccinellid females enabled a more detailed analysis of the effects of oviposition-detering larval tracks.

In order to find out whether repellent effects are associated with the oviposition-detering effects of larval tracks, the searching behaviour of single *C. limbifer* females was compared on simultaneously provided clean substrates and substrates with either conspecific or *C. undecimnotata* larval tracks. The mobility of single females was recorded by EthoVision, a computer-aided automatic video tracking system, which enables continuous monitoring of small objects within selected areas of an arena.

MATERIALS AND METHODS

Insects

Experiments were done using *Cycloneda limbifer* Casey (origin Cuba 1996) and *Ceratomegilla undecimnotata* (Schneider) [= *Semiadalia undecimnotata* (Schneider)] (origin North Bohemia, Czech Republic). Females used in experiments were 10-25 days old. The laboratory culture of *C. limbifer* was reared on *Aphis fabae* Scopoli, and that of *C. undecimnotata* on *Acyrtosiphon pisum* Harris. Cultures of both aphids were maintained on horse bean, *Vicia faba* L.

Experimental design

The effect of larval tracks on the behaviour of

females of the aphidophagous ladybird *C. limbifer* was studied in experiments similar in design to those used previously (RŮŽIČKA 1997b, 2001). The behaviour of a female was monitored on a clean substrate and an adjacent substrate with larval tracks within a circular arena (Fig. 1). The arena was the bottom of glass Petri dish, 18.5 cm in diameter. The rim of the dish was painted with Fluon (polytetrafluorethylene), which prevented the coccinellid from leaving the arena. The test substrates consisted of strips (40 x 200 mm) of transparent plastic sheet transversally folded every 10 mm, which resulted in a total length of 130 mm. The transparency of the material enabled females to be monitored on both the upper and lower surfaces of each strip. The strips were placed parallel and 2.5 cm apart, each inside a 53x145mm rectangle substrate zone, within the monitored circular arena. They were fixed to the bottom of the Petri dish with narrow strips of clear adhesive tape. The substrate zones covered 57% of the area of the circular arena.

In order to ensure recording of females present also on the margin of substrates, the substrate zones around the folded strips were slightly larger than the substrates. The positions of a female on the test substrates and outside substrate zones were recorded for 30 minutes with a computerised video tracking system. The monitoring started three minutes after the female was carefully placed in the centre of the arena. In order to avoid effects of bias the substrates with larval tracks were placed alternately in the left and right rectangles. In addition, blank tests with two clean substrates were carried out to reveal whether females had a preference for one of the two rectangles, which would indicate a bias due to, e.g. temperature, light intensity or geomagnetism. The behaviour of each female was monitored first in a blank test and then, after 5-10 minutes, in a choice test. This was replicated 14 times. No female laid eggs during the tests.

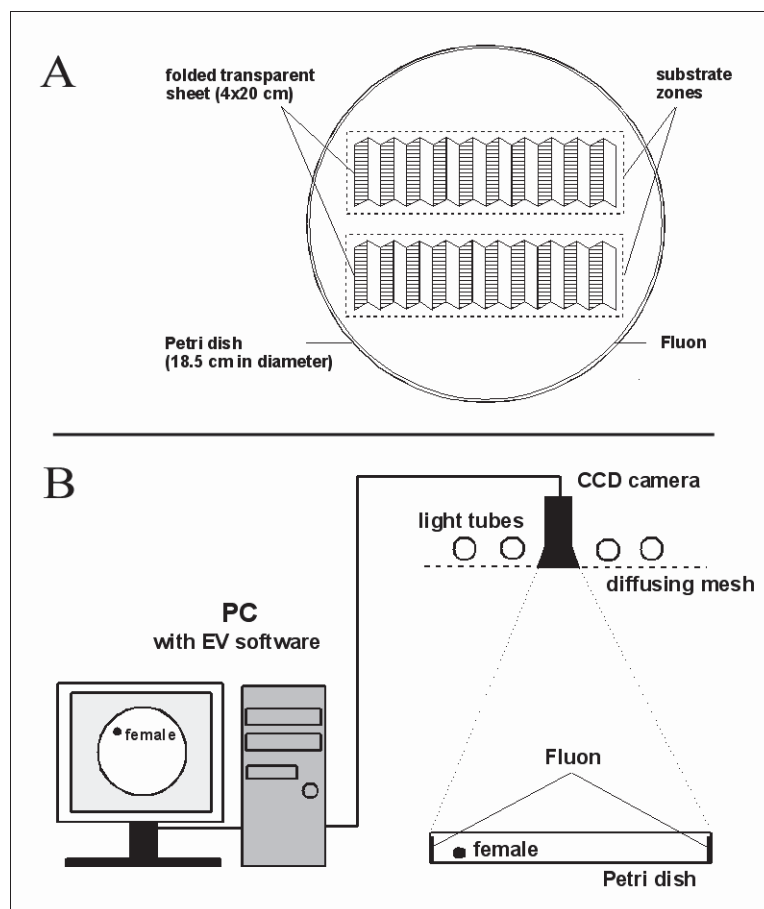


Fig. 1. Diagram of the arena (A) with two substrates and the monitoring apparatus (B). Fluon (polytetrafluorethylene) painted on inner wall of Petri dish.

Contamination with larval tracks

A pair of plastic strips was exposed to 40 unfed first instar conspecific or heterospecific larvae for 4 hours in a Petri dish, 18.5 cm in diameter. The inner rim of the dish was painted with Fluon to keep larvae in the dish. Strips were used for experiments within 6 hours of exposure to larvae.

Video tracking

The experiments were carried out in a dark room (2.6H2.7H2.7 m) illuminated from above by a series of eight 150 cm long fluorescent tubes (Narva LS 65 W-1 coolwhite). Diffused lighting was achieved by placing a thin white cloth under

the lamps. The light intensity at floor level in the arena was 800 Lux. Temperature in the room during the experiments was kept at 26 ± 1 °C. A Petri dish with a beetle in it was placed on a white sheet of paper. White was used to ensure a high contrast between the background and the beetle, necessary for detection by the computer. The experimental arena was scanned by a colour CCD camera equipped with a zoom lens and fixed to the ceiling above the centre of the arena. The composite video signal from the camera was fed into a computerised video tracking system placed outside the room. The recording system consisted of a video monitor (Sony), a computer (486DX2, 66 Mhz) with a frame grabber (Targa Plus, TrueVision) and EthoVision software (Noldus Information Technology, 1997). The location of a

beetle in the arena was determined automatically by the software using a grey scaling method of object detection. The co-ordinates of the centre of the animal's body were calculated using a spatial resolution of 254H238 pixels. Tracking was done 10 times per second which was the highest possible sample rate (BELL 1991) taking into consideration the speed of the processor and storage capacity of the computer. Nevertheless, this gave an accurate representation of the track.

Data analysis

The digitised paths of individual beetles were used to calculate distances walked and time spent on each of the two test substrates and on the surrounding glass. For details of the algorithms used in the data analysis see Noldus Information Technology (1997). Female behaviour on both substrates was compared in three subsequent periods: 0-10, 10-20 and 20-30 minutes. Differences in the time spent on the two substrates were tested using non parametric Wilcoxon signed paired sample test (SIEGEL & CASTELLAN 1988). The same test was used to compare distance walked and speed of movement on the substrates.

RESULTS

Blank tests

The effect of bias on individual females of *C. limbifer* walking on two clean substrates was not significant. The results for females on the two clean substrates, in the first choice test with conspecific (values in parenthesis) and the second, with heterospecific larval tracks (values in brackets), revealed no significant bias in the time spent on substrates in the left and right positions ($P=0.5830$), [$P=0.8077$]. The values for the periods 0-10, 10-20 and 20-30 minutes were ($P=0.3258$), [$P=0.3910$]; ($P=0.9515$), [$P=0.3575$] and ($P=1$), [$P=0.1937$]. Total distances walked by females in the blank tests on the right and left substrates were similar ($P=0.7148$), [$P=0.7148$]. Records of the tracks of the most representative female, i.e. the one with the ratio of the distances

walked on the two substrates nearest to the average value, in each blank test is illustrated in Fig. 2. The distances walked during the three subsequent periods of 10 minutes were similar ($P=1$), [$P=0.5416$]; ($P=0.1040$), [$P=0.6698$] and ($P=0.7148$), [$P=0.5416$] (Fig. 3 and 4). The average speed of females on clean substrates in the left and right positions when associated with conspecific larval tracks was 6.7 mm/sec and 6.0 mm/sec. The average speed of females on clean substrates in the left and right positions when associated with tracks of heterospecific larvae was 5.6 mm/sec and 5.1 mm/sec. In both blank tests, the speed of walking on clean substrates, in the right and in the left position, did not differ either in the whole test ($P=0.3258$), [$P=0.5416$], or in three consequent periods ($P=0.3590$), [$P=0.8311$]; ($P=0.9700$), [$P=0.5771$], and ($P=0.1940$), [$P=0.1040$] (Fig. 5).

During the blank tests, females of *C. limbifer* spent (21 %) and [18 %] of the total time on the glass bottom of the Petri dish outside substrate zones. The average distances ($0\sqrt{SE}$) walked on the glass were (527 $\sqrt{92}$ cm) and [392 $\sqrt{88}$ cm], i.e. (40 %) and [34 %] of the total distance walked in the monitored area. The average speed of females on the glass away from the substrates was (13.8 mm/sec) and [12.6 mm/sec].

Choice experiments with fresh tracks of conspecific larvae

The total residential time and the distance walked on substrates with fresh tracks of unfed conspecific first instars were significantly longer than on clean substrates ($P=0.0134$ and $P=0.0203$). The average speed of females was 10.9 mm/sec on the clean substrate and 8.9 mm/sec on the substrate with tracks. The average speed on both substrates in the test did not differ significantly ($P=0.1531$).

Females of *C. limbifer* spent significantly longer on substrates with tracks than on clean substrates only during the first and the second period of 10 minutes ($P=0.0353$ and $P=0.0203$). In the last period, the difference in favour of the substrate with tracks was not significant ($P=0.5830$) (Fig. 3). Also distances walked on substrates with larval tracks were significantly

longer than on clean substrates in the first and second period ($P=0.0245$ and $P=0.0419$), but not significantly so in the last period ($P=1$). Walking speed of females on substrates with tracks was significantly lower than on clean substrates only

in the middle period, i.e. between 10-20 minutes ($P=0.0250$), but not in the first and the last periods ($P=0.6770$), and ($P=0.6360$), (Fig. 5). A record of the tracks of the most representative female is illustrated in Fig. 2.

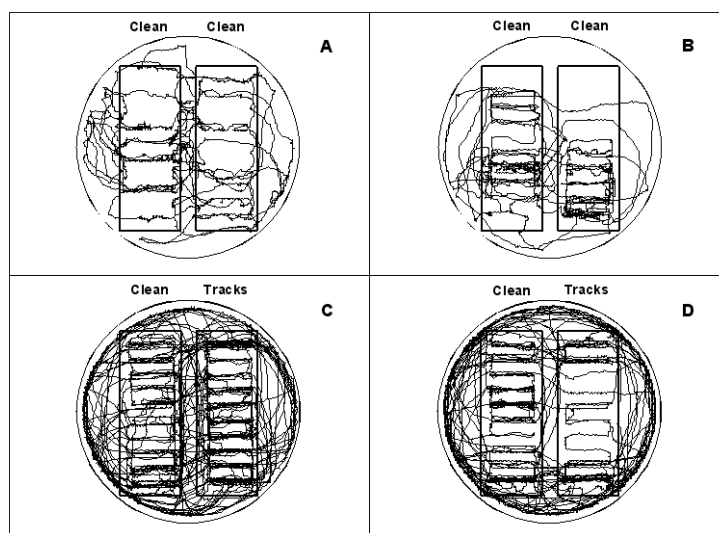


Fig. 2. Tracks of average *Cycloneda limbifer* females in blank tests (A and B) and in choice tests with conspecific (C) and *Ceratomegilla undecimnotata* (D) larval tracks.

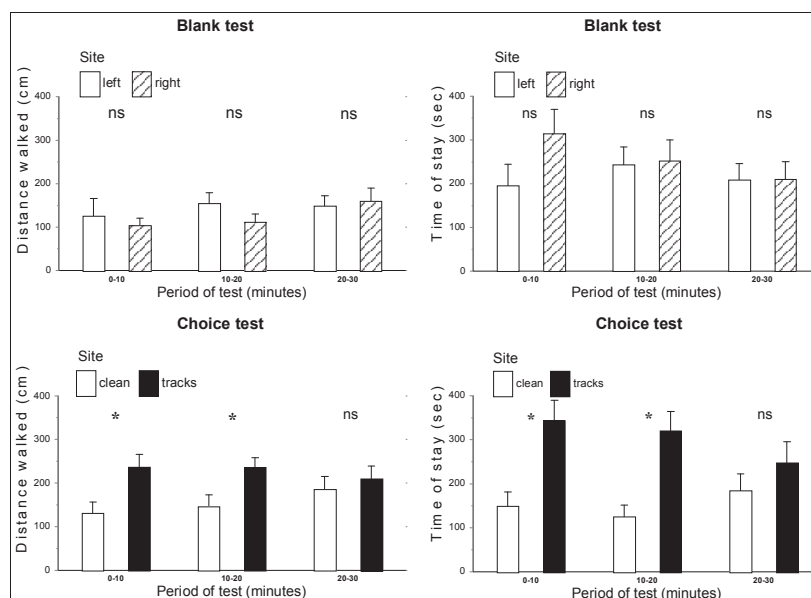


Fig. 3. Effects of conspecific larval tracks on the behaviour of females of *Cycloneda limbifer*. Results (mean \pm SE) both for the behaviour on two clean substrates in blank tests and on one clean and one contaminated substrate in subsequent choice tests. Wilcoxon paired sample test (two-tailed P value), * = $P < 0.05$, ns = not significantly different ($P \geq 0.05$).

During the tests, females of *C. limbifer* spent 24 percent of the time on the glass outside substrate zones. The average distance walked by a female on the glass was 863 ± 158 cm (43% of the total distance walked in monitored area). The average speed of females on glass outside substrate zones was 19.8 mm/sec.

Choice experiments with tracks of *C. undecimnotata* larvae

The total residential time and the distance walked on substrates with fresh tracks of unfed heterospecific first instars were significantly shorter than on clean substrates [$P=0.0023$ and $P=0.0134$]. The average speed of females during the choice test was 7.5 mm/sec on the clean substrate and 9.2 mm/sec on the substrate with tracks. The speed on substrates with tracks was significantly higher than on clean substrates

[$P=0.0107$].

C. limbifer spent significantly less time on substrates with fresh tracks of unfed first instars of *C. undecimnotata* than on clean substrates in the second period (10-20 minutes) of the test [$P=0.0040$]. Differences in the first and the last period of 10 minutes were not significant [$P=0.1189$ and $P=0.2166$] (Fig. 4). The distances walked on clean substrates were significantly longer than on substrates with tracks of heterospecific larvae during the second period (10-20 minutes) of the test [$P=0.0295$], but not in the first and the last period [$P=0.0906$ and $P=0.1726$] (Fig. 4). Walking speed of females on substrates with tracks was also significantly higher than on clean substrates only in the middle period of the test [$P=0.0005$], but not in the first (0-10 minutes) and the last (20-30 minutes) periods [$P=0.4631$ and $P=0.583$] (Fig. 5). A record of the track of the most representative female is illustrated in Fig. 2.

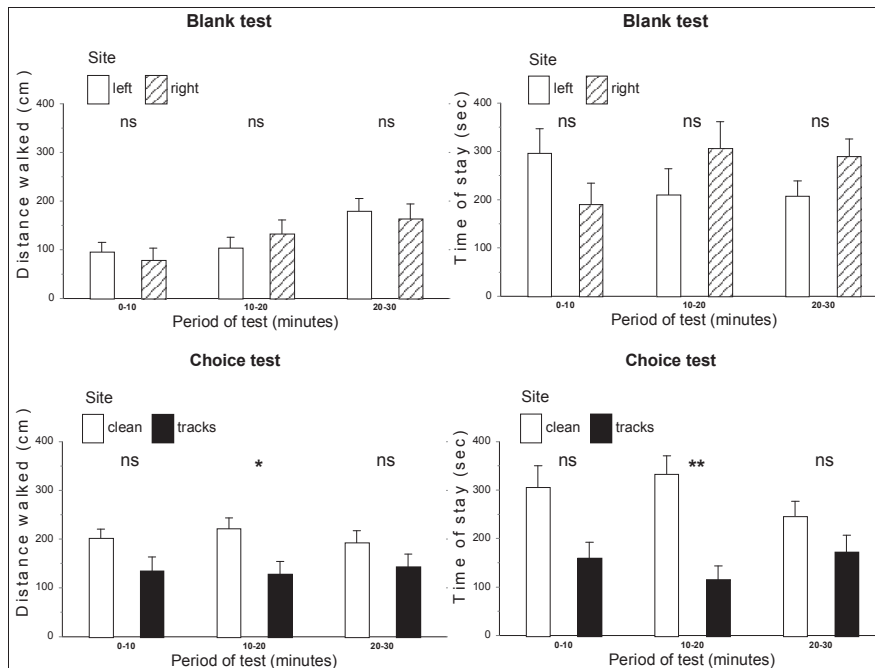


Fig. 4. Effects of larval tracks of *Ceratomegilla undecimnotata* on the mobility of *Cycloneda limbifer*. Results are for the behaviour (mean \pm SE) on two clean substrates in blank tests and on one clean and one contaminated substrate in subsequent choice tests. Wilcoxon paired sample test (two-tailed P value), ** = $P < 0.01$, * = $P < 0.05$, ns = not significantly different ($P \geq 0.05$).

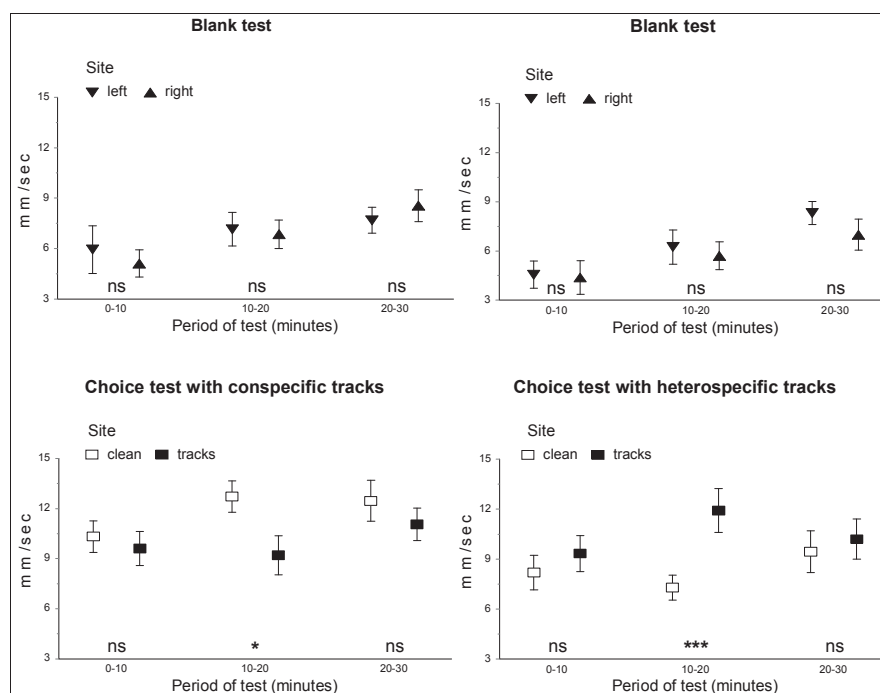


Fig. 5. The speed of movement (mean ∇ SE) of *Cyclonebda limbifer* females on two clean substrates in blank tests and on a clean substrate and substrate with tracks of conspecific or *Ceratomegilla undecimnotata* larvae in subsequent choice tests. Wilcoxon paired sample test (two-tailed P value), *** = $P < 0.001$, * = $P < 0.05$, ns = not significantly different ($P \geq 0.05$).

During the tests, females of *C. limbifer* spent 26 percent of the time on the glass outside substrate zones. The average distance (0∇ SE) walked by a female on the glass was $937 \nabla 150$ cm, (48 % of the total distance walked in monitored area). The average speed of females on the glass was 19.1 mm/sec.

DISCUSSION

Adult coccinellids usually do not stay on plants very long. If not laying eggs, they walk or fly away after several minutes, exceptionally after hours. Therefore, the presence of larval tracks is most likely to change the searching behaviour of females soon after their arrival on a plant. Automatic monitoring of females of *C. limbifer* provided considerably more information on the effects on their behaviour of substrates with larval tracks than did faecal spot densities left by females in choice tests designed to study these effects over 20 hours (RŮŽIČKA 2001).

The current results confirm a former assumption that the higher densities of faecal spots left by females on clean substrates than on those with larval tracks of *C. undecimnotata* indicate a repellent effect of contaminated substrates (RŮŽIČKA 2001). Residential time and total distance walked by *C. limbifer* females on clean substrates were significantly longer than on substrates with heterospecific tracks. This effect was strongest during the middle period (10-20 minutes) of the test. Also, the speed of females was higher on contaminated than on clean substrates at this time.

The analysis revealed that the fresh tracks of conspecific larvae affect the searching behaviour of *C. limbifer* females. In the first 20 minutes of the test, residential time and the distance walked were significantly higher on substrates with conspecific tracks than on clean substrates. Both parameters were also significantly lower on clean substrates over the whole 30 minutes of this test. This effect of larval tracks was not evident in the previous study (RŮŽIČKA 2001). In addition, the

speed of females was higher on contaminated than on clean substrates in the middle period. This effect of fresh conspecific tracks was surprising, because the oviposition-detering effect of conspecific larval tracks is at least as strong as the oviposition-detering effect of heterospecific tracks (RŮŽIČKA 2001). This is the first report that larval tracks can increase the time of stay and decrease the speed of search of conspecific females in an insect predator. Fresh tracks of conspecific first instar larvae may indicate, at least in some coccinellid species, that prey might be present, even though the tracks indicate it is an unsuitable site for oviposition.

In the absence of aphids, the effect of conspecific tracks on *C. limbifer* declined after 20 minutes. Results confirm that the strongest effects of larval tracks on female mobility can be expected shortly after their arrival on a plant. BÄNSCH (1966) observed that adult coccinellids search model plants without aphids for 23 minutes.

Larvae of the pyralid *Ephestia kuehniella* Zeller secrete an oviposition-detering pheromone from salivary glands and contaminate their food with the secretion (CORBET 1971). While low numbers of larvae attract conspecific females to lay eggs, high numbers deter them (CORBET 1973). Females of another species, *Plodia interpunctella* (Hübner), lay significantly more eggs in sites contaminated with 1 or 5 larvae than on clean sites, but lay significantly fewer eggs on sites contaminated with 10 larvae (PHILLIPS & STRAND 1994). A similar response is not observed in aphidophagous predators. The oviposition-detering effect of larval tracks steadily increases with increase in density of tracks (RŮŽIČKA 1997a; DOUMBIA et al. 1998) as well as size of larvae (RŮŽIČKA 1997b).

Chemical analysis of the larval tracks of the coccinellid *Adalia bipunctata* (L.) revealed a wide spectrum of semiochemicals, mainly hydrocarbons (HEMPTINNE et al. 2001), however, effects of individual compounds or sets of compounds on conspecific females are unknown. The strong intraspecific oviposition-detering effect of conspecific larval tracks (RŮŽIČKA 2001) and their effects on the foraging of *C. limbifer* may either be stimulated by the same or different substances present in the tracks.

This study showed that the fresh tracks of *C. undecimnotata* larvae and those of conspecific larvae affect the searching of *C. limbifer* females differently. This was unexpected because the oviposition-detering effects of fresh conspecific and heterospecific larval tracks were almost identical (RŮŽIČKA 2001).

The difference in the effect of fresh tracks of conspecific and heterospecific first instar larvae on the searching behaviour of females is here reported in aphid predators for the first time. The different behaviour of females on substrates with conspecific tracks can have an adaptive significance. Fresh larval tracks may stimulate females to search sites more thoroughly, because the food is likely to be present. The prolongation of the search on sites with tracks may also give a better assessment of the ratio of prey to conspecific competitors. This may enable females to more effectively assess site quality.

ACKNOWLEDGEMENTS

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REFERENCES

- BÄNSCH, R. 1966. On prey seeking behaviour of aphidophagous insects. Pp. 123-128 in: I. HODEK (Ed.). *Ecology of Aphidophagous Insects*. Prague: Academia.
- BELL, W.J. 1991. *Searching Behaviour: The Behavioural Ecology of Finding Resources*. London: Chapman & Hall.
- CORBET, S.A. 1971. Mandibular gland secretion of larvae of the flour moth, *Anagasta kuehniella*, contains an epideictic pheromone and elicits oviposition movements in a hymenopteran parasite. *Nature* 232: 481-484.
- CORBET, S.A. 1973. Oviposition pheromone in larval mandibular glands of *Ephestia kuehniella*. *Nature* 243: 537-538.

- DOUMBIA, M., J.-L. HEMPTINNE & A.F.G. DIXON 1998. Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia* 113: 197-202.
- FERRAN, A. & A.F.G. DIXON 1993. Foraging behaviour in ladybird larvae (Coleoptera: Coccinellidae). *European Journal of Entomology* 90: 383-402.
- HEMPTINNE, J.-L. & A.F.G. DIXON 1991. Why ladybirds have generally been so ineffective in biological control? Pp. 149-157 in L. POLGÁR, R.J. CHAMBERS, A.F.G. DIXON & I. HODEK (Eds). *Behaviour and Impact of Aphidophaga*. The Hague: SPB Academic Publishing.
- HEMPTINNE, J.-L., G. LOGNAY, M. DOUMBIA & A.F.G. DIXON 2001. Chemical nature and persistence of the oviposition deterring pheromone in the tracks of the larvae of the two spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). *Chemoecology* 11: 43-47.
- KUCHLEIN, J.H. 1966. Some aspects of the prey-predator relation. Pp. 237-242 in I. HODEK (Ed). *Ecology of Aphidophagous Insects*. Prague: Academia.
- MARKS, R.J. 1977. Laboratory studies of plant searching behaviour by *Coccinella septempunctata* L. larvae. *Bulletin of Entomological Research* 67: 235-241.
- Noldus Information Technology 1997. *EthoVision: Video Tracking, Motion Analysis & Behavior Recognition System*. Reference Manual, Version 1.90., Wageningen.
- PHILLIPS, T.W. & M.R. STRAND 1994. Larval secretion and food odors affect orientation in female *Plodia interpunctella*. *Entomologia Experimentalis et Applicata* 71: 185-192.
- RŮŽIČKA, Z. 1994. Oviposition-detering pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae). *European Journal of Entomology* 91: 361-370.
- RŮŽIČKA, Z. 1997a. Persistence of the oviposition-detering pheromone in *Chrysopa oculata* (Neur.: Chrysopidae). *Entomophaga* 42: 109-114.
- RŮŽIČKA, Z. 1997b. Recognition of oviposition-detering allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae). *European Journal of Entomology* 94: 431-434.
- RŮŽIČKA, Z. 1998. Further evidence of oviposition-detering allomone in chrysopids (Neuroptera: Chrysopidae). *European Journal of Entomology* 95: 35-39.
- RŮŽIČKA, Z. 2001. Oviposition responses of aphidophagous coccinellids to tracks of coccinellid (Coccinellidae) and chrysopid (Chrysopidae) larvae. *European Journal of Entomology* 98: 183-188.
- SIEGEL, S. & N.J. CASTELLAN JR. 1988. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill Book Company.
- SOLOMON, M.E. 1949. The natural control of animal populations. *Journal of Animal Ecology* 18: 1-35.
- SOLOMON, M.E. 1964. Analysis and Processes Involved in the Natural Control of Insects. Pp. 1-54 in J.B. CRAGG (Ed). *Advances in Ecological Research* 2. London and New York Academic Press.
- YASUDA, H., T. Takagi & K. Kogi 2000. Effects of conspecific and heterospecific larval tracks on the oviposition behaviour of the predatory ladybird *Harmonia axyridis* (Coleoptera, Coccinellidae). *European Journal of Entomology* 97: 551-553.

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PREDATORS AND PARASITOIDS ON DIFFERENT CEREAL APHID SPECIES UNDER CAGED AND NO CAGED CONDITIONS IN HUNGARY

Z. BASKY

BASKY, Z. 2003. Predators and parasitoids on different cereal aphid species under caged and no caged conditions in Hungary. Pp. 95-101 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

Wheat plants, randomly chosen, were infected with *Diuraphis noxia*, *Sitobium avenae*, *Rhopalosiphum padi* and *Metopolophium dirhodum*, respectively, regardless of the presence or absence of other aphids. Half of the artificially infected plants were caged whereas the other half was left no caged. One month after artificial aphid infection plants were sampled weekly, and insects were counted.

R. padi was the most abundant species, followed by *S. avenae*, *M. dirhodum* and *D. noxia* on caged tillers. Significant relationships were found between *C. septempunctata* and *R. padi* densities and between *Aphidius ervi* and *S. avenae* densities. Activity of parasitoids was hampered by hyperparasitoids. *Chalcididae* hyperparasitoids were more than twice as abundant as parasitoids.

D. noxia was ca. ten to twenty times more frequent on no caged tillers, compared to other cereal aphid species. Populations of indigenous aphid species: *R. padi*, *S. avenae* and *M. dirhodum* were under the economic threshold on the no caged tillers. The results suggest that the indigenous aphid species were more influenced by local natural enemies than *Diuraphis noxia* predators and parasitoids presented in this study were not able to keep *D. noxia* populations under economic injury level.

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INTRODUCTION

Cereals are one of the main staple crops worldwide (FAO 2001) with the largest area in the temperate zone. Several species of pests attack cereals (AFONINA et al. 2001). Aphids (Homoptera Aphididae) are one of the most important pests of cereals, causing both direct damage by feeding and indirect damage by transmitting plant viruses (QUIROZ 1992). To sustain cereal production and profitability, attempts to decrease aphid damage by using resistant cultivars and enhancing naturally occurring biological control have been made (STECHMANN 1986). However, the introduction of resistant cultivars resulted in developing new aphid biotypes which are able to damage resistant

cultivars (e.g., NIASSY et al. 1987; OGECHA et al. 1992; PUTERKA et al. 1992; MILLER et al. 1994; BASKY et al. 2001). Aphid resistant cultivars may negatively impact the third trophic level (PRICE 1986). Therefore the enhancement of predator and parasitoid activity in a growing system that allows natural enemies to maintain aphid populations below the economic injury level remains a desirable goal (MARASAS et al. 1997).

This study reports the result of a cage experiment where susceptible wheat plants infected naturally by aphids and natural enemies, were artificially infected with indigenous cereal aphids and with the recently occurred *Diuraphis noxia* (Kurdjumov) (BASKY & EASTOP 1991). The aim of this study was to monitor aphid, predator and parasitoid density under caged and

no caged conditions between tillering and ripening.

MATERIAL AND METHODS

The trial was carried out in a suburb of Budapest (18°53'E 47°35'N, 342 m a.s.l.) on a 2 ha wheat field.

Artificial infection

Winter wheat variety "MV 17" was sown at a seed rate of 220 kg/ha on 13 November. When the plants reached the growth stage GS 30 (TOTTMAN & BROAD 1987) beginning of stem elongation on 11 May (2001), randomly chosen groups of 10-12 tillers were artificially infected with aphids.

Plants were infected regardless of the presence or absence of other aphids and natural enemies.

Five aptera or L₄ nymph individuals of the indigenous cereal aphid species: *Sitobion avenae* (Fabr.), *Rhopalosiphum padi* (L.), or *Metopolophium dirhodum* (Walker) and the newly occurred *Diuraphis noxia* (Kurdjumov), respectively were used to infect wheat plants. Half of the artificially infected plants were caged the other half was left no caged. Twenty-five pairs of caged and no caged group of tillers were infected with different aphid species. Each aphid species was released on other twenty-five pairs of caged and no caged group of tillers. The distance between caged and no caged pairs was 1.5 m and 3 m between pairs. Five pairs of caged and no caged groups of tillers were infected in each of five replicate blocks at each aphid species yielding a total of 200 plants.

Sampling

Sampling started one month after the artificial aphid infection of the plants. Five pairs of caged and no caged tillers infected with different aphid species, selected at random, were sampled destructively at weekly intervals for five weeks starting on 11 June. The plants were individually

placed into Berlese funnel for 5 days to extract insects. Afterwards, plants were transferred to emergence canisters for one week to collect emerging parasitoids. The numbers of *Aphidius* and *Aphelinus* - type mummies were counted from both the extracted samples and dry plant material. The numbers of different aphid species were counted. The numbers of each species of adult parasitoid and hyperparasitoid from Berlese funnels and the emergence canisters were counted, species were identified.

Data analysis

Analysis of covariance using the sampling date, isolation level (cage vs. no cage) and artificial aphid infection as categorical variables and number of predators as continuous predictor were used to identify the effect of these variables on the number of different aphid species.

The effect of parasitoids was calculated as a regression between the number of the most frequent parasitoid (*Aphidius ervi* Haliday) and the numbers of *Diuraphis noxia*, *S. avenae*, *R. padi* and *M. dirhodum* on caged and no caged tillers.

The similarity between cage – no cage were calculated by the Renkonen - index (RENKONEN 1938)

Statistical significance of goodness of fit of numbers of different species collected from caged and no caged tillers was tested by Yates corrected Chi-square test.

Analyses were made using the Statistica program package (STATISTICA 1997)

RESULTS

Aphids

Rhopalosiphum padi reached the highest numbers among the aphid species, followed by *S. avenae*, *M. dirhodum* and *D. noxia* on the caged tillers (Fig.1). *R. padi* was the dominant naturally occurring aphid species; it was present in 92 % of the cages, although only 25 % of the cages were artificially infected with this species. *S. avenae*

was present in 52 % of the cages followed by *M. dirhodum* and *D. noxia* 41 and 37 %, respectively. *R. padi* colonised winter wheat more frequently compared to other aphid species.

However, on the no caged tillers *D. noxia* was the prevailing aphid species, its abundance was

ten times higher compared to *S. avenae* and *R. padi* and twenty times higher than that of *M. dirhodum* (Fig. 2). *D. noxia* was present on 39 % of the no caged tillers. *S. avenae* infected 49 % of no caged tillers, followed by *R. padi* and *M. dirhodum* 40 and 29 %, respectively.

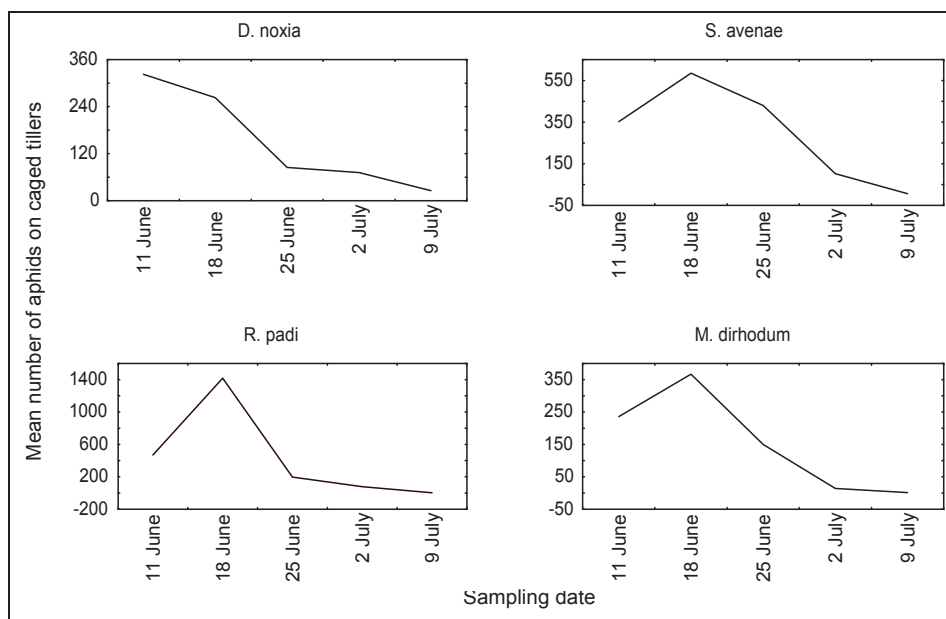


Fig. 1. Seasonal abundance of cereal aphids in the cages.

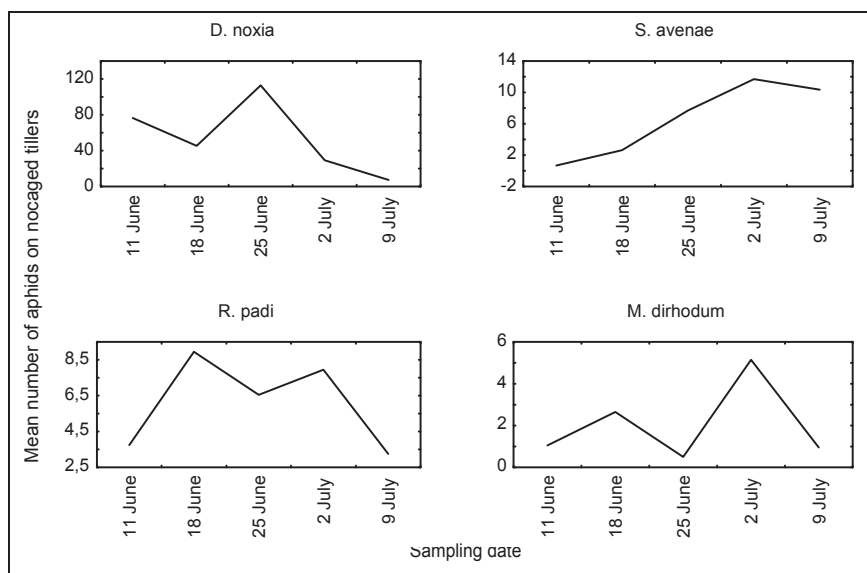


Fig. 2. Seasonal abundance of cereal aphid species on no caged tillers.

Predators and parasitoids

The survey yielded 10 species of aphidophagous insects associated with cereal aphids. The ladybird *C. septempunctata* (Coccinellidae) was the most abundant predator, 67 % of the predators belonged to *C. septempunctata*. Hoverflies (Syrphidae) and lacewings (Chrysopidae) comprised only 33 % of the predators. -96% of the collected predators were in the cages (Fig 3).

Aphidius - type mummies infecting mainly *S. avenae* were 5.5 times more abundant on the caged than on no caged tillers. *Aphelinus* - type

mummies, always found on *Diuraphis noxia* hosts, were 5 times more frequent on caged than no caged tillers.

Seventy eight percent of the emerged adult parasitoids were *Aphidius ervi*.

Apart from *A. ervi*, *Aphidius uzbekistanus* Luzhetskii, *Diaretiella rapae* (M'Intosh), *Ephedrus plagiator* (Nees), *Praon volucre* (Haliday) and *Aphelinus* spp. parasitoid species were present. The majority (94%) of the hyperparasitoids belonged to the Chalcididae family. The number of hyperparasitoids was more than twice as much at that of parasitoids (Fig 4).

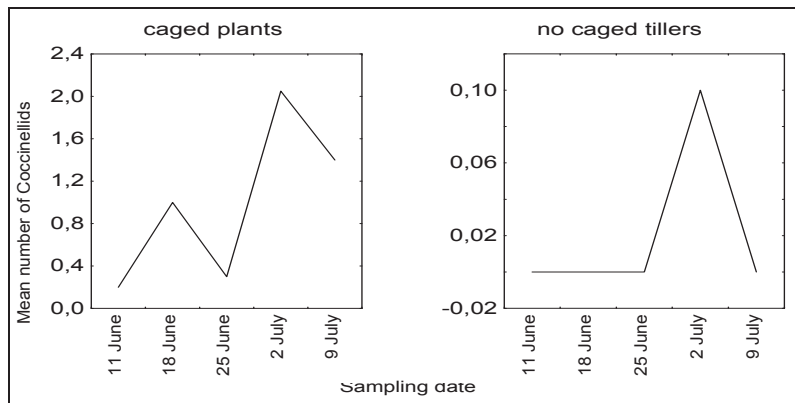


Fig. 3. Seasonal abundance of Coccinellids on no caged tillers.

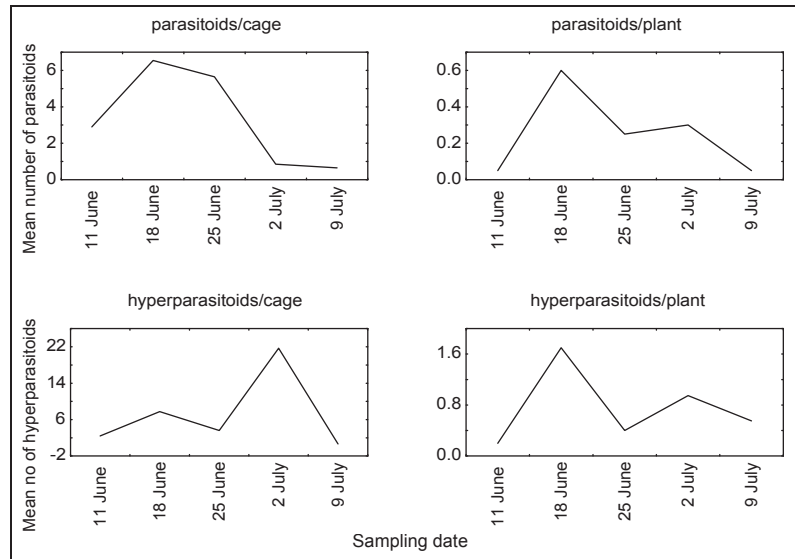


Fig. 4. Seasonal abundance of parasitoids and hyperparasitoids on caged and no caged tillers.

Relationships between aphids and natural enemies

Analysis of covariance revealed significant relationship between sampling date, isolation level, artificial aphid infection, number of *C. septempunctata*, and number of *R. padi*, *S. avenae*, *M. dirhodum* and *D. noxia* (adjusted $R^2=0.17$, $=$, 0.13 , 0.28 and 0.18 , R^2 respectively. $F=2.07$, 1.75 , 2.98 and 2.12 , respectively $df= 40$, 158 , $P<0.00$) for the whole model. However, within the whole model the only significant relationship occurred between number of *C. septempunctata* and that of *R. padi* at $P<0.10$ ($P=0.06$, $F=3.37$). The significant relationship between number of *C. septempunctata* and *R. padi* is in agreement with the observations that relatively few *R. padi* remained in cages where *C. septempunctata* larvae were present.

However, the number of *C. septempunctata* did not affect significantly those of *S. avenae*, *M. dirhodum* and *D. noxia*. It is in agreement with the observations that *D. noxia* survived in large numbers in cages containing *C. septempunctata*.

Sampling date and isolation level significantly affected aphid numbers. Artificial aphid infection significantly affected number of *D. noxia* and *R. padi*, but not of *S. avenae* and *M. dirhodum*.

In the cages, the aphid/parasitoid ratio was highest for *R. padi* (132 aphids/parasitoid, followed by *S. avenae* (86 aphids/parasitoid), *M. dirhodum* (45 aphids/parasitoid), and *D. noxia* (39 aphids/parasitoid).

While on the no caged tillers the aphid/parasitoid ratio was the highest for *D. noxia* (150 aphids/parasitoid, and was much lower for *R. padi*, *S. avenae* and *M. dirhodum* (19, 15 and 7 aphids/parasitoid, respectively). The parasitoid/hyperparasitoid ratio was higher on no caged tillers than in the cages (3.0 vs. 2.6, parasitoid/hyperparasitoid respectively).

Simple linear regression analyses revealed significant relationship between *Aphidius ervi* and *Sitobion avenae* (Adjusted $R^2=0.83$ $F=37.42$ $P<0.00$) on no caged tillers. The relationship was not significant between *Aphidius ervi* and the other aphid species regardless of the isolation level. There was no significant regression either between the numbers of predators and numbers of

R. padi, *M. dirhodum* and *D. noxia* or between the numbers of parasitoids and hyperparasitoids.

Cage versus no cage

The low Renconen index value (0.3527) indicated that the community structure of aphids and natural enemies was different on caged and no caged tillers. Yates corrected Chi-squared test revealed significant differences between the frequencies of different aphid species on caged and no caged tillers. Yates corrected Chi² value was the highest for *D. noxia* (Chi²=9257, $P=0.000$). The high Chi² value reflects that *D. noxia* was the least abundant species in the cages, but it was the most abundant species on the no caged tillers. *R. padi* was the most abundant in the cages (Chi²=1256 $P=0.000$), it was less abundant than *D. noxia* and *S. avenae* on the no caged tillers. *S. avenae* (Chi²=881 $P=0.000$) was the second most abundant aphid species in the cages and it was the second most abundant on the no caged tillers. *M. dirhodum* (Chi²=634 $P=0.000$) was the third most abundant cereal aphid in the cages and it was the least abundant on the no caged tillers.

There was a significant difference between abundance *C. septempunctata* and that of hyperparasitoids on no caged and caged tillers (Chi² was 5.25 and 7.49, respectively $P=0.000$). However, the abundance of hover flies, lacewings and parasitoids did not differ significantly between caged and no caged tillers.

DISCUSSION

R. padi, *S. avenae*, *M. dirhodum* and *D. noxia* populations reached very high numbers on artificially- infected caged tillers. The high aphid abundance in the cages was probably due to successful artificial aphid infection. On the other hand, cages blocked aphid emigration. Cages prevented alate aphids to leave the host plants. Therefore several generations developed on these plants resulting in very high aphid populations. Cages blocked natural enemy emigration as well, resulting in much higher natural enemy abundance in cages than on no caged tillers.

Although the majority of predators and parasitoids were in the cages, the high number of aphids in cages indicated that aphid reproduction rate was higher than the consumption rate of predators or the reproduction rate of parasitoids.

Abundance of indigenous aphid species was under economic injury level in spite of artificial aphid infection on no caged tillers, indicating that naturally occurring natural enemies were able to control indigenous aphid species in spite of the artificial aphid introduction. However, *D. noxia* surpassed the economic injury level. It was 10-20 times more abundant than indigenous aphid species. *D. noxia* feeds inside the rolled leaves (AALBERSBERG 1988) predators cannot easily reach *D. noxia* individuals. Colonies of other cereal aphids are exposed to predators on the extended leaf surfaces (REED et al. 1991). The lower proportion of indigenous cereal aphids on no caged tillers indicated that *C. septempunctata*, syrphid and chrysopid predators limited the numbers of *R. padi*, *S. avenae* and *M. dirhodum* more efficiently than those of *D. noxia*. The significant relationship between number of *C. septempunctata* and number of *R. padi* supported the assumption that *C. septempunctata* efficiently suppressed *R. padi*.

The significant relationship between *A. ervi* and *S. avenae* indicated that this aphid was efficiently suppressed by *A. ervi* on no caged tillers. *A. ervi* was the most frequent parasitoid present in this study. *A. ervi* more often parasitized *S. avenae* than *R. padi*, *M. dirhodum* and *D. noxia*. This is due to host specialisation of this parasitoid. *Aphidius ervi* is common on *Sitobion avenae* (STARY 1973; ABO KAF 1991). However, hardly any parasitoids attacked *R. padi* and *M. dirhodum*. *Aphelinus* spp. always attacking *D. noxia* was the second most abundant parasitoid. However, it was not abundant enough to efficiently decrease the number of *D. noxia* below the economic injury level.

Higher parasitoid/hyperparasitoid rate occurred on no caged tillers than on caged ones. Although hyperparasitoids were closed in the cages together with aphids and parasitoids; therefore they could easily reproduce on parasitized mummies. The lower hyperparasitoid rate in the cages indicated that hyperparasitoids continued to arrive as the season progressed. High

hyperparasitisation often occurs in the *Sitobion avenae* - *Aphidius ervi* host - parasitoid relationship (ABO KAF 1991).

The community structure of aphids and natural enemies is significantly different on caged and no caged tillers (Renkonen index). The relative abundance of aphids was significantly higher on caged than on no caged tillers. The high aphid abundance in the cages was partly the result of the blocked aphid emigration. Alata aphids left no caged wheat when they developed. While in the cages they continued feeding and producing progenies as long as the wheat was suitable for aphid feeding. Therefore the number of aphids on caged tillers was much higher than on no caged ones.

The relative abundance of hover flies, lacewings and parasitoids did not differ significantly on caged and no caged tillers.

Based on these results, it can be concluded that the natural enemy complex played a substantial role in suppressing populations of indigenous aphid species under no caged conditions. The number of naturally occurring and artificially introduced indigenous aphid species was below the economic threshold during the survey under no caged conditions. However, *D. noxia* originated from artificial infection built up high populations on no caged tillers. It indicates that parasitoids and predators present in this study were not able to maintain the *D. noxia* infection below the economic injury level.

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REFERENCES

- ABO KAF, N. 1991. Parasitic Hymenoptera associated with cereal aphids in fields of wheat and barley in the region of Lublin, Poland. Pp. 17-21 in L. POLGÁR, R.J. CHAMBERS, A.F.G. DIXON & I. HODEK (Eds). *Behaviour and impact of Aphidophaga*. SPB

- Academic Publishing bv, The Hague, The Netherlands.
- AFONINA, V.M., V.B. TSHERNYSHEV, I.I. SOBOLEVA-DOKUCHAEVA, A.V. TIMOKHOV, O.V. TIMOKHOVA & R.R. SEIFULINA 2001. Arthropod complex of winter wheat crops and its seasonal dynamics. Integrated Control in Cereal Crops. *IOBC wprs Bulletin* 24: 153-163.
- AALBERSBERG, Y.K. 1988. Natural enemies and their impact on *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae) populations. *Bulletin of Entomological Research* 78: 111-120.
- BASKY, Z. & V.F. EASTOP 1991. *Diuraphis noxia* in Hungary. *Newsletter barley Yellow Dwarf* 4: P. 34.
- BASKY, Z., R.L. HOPPER, J. JORDAAN & T. SAAYMAN 2001. Biotypic differences in Russian wheat aphid (*Diuraphis noxia*) between South African and Hungarian agro-ecosystems. *Agriculture, Ecosystems and Environment* 83: 121-128.
- FAO 2001. *Production Yearbook* (1999). (Vol. 53), FAO, Rome, Italy.
- MARASAS, C., P. ANANDAJAYASEKERAM, V.L. TOLMAY, D. MARTELLA, J.L. PURCHASE & G.J. PRINSLOO 1997. Socio-economic impact of the Russian wheat aphid control research program. *Southern African Centre for Cooperation in Agriculture and Natural Resources & Training*; P/Bag 00108, Gaborone, Botswana.
- MILLER, H., D.R. PORTER, J.D. BURD, C.W. MORNHINWEG & R.L. BURTON 1994. Physiological effects of Russian wheat aphid (Homoptera: Aphididae) on resistant and susceptible barley. *Journal of Economic Entomology* 87: 493-499.
- NIASSY, A., J.D. RYAN & D.C. PETERS 1987. Variation in feeding behaviour, fecundity and damage of biotypes B and E of *Schizaphis graminum* (Homoptera: Aphididae) on three wheat genotypes. *Environmental Entomology* 16: 1163-1168.
- OGECHA, J., J.A. WEBSTER & D.C. PETERS 1992. Feeding behaviour and development of biotypes E, G, H of *Schizaphis graminum* (Homoptera: Aphididae) on 'Wintermalt' and 'Post' barley. *Journal of Economic Entomology* 85: 1522-1526.
- PUTERKA, G.J., J.D. BURD & R.L. BURTON 1992. Biotypic variation in a worldwide collection of Russian wheat aphid (Homoptera, Aphididae). *Journal of Economic Entomology* 85: 1497-1506.
- PRICE, P.W. 1986. Ecological aspects of host plant resistance and biological control: Interactions among three trophic levels. Pp. 11-30 in D.J. BOETHEL & R.D. EIKENBARY (Eds). *Interactions of Plant Resistance and Parasitoids and Predators of Insects*. Ellis Horwood, Ltd., Chichester.
- REED, D.K., J.A. WEBSTER, B.G. JONES & J.D. BURD 1991. Tritrophic Relationships of Russian Wheat Aphid (Homoptera: Aphididae), a Hymenopterous Parasitoid (*Diaretiella rapae* McIntosh), and Resistant and Susceptible Small Grains. *Biological Control* 1: 35-41.
- RENKONEN, O. 1938. Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. *Annales Zoologici Societatis Zoologicae - Botanicae Fennicae Vanamo* 6: 1-231.
- QUIROS, C., R.M. LISTER, R.H. SHUKLE, J.E. ARAYA & J.E. FOSTER 1992. Selection of symptom variants from the NY-MAV strain of barley yellow dwarf virus and their effects on the feeding behaviour of the vector *Sitobion avenae* (Homoptera: Aphididae). *Environmental Entomology* 21: 376-381.
- STARÝ, P. 1973. A review of the *Aphidius* – species (Hymenoptera, Aphidiidae) of Europe. *Annotationes Zoologicae et Botanicae* 84: 85 pp.
- STATISTICA 1997. *Statsoft*. Tulsa, Oklahoma, USA
- STECHMANN, D.H. 1986. Cereal aphids – Aphidophaga associations in hedges and fields: Can habitat interaction contribute to integrated pest management? Pp. 273-278 in I. HODEK (Ed). *Ecology of Aphidophaga*. Academia Prague & Dr. W. Junk, Dordrecht.
- TOTTMAN, D.R. & A. BROAD 1987. Decimal code for the growth stage of cereals. *Annales of Applied Biology* 110: 683-687.

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INTRAGUILD PREDATION AMONG THE APHIDOPHAGOUS LADYBIRD BEETLES *Harmonia axyridis* PALLAS AND *Coccinella undecimpunctata* L. (COLEOPTERA: COCCINELLIDAE): CHARACTERIZATION OF THE DIRECTION AND SYMMETRY

S. FÉLIX & A.O. SOARES

FÉLIX, S. & A.O. SOARES 2003. Intraguild predation among the aphidophagous ladybird beetles *Harmonia axyridis* Pallas and *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae): characterization of the direction and symmetry. Pp. 103-106 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

Direction and symmetry of intraguild predation (IGP) between all developmental stages of the aphidophagous *Harmonia axyridis* Pallas and *Coccinella undecimpunctata* L. were characterized.

Our results revealed that *H. axyridis* predation level was significantly higher than *C. undecimpunctata* and eggs were the more vulnerable developmental stage. Significantly asymmetric IGP on eggs occurred after the second and fourth larval stages of *H. axyridis* and *C. undecimpunctata*, respectively. Asymmetric IGP on pupas exclusively occurred in the presence of the fourth larval stage of *H. axyridis*.

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INTRODUCTION

Intraguild predation is the killing and consumption of a species that uses similar resources being potential competitors. It is a common and often important interaction. In a diverse array of communities, IGP occurs among members of the same guild (POLIS & HOLT 1992). The aggressor is the intraguild predator (IG predator), the victim the intraguild prey (IG prey), and the common resource is the extraguild prey (LUCAS et al. 1998). IGP is considered to be an extreme form of competition or a type of classical predation that may affect the distribution, abundance and evolution of the animal species. IGP not only provides an additional food resource to the IG predators, but it may reduce inter- or intraspecific competition and predation risk for the extraguild prey when mutual IGP occurs (POLIS et al. 1989; POLIS &

HOLT 1992; LUCAS et al. 1998; YASUDA et al. 2001). IG prey populations may suffer local extinctions due to IGP, which represents an important mortality factor (LUCAS et al. 1998).

The two most important factors that determine the symmetry and the direction of IGP are the size and the degree of feeding specificity exhibited by the protagonists. IGP occurs mainly with generalist predators attacking prey of smaller size, including conspecifics (POLIS et al. 1989; POLIS & HOLT 1992; LUCAS et al. 1998). The size of the prey attacked generally increases with the size / age of the IG predator (SABELIS 1992), with smaller individuals being more vulnerable to a larger number of predators (WERNER & GILLIAM 1984; LUCAS et al. 1998). In ladybird beetles, large species usually take advantage of small ladybird species in terms of food consumption, and this could result in asymmetrical interactions between the two species (OBRYCHI et al. 1998). A

specialized predator should be less adapted to attack a nonpreferred prey, a disadvantage when confronted with a generalist predator (LUCAS et al. 1998).

Coccinella undecimpunctata L. is a native aphidophagous predator of the Azorean ecosystems, which can be found mostly by the sea (salt lands) and also in plants and flowers from where they feed on pollen (RAIMUNDO & ALVES 1986). *Harmonia axyridis* Pallas is a palearctic species native from Asia (TAN 1946, 1949; KOMAI 1956; IABLOKOFF-KHNZORIAN 1982). An euryphagous predator which prefers aphids (HUKUSIMA & KAMEI 1970; HUKUSIMA & OHWAKI 1972; IABLOKOFF-KHNZORIAN 1982; OSAWA 1992), psyllids (FYE 1981; DREA & GORDON 1990), coccids (MCLURE 1987; HODEK & HONĚK 1988), the immature stages and eggs of lepidopteran (SCHANDERL et al. 1988; DREA & GORDON 1990), and spider mites (DREA & GORDON 1990; CLOUTIER & CLOUTIER 1991; LUCAS et al. 1997). It was found to be the best biological agent tested in laboratory against many phytophagous species. The possibility to rear this ladybird beetle successfully on eggs of *Ephestia kuehniella* Zeller (SCHANDERL et al. 1988) favors its mass production to sustain inundative releases. However, studies on the possible negative impacts of its presence on native ladybird beetles and on other non-target arthropods are rarely performed (LUCAS et al. 2002).

The aims of this study were to characterize the (i) direction and (ii) the symmetry of intraguild predation (IGP) between the aphidophagous *H. axyridis* and *C. undecimpunctata*.

MATERIAL & METHODS

H. axyridis individuals were mass reared at 22 ± 1 °C, with 75 ± 5 % RH and a photoperiod of 16L:8D, using fluorescent lamps (Philips ref.: TDL 23W/54 and TDL 18W/54). Coccinellids were fed a mixture of *Aphis fabae* Scopoli and *Myzus persicae* (Sulzer), and eggs of *Ephestia kuehniella* Zeller. *C. undecimpunctata* adults were collected in S. Maria Island and reared under the same biotic and abiotic conditions.

Predation level, direction and symmetry of IGP were characterized and compared between all developmental stages (eggs, 4 larval stages, pupae

and adults) of *H. axyridis* and *C. undecimpunctata*.

As there are no possible interaction respectively between eggs and pupae of the two species, there remain 45 experimental combinations. Larvae and adults used in the experiments were 24h old. Prior to the beginning of the tests, second to fourth instars larvae and adults were starved for 24h then, they were weighed on a 10^{-4} mg Mettler AM 50 analytical balance. First instars larvae were not starved they were also weighed before the experiments. One-weighted individuals of one species of ladybirds was placed with a weighed individual of the other species in a 2L transparent plastic box that contains also a potted broad bean without aphid. Twenty-four hours later, the box was checked to determine which species survived if any. There were 15 replicates for each combination.

The natural mortality of each developmental instar of the two species was used as a control. A single individual of each instar was kept for 24h in a 2L transparent plastic box with a broad bean without aphid. There were 3 replicates for each instar.

All trials were performed at 20 ± 1 °C, 75 ± 5 % of RH and a photoperiod of 16L:8D, under fluorescent lamps (Philips ref.: TDL 23W/54 and TDL 18W/54).

A symmetry index was adapted from LUCAS et al. (1998) and expresses the number of replicates in which a given predator was eaten over the total numbers of replicates in which there was IGP for a particular combination of predator.

Statistical analysis

The symmetry indices for each combination were compared to a theoretical index of 50% corresponding to a symmetric interaction, using a Chi-square test (χ^2 , $P < 0.05$) (SPSS PRODUCTION FACILITY 2001).

RESULTS

Among all significantly asymmetric combinations, *H. axyridis* was IG predator in 16 times and *C. undecimpunctata* only in 3 combinations. IGP were not significantly

asymmetric in 19 combinations and symmetric in one of them. Absence of IGP was observed 6 times. Among all combinations with *H. axyridis* adults except on pupae and adult, the IGP was significantly asymmetric. On the other hand, in all combinations of *C. undecimpunctata* adults, significantly asymmetric IGP only occurred on

eggs. IGP between adults did not occurred significantly asymmetric IGP, on pupae, exclusively occurred in the presence of the fourth larval stage of *H. axyridis*. Larvae of both species attacked heterospecific. In general, predation rate of immature stages of *H. axyridis* is higher (Fig. 1).

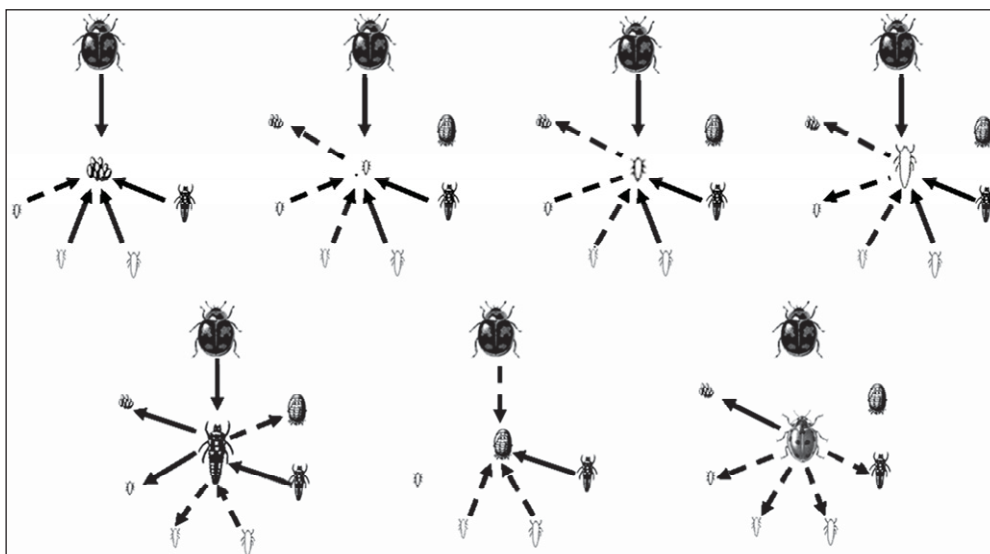


Fig. 1. Representation of the intraguild predation (IGP), between various developmental stages of *H. axyridis* and *C. undecimpunctata*. Legend: Close arrow - significant asymmetry IGP; Dashed arrow - not significantly asymmetric IGP; Dashed line- symmetric IGP; Lack of arrows and lines- absence of IGP; *C. undecimpunctata*: in central position (χ^2 , $df=1$, $P < 0.05$).

DISCUSSION

We characterized, under controlled conditions, the direction and symmetry of IGP between *H. axyridis* and *C. undecimpunctata*. Among all combinations tested, 19 of them were found to be significantly asymmetrical, with a 16 combinations having *H. axyridis* as the IG predator and only in 3 of them *C. undecimpunctata* was the IG predator. Those results are according with our previously prediction in which *H. axyridis* would be the aggressor (IG predator) and *C. undecimpunctata* the victim (IG prey) in most of the combinations among their developmental stages.

Eggs were the most vulnerable developmental stage. We think that ease capture, in consequence of immobility, is the main reason for their vulnerability. It seems, however, that pupae's

immobility do not confers any disadvantaged in this biotic relation because they were almost invulnerable to IGP, the biggest body size, can contribute to its lower vulnerability.

Concerning the combinations between the larval stages, the differences size of IG predator and IG prey could determine the direction and symmetry.

In all combinations with adults versus either larval stages or eggs, adults took advantage, mainly *H. axyridis*. However IGP between adults did not occurs.

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REFERENCES

- CLOUTIER, C. & C. CLOUTIER 1991. Les solutions biologiques de la lutte pour la répression des insectes et acariens ravageurs des cultures. Pp. 19-88 in C. VINCENT & D. CODERRE (Eds). *La Lutte Biologique*. Gaent Morin Éditeur, Québec. 671 pp.
- DREA, J.J. & R.D. GORDON 1990. Coccinellidae. Pp. 19-40 in D. ROSEN (Ed). *Armored Scale Insects-Their Biology, Natural Enemies and Control* Vol. 4B. New York; Amsterdam: Elsevier. 688 pp.
- FYE, R.E. 1981. Rearing and release of coccinellids for potential control of pear Psylla. *Agricultural Research Service (Western Region)* 20: 1-9.
- HODEK, I. & A. HONĚK 1988. Sampling, rearing and handling of aphid predators. Pp. 311-321 in A.K. MINSK & P. HARREWIJN (Eds). *Aphids-their Biology, Natural Enemies and Control*. vol. 2B. Elsevier Science Publishers B. V., Amsterdam. 364 pp.
- IABLOKOFF-KHNZORIAN, S.M. 1982. *Les coccinelles; Coléoptères-Coccinellidae*. Société Nouvelle des Éditions Boubée. Paris. France. 568 pp.
- KOMAI, T. (1956). Genetics of ladybeetles. *Advances in Genetics* 8: 155-189.
- LUCAS, E., D. CODERRE & C. VINCENT 1997. Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. *Entomologia Experimentalis et Applicata* 85: 151-159.
- LUCAS, E., D. CODERRE & J. BRODEUR 1998. Intraguild predation among aphids predators: characterization and influence of extraguild prey density. *Ecology* 79: 1084- 1092.
- LUCAS, E., I. GAGNE & D. CODERRE 2002. Impact of the *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology* 99: 457-463.
- OBRYKI, J.J., K.L. GILES & A.M. ORMORD 1998. Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia* 117: 279-285.
- OSAWA, N. 1992. A life table of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in relation to the aphid abundance. *Japanese Journal of Entomology* 60: 575-579.
- MCLURE, M.S. 1987. Potencial of the asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosa* Bean & Godwin (Homoptera: Margarodidae) in the United States. *Environmental Entomology* 16: 224-230.
- POLIS, G.A. & R.D. HOLT 1992. Intraguild predation: The dynamics of complex trophic interactions. *Trends in Ecology and Evolution* 7: 151-154.
- RAIMUNDO, A.A.C. & L.L.G ALVES 1986. *Revisão dos coccinélidos de Portugal*. Publicações da Universidade de Évora, Évora. 103 pp.
- SABELIS, M.W. 1992. Predatory arthropods. Pp. 225-264 in M.J. CRAWLEY (Ed). *Natural Enemies*. Blackwell Scientific Publications, Oxford. 592 pp.
- SCHANDERL, H., A. FERRAN & V. GARCIA 1988. L' élevage de deux coccinelles *Harmonia axyridis* et *Semiadalia undecomnotata* à l' aide d' oeufs d' *Anagasta kuehniella* tués aux rayons ultraviolets. *Entomologia Experimentalis et Applicata* 49: 417-421.
- TAN, C.C. 1946. Mosaic Dominance in the inheritance of color patterns in the Ladybird Beetle, *Harmonia axyridis*. *Genetics* 31: 195-210.
- TAN, C.C. 1949. Seasonal Variations of color patterns in *Harmonia axyridis*. Proceedings of the 8th International Congress Genetic: 669-670.
- WERNER, E.E. & J.F. GILLIAM 1984. The ontogenetic niche and species interactions in size- structured populations. *Annual Review of Ecology and Systematics* 15: 393-425.
- YASUDA, H., T. KIKUCHI, P. KINDLMANN & S. SATO 2001. Relations between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior* 14: 373-384.

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APPROACH TO THE KNOWLEDGE OF COCCINELLIDADE (COLEOPTERA) SPECIES DIVERSITY OF MADEIRA AND PORTO SANTO ISLANDS

A.O. SOARES, R.B. ELIAS & A. RAIMUNDO

SOARES, A.O., R.B. ELIAS & A. RAIMUNDO 2003. Approach to the knowledge of Coccinellidae (Coleoptera) species diversity of Madeira and Porto Santo islands. Pp. 107-112 in A.O. SOARES, M.A. VENTURA, V. GARCIA & J.-L. HEMPTINNE (Eds) 2003. Proceedings of the 8th International Symposium on Ecology of Aphidophaga: Biology, Ecology and Behaviour of Aphidophagous Insects. *Arquipélago*. Life and Marine Sciences. Supplement 5: x + 112 pp.

We present a list of coccinellids collected in Madeira archipelago and notice the presence of two new species; of *Scymnini*; *Scymnus (Scymnus) abietis* (Paykull) and *Nephus hieki* Fürsch. We analyse the distribution and abundance at the community level, using the following measures: species richness index, abundance and relative abundance, similarity index, diversity, and evenness. 13 species from 3 families were recorded. *Hippodamia variegata* was the most abundant one with 29.7 % of the 141 specimens collected. Two main groups of relative abundance were identified. The first group included the 6 most common *H. variegata*, *S. interruptus*, *C. arcuatus*, *C. septempunctata*, *S. levaillanti* and *R. litura* and the second one included *S. abietis*, *L. lophante* and *R. chrysomeloides*. Diversity index values are relatively high. The 6 most common species comprised more than 90 % of the individuals without a very different relative abundance.

Many factors other than extinction and immigration could explain the variation of the number of species on islands. The highest number of species collected in Madeira island, compared to Porto Santo, could be related with its higher elevation, soil and substrate types, plant species richness, number of habitat, habitats diversity, structure and heterogeneity of the former.

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INTRODUCTION

According to the MACARTHUR and WILSON'S (1967) equilibrium theory of island biogeography, the number of species on islands balances regional process governing immigration against local process governing extinction. The immigration rate of new species to the island will be dependent on the potential mainland colonists and the extinctions rate increases with the number of species already present on the island. The extinction rate through competition between species on islands increases more rapidly as species diversity also increases. According to the same model, small and more isolated islands are thought to support fewer species. However, many

factors not included in the model, other than extinction and immigration, could explain the variation on the number of species on islands such as elevation, number of soil types, substrate types, plant species richness, number of habitats, habitat diversity, structure and heterogeneity (BORGES 1992; BORGES & BROWN 1999).

Species diversity is an expression of community structure. High species diversity indicates a highly complex community, for a greater variety of species allows for a larger array of species interactions (ZAR 1984). Information on community characteristics, mainly diversity, has remained a central issue in ecology and measures of diversity are frequently seen as indicators of the stability and maturity of the

community and the well being of ecological systems. Diversity can be divided into two components: the variety or species richness and the relative abundance of species or heterogeneity (MAGURRAN 1991). Diversity measures can be a useful tool in environmental monitoring and conservation management (MAGURRAN 1991), used to evaluate how far the impact of immigration, extinctions and environmental factors, namely human activity, can affect its components. Thus all information concerning previous history of the community, such as the permanence of community in time is very important.

The main characteristics of the Madeiran archipelago are as follows. *Geography and geology*: located in the North Atlantic Ocean between 32°20'-33°10' N latitude and 16°20'-17°20' W longitude. Is 978 km distant from Lisbon and 630 km from the west coast of Morocco, to the Azores it roughly 800 km and to Canary Islands 380 Km. It is formed by two main islands (Madeira - 728 km² and Porto Santo - 57 km²) and three small islands located at 24 km southeast of Madeira (Chão, Deserta Grande e Bugio). Pico Ruivo (1862 m) and Pico do Facho (478 m) are Madeira's and Porto Santo's highest elevations. The archipelago has a volcanic origin. It was formed 60-70 million years ago but Porto Santo has been subaerial for only 12-13 million years whereas Madeira has been aerial for 2-3 million years. *Climate*: Mediterranean type, rather homogenous, but varies depending on the elevation and exposure. The annual precipitation varies much depending on the altitude (Funchal, 645 mm; Encumeada 2675 mm and Porto Santo 338 mm). Monthly temperatures range from 6 to 20 °C, depending on the region. Porto Santo is semi-arid. *Vegetation*: Madeira presents an evergreen laurel forest, called laurisilva, which covers about 10 % of the island. The vegetation on most of the southern part of the island, as well as along portions of the northern coast and into the valleys presents many introduced plants and

trees. The natural vegetation of Porto Santo has also been totally destroyed. It was probably thermophilous laurel forest (KARSHOLT 2000).

Term community used in this work, has its broadest sense, *i.e.*, a set of coccinellid individuals present in a given habitat at a particular time (HODEK & HONĚK 1996). Thus we will consider each island as a whole despite the differences in habitats and the mosaic of environments that each habitat can have. The aims of this work were (i) to provide a contribution to the knowledge of the biological control agents of the *Coccinellidae* family, in Madeira Archipelago (ii) to characterise species diversity of the *Coccinellidae* community, and (iii) to test the species-area hypothesis, which predicts that assemblages will be more species rich on larger islands.

MATERIAL & METHODS

Twenty-three sampling sites located in Madeira and Porto Santo was selected. In which one 30 samples were taken [MADEIRA: Funchal (1), Camacha (1), Santo da Serra (2) Caniçal (1), Câmara de Lobos (1), Quinta Grande (1), Anjos (1), Laranjeiras (1), Porto Moniz (1), Seixal (1), Chão da Ribeira (1), Santana (2), Faial (1), Cural das Freiras (1), Fajã da Rocha do Barco (1); PORTO SANTO: Pico do Castelo (1), Fonte da Areia (1), Aeroporto (1), Portela (2) and Pedrogal (1)] (Fig. 1). Depending on the type of vegetation, different methods were used such as direct observation, beating and sweeping methods, collecting the ladybeetles with a suction tube aspirator. We never took more than an hour in each plot. The collected specimens were preserved in 70% alcohol and afterwards mounted and classified. The specimens collected are deposited at the Ecology Section of the Biology Department of the Azores University (ref. CC-UA-SC-MAD).

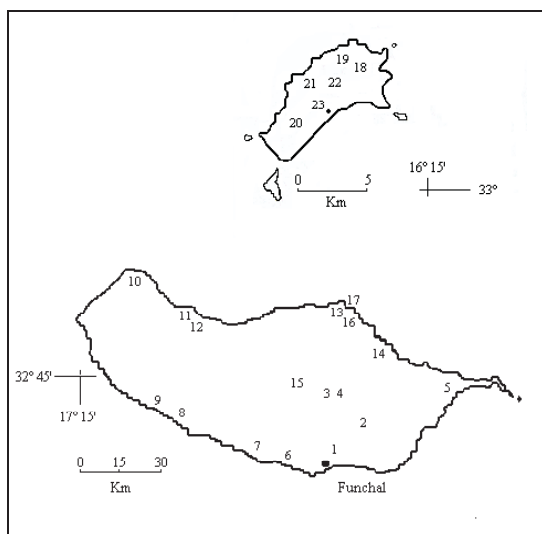


Fig. 1. Madeira and Porto Santo Islands with reference to the 23 sites; 1-Funchal, 2-Camacha, 3 and 4-Santo da Serra, 5-Caniçal, 6-Câmara de Lobos, 7-Quinta Grande, 8-Anjos, 9-Laranjeiras, 10-Porto Moniz, 11-Seixal, 12 Chão da Ribeira, 13 and 16-Santana, 14-Faial, 15-Curral das Freiras, 17-Fajã da Rocha do Barco, 18-Pico do Castelo, 19-Fonte da Areia, 20-Aeroporto, 21 and 23-Portela and 22-Pedrogal.

To characterise the community structure of the *Coccinellidae* fauna, the following measures of diversity were used:

Species richness index (D): Species richness provides an extremely useful measure of diversity. A number of simple indices have been derived using some combination of S (number of species recorded) and N (total number of individuals summed over all species) such as the Margalef's index (MAGURRAN 1991):

$$D_{Mg} = \frac{(S-1)}{\ln N} \quad (1)$$

Abundance (n_i) and relative abundance (p_i): Relative proportions of different species in the community can be measured. The abundance and relative abundance express the total number of individuals collected and the distribution of individuals among species, respectively. If n₁, n₂, n₃, ... n_i, are the abundance of species 1, 2, 3 ..., i, the relative abundance expressed in percentage, becomes (MAGURRAN 1991):

$$p_i = \left[\frac{n_i}{(n_1 + n_2 + n_3 \dots + n_i)} \right] 100 \quad (2)$$

Similarity index (C_s): This is a simple measure of the extent to which two habitats have species (or individuals) in common. Applied as defined, purely in terms of species number, this coefficient gives equal weight to all species and hence tends to place too much significance on the rare species, whose capture will depend heavily on chance (SOUTHWOOD & HENDERSON 2000). In this case we use this index to evaluate to which extent two species have common habitats. It was calculated from the Czekanowski or Sørensen equation:

$$C_s = \frac{2j}{(a+b)} \quad (3)$$

where *j* is the number of habitats common to the two species, and *a* and *b* are the total numbers of habitats, where the species are present, respectively.

Diversity index (H'): Species diversity (sometimes called species heterogeneity), a characteristic unique to the community level of biological organisation, is an expression of community structure. Diversity can be measured recording the number of species and describing their relative abundance, (MAGURRAN 1991). We used the Shannon and Wiener diversity index. It assumes that individuals are randomly sampled from an "indefinitely large" population (PIELOU 1975), and is calculated from the equation:

$$H' = -\sum p_i \log p_i \quad (4)$$

where p_i is the proportion of individuals found in *i*th species estimated as

$$p_i = \frac{n_i}{N} \quad (5)$$

Evenness (J): This diversity index takes into account both species richness and evenness of the individuals' distribution among the species. Evenness (also referred as homogeneity) may be

expressed by considering how close a set of observed species abundances is to those from an aggregation of species having maximum possible diversity for a given N and S (ZAR 1984). It is calculated as follows:

$$J = \frac{H'}{H'_{\max}} \quad (6)$$

H'_{\max} is the maximum possible diversity for a collection of N individuals in a total of S species, when the N individuals are distributed as evenly as possible among the S species. It is calculated as follows:

$$H'_{\max} = \log S \quad (7)$$

J is constrained between 0 and 1 with 1 representing a situation in which all species are equally abundant.

RESULTS & DISCUSSION

Species richness and species richness index (D):

We collected 141 specimens distributed by 13 species of 9 genus, 4 tribes and 3 subfamilies.

For the first time it was recorded the presence of *Scymnus (Scymnus) abietis* (Paykull) and *Nephus hiekei* Fürsch in Madeira archipelago. In Porto Santo Island we collected *Coccinella septempunctata* L. and *Hippodamia variegata* (Goeze) (Table 1). Among all the *Coccinellidae* species already known from Madeira archipelago (33 species) (JANSSON 1940; LUNBLAD 1958; BIELAWSKY 1963; MITTER 1984; FÜRSCHE 1987; RAIMUNDO & LVES 1986; ERBER & HINTERSEHER 1988, 1990; ERBER 1990; ERBER & AGUIAR 1996) we r ecollected 33% (11 species), from which some of them were little abundant. The short period of time selected to carry out the samples, could explain the reason of the low number of species recollected.

Many factors other than extinction and immigration could explain the variation on species numbers on islands. For instance, elevation, number of soil types, substrate types, plant species richness, number of habitats, habitat diversity, structure and heterogeneity (BORGES 1992; BORGES & BROWN 1999). Thus, the higher variability of environmental conditions in Madeira island could explain the higher number of species collected.

Table 1

List of coccinellid species collected on Madeira (Mad) and Porto Santo (Ps) Islands. Legend: + Present on island; * New species to the archipelago

Subfamilies	Tribes	Genus	Species	Mad	Ps	Note
Scymninae	Scymnini	<i>Stethorus</i>	<i>S. wollastoni</i> Kapur	+		
		<i>Clitostethus</i>	<i>C. arcuatus</i> (Rossi)	+		
		<i>Scymnus</i>	<i>S. interruptus</i> (Goeze)	+		
			<i>S. levaillanti</i> Muls.	+		
			<i>S. abietis</i> (Paykull)	+		*
		<i>Nephus</i>	<i>N. flavopictus</i> Woll.	+		
<i>N. hiekei</i> Fürsch	+			*		
Coccidulinae	Coccidulini	<i>Lindorus</i>	<i>L. lophante</i> (Blaisds.)	+		
		<i>Rhizobius</i>	<i>R. litura</i> F.	+		
			<i>R. chrysomeloides</i> (Herbst.)	+		
Coccinellinae	Coccinellini	<i>Adalia</i>	<i>A. decempunctata</i> (L.)	+		
		<i>Coccinella</i>	<i>C. septempunctata</i> (L.)		+	
	Hippodamiini	<i>Hippodamia</i>	<i>H. variegata</i> (Goeze)	+	+	

The values of species richness based on the number of species, were 2.627 and 2.519 to the archipelago and Madeira Island alone, respectively (Table 2).

Abundance (n_i) and relative abundance (p_i):
 In figure 2, values of abundance and relative

abundance are given. Almost 75% of all individuals collected (n_i =89) belong to the following species: *H. variegata* (n_i =42, p_i =29.7%), *Scymnus interruptus* (Goeze) (n_i =29, p_i =20.6%) and *Clitostethus arcuatus* (Rossi) (n_i =18, p_i =12.8%). Those values rise up to 81%

($n_i=101$) and 87% ($n_i=112$) when we include *C. septempunctata* and *Scymnus levaillanti* Mulsant, respectively. The rare species collected, with a uniform distribution of the individuals, were *S. abietis*, *Lindorus lophante* (Blaisds.) and *Rhizobius chrysomeloides* (Herbst.), with only one female in each (0.7%).

Table 2

Data characterising the Coccinellid community from Madeira; S_r - species richness; D_{Mg} - species richness index, H' - diversity index, $H'_{m\acute{a}x}$ -the maximum possible diversity and J-evenness. Legend: Mad- Madeira island; Ps-Porto Santo island

Indices	S_r	D_{Mg}	H'	$H'_{m\acute{a}x}$	J'
Values (Mad+Ps)	13	2.627	0.875	1.114	0.785
Values (Mad)	12	2.519	0.764	1.079	0.708

Similarity index (Cs): *H. variegata* (s= 1, 4, 7, 8, 9, 10, 14, 15(2x), 17) and *S. interruptus* (Goeze) (s= 4, 8, 9, 11, 12, 13, 14, 15, 16 e 17) were found in 10 samples. *S. levaillanti* were found in 7 samples (s= 7, 9, 10, 13, 24, 16, 17), *C. arcuatus* and *R. litura* in 3 samples (s= 9, 15, 16 and s= 2, 3, 12, respectively). The highest values of similarity were obtained in the following species combinations: *H. variegata*/ *S. interruptus*, *H.*

variegata/ *S. levaillanti* and *S. interruptus*/ *S. levaillanti*. The similarity index values in the following combinations *C. arcuatus* - *S. interruptus* and *C. arcuatus* - *S. levaillanti* were, 0.46 and 0.40 respectively (Table 3). Higher values of similarity suggest the possibility of population's niche apportionment and interaction such as competition and intraguild predation.

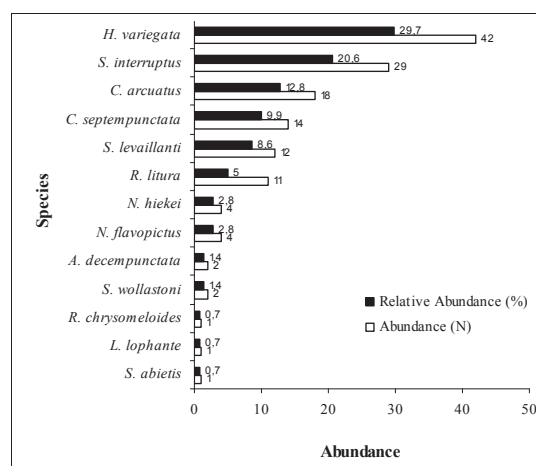


Fig. 2. Absolute and relative number of specimen and among species (Relative Abundance-%) found in Madeira and Porto Santo islands.

Table 3

Similarity index values (Czekanowski or Sørensen) between the most abundant species.

	<i>H. variegata</i>	<i>S. interruptus</i>	<i>S. levaillanti</i>	<i>R. litura</i>	<i>C. arcuatus</i>
<i>H. variegata</i>	—	0.60	0.59	0	0.31
<i>S. interruptus</i>		—	0.59	0.15	0.46
<i>S. levaillanti</i>			—	0	0.40
<i>R. litura</i>				—	0
<i>C. arcuatus</i>					—

Diversity index (H): Relatively high values of diversity were obtained in archipelago (Madeira and P. Santo) and in Madeira island (Table 2). Despite a high relative abundance of *H. variegata* in the community, we found that half of the species had more than 90% of the individuals. The relative abundance of the 6 commonest species was high, with abundance ranging from 5 to 29.7%. Diversity index and maximum possible diversity, were slightly different (Table 2). The lowest value of the diversity index obtained in Madeira island (0.764) when compared to the one

of the archipelago (0.875) can be explained by the absence of *C. septempunctata* in Madeira island.

Evenness (J): The maximum evenness is obtained when values of diversity index and maximum possible diversity are the same (Table 2). Despite not having an identical distribution of individuals among species, we found that the community presented two groups in which the relative abundance wasn't very different. The first group includes the 6 common species and the second one, the other species in which we recorded a uniform distribution of the individuals.

In our opinion this fact contributes to the relatively high values of evenness.

The amount of time spent in sampling and the temporal and spatial variations in the abundance of *Coccinellidae*, related with the life cycle of each species are, in our opinion, the main restriction to the utilization of these results in the characterisation of the distribution and abundance of the entire coccinellid community. Exhaustive sampling programmes must be carried out in order to evaluate seasonal and annual community structure. The approach that we are proposing to know species diversity in Madeira and Porto Santo islands, can be a useful tool in environmental monitoring and conservation management, and can be used to evaluate how far the impact of immigration, extinction and environmental factors namely human activity, may affect its components.

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REFERENCES

- BORGES, P.A.V. 1992. Biogeography of the Azorean Coleoptera. *Boletim Museu Municipal do Funchal* 44: 5-76.
- BORGES, P.A.V. & V.K. BROWN 1999. Effect of island geological age on the arthropod species richness of Azorean pastures. *Biological Journal of the Linnean Society* 66: 373-410.
- BIELAWSKY, R. 1963. Coccinellidae (Coleoptera) von Madeira. *Communications in Biology* 25: 72-102.
- ERBER, D. 1990. New and little known Coleoptera from Madeira. Results of excursions to Madeira in the years 1986-1990. *Boletim Museu Municipal do Funchal* 42: 147-181.
- ERBER, D. & W. HINTERSEHER 1988. Contribution to the knowledge of the Madeira beetles. *Boletim Museu Municipal do Funchal* 40: 139-214.
- ERBER, D. & W. HINTERSEHER 1990. Additional notes to the Knowledge of the Madeira beetles. *Boletim Museu Municipal do Funchal* 42: 141-146.
- ERBER, D. & A.M.F. AGUIAR 1996. New reworkable species of the coleopterous fauna of Madeira. *Boletim Museu Municipal do Funchal* 48: 41-62.
- FÜRSCH, H. 1987. Die Scymninae der Kanaren, Azoren und Madeiras. *Acta Coleopterologica* 3: 1-14.
- HODEK, I. & A. HONĚK 1996. *Ecology of Coccinellidae*. Dordrecht: Kluwer Academic Publishers. 260 pp.
- JANSSON, A. 1940. Die Arthropodenfauna von Madeira nach den Ergebnissen von Prof. Dr. O. Lundblad Juli-August. XXIX. Coleoptera: Sämtliche Familien unter Ausschluss der familie der Carabidae, Dytiscidae, Hydrophilidae und der Gattung Cryptophagus Herbst aus der Familie Cryptophagidae. *Arkiv för Zoologi* 30: 1-64.
- KARSHOLT, O. 2000. Contribution to the Lepidoptera fauna of the Madeiran Islands. *Beiträge zur Entomologie*: 397-405.
- LUNDBLAD, O. 1958. Die Arthropodenfauna von Madeira nach den Ergebnissen der Reise von Prof. Dr. O. Lunblad Juli-Augustus 1935. XXXV. Die Käferfauna der Insel Madeira. *Arkiv för Zoologi* 11: 461-524.
- MACARTHUR, R.H. & E.O. WILSON 1967. *The theory of island biogeography*. Princeton: Princeton University Press. 203 pp.
- MAGURRAN, A.E. 1991. *Ecological diversity and its measurement*. Cambridge: Chapman and Hall. 179 pp.
- MITTER, H. 1984. Beitrag zur Kenntnis der Käferfauna der Insel Madeira. *Bocagiana* 80: 1-7.
- PIELOU, E.C. 1975. *Ecological Diversity*. New York: Wiley & Sons Inc. 165 pp.
- RAIMUNDO, A.A.C. & M.L.L.G. ALVES 1986. *Revisão dos Coccinélidos de Portugal*. Évora, Publicações da Universidade de Évora. 103 pp.
- SOUTHWOOD, T.R.E. & P.A. HENDERSON 200. *Ecological methods* (3rd ed.). London: Chapman and Hall. 575 pp.
- ZAR, J.H. 1984. *Biostatistical analysis* (2nd ed.). New Jersey: Prentice-Hall. 718 pp.

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