The spatial dynamics of the omnivorous Heteroptera *Anthocoris nemoralis*: Effects of host plants and prey

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By

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Abstract

True omnivores are organisms that feed on both plant material and prey. It has recently become evident that omnivory is widespread in many food webs; many species once considered exclusively predaceous have been found to exhibit omnivorous feeding habits. There is, therefore, increasing interest in the ecological implications of omnivory, particularly in understanding the effects of omnivory on community structure. Reduced dependence on prey as an exclusive food source can lead to de-coupling of the population dynamics of the omnivore and its prey. In addition to serving as a food source, plants may provide omnivores with other resources such as oviposition sites and shelter. Ecologists are now attempting to determine whether omnivores have a destabilizing effect on ecological systems, or if, in contrast, omnivory can moderate oscillations and reduce ecosystem disturbances resulting from outbreaks or extermination of herbivores.

In order to understand the unique influence of omnivores on the ecological systems which they inhabit, the factors affecting their temporal and spatial population dynamics must be understood. Since omnivores are dependent for their subsistence on both prey and plants, they may be influenced by changes in quality and quantity of both these food sources and their population dynamics are thus likely to be fundamentally different from those of pure carnivores.

This research has focused upon elucidating the importance of various plant and prey factors in determining the population dynamics of the omnivorous bug *Anthocoris nemoralis* (Heteroptera: Anthocoridae), and its movement between plants. In addition, the research aimed to reveal the impact of plant/omnivore interactions on prey population density. Finally, the possibility of implementing of this knowledge

for improved biological control of the pear psylla (*Lat. Name*) in pear orchards was explored.

The research was conducted in two parallel systems: a natural ecosystem comprised of four tree species and their specific psylla, and an agroecosystem consisting of pear orchards and the pear psylla. This project was carried out over a period of 6 years in the upper Galilee in natural woodlands, in orchards, and in the laboratory.

Capture-recapture experiments revealed that adult *A. nemoralis* bugs actually move among trees in the natural habitat. This finding supported my basic thesis that individual dispersion is one of the factors responsible for changes in the density of the bug population. The results of these experiments also showed that the wing load ratio was lower in dispersers than in non-dispersers.

The effect of plant species on *A. nemoralis* oviposition preference and egg hatching success was examined in choice experiments conducted in the laboratory using pairs of branches from different trees. Significant differences in both parameters were found among the plants. There was some indication that *A. nemoralis* females tend to avoid ovipositing in plants where hatching success is low.

The effect of plant species on time allocation by *A. nemoralis* on prey-less branches was evaluated in a non-choice lab experiment. There was variation in the bugs' allocation of time to different parts of the same plant, and to the same part in different plants. This variation in time allocation indicates that the plant fulfils several functions for the bugs, and that plant quality assessment in one function can differ from the quality assessed in another. The results of these experiments support my hypothesis that plant species preference in *A. nemoralis* is unrelated to prey.

The effects of several plant/prey diet combinations on developmental rate, survival, fecundity and nutritional status of *A. nemoralis* at different developmental stages were evaluated in a series of lab experiments.. The results of these experiments indicate that:

1. Development and survival rate of the bugs was highest on a combined diet of plant foliage and prey in all plant systems. In other words, a plant + prey diet was more suitable for *A. nemoralis* than a diet of prey alone.
2. Nutritional differences were detected among bugs reared on the combined diet of plant + prey in the different systems, although no differences were found in other performance parameters (survival rate and longevity).
3. Wing load ratio was lowest in bugs that were reared on the most optimal plant system, i.e. the system that supported bugs with the highest nutritional status).
4. In the combined diet of foliage + pollen + prey, there was a difference in fat content among nymphs reared on the four plant systems. No differences were detected in other performance parameters (survival, developmental rate and protein content).
5. The fecundity and survival rate of females differed among similar diet combination on different plant systems, or different diet combinations in the same plant system.

The significant conclusions gained from this series of experiments were (a) biochemical differences are a more sensitive measure of a diet's nutritional contribution then other performance parameters such as survival or development rate; (b) quality differences within a resource category have an effect on the nutritional status of *A. nemoralis (*e.g. the pollen of *Rhamnus alaternus* was superior to the

pollen of *Laurus nobilis*); and (c) bugs developing on higher quality plant systems are potentially better dispersers.

The data obtained from this series of experiments support my hypothesis that variation in the nutritional quality of both plant and prey in a habitat determines the size of the *A. nemoralis* population by affecting development, survival and fecundity.

The dynamics of omnivore, herbivore and carnivore populations on the four plant species in the natural woodland were observed and recorded once every two weeks for 3 years. The results indicate that the population density of *A. nemoralis* varies among the trees during the course of a season. There were differences between the variations observed in adult and nymph populations. The data show that each of the four plant species examined plays a different ecological role in the population dynamics of *A. nemoralis: Pistacia lentiscus* is a permanent source; *Rhamnus alaternus* is a temporary source; *Laurus nobilis* is a long term sink; and *Pyrus syrica* is a temporary sink. Another conclusion gained from these observations is that the movement of *A. nemoralis* among the trees is determined by the relative value of available plant and prey resources.

Differences in protein content were found among the bugs collected on the 4 plant species. The pattern of differences was similar to that found in laboratory experiments, although the protein content was higher in laboratory reared specimens. Testing of lipid levels revealed a pattern opposite to that found in the lab; the highest level was found in bugs collected from *Laurus*. It was concluded from these results that comparative data on lipid content of *A. nemoralis* could be relevant to dispersal .

Wing load ratio was found to be highest among bugs collected from *Pyrus,* and lowest was in bugs collected from *Pistacia*. These facts support the hypothesis that individuals developing on higher quality plant systems have a lower wing load, which

contributes to higher fitness in an unstable habitat. Wing load was also found to be lower in males than in females, implying that there are differences between between males and females in fitness components that are expressed as morphometric traits. For males higher fitness takes the form of improved flight capability, which can lead to a greater number of copulations.

Diet experiments and field observation results support the assumption that the spatial and temporal dynamics of *A. nemoralis* are correlated with its nutritional status on different plants during the season. It was concluded that the *A. nemoralis* population in Mediterranean woodland should be considered a dynamic metapopulation system, where some of the trees are sources and some sinks. The movement of bugs between the trees is a function of the availability and relative value of both plant and prey resources.

The rate of predation of the *Rhamnus* psylla by *A. nemoralis* was tested in a laboratory experiment. Fewer psylla were consumed on *Pyrus* then on *Pistacia*, leading to the conclusion that changes in plant utilization by *A. nemoralis* influence prey population density.

The impact of intra-guild interactions on *A. nemoralis* and its prey was studied in a series of laboratory experiments. The omnivore proved more sensitive to intra-guild predation than were other guild members in the system. In addition, significantly fewer psylla were consumed when *A. nemoralis* and the lacewing *Chrysoperela carnea* shared the same arena, although very little intra-guild predation occurred. These results show that actual intra-guild predation need not be present in order for intra-guild interactions to have an impact upon prey density; the presence of another predator is sufficient to have an impact.

The population dynamics of pear psylla, *A. nemoralis* and other psylla natural enemies were recorded during six years of observations in a pesticide-free pear orchard. It was concluded from these observations that *A. nemoralis* has the potential to control the population of pear psylla in orchards in the upper Galilee. The main obstacle to effective control is the predator's late entrance into the orchards. The results of this research indicate that pear orchards are only one of many temporary habitats visited by *A. nemoralis* as it moves among different species of plants in numerous habitats throughout the region. During periods when the pear psylla population reaches economically-damaging proportions in pear orchards, the natural habitat offers combinations of plant and prey resources that are of higher quality than the orchard.

In order to alleviate this situation and improve pear psylla control, a field experiment was conducted to test the impact of *R. alaternus* on pear psylla populations on pear trees. The results showed that psylla survival was lower on pear trees adjacent to *Rhamnus* than on adjacent pear trees enclosed in insect cages, or on pear trees at least 500 meters distant. It was concluded that planting *R. alaternus* as hedgerows around pear orchards may enhance biological control of the pear psylla by *A. nemoralis.*