# The influence of plant structure on searching behaviour in the ladybird, *Scymnus nigrinus* (Coleoptera: Coccinellidae)

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**Abstract.** The foraging behaviour of all developmental stages of the ladybird, *Scymnus nigrinus*, when searching for its prey, *Schizolachnus pineti*, on pine trees was examined. Foraging was characterized by a high inter-individual variability but patterns did not differ significantly between larvae and adults. All stages spent most of their time searching on needles, on which their prey feeds, and remained mainly in the upper and outer parts of the plant which have a higher needle density in comparison with the interior plant parts. Older stages showed a higher voracity than those younger, but all had a similar predation success when attacking an individual prey. All stages spent a high amount of observation time feeding on honeydew from *S. pineti*.

## INTRODUCTION

Usually optimal foraging behaviour represents a compromise between benefits achieved (e.g. finding of food, mates or shelter) and costs arising (e.g. risk of mortality, energy consumption) (Bell, 1990). Theoretically, a forager should try to achieve a maximum of energy gain or reproductive success at a minimum of expense (e.g. Charnov, 1976; Stephens & Krebs, 1986). For an insect predator searching for food, the optimal compromise between cost and benefit is influenced by a number of environmental factors, among them prey distribution, prey availability and plant structure. This last may provide information to a searching predator but also hinder its activities. Coccinellid beetles, for example, may use prominent structures such as twigs, pronounced leaf veins or leaf edges for orientation (e.g. Bänsch, 1964; Shah, 1982; Kareiva & Sahakian 1990; Ferran & Deconchat, 1992). Conversely, hairs or waxes on the plant surface may influence coccinellid movements negatively (e.g. Shah, 1982; Carter et al., 1984; Quilici & Iperti, 1986). Also, coccinellids may have more difficulties to find prey on spatially diverse plant structures than in a homogeneous environment (Kareiva, 1985; Sheehan, 1986).

Usually coccinellids search randomly rather than systematically for prey, as demonstrated by their frequent returns to the same places on a plant (Banks, 1957). Once they encounter prey, or at least honeydew (Carter & Dixon, 1984a) during their search, they switch to an intensive area restricted search (Banks, 1957; Nakamuta, 1985), whose duration depends on the degree of satiation (Dixon, 1959; Carter & Dixon, 1984b). However, the transition between extensive and intensive search shows a considerable individual variation, allowing a high degree of adaptation to short-term fluctuations in prey availability (Ferran et al., 1994).

In the present study the foraging behaviour of the ladybird, *Scymnus nigrinus* Kugelann (Coleoptera: Coccinellidae) on individuals of *Pinus sylvestris* L. infested by the grey needle conifer aphid, *Schizolachnus pineti* (F.) (Homoptera, Aphidoidea: Lachnidae) was examined. *S. nigrinus* is a habitat specialist on conifers, particularly on pines (Klausnitzer, 1967; Majerus, 1994), where it feeds on aphids and adelgids (Börner & Heinze, 1957; Klausnitzer, 1967; Majerus, 1994). Adults hibernate in bark crevices and between pine buds (Hodek, 1973; Majerus, 1994). In late spring and early summer, females lay single eggs under the membraneous ligula at the base of the pine needles. The first instar larva, which is approximately 0.9–1.0 mm long, hatches about ten days after oviposition. Larval development lasts at least 17 days. The grey pine needle aphid, *S. pineti* feeds also exclusively on pines, where it forms dense linear colonies on the outer side of the needles (Leonhardt, 1940; Kidd, 1982).

Searching behaviour and resource utilization of all larval instars and of hibernated and newly emerged adults were analysed. The following were tested: (1) whether different beetle stages differ in their search patterns; (2) whether differences in plant structure (smooth and rough surfaces) and plant architecture (differences in needles density in particular tree sectors) influence foraging behaviour and (3) whether foraging and predation success differed between larval instars and adults.

## MATERIAL AND METHODS

### Insects

Colonies of *S. pineti* were established on potted individuals of *P. sylvestris* and held at 20°C, 65–70% rh, 2,000 lux and 16 L : 8 D period in a climate chamber. *S. nigrinus* adults were collected after hibernation (= last-year adults) on Scots pines near Bayreuth, south-eastern Germany, in April 1994. First instar larvae were obtained exclusively from a laboratory stock of *S. nigrinus* established with hibernated adults. Second to fourth instar larvae were obtained both from the laboratory stock and from field samples. Adults of the new generation (= current-year adults) originated exclusively from the laboratory culture. All *S. nigrinus* were kept in a climate chamber under the same conditions as their prey. Larvae and adults were held individually in plastic boxes (13 cm × 13 cm × 6 cm) and transparent plastic cylinders (dia 5 cm, height 10 cm), respectively, together with *S. pineti* on pine twigs, honeydew droplets and wet filter paper. To standardize their level of hunger, L3, L4 and adults were deprived of food for a 24 h period before the experiment was started. L1 and L2, which are more sensitive to starvation, were deprived of food three hours before the experiment was started.

### Plants

The animals were observed on three year old potted pines which consisted of a main stem, four side-shoots and a central shoot. Three different structural elements were distinguished: needle surface, shaft and bark (Fig. 1). Needle surfaces are linear and smooth, shafts are rough membranes at the transition between needles and bark. The bark is also rough but in contrast to the more one-dimensional needle, it is a planar, two-dimensional structure. Furthermore, the needle densities differed between different parts of the pines: areas with high needle density in the upper, peripherical regions of a pine tree passed gradually into areas with lower needle density and needle-free parts in the lower parts of a tree. For an easier description of the "within-tree position" of the *S. nigrinus* larvae or adults, the pines were divided into 4 cm-sectors (Fig. 1). Sectors I to V ran down from the top to the bottom of the main shoot, sectors VI comprised all outer part of the side shoots, and sectors VII the inner parts of the side shoots.

### Analysis of foraging behaviour and foraging success

L3 (n = 14), L4 (n = 18) and adults (n = 9 for last-year adults; n = 19 for current-year adults) of *S. nigrinus* were released individually at the bottom part of a potted pine (sector V). They were observed either until they left the tree, or until they had rested for more than 2 h without movement. The very small L1 (n = 14) and L2 (n = 13) were observed on single twigs under a binocular microscope until they either
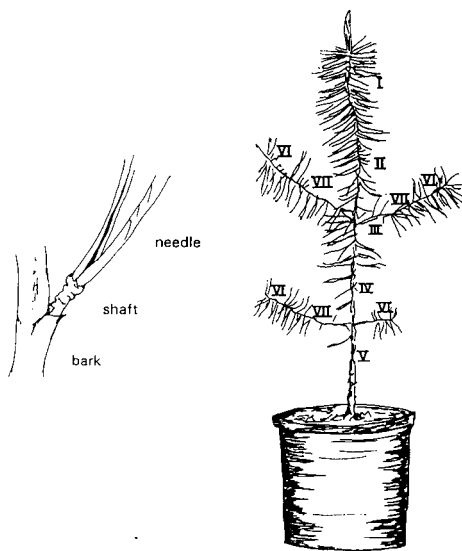
Fig. 1. A sketch of a pine tree indicating the different plant sectors (I–VII) and the three structural components, needle surface, shaft and bark.

left the twig or rested for more than 2 h (release point: bark at the base of the twig). On each host plant or twig between 9 and 18 needles were infested by *S. pineti*. These colonies were distributed irregularly on the plant, similar to the situation in nature.

During any individual observation the following parameters were noted: 1) time spent for searching on bark, shaft or needle surface; 2) time spent for feeding on aphids or aphid honeydew; 3) time spent in particular plant sectors (see Fig. 1; only for L3, L4, current-year adults and last-year adults); 4) number of needles searched; 5) number of attacks upon *S. pineti*; 6) number of consumed *S. pineti*.

## RESULTS

### Structural characteristics of the host plant and distribution of *S. pineti*

Both the average number of needles (Kruskal-Wallis-ANOVA: $H = 180$; $df = 6$, $p < 0.001$) and the average number of colonies of *Schizolachnus* ($H = 109$; $df = 6$, $p < 0.001$) per unit branch length differed significantly between the seven sectors defined for the plants (see Fig. 1). The highest needle density occurred in the outer and upper sectors. The number of needles per sector decreased on the inner parts of the twigs and was lowest on the main stem. Also, significantly more *S. pineti* colonies fed in the outer areas of the plants than in the inner parts or on needles bearing from the stem. However, differences between sectors in the number of *S. pineti* colonies per 100 needles could not be detected ($H = 10$; $df = 6$, $p = 0.134$). Thus, the higher number of colonies, and consequently the higher number of prey available in the outer and upper sectors, resulted from the higher number of needles in those areas.

### Time allocation and searching behaviour in different stages of *S. nigrinus*

The average observation time between release and plant leave or inactivity varied considerably between the different stages. However, due to a high inter-individual variability in time allocation, these differences were not significant ($H = 4$; $df = 5$, $p = 0.597$; Tab. 1), although L1 and L2 searched only single twigs instead of the whole plant and a shorter searching time might have been expected. For adults, observation time ended in 95% of observations because they ceased movement, whereas for the larvae inactivity ended the observation ended in only 26%. Normally they left the tree or twig searching (67%) or sometimes fell from the tree (7%).

After their release at the bottom of the tree, 74% of L3 and 57% of L4 first ascended the apex of the tree, while 67% of the current-year adults first visited one of the peripherical branches. These adults visited significantly more often peripherical sectors in comparison with the larvae ($H = 9.22$; $n = 43$; $p < 0.01$).

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TABLE 1. Observation time and number of searched needles by *Scymnus nigrinus* in relation to beetle age (means ± S.E.). Within each column, means sharing the same letter do not differ significantly at $p < 0.05$ (Mann-Whitney U-test).

| Stage of *Scymnus nigrinus* | Observation time (sec) | No. needles visited per observation | No. needles visited per hour |
|---|---|---|---|
| L1 | 5,457 ± 1,361[a] | 7.1 ± 1.9[a] | 11.7 ± 4.5[a] |
| L2 | 9,388 ± 2,280[a] | 13.2 ± 4.0[bc] | 8.7 ± 3.3[a] |
| L3 | 8,762 ± 1,823[a] | 18.8 ± 5.0[bc] | 9.6 ± 2.9[a] |
| L4 | 12,314 ± 2,843[a] | 41.5 ± 11.2[c] | 16.3 ± 3.3[a] |
| adult (new) | 9,913 ± 2,425[a] | 15.4 ± 4.9[b] | 11.7 ± 2.9[a] |
| adult (old) | 6,883 ± 1,608[a] | 21.3 ± 4.9[bc] | 8.8 ± 0.6[a] |

On average, L1, L3 and L4 spent between 50% and 60% of their time budget to search on the plant for resources, while L2 and adults allocated only between 30 and 35% of their time for searching (Fig. 2). However, no means differed significantly due to the high inter-individual variability.

There were also age-dependent differences in the relative time spent on needle surface, shaft and bark. The ratio of searching time spent on needle surfaces increased continuously from L1 to current-year adults. Last-year adults searched longer on shaft and bark than current-year adults.

These differences could be related to some extent to the individual behaviour when searching a needle. Older stages examined significantly more often the complete needle, while younger stages often remained on the shaft and did not move to the needle surface (Fig. 3: H = 24; n = 85, p < 0.001). Small larvae had difficulties to surmount the distance between the membraneous shaft ligula and the needle. Particularly, L1 returned to the bark very often after having searched intensively on the shaft, instead of continuing the search on the needle surface where the prey was feeding. There were also significant differences between stages in the number of needles searched during the observation time. L1 searched fewer needles than all other stages, while L4 showed the highest searching activity (Tab. 1). No differences could be detected in the average number of visited needles per hour.

On average, L3, L4 and current-year adults spent more than half of their time on the outer and upper part of the tree (Fig. 4) where needle densities were highest. For all three stages, the time spent in a tree sector was correlated with the specific needle density in these sectors (Spearman's rank correlation: L3: rs = 0.624, n = 47, p < 0.001; L4: rs = 0.603, n = 82, p < 0.001 ; adults: rs = 0.546, n = 70, p < 0.001).

Foraging success and resource exploitation

*S. nigrinus* larvae discovered between 0 and 5 colonies during their observation. They tended to detect larger colonies easier than smaller colonies, since the average size of detected colonies (2.98 individuals per colony, SD = 2.68) was higher than the average size of all colonies present on the tree (2.47 individuals per colony, SD = 1.10). There was a strong tendency of increasing foraging success with larval age, although their means did not differ significantly (Tab. 2; H = 8, df = 3, p = 0.168). Both last-year and current-year adults had a similar success as third instar larvae.
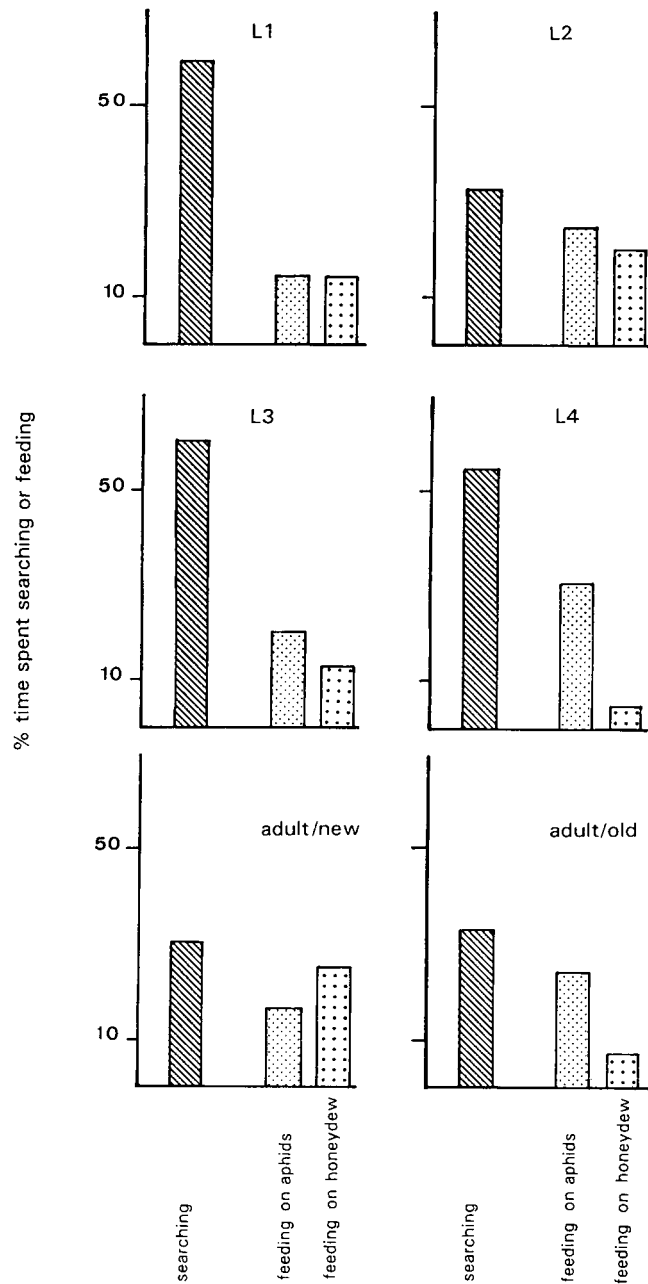
Fig. 2. Relative time spent searching (hatched bars), feeding on aphids (fine-dotted bars) and feeding on honeydew (coarse-dotted bars) by various stages of *Scymnus nigrinus* (means). Within each pattern, no means differed between stages at $p < 0.05$ (Mann-Whitney U-test). The means presented for each *S. nigrinus* stage do not sum up for 100% since other activities (resting, cleaning) are not included in the figure.

TABLE 2. Foraging success of *Scymnus nigrinus* in relation to beetle age. Within each column, means sharing the same letter do not differ significantly at p < 0.05 (Mann-Whitney U-test).

| Stage of *Scymnus nigrinus* | Discovered colonies | | | No. consumed aphids/observation (mean ± S.E.) | No. consumed aphids/hour (mean ± S.E.) |
|---|---|---|---|---|---|
| | Min | Max | x̄ ± S.E. | | |
| L1 | 0 | 1 | 0.4 ± 0.1ᵃ | 0.1 ± 0.1ᵃ | 0.1 ± 0.1ᵃ |
| L2 | 0 | 2 | 0.6 ± 0.2ᵃ | 0.6 ± 0.3ᵇ | 0.3 ± 0.1ᵇ |
| L3 | 0 | 2 | 0.9 ± 0.2ᵃ | 0.9 ± 0.3ᵇ | 0.4 ± 0.1ᵇ |
| L4 | 0 | 5 | 1.7 ± 0.4ᵃ | 1.9 ± 0.5ᵇ | 0.5 ± 0.2ᵇ |
| adult (new) | 0 | 4 | 1.0 ± 0.3ᵃ | 1.0 ± 0.3ᵇ | 0.4 ± 0.1ᵇ |
| adult (old) | 0 | 3 | 1.1 ± 0.3ᵃ | 1.6 ± 0.5ᵇ | 0.7 ± 0.3ᵇ |

The success of the subsequent attacks depended significantly on the size of the aphid (oneway-ANOVA: F = 12.42, df = 4; p < 0.001). Small aphids, e.g., first instar larvae, were easier to subdue than those larger, e.g., fourth instar larvae and adults. However, there were no stage-specific differences in overcoming success between the various *S. nigrinus* stages (oneway-ANOVA: F = 0.719, df = 5, p = 0.610). Only the first instar larvae tended to be less successful during an attack. In most cases, any *S. nigrinus* was able to consume only one aphid per colony of *S. pineti* discovered. Usually, the other aphids left their feeding place and the needle in response to the coccinellid attack and the subsequent defense of the aphid attacked. Only exceptionally, *S. nigrinus* was able to consume two aphids of the same colony on the same needle.

The average number of consumed *S. pineti* increased significantly with the beetle's age (Tab. 2), both per total observation time (H = 14, df = 5, p = 0.018) and per unit observation time (H = 15, df = 5, p = 0.017). It ranged between 0.1 aphids per hour in L1 and 0.5 aphids per hour in L4. Adults did not differ significantly from L2 to L4 (Tab. 2).

All stages except L4 and last-year adults spent a similar amount of time for consuming aphids and feeding on aphid honeydew (Fig. 2). Larvae resolved crystalline honeydew by the release of digestion fluid and external digestion and ingested it subsequently with their sickle-shaped mandibles. Usually, newly hatched first instar larvae were able to complete their development until moulting into the second instar if fed with honeydew of *S. pineti* (n = 7 out 8 individuals) exclusively and showed normal development if provided
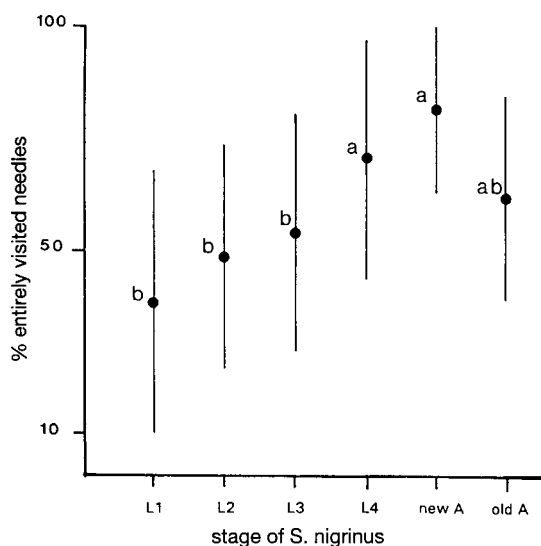


Fig. 3. Proportion of entirely searched needles [(shaft + needle searched)/(shaft + needle surface searched plus only shaft searched)] in various stages of *Scymnus nigrinus* (mean ± S.E).

% of time spent in the sections

100

50

0

L3      L4    new adult

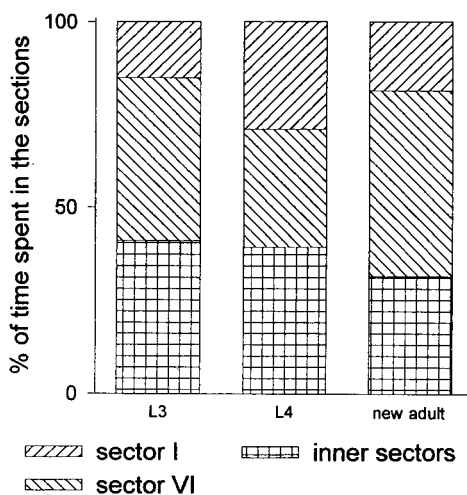⬚⬚⬚ sector I    ⬚⬚⬚ inner sectors

⬚⬚⬚ sector VI

Fig. 4. Time allocation (in percent) in different tree sectors by L3, L4 and adult *S. nigrinus*.

with *S. pineti* after moulting into the second instar.

DISCUSSION

The foraging behaviour of *S. nigrinus* was characterized by a high inter-individual variability, a feature which is typical for many coccinellids (e.g. Ferran & Dixon, 1993; Ferran et al., 1994; Frazer & MacGregor, 1994; Kauffman & LaRoche, 1994). Although adult ladybirds, in contrast to larvae, are able to use visual cues for foraging (Hodek, 1973; Nakamuta, 1984; Said et al. 1985; Obata, 1986; Collet, 1988), larvae and adults of *S. nigrinus* differed only slightly in their searching patterns. A similar result was obtained by Kauffman & LaRoche (1994) who compared the searching behaviour of second instar, fourth instar and adult *Scymnus frontalis* (F.) on wheat infested with *Diuraphis noxia*. Again, there was little difference in searching patterns between *S. frontalis* larvae and adults.

Both larvae and adults of *S. nigrinus* spent most of their time on needle surfaces, the plant structure where their prey, *S. pineti*, was feeding. The almost one-dimensional structure of the needle may be one reason for the small differences in searching patterns. Needles "guide" larvae and adults and determine their search path. An "area restricted search" with many sharp turns, typical for many coccinellids (e.g., Banks, 1957; Carter & Dixon, 1982; Nakamuta, 1985; Kareiva & Odell, 1987), is thus prevented by the limited space. Furthermore, *S. pineti* colonies often disperse after an attack of *S. nigrinus*, especially if the attacked individual was defending itself heavily (Völkl & Stadler, 1996). Thus, both *S. nigrinus* larvae and adults usually continued an "extensive search" after having consumed their prey. Searching pattern may change if other prey, e.g., the adelgid *Pineus pini*, is available on the stem. In this case, both larvae and adults displayed the typical "area restricted search" and remained on the bark in the vicinity of *P. pini* aggregations for long time intervals.

The host plant's structural heterogeneity influenced the foraging of *S. nigrinus*. Plant heterogeneity occurred on two levels: first, the smooth linear needle surface can be distinguished from the rough shaft membranes and from the coarse bark. Second, the needle density was much higher in the peripherical parts of the tree and decreased towards the inner and lower sectors (Fig. 1). The surface structure influenced mainly first and second instar larvae, which had difficulties to take the short "step" from shaft to needle surface. Therefore, younger larvae searched less needles entirely, and spent less time on the surface, than older stages. In contrast, adult *Anatis ocellata* (L.) visited regularly the shaft only but not the needle surface when searching on pines (Kesten, 1969). In this species, the behaviour was not size-related, particularly since larvae were regularly searching entire needles. Another phenomenon observed was that last-year adults spent consistently

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more time on bark and shaft than current-year adults. One reason for the difference might be a search for suitable oviposition sites which are, usually, located under the shaft or, sometimes, in bark crevices.

The higher needle density in the upper and outer sectors influenced strongly the "within-plant place allocation" of older S. nigrinus stages, which spent most of their time in the peripherical and upper plant sectors. The time spent in a particular plant sector was correlated with the needle density. Therefore, needle density appears to be the most important factor determining the comparably long time spent in the peripherical and upper sectors of the tree. Other factors such as positive phototaxis and negative geotaxis (Dixon, 1959) might be supplementary explanations for time spent on the main shoot.

There was a strong tendency that older larvae and adults found more S. pineti colonies per unit time than small larvae. One reason for this might be that younger larvae remained more often on the shaft (Fig. 3) where no hosts were available. As is typical for ladybirds, older stages also showed a higher voracity than those younger (e.g. Hodek, 1973; Hattingh & Samways, 1991; Richards & Goletsos, 1991; Ofuya, 1995). However, the proportions of successful attacks after a prey colony was located did not differ greatly between the stages. The L1 and L2 tended to be less successful, but the differences were not significant. This could be explained by a contrary effect of the size of the S. nigrinus larvae. The smaller larvae were often not noticed by the aphids and could attack an aphid without being molested. Although earlier perceived by the aphids the larger larvae had less difficulties to subdue an aphid even if it started to defend itself. Instead, the success of an attack was determined mainly by aphid size, with larger aphids being less vulnerable to S. nigrinus attacks than those smaller.

A striking result was the high amount of time spent both by larvae and adults for feeding on honeydew. Adults of predatory ladybirds are known to utilize honeydew, or other food such as pollen, regularly as alternative food to survive periods of prey shortage (Hodek, 1973; Majerus, 1994). However, in S. nigrinus both larvae and adults commonly fed on honeydew despite the presence and availability of their essential prey, S. pineti. For larvae, the uptake of honeydew is facilitated by the morphology of its mouthparts (Ricci, 1979) which enable S. nigrinus to ingest it like prey. One important function of larval honeydew uptake for S. nigrinus might be an increase in the probability of survival, especially in the first instar. For them the ability to develop successfully on honeydew might serve as an alternative mechanism to increase the survival time until the first prey is found. As S. nigrinus females lay their eggs singly, the newly hatched larvae are unlikely to feed on those of their siblings. Such sibling cannibalism is widespread in coccinellids which lay their eggs in batches. It is assumed that this extends the survival time until the first aphid prey will be found (e.g. Banks, 1956; Kawai, 1978; Osawa, 1992; Agarwala & Dixon, 1992).

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