

Food remains in the guts of *Coccinella septempunctata* (Coleoptera: Coccinellidae) adults and larvae

HOLGER TRILTSCH

Federal Biological Research Centre for Agriculture and Forestry, Institute of Integrated Plant Protection, Stahnsdorfer Damm 81,
D-14532 Kleinmachnow, Germany; e-mail: h.triltsch@bba.de

Key words. *Coccinella septempunctata*, Coccinellidae, food remains, gut dissection, Aphididae, aphids, non-aphid prey, Thysanoptera, Chrysomelidae, *Oulema* spp.

Abstract. From 1994–1997 the food of *Coccinella septempunctata* L. was investigated on the basis of gut dissections of adults and larvae collected in the field. Additionally, the gut contents of adults fed under laboratory conditions were investigated. The likelihood of recovering different prey types during gut dissection was variable, which will be illustrated by presenting some common prey fragments. The food eaten by adult *C. septempunctata* throughout a year was studied at a locality in Berlin-Staaken. Ladybirds were collected from March 1994 until November 1997 in different crops and habitats on roughly a monthly basis. Aphid feeding was detectable from April until October. In May and June they were the most frequent food type. Fungal spores, in most cases the conidia of *Alternaria* spp., became most frequent in July. Additionally non-aphid arthropods were frequently preyed upon in July. A very common non-aphid prey item were thrips. Pollen was important in May and September. Comparing the food components of newly emerged adults with those of overwintered adults some remarkable differences were detected. In newly emerged adults non-aphid arthropods and fungal spores were much more frequent than in overwintered adults whereas aphids were less frequently found. The diet of adults and larvae was also investigated in June and July in cereal fields at two other localities, Northern Flaeming and Magdeburger Boerde. No difference in adult diet was found between the three localities. The composition of the larval diet was relatively similar to that of the adults.

INTRODUCTION

Coccinella septempunctata L. is the dominant aphidophagous ladybird in a wide range of agricultural crops and other habitats. In Germany and other European countries this species, together with syrphid larvae, is considered to be the most important predator regulating aphid population dynamics in cereals (Triltsch, 1997a; Freier et al., 1998).

It is known that aphidophagous ladybirds consume different food types because aphids are abundant only during a restricted time period. More than 20 aphid species were listed as essential prey of *C. septempunctata* by Hodek & Honěk (1996). Besides this there are other arthropod prey items documented in the literature, e.g. other Sternorrhyncha (Psyllidae, Aleyrodidae, Coccidae), Acari, Thysanoptera, and larvae of Diptera, Coleoptera, and Lepidoptera (Schilder & Schilder, 1928; Kanervo, 1940; Hodek, 1967, 1970; Singh et al., 1991). As with many other coccinellid species several reports exist on the cannibalistic behaviour of *C. septempunctata* (e.g. Takahashi, 1989; Agarwala & Dixon, 1992). Nevertheless there are also some vegetarian food components observed in the diet of aphidophagous ladybirds, e.g. pollen, nectar, and fungal spores (Putman, 1964; Hemptinne & Desprets, 1986; Hemptinne et al., 1988). Because of differences in the nutritive suitability of food types it is important to distinguish between essential and alternative food types (Hodek, 1967, 1970). Food which only provides energy to survive in periods of aphid scarcity, but does not allow ovariole ripening and the completion of juvenile development, is characterised as alternative food.

In recent years the list of aphid species and other components of *C. septempunctata* diet is getting larger. But most of our knowledge about different foods and their suitability is based on feeding experiments under laboratory conditions or on field observations of individual ladybirds. From a single observation in the field it is difficult to decide whether consuming a certain food item is a common behaviour or not. Therefore, relatively little is known about the diet composition of *C. septempunctata* and the relative importance of the food types mentioned above under field conditions.

To get more information, gut dissections of field sampled *C. septempunctata* were performed. Previously this method was widely used to study the food range of some polyphagous predators, such as carabid beetles (e.g. Sunderland, 1987; Sunderland et al., 1987, 1995). Gut dissection gave interesting results on the pollinivory of *Propylea quatuordecimpunctata* (L.) and *Adalia bipunctata* L. in early spring (Hemptinne & Desprets, 1986; Hemptinne et al., 1988). For the genus *Coccinella* two gut content studies were undertaken in some Nearctic species (Forbes, 1883; Putman, 1964).

The main objective of this study was to examine the diet of *C. septempunctata* under field conditions in association with a critical evaluation of the gut dissection method. The following topics were of interest. First, the adults of *C. septempunctata* were collected at an agricultural area in different crop and non-crop habitats throughout the whole year to look for seasonal changes in diet composition. Second, during June and July, when *C. septempunctata* reproduces in cereals, adults and larvae were

collected at three localities. The differences in diet composition between localities and developmental stages were thus analysed. New generation adult *C. septempunctata* often emerge at the end of cereal aphid infestation (Triltsch, 1997a). These newly emerged adults need food to accumulate fat reserves whereas overwintered adults need the aphid food essential for reproduction. It was of interest to investigate if the described variation in aphid availability in connection with different ladybird physiology caused changes in the composition of their diet. Therefore the diet of newly emerged and overwintered adults was compared. Some preliminary results of the first two years of this study were already presented for adult *C. septempunctata* (Triltsch, 1997b). Now a more detailed picture is given and results from investigations of larvae are added.

Moreover, a description of prey fragments and other food items frequently found in the alimentary canal is given. In addition, difficulties to identify certain prey types will be illustrated using examples of some experimental work in the laboratory. In feeding experiments two prey types, previously never found in the alimentary canal but mentioned as prey of aphidophagous ladybirds, namely ladybird eggs and larvae of *Oulema* spp. (Coleoptera: Chrysomelidae), were studied. Cannibalism on eggs is well documented in the literature (e.g. Banks, 1956; Agarwala & Dixon, 1992). Feeding on *Oulema* spp. larvae was reported for *P. quatuordecimpunctata* (Rogers et al., 1972). Other ladybird species are also successfully fed on Chrysomelidae (Hazzard & Ferro, 1991). While invading cereal fields *C. septempunctata* probably often encounter *Oulema* spp. larvae because they are a very common pest of these crops. Therefore, feeding on these chrysomelid species could be of importance.

MATERIAL AND METHODS

Sources of material used for gut dissection

From 1994 to 1997 *C. septempunctata* individuals, 20 to 40 in each sample, were collected at three agricultural localities. At locality Berlin-Staaken (BS) adults of *C. septempunctata* were collected throughout the whole year in different crop and non-crop habitats according to the frequency of their occurrence. From March 1994 until November 1997 41 different samples were collected in an agricultural area of about 10 km² with less fertile soils, relatively small fields (around 10 ha) and numerous woody islands. The dominant crop is winter rye. Other typical crops are the spring cereals, i.e. oats and spring wheat. Data collected over the above time span were divided into monthly intervals. This allows the analysis of changes in the frequency of food types during the course of a year based on a larger number of dissected individuals. The gut contents of newly emerged adults and the old generation, were compared in samples collected in June, July, and August. In *C. septempunctata* the elytra of newly emerged adults are lighter in colour (Hodek & Honěk, 1996) and also more flexible. It is thus relatively easy to distinguish them from overwintered adults.

At Northern Flaeming (NF) and Magdeburger Boerde (MB) ladybird adults were collected in June and July, when they reproduce in cereal fields. In most cases enough *C. septempunctata* were found in winter wheat fields; otherwise adjacent fields were chosen for additional collecting. There was no investigation in 1997 at MB due to very low ladybird densities.

Locality NF is situated 40 km south of Berlin. By the size of fields (15–20 ha) and abundant winter rye it is similar to locality BS. In contrast the locality MB, situated 120 km west of Berlin, is an important agricultural area with highly fertile soils. It is characterised by larger fields (40–80 ha), and the dominant crop is winter wheat. The data from all localities were analysed per month.

Third and fourth instar *C. septempunctata* larvae were collected for gut dissection from 1995, at the BS and NF sites. There are two samples from winter wheat fields at NF and five samples from oat fields at BS. These data were also analysed per month.

All ladybird individuals were captured by sweepnetting or after visual searches. The ladybirds were carried to the laboratory in a cool-box ($9 \pm 2^\circ\text{C}$). They were then rendered inactive at -20°C and killed in 80% ethanol. This procedure was necessary to prevent any excretion.

While collecting ladybird individuals for gut dissection, additional plant material (flowers and leaves, particularly with fungal spores on their surface) and potential prey arthropods were also sampled. That material was useful in identifying prey fragments present in the gut samples. From these studies a catalogue of food remains frequently found in the guts of *C. septempunctata* adults and larvae was created.

Gut dissection

The alimentary canal of each individual was removed by dissection under a binocular microscope and the food remains were inspected in glycerol. Food remains were classified as: (1) aphids, (2) non-aphid arthropods, (3) fungal spores, (4) pollen and other plant material, (5) inorganic material, and (6) unidentifiable items. Frequency of a certain food type was then the percentage (%) of individuals of each sample containing that type of food remains. The "combined meal" category includes cases where more than one food type were found in a single gut. This category was defined according to Sunderland et al. (1995) as the percentage of individuals with food in their gut.

A more detailed identification of prey species within the category "non-aphid arthropods" was performed from 1995. Therefore the frequency of certain non-aphid arthropod species is based on less data. In some cases it was not possible to make a definite classification within "non-aphid arthropods" and this relatively large category was not divided.

Feeding experiments

Prey types were studied in an air conditioned laboratory ($20 \pm 3^\circ\text{C}$, $65 \pm 5\%$ RH, 16L : 8D). Adults of *Coccinella septempunctata*, 10 individuals in each experiment, were kept individually in small plastic vials (100 ml) for 3 days without any food. After that the beetles were fed with 10–20 *C. septempunctata* eggs/d or 1 *Oulema* spp. larva/d for 5 days and then dissected.

RESULTS

Identification and morphological appearance of common food remains

A collection of some common food remains present in the gut of adult and larval *C. septempunctata* are shown in Figs 1–5. Gut dissection of field collected individuals as well as of those fed under laboratory conditions indicate a very different degree of food recovery in the alimentary canal. If *C. septempunctata* adults were fed with eggs of their own species no remains were recovered which would allow their identification. Additionally, after feeding on *Oulema* spp. larvae, it was quite difficult to find any characteristic food remains. In most cases only

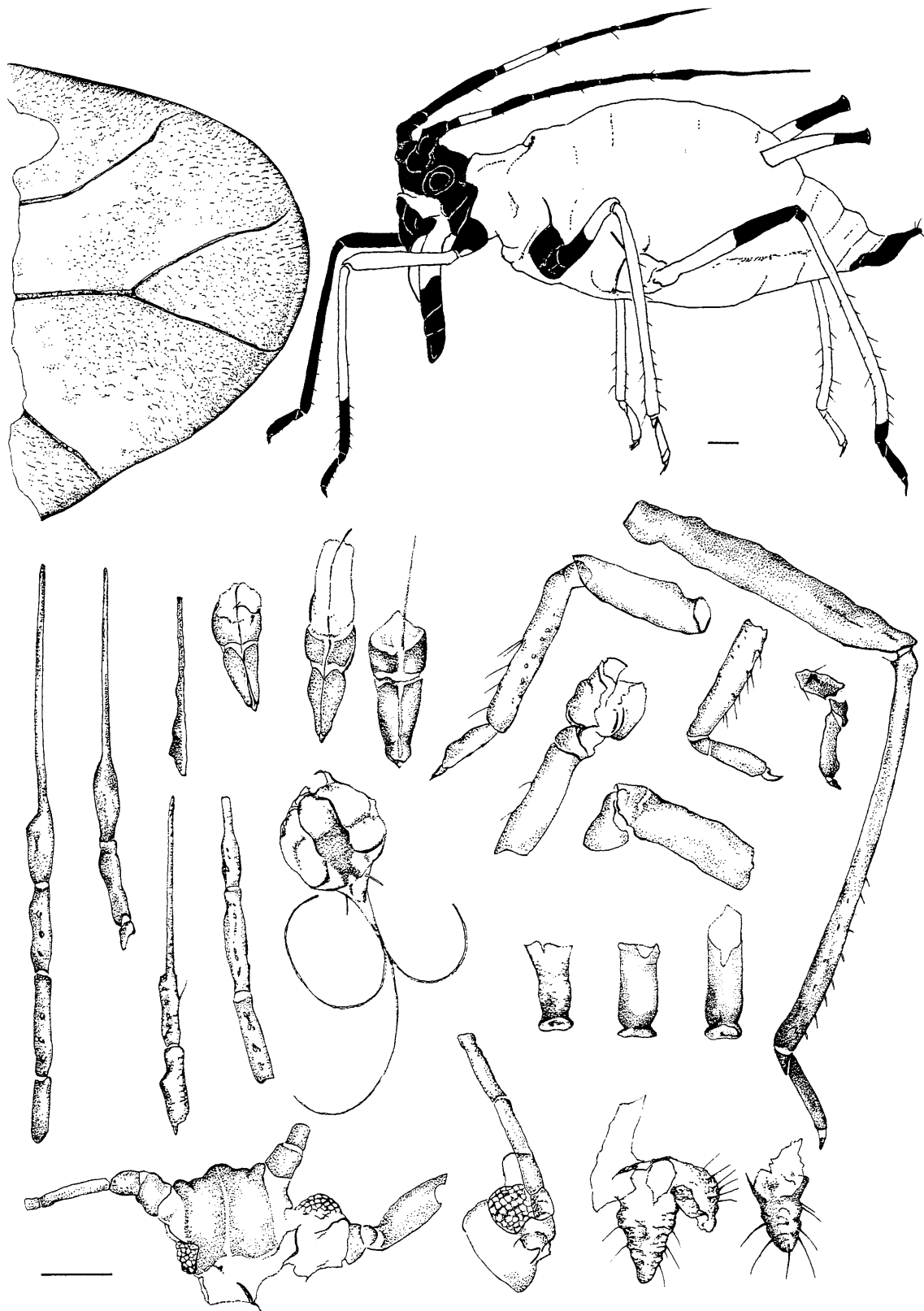


Fig. 1. Aphid remains in the guts of *Coccinella septempunctata* and their possible site of origin on an intact aphid prey (black body parts). Scale bar = 0.1 mm.

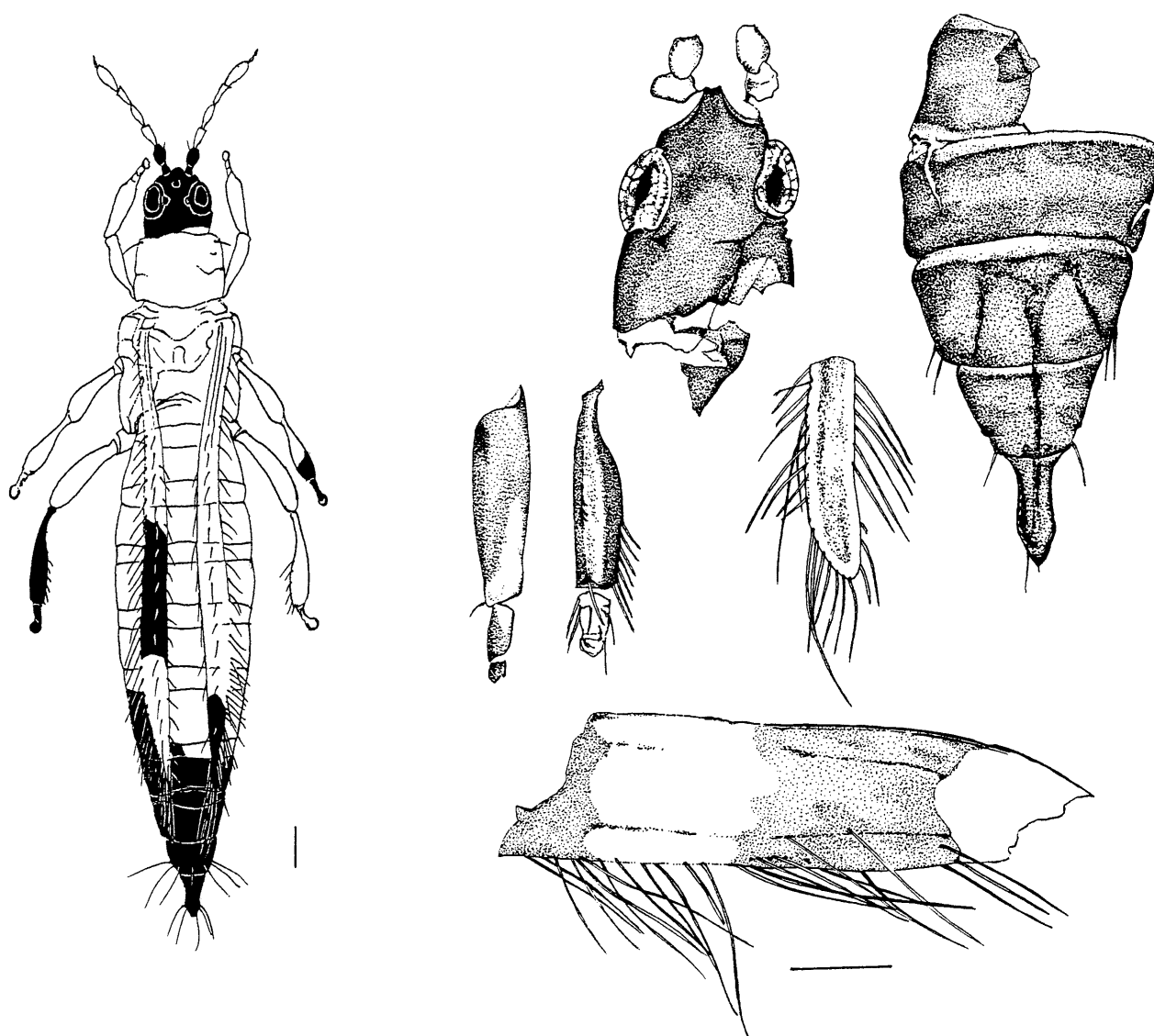


Fig. 2. Remains of Thysanoptera in the guts of *Coccinella septempunctata* and their possible site of origin on an intact prey individual (black body parts). Scale bar = 0.1 mm.

single setae were traceable (Fig. 3). On the other hand, smaller prey animals like aphids or Thysanoptera are easily detectable during gut dissection (Figs 1, 2). These smaller arthropods are completely devoured by *C. septempunctata*, which makes it easy to find typical chitin fragments or in some cases nearly intact bodies (especially of Acari, Collembola and Thysanoptera), only parts of larger arthropods are eaten. During feeding experiments with *Oulema* spp. larvae it was observed that *C. septempunctata* fed only on the soft abdominal part of the larva but never on the head. Therefore in larger prey arthropods the success of prey recovery during gut dissection depends largely on the amount of sclerotized body

parts eaten. Coccinellid larvae were easily detectable as prey (Fig. 4).

In Table 1 an example is given for the body parts recovered from *C. septempunctata* feeding on aphids. However, no conclusions on the number of aphids eaten can be easily drawn from the values presented here, because several fragments of head, antenna, femur, and tibia, may have originated from the same prey individual. Nevertheless, there are some body parts, e.g. the ultimate rostral segment, which were found to be seldom destroyed. The nomenclature of aphid body parts follows Miyazaki (1987).

TABLE 1. Number of aphid body fragments found in the guts of two adult *Coccinella septempunctata* (a female and a male) collected at Northern Flaeming from winter wheat in July 1996.

	Head without appendices	Antenna	Clypeus/ Rostrum	Femur/Tibia	Tarsus	Siphunculus	Other parts	Total
Female	13	31	5	129	29	5	82	294
Male	7	13	4	55	9	5	30	123

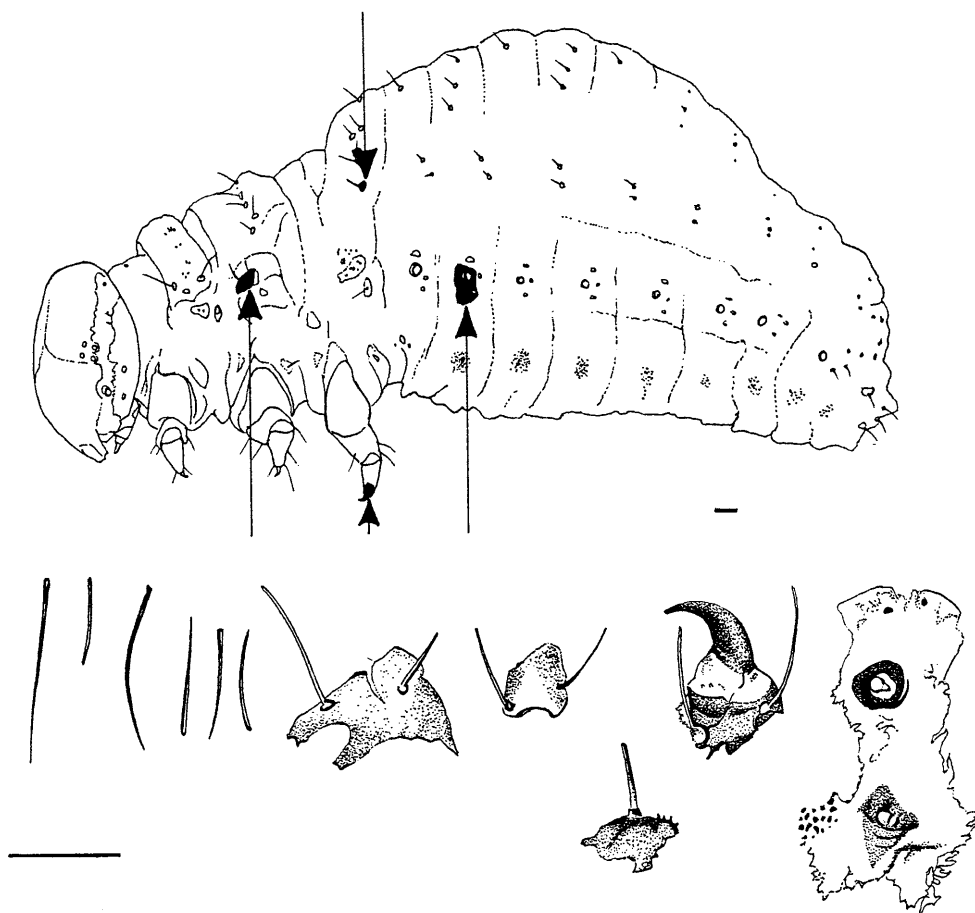


Fig. 3. Remains of *Oulema* spp. larvae in the guts of *Coccinella septempunctata* and their possible origin from the prey (black body parts). Scale bar = 0.1 mm.

Adult food throughout a year

Remarkable changes in the frequency of consumption of certain food types were observed during the course of a year (Table 2). Feeding on aphids was detectable from April to October. Aphids were the most frequent food type in May and June. The highest proportion of *C. septempunctata* adults with aphid remains was observed in June (88.5%). At the same time the proportion of individuals with an empty gut was lowest. Like aphids, non-aphid arthropods were consumed from April until October, but generally not so frequently. A relatively high frequency of feeding on non-aphid arthropods was observed in May, July, and August. It was possible to identify the prey arthropods as belonging to Thysanoptera, Collembola, Acari, Hymenoptera, Diptera (larvae), Coccinellidae (larvae), and probably Chrysomelidae (larvae). Non-aphid arthropods appear to be less frequent sources of food during June when aphids were most frequently consumed. Surprisingly, fungal spores were found to be nearly as frequent as aphids in *C. septempunctata* guts. During this study 1,146 adult *C. septempunctata* were collected at locality BS. In the guts of 507 of these individuals aphid remains were found and in 484 individuals fungal spores were present. Non-aphid arthropods were found in only 144 of all dissected adults. Fungal spores were the most frequent food type detected during gut dis-

section, especially in the second half of the year. It was possible to identify conidia of *Alternaria* spp. and other Moniliales, and also uredospores of *Puccinia* spp. (Barnett, 1960). Conidia of *Alternaria* spp. (Fig. 5) were the most frequent and numerous fungal spores found in the gut of *C. septempunctata* (around 80% of all cases). Pollen and plant material was present in the alimentary canals of dissected *C. septempunctata* from April until November. There were two periods of frequent pollen feeding, a first peak in May and another in September. Observations in the field and gut dissection results indicate feeding on the pollen of *Ribes* spp., *Stellaria* spp., *Pinus* spp., *Solidago* spp., *Tanacetum vulgare* L., and Gramineae. Another diet component found relatively frequently during gut dissection was inorganic material (Fig. 5).

Feeding on more than one of the mentioned food types, defined as a "combined meal", was frequently found. In July a "combined meal" was observed in 84.4% of *C. septempunctata* adults with food in their gut. Nevertheless about 5–10% of the dissected individuals contained no identifiable remains in their guts. From November to March no visible food remains were found in more than 75% of the adults investigated.

An interesting observation arose from a comparison between newly emerged and overwintered adults in June–August. Whereas the frequency of pollen and inor-

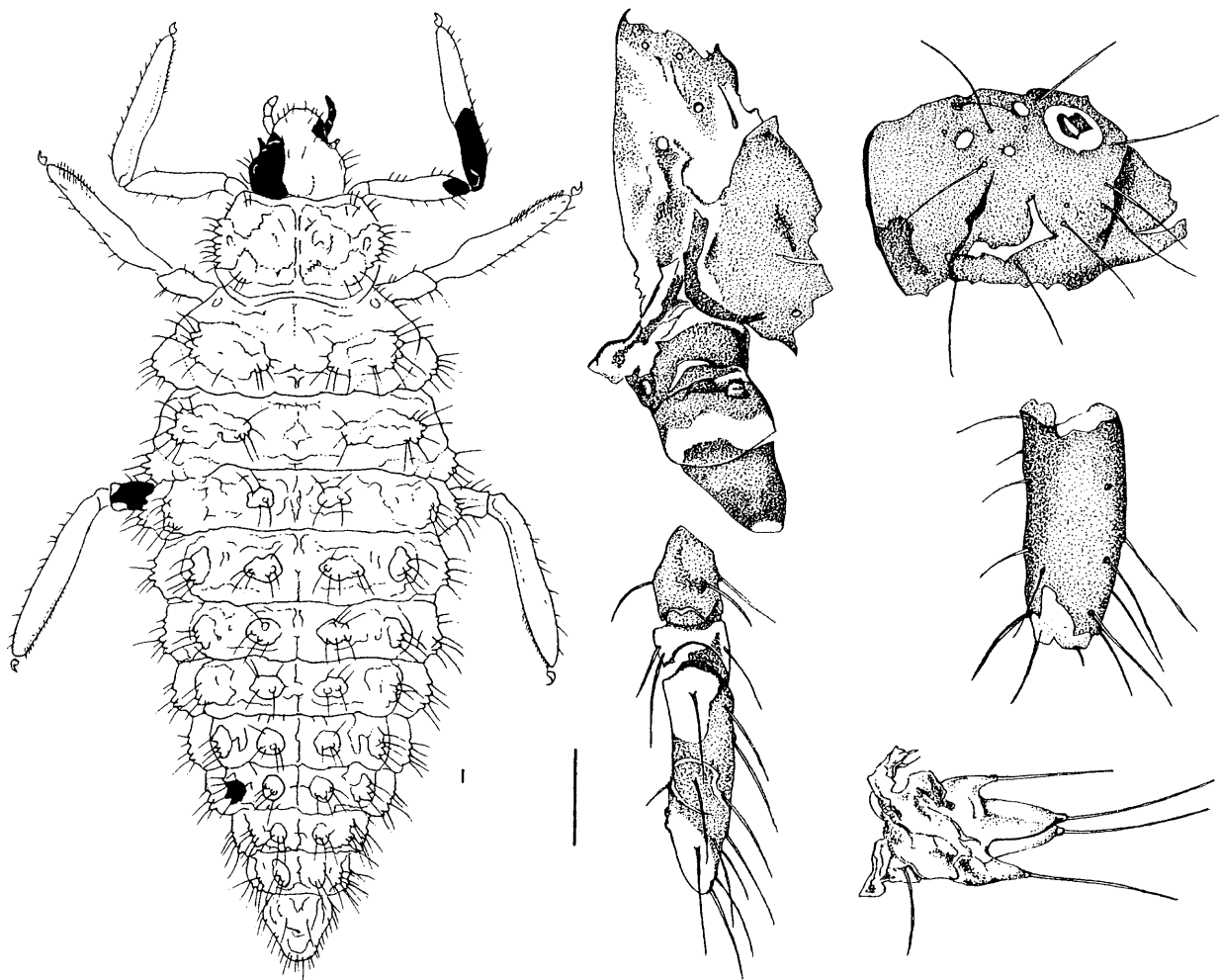


Fig. 4. Remains of coccinellid larvae in the guts of *Coccinella septempunctata* and their possible site of origin on an intact prey individual (black body parts). Scale bar = 0.1 mm.

ganic material was nearly at the same level in both groups, some considerable changes were observed in the frequency of aphids, non-aphid arthropods, and fungal spores in their diet. In newly emerged adults non-aphid arthropods and fungal spores were much more frequent than in the diet of overwintered adults, while aphids were less frequent (Fig. 6). To a certain degree that change in

diet composition was also observed by comparing the results between June and July (Table 2).

Adult and larval food in June and July

The frequency of food types in the guts of adults was very similar at the three localities (Table 3). The typical change in food composition from June to July, previously

TABLE 2. Frequency of food types in the gut of adult *Coccinella septempunctata* collected at Berlin-Staaken in 1994–1997.

Month	Habitat/crop	Number of adults dissected (samples)	Proportion (%) with							
			remains of aphids	non-aphid arthropods	fungal spores	pollen	inorganic material	not identified	empty gut	combined meal ^a
Feb	hibernacula	42 (1)	0	0	0	0	0	16.7	83.3	0
Mar	hibernacula	98 (4)	0	0	0	0	1.0	2.0	97.0	0
Apr	hibern., fallow	65 (2)	10.8	10.8	15.4	9.2	9.2	16.9	43.1	9.2
May	fallow, oat, rye	110 (4)	50.0	27.3	45.5	22.7	49.1	10.9	9.1	70.0
Jun	oat, wheat	261 (10)	88.5	12.6	56.3	7.3	39.5	3.1	1.5	68.9
Jul	oat	138 (4)	82.6	34.8	86.2	14.5	24.6	5.8	2.9	84.4
Aug	fallow, oat, maize	67 (3)	44.8	23.9	68.7	13.4	41.8	6.0	7.5	75.8
Sep	fallow, grassland	176 (6)	36.4	9.7	55.1	23.3	24.4	7.4	24.4	69.2
Oct	fallow, hibern.	125 (3)	4.8	0.8	12.0	1.6	12.0	8.0	75.2	51.6
Nov	fallow, hibern.	32 (2)	0	0	0	3.1	0	0	96.9	0
Dec	hibernacula	32 (2)	0	0	0	0	0	0	100.0	0

^aProportion of individuals with more than one food type in gut as percentage of the number of individuals with food in gut.

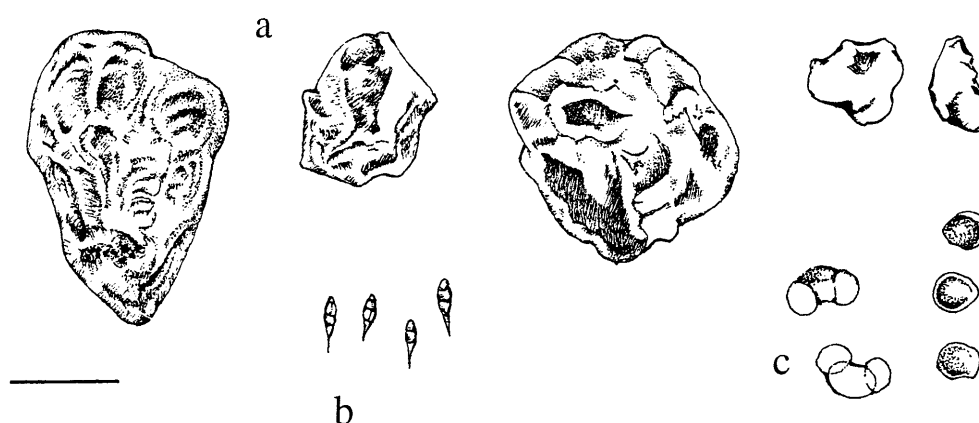


Fig. 5. Inorganic material (a), fungal spores (b), and pollen (c) in the guts of *Coccinella septempunctata*. Scale bar = 0.1 mm.

observed at locality BS, was also found at localities NF and MB. Non-aphid arthropods as well as fungal spores and pollen became more frequent in July whereas the frequency of aphid remains slightly decreased at locality BS and NF but not at MB. Moreover, the frequency of individuals with a "combined meal" increased from June to July.

Some preliminary results of the gut dissections of *C. septempunctata* larvae are given in Table 4. Compared with the adults these data are derived from a smaller number of individuals. Therefore only general trends will be described. Aphids were the most frequent food type in June and July. The remarkably increased frequency of fungal spores in July, previously observed in adult *C. septempunctata*, was also true for larvae. Non-aphid arthropods were detected in larval guts as frequently as in those of adults. On the other hand, pollen and inorganic material were less frequently found in larvae. Another distinction between larval and adult diet was observed through a closer inspection of the non-aphid prey. In July 1995–1997, mean frequency (%) of feeding on coccinellid larvae was significantly higher ($P < 0.05$) in larvae (4.7 ± 4.19 , $n = 5$) compared to adults (0.8 ± 1.19 , $n = 10$). The most frequent non-aphid prey found in both larvae and adults were Thysanoptera. During July this prey amounted to 66% of all detected non-aphid arthropods fed upon by larvae. The amount for adults was 40%. Because relatively large body fragments of Thysanoptera

were found in the gut it was tried to quantify consumption rates on that prey animal. While dissecting 27 *C. septempunctata* larvae, collected in a wheat field at locality NF on 18 July 1995, 32 Thysanoptera individuals were found.

DISCUSSION

Evaluation of gut dissection method

It was shown that the gut dissection method is only suitable for a limited study of the food eaten by *C. septempunctata*. Animal prey without sclerotized parts, like coccinellid eggs, were not detectable. Larger prey with little sclerotization could therefore be easily overlooked during gut dissection. Hence, consumption of certain insect larvae, e.g. those of *Oulema* spp., is very difficult to prove. On the other hand, small prey animals, especially aphids and Thysanoptera, were easily detected. Moreover, it seems to be possible to quantify consumption of those prey animals by *C. septempunctata*. Thysanoptera were completely devoured by *C. septempunctata* adults and larvae and relatively large body fragments were found in the gut (Fig. 2). Aphid remains found in the gut were more crushed when compared to those of the Thysanoptera. Therefore quantification of aphid consumption is more difficult. Some preliminary experiments, where *C. septempunctata* adults were fed a certain number of aphids before dissection, showed a significant relationship between the number of aphids eaten per day and the

TABLE 3. Frequency of food types in the gut of adult *Coccinella septempunctata* collected at three localities in June and July 1994–1997.

Month, locality	Cereal crop	Number of adults dissected (samples)	Proportion (%) with							
			remains of aphids	non-aphid arthropods	fungal spores	pollen	inorganic material	not identified	empty gut	combined meal ^a
June										
BS	oat, wheat	261 (10)	88.5	12.6	56.3	7.3	39.5	3.1	1.5	68.9
MB	oat, wheat	157 (6)	89.2	14.6	43.3	1.3	51.0	4.5	3.2	71.7
NF	wheat	248 (10)	77.4	16.9	51.6	16.9	20.6	1.6	5.6	62.1
July										
BS	oat	138 (4)	82.6	34.8	86.2	14.5	24.6	5.8	2.9	84.4
MB	wheat	50 (3)	90.0	24.0	62.0	10.0	22.0	0.0	1.4	79.6
NF	wheat	202 (7)	74.8	20.3	72.3	27.2	20.3	4.5	9.8	81.9

^aProportion of individuals with more than one food type in gut as percentage of the number of individuals with food in gut.

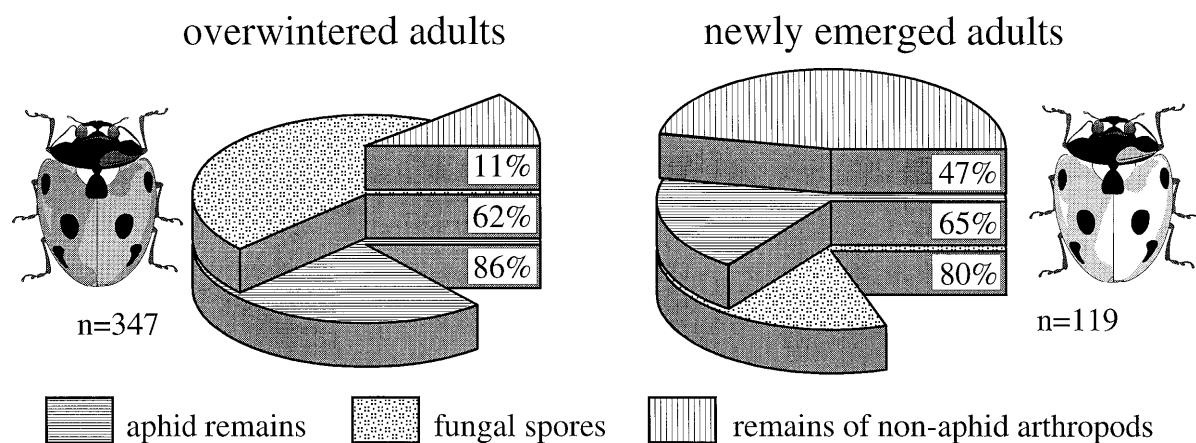


Fig. 6. Frequency of aphids, non-aphid arthropods, and fungal spores in the guts of overwintered and newly emerged adult *Coccinella septempunctata* collected at Berlin-Staaken in June, July, and August 1994–1997.

number of aphid body fragments present in the gut. For quantification two aphid body fragments, the ultimate rostral segment and the tarsus, were chosen. The quantity of aphids was estimated for the two ladybird individuals which were presented in Table 1. The calculated consumption was 12–16 aphids for the female and 5–9 aphids for the male adult (Triltsch, unpubl.). Gut dissection could be a suitable method for studying aphid feeding by *C. septempunctata* in the field if it is combined with an aphid abundance estimation at that point when the ladybirds were collected. While dissecting ladybird samples further interesting data can be obtained, e.g. beetle size, sex ratio, stage of ovariole ripening, and parasitization. In addition to the ladybird and aphid density data this offers the chance of a more detailed life cycle study (Triltsch & Freier, 1998).

Besides the incomplete food record mentioned above another problem emerges from the gut dissection method. The presence of a certain food in the alimentary canal gives no clue to its suitability or digestibility. Moreover it is not clear whether a certain food was intentionally chosen. It could also be swallowed accidentally when preying on another food item not detected in the gut. This might be the case when some fungal spores were consumed. Previously Putman (1964) suggested a connection between feeding on honeydew and the presence of *Alternaria* spp. conidia. If fungal spores are mostly accidentally taken in during feeding on honeydew the results presented here indicate very extensive consumption of non-

eydew. That behaviour has already been recorded in predaceous coccinellids (Zoebelein, 1955; Carter & Dixon, 1984). However, conidia of *Alternaria* spp. were found in very high numbers per dissected individual, also in the absence of aphids. In addition, plant parasitic fungi were observed. For these reasons it seems unlikely that feeding on fungal spores by *C. septempunctata* is exclusively accidental. Polyphagy, i.e. feeding on pollen, fungal spores, and aphids, has been observed in other closely related ladybird species (e.g. Putman, 1964; Hukusima & Itoh, 1976; Ricci, 1986). But nothing is yet known about the nutritional value of fungal spores to *C. septempunctata* and additional work is needed.

Another surprising observation was the relatively high frequency of inorganic material in the gut of *C. septempunctata*. The frequent detection of food components without any clear nutritional value, in our case soil particles and perhaps conidia of *Alternaria* spp., leads to the hypotheses that *C. septempunctata* is a careless predator and consumer and does not cautiously investigate its food before feeding on it. However, such a hypothesis seems to be unrealistic. While searching for food a ladybird permanently touches the substrate with its maxillary palps which are equipped with numerous sensory receptors (Barbier et al., 1996). These maxillary palps are also involved in prey recognition. The observed preference for certain prey types, e.g. Thysanoptera as a non-aphid animal prey, is another indication of an active food choice by *C. septempunctata*. If *C. septempunctata* is able to recog-

TABLE 4. Frequency of food types in the gut of larval *Coccinella septempunctata* collected at three localities in June and July 1994–1997.

Locality	Cereal crop	Number of adults dissected (samples)	Proportion (%) with							
			remains of aphids	non-aphid arthropods	fungal spores	pollen	inorganic material	not identified	empty gut	combined meal ^a
June										
BS	oat, wheat	61 (2)	77.0	18.0	16.4	4.9	11.5	11.5	11.5	46.3
July										
BS	oat	41 (3)	85.4	14.6	61.0	7.3	9.8	4.9	9.8	78.4
NF	wheat	73 (2)	91.8	30.1	89.0	0.0	2.7	17.8	1.4	88.9

^aProportion of individuals with more than one food type in gut as percentage of the number of individuals with food in gut.

nise all its food components then there must exist non-nutritional reasons for selecting certain prey types. It is conceivable that the presence of *Alternaria* spp. spores in an aphid colony may be an indicator of the age of the colony. In older aphid colonies accumulated honeydew provides a suitable substrate for the growth of that fungus. Usually ladybird food is only judged from a nutritional point of view. The possibility that food may provide information about habitat quality is often overlooked.

Diet composition under field conditions

As it is shown in Table 2 adults feed from April to October. *Coccinella septempunctata* was able to track down aphids during the whole period of feeding activity. However, only in June and July were aphids consumed by more than 50% of the adults investigated. Fungal spores were consumed by more than half of the dissected adults from June to September. Considering all 1146 *C. septempunctata* adults collected at locality BS, feeding on fungal spores was nearly as frequent as feeding on the essential aphid prey. This was an unexpected result and we are far from having a satisfactory explanation for this phenomenon. It is imaginable that it indicates frequent feeding on honeydew. On the other hand the gut dissection method could favour suggestion that fungal spores are frequently eaten, because an indigestible component is detectable in the whole alimentary canal. Frequent feeding on fungal spores has been already observed in closely related ladybird species. Putman (1964) found pollen, fungal spores, aphids, and other arthropods in the gut of *Coleomegilla maculata lengi* Timb. A diet consisting of pollen, fungal spores, mites, and Thysanoptera was observed in *Tytthaspis sedecimpunctata* (L.) by Ricci (1986). The phylogenetic closeness of the Coccinellini and Tytthaspidini tribes has been stated by several authors (e.g. Kovář, 1996; Klausnitzer & Klausnitzer, 1997). It is well documented that there are aphidophagy, mycophagy, and phytophagy represented in the subfamily Coccinellinae but our knowledge about food relations of coccinellids is still fragmentary (Hodek & Honěk, 1996; Klausnitzer & Klausnitzer, 1997).

Non-aphid arthropods became relatively common in July. While comparing the diet of newly emerged adults with that of overwintered adults the increased frequency of feeding on non-aphid arthropods was more evident. Previously Sunderland (unpubl.) observed such a change in prey eaten by *C. septempunctata* during the summer, and Thysanoptera were also recorded as important non-aphid prey. Newly emerged *C. septempunctata* adults often have to start their lives under unfavourable food conditions. Most of the formerly abundant aphid populations in cereals, which were intensively exploited by ladybirds in the preceding larval stage, have disappeared due to changes in plant quality and predation. Under such circumstances Thysanoptera appear to be the favoured substitute animal food. It was noteworthy that both adults and larvae preferred Thysanoptera as non-aphid prey.

Pollen was important as a food source in May and September. Pollinivory in spring has been previously observed in *A. bipunctata* and *P. quatuordecimpunctata*. In

A. bipunctata it was shown with feeding experiments that pollen represents an alternative food source. It enables the females to promptly oviposit at the time of aphid population increase (Hemptinne & Desprets, 1986; Hemptinne et al., 1988). In the present study pollinivory was recorded frequently in September and to a certain degree during the whole period of feeding activity. For instance, during wheat flowering it was possible to find some wheat pollen in the gut of *C. septempunctata* adults.

A comparison of *C. septempunctata* adult food during June and July at three different agricultural localities showed no remarkable differences. Furthermore, adults and larvae fed on similar prey items. A similarity between larval and adult diet in different habitats was also observed in *T. sedecimpunctata* by Ricci (1986).

Predation on coccinellid larvae was significantly more frequent in *C. septempunctata* larvae than in adults but is generally relatively seldom. Previously Takahashi (1989) observed that feeding on ladybird larvae is more common in larvae than in adults. Predation on ladybird eggs that is considered to be the most important cannibalistic behaviour (e.g. Takahashi, 1989; Agarwala & Dixon, 1992) was not detectable by gut dissection.

ACKNOWLEDGEMENTS. The author acknowledges the "Deutsche Forschungsgemeinschaft" (DFG) for funding the researcher and the Federal Biological Research Centre for Agriculture and Forestry for facilitating the research. I would like to thank very much my family team Anett and Marlene for their help in collecting ladybirds. I am grateful to K. Sunderland for providing me with his unpublished material on ladybird gut dissections which focused my attention to changes in ladybird animal food during June/July. I thank K. Lindner for assistance in identifying fungal spores and U. Vetter for reading the English manuscript. I am also grateful to three anonymous referees for their critical reviews.

REFERENCES

- AGARWALA B.K. & DIXON A.F.G. 1992: Laboratory studies of cannibalism and interspecific predation in ladybirds. *Ecol. Entomol.* **17**: 303–309.
- BANKS C.J. 1956: Observations on the behaviour and mortality in Coccinellidae before dispersal from the egg shells. *Proc. R. Entomol. Soc. Lond. (A)* **31**: 56–60.
- BARBIER R., LE LANNIC J. & BRUN J. 1996: Récepteurs sensoriels des palpes maxillaires de coccinellidae adultes aphidiphages, coccidiphages et phytophages. *Bull. Soc. Zool. Fr.* **121**: 255–268.
- BARNETT H.L. 1960: *Illustrated Genera of Imperfect Fungi*. Burgess, Minneapolis, 225 pp.
- CARTER M.C. & DIXON A.F.G. 1984: Honeydew: An arrestant stimulus for coccinellids. *Ecol. Entomol.* **9**: 383–387.
- FORBES S.A. 1883: The food relations of the Carabidae and Coccinellidae. *Bull. Illinois St. Lab. Nat. Hist.* **1**: 33–60.
- FREIER B., MÖWES M. & TRILTSCH H. 1998: Beneficial thresholds for *Coccinella 7-punctata* L. (Col., Coccinellidae) as a predator of cereal aphids in winter wheat – results of population investigations and computer simulations. *J. Appl. Entomol.* **122**: 213–217.
- HAZZARD R.V. & FERRO D.N. 1991: Feeding response of adult *Coleomegilla maculata* (Col.: Coccinellidae) to eggs of Colorado potato beetle (Col.: Chrysomelidae) and green peach

- aphids (Homoptera: Aphididae). *Envir. Entomol.* **20**: 644–651.
- HEMPTINNE J.-L. & DESPRETS A. 1986: Pollen as a spring food for *Adalia bipunctata*. In Hodek I. (ed.): *Ecology of Aphidophaga*. Academia, Prague, pp. 29–35.
- HEMPTINNE J.-L., NAISSE J. & OS S. 1988: Glimps of the life history of *Propylea quatuordecimpunctata* (L.) (Col.: Coccinellidae). *Med. Fac. Landbouww. Rijksuniv. Gent* **53**: 1175–1182.
- HODEK I. 1967: Bionomics and ecology of predaceous Coccinellidae. *Annu. Rev. Entomol.* **12**: 79–104.
- HODEK I. 1970: Coccinellids and modern pest management. *Bio-science* **20**: 543–552.
- HODEK I. & HONĚK A. 1996: *Ecology of Coccinellidae*. Kluwer, Dordrecht, 464 pp.
- HUKUSIMA S. & ITOH K. 1976: Pollen and fungus as food for some coccinellid beetles. *Res. Bull. Fac. Agric. Gifu Univ.* **39**: 31–38.
- KANERVO V. 1940: Beobachtungen und Versuche zur Ermittlung der Nahrung einiger Coccinelliden. *Ann. Entomol. Fenn.* **6**: 89–110.
- KLAUSNITZER B. & KLAUSNITZER H. 1997: *Marienkäfer: Coccinellidae*. 4th ed. Westarp-Wiss., Magdeburg, 176 pp.
- KOVÁŘ I. 1996: Phylogeny. In Hodek I. & Honěk A.: *Ecology of Coccinellidae*. Kluwer, Dordrecht, pp. 19–31.
- MIYAZAKI M. 1987: Morphology of aphids. In Minks A.K. & Harrewijn P. (ed.): *Aphids. Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 1–25.
- PUTMAN W.L. 1964: Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. *Can. Entomol.* **96**: 1149–1155.
- RICCI C. 1986: Food strategy of *Tytthaspis sedecimpunctata* in different habitats. In Hodek I. (ed.): *Ecology of Aphidophaga*. Academia, Prague, pp. 311–316.
- ROGER C.E., JACKSON H.B., ANGALET G.W. & EIKENBARY R.D. 1972: Biology and life history of *Propylea 14-punctata* (Col.: Coccinellidae), an exotic predator of aphids. *Ann. Entomol. Soc. Am.* **65**: 648–650.
- SCHILDER F.A. & SCHILDER M. 1928: Die Nahrung der Coccinelliden und ihre Beziehung zur Verwandtschaft der Arten. *Arb. Biol. Reichsanstalt* **16**: 213–282.
- SINGH T.V.K., SINGH K.M. & SINGH R.N. 1991: Influence of intercropping: III. Natural enemy complex in groundnut. *Indian J. Entomol.* **53**: 333–368.
- SUNDERLAND K.D. 1987: A review of methods of quantifying invertebrate predation occurring in the field. *Acta Phytopath. Entomol. Acad. Sci. Hung.* **22**: 13–34.
- SUNDERLAND K.D., CROOK R.J., STACEY D.L. & FULLER B.J. 1987: A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *J. Appl. Entomol.* **24**: 907–933.
- SUNDERLAND K.D., LÖVEI G.L. & FENLON J. 1995: Diets and reproductive phenologies of the introduced ground beetles *Harpalus affinis* and *Clivinia australasiae* (Coleoptera: Carabidae) in New Zealand. *Aust. J. Zool.* **43**: 39–50.
- TAKAHASHI K. 1989: Intra- and inter-specific predations of lady beetles in spring alfalfa fields. *Jpn. J. Entomol.* **57**: 199–203.
- TRILTSCH H. 1997a: Der Marienkäfer *Coccinella septempunctata* L. im Komplex Winterweizen-Getreideblattlaus-Antagonist. *Agrarökologie* **24**: 1–159.
- TRILTSCH H. 1997b: Gut contents in field sampled adults of *Coccinella septempunctata* (Col.: Coccinellidae). *Entomophaga* **42**: 125–131.
- TRILTSCH H. & FREIER B. 1998: Investigations on differences between ladybird populations (Col., Coccinellidae) at three localities. *IOBC/WPRS Bull.* **21**: 113–124.
- ZOEBELEIN G. 1955: Der Honigtau als Nahrung der Insekten. *J. Appl. Entomol.* **38**: 369–416.

Received October 26, 1998; accepted March 19, 1999