6 FOOD RELATIONS

6.1 Food range

The food of *Coccinellidae* has always been actively studied, largely because of the economic impact of most species. Unfortunately the prey-predator relations have mostly been studied by observing what the coccinellids happen to be eating, sometimes only by noting occurrence together of predator and prey on the same plant, etc. The reliability of the lists of data accumulated in this way (Schilder and Schilder 1928, Balduf 1935, Fulmek 1957, Börner and Heinze 1957, Kaddou 1960, Kurir 1964,) was questioned already by Thompson (1951): "The various species of ladybirds do not actually feed or at least feed habitually on all the various host insects with which they are associated in the records." Thompson warned further that: "The gradual accumulation of such records in the literature finally gives a picture which may be completely inaccurate in so far as the real behaviour and food habits of the species are concerned."

A short but critical survey of the food relations of central European *Coccinellidae* has been made by Klausnitzer (1966). An exact picture of the relationship of coccinellids to food can only be gained by a systematic study, preferably experimental, of individual species. Then it becomes gradually apparent that even within individual tribes, there are various specialisations in the feeding of the various members. Thus, for example, in the generally aphidophagous tribe *Coccinellini* there are also non-predaceous species, such as the phytophagous *Bulaea lichatschovi* (Capra 1947, Dyadechko 1954, Savoïskaya in Hodek 1966, p. 141; 1970a) and the mycophagous *Tytthaspis sedecimpunctata* (Dauguet 1949, Turian 1969). Within the same tribe there are further species which specialize on immature stages of *Coleoptera*, such as *Aiolocaria spp.* (Iwata 1932, 1965, Savoïskaya 1970b) and *Calvia quinquedecimguttata* (Kanervo 1940) which feed on pre-imaginal stages of *Chrysomelidae*, or *Neocalvia spp.* which prey on larvae of mycophagous coccinellids of the tribe *Psylloborini* (Camargo 1937). Thus, not only entomophagy, but also phytophagy and mycophagy are represented in the tribe *Coccinellini;* phytophagy is normal in the subfamily *Epilachninae*, and mycophagy in the tribe *Psylloborini*. The classification of coccinellids is still partially artificial and thus discussing the food specialization of a whole tribe cannot but have its limitations (Tab. 6.01).

The natural food range of a certain coccinellid species can be ascertained by several ways. The classic method is the microscopic detection and identification of prey remnants from the guts or excreta (Forbes 1883, Putman 1964) which can be compared with the whole specimens of insects from the same community. Three more refined methods are rather time consuming, but they have general application. In the precipitin test (Dempster 1960, Loughton at al. 1963, Rothschild 1966) the specific proteins of the prey are identified by their reaction with the serum of a sensitized mammal (usually a rabbit). Limitations of this method are discussed by Southwood (1966, pp. 250—1).

Tab. 6.01 Food of *Coccinellidae* (Compiled from Balduf 1935 and Sasaji 1971) 1)

Subfamily *Sticholotinae*	
tribe *Sukunahikonini*	coccids, *Diaspinae*
tribe *Serangini*	aleyrodids
tribe *Sticholotini*	coccids, *Diaspinae*
(Pharini)	*Diaspinae*
(Microweiseini)	principally coccids, chiefly *Diaspinae (Aspidiotus Chionaspis)*
Subfamily *Scymninae*	
tribe *Stethorini*	phytophagous mites
tribe *Scymnini*	62 % coccids. 23 % aphids
individual genera	extensive specialisation
Clitostethus	*Aleyrodidae*
Lioscymnus	
Diomus	*Pseudococcus*
Nephus	
Sidis	
Parasidis	
Cryptolaemus	
Pseudoscymnus	
Platyorus	aphids
Scymnus (Pullus)	
Scymnus (Scymnus)	
tribe *Aspidimerini*	aphids
tribe *Hyperaspini*	75 % coccids — *Coccinae (Pseudococcus, Phenacoccus, Ripersia)*
tribe *Ortaliini*	psyllids, *Flatidae*
Subfamily *Chilocorinae*	
tribe *Telsimiini*	coccids, *Diaspinae*
tribe *Platynaspini*	? aphids
tribe *Chilocorini*	75 % coccids, aphids
Subfamily *Coccidulinae*	
tribe *Coccidulini*	all but one sp. coccids
(Rhizobiini)	51 % *Diaspinae*. 35 % *Coccinae*. 14 % *Lecaniinae*
tribe *Exoplectrini*	*Icerya* and its nearest relatives
tribe *Noviini*	*Icerya* and its nearest relatives
Subfamily *Coccinellinae*	
tribe *Coccinellini*	85 % aphids. also psyllids. *Chrysomelidae*
(Hippodamiini)	76 % aphids
(Synonychini)	aphids
Neda	coccids
Archaioneda	coccids
(Cheilomenini)	72 % aphids, coccids, *Aleyrodidae*
(Veraniini)	aphids, phytophagous
tribe *Psylloborini*	*Erisyphe* (mildew)
Subfamily *Epilachninae*	
tribe *Epilachnini*	phytophagous
(Azyini)	*Diaspinae*
(Oeneini)	*Aleyrodidae*
(Scymnillini)	*Aleyrodidae*

---

1) Tribes in brackets are not considered in the modern system of *Coccinellidae;* the position of the last three tribes is not clear.

The precipitin test is unsuitable for quantitative studies and is, therefore, of limited use with voracious predators; for these the method of radio-isotope labelled prey could be of value (surveyed by Southwood 1966). An approximate measure of the number of prey eaten might be obtained from the level of radioactivity in the predator.

Putman (1965) determined the food of predators of phytophagous mites (other than coccinellids) in orchards by paper chromatography.

In nearly the whole of this section (6.1) we shall be dealing with predaceous *Coccinellidae*; these constitute the majority of the species and are of interest from the point of view of biological and integrated control. Chapter 6.15 will be devoted to myco- and phytophagous coccinellids.

6.11 Food specificity of predaceous Coccinellidae

Predaceous coccinellids have a wide range of accepted food. Apart from feeding on *Homoptera* and phytophagous mites, they often prey also on young instars of *Lepidoptera*, *Coleoptera* and *Hymenoptera*, small nematocerous *Diptera* and *Thysanoptera*. The larvae always prey on the same prey as the adults. Hence it is the adults which select a certain type of food for the larvae while laying their eggs (Way in Hodek 1966 p. 91), for the larvae are much less mobile and even appear to be unable to choose between suitable and toxic food (Blackman 1967b) (see 6.1123). Furthermore, the selection of food depends to a great extent on the adult preference for a certain habitat (see chapter 5).

When suitable food is in short supply the adult coccinellids are able to starve for quite a long time, to take only a limited amount of food, or, what is most important, they can switch to a different substitutive food, whether this be of insect (as mentioned above) or plant origin. Coccinellids have even occasionally been reported biting fairly strongly into human skin (Svihla 1952).

Some cases of phytophagy which have been reported are probably the result of an error of observation; in reality minute insect prey is being eaten (e. g. larvae of *Thysanoptera*) but this was overlooked by the observer. In other cases the reported phytophagy may represent a form of drinking; this is particularly true for the feeding on young leaves in spring by adults which have emerged from hibernation quarters and the feeding very probably augments the reduced water level in the body (e. g. the observation by Brassler 1930 on *Coccinella septempunctata*).

6.111 Substitution food of plant origin

Among food of plant origin, pollen and nectar both from flowers and from extrafloral nectaries form immensely important food for even explicitly carnivorous coccinellids. This plant food allows the coccinellids to survive with a reduced mortality when insect food is scarce for a while and then they can resume oviposition immediately the insect prey re-appears, as has been described, for example, for *Coccinella undecimpunctata aegyptiaca* by Ibrahim (1955b) (see also 6.23). Similar data have been recorded for other coccinellids (for *Hippodamia tredecimpunctata* and *Anisosticta novemdecimpunctata* by Goidanich 1943, for *Exochomus flavipes* by Geyer 1947, for *Chilocorus bipustulatus* by Yinon 1969a, for *Coccinella septempunctata* and *Coccinula quatuordecimpustulata* by Savoïskaya 1970a and for *Anatis ocellata* by Allen et al. 1970).

Alternatively, feeding on pollen enables reserves to be accumulated for a long-term cessation of feeding during dormancy (Hagen 1962). Pollens from different plants have, of course, different compositions (e. g. the pollen of *Pinus* contains much less protein than other pollens used) and therefore are not equally adequate as food for coccinellids (Smith 1960, 1961b). *Coleomegilla maculata* may even complete its full development on pollen of a number of plants (*Zea mays*, *Betula populifolia*, *Cannabis sativa*, *Carpinus caroliniana*) equally successfully as on aphids (Smith 1960); the species may actually prefer pollen to aphids (Ewert and Chiang 1966), and this euryphagy is a characteristic of this species (see 6.12). Other species studied (*Cycloneda sanguinea*, *Coccinella trifasciata*) cannot successfully complete their development if fed only on pollen (Smith 1961b).

Particularly the high-altitude Alpine coccinellid species, such as *Coccinella reitteri* or *Spiladelpha barovskii kritschenkoi* are also adapted to feeding on pollen, often on edelweiss (*Leontopodium alpinum*), because their habitats often lack aphids (Savoïskaya 1970a).

Extrafloral nectaries were reported to provide substitution food for coccinellids as early as 1933 by Watson and Thompson (1933) for *Leis conformis* (the plant was *Crotalaria striata*) and more recently, for example, by Putman (1955) for *Stethorus punctillum* (on young leaves of peach trees) and by Ibrahim (1955b) for *Coccinella undecimpunctata aegyptiaca* (the nectaries are at the midrib of cotton leaves).

6.112 Unsuitable insect food

The great variety of food consumed by predaceous coccinellids led to the assumption that food specificity in coccinellids exists only between major taxonomic groupings. Observed acceptability has been mistaken for real suitability of prey, even by experienced workers. Balduf (1935) concluded, on the basis of a survey of accepted food, that *Coccinellidae* of the tribes *Hippodamiini* and *Coccinellini* are mostly aphidophagous and that "no special groups of aphids are selected by them." In a special study of food of coccinellids, Kanervo (1940) states that he treated the six species of aphids he used to feed his coccinellids as a complex because "it appeared that the experimental animals (i. e. the coccinellids) did not make any great distinction between individual species (of aphids)". Such an assumption has long been accepted even though contradictory evidence has been reported.

6.1121 Rejected prey

Since as early as 1907, observations were published that some aphids are not acceptable to certain coccinellids. The example of the aphid *Macrosiphum aconitum* feeding on *Aconitum*, which contains the poisonous compound aconitin (Hawkess 1920), is particularly relevant to the following section (6.1122). In other examples, unpalatability seems to have been due to an intensive colouration of aphids (Johnson 1907) or a waxy surface, as in *Brevicoryne brassicae*.

Telenga and Bogunova (1936) observed that the coccinellid *Harmonia axyridis* refuses *B. brassicae* in the field. This has also been shown experimentally; adults which were transferred from the aphid *Hyalopterus pruni* to *B. brassicae* reduced their food consumption by 90 % within 8 days, and the females ceased oviposition. George (1957) also noticed that *B. brassicae* was avoided by *Coccinellidae*.

Hyalopterus pruni itself is rejected immediately a larva of *Adalia decempunctata* pierces the body wall. In subsequent attacks this aphid is rejected as soon as the coccinellid touches it with its palps (Dixon 1958). *H. pruni* was already described as unsuitable for *A. bipunctata* by Hawkes (1920) who wrote: "This aphis has a grey-green mealy exudation which fills the stomata of the larvae and so kills them". By contrast, Hodek (1959) found this aphid to be the essential food for *C. septempunctata* in spite of the waxy covering, for the larvae successfully completed their development when feeding exclusively on this aphid.

Anisosticta bitriangularis and *Hyperaspis spp.* refuse *Schizolachnus piniradiatae* and starve when no other food source is available (Gagné and Martin 1968).

A similar study was made over 40 years ago on the famous *Rodolia cardinalis.* This coccidophagous ladybird did not prey on its normal host *Icerya purchasi* if the latter had fed on *Spartium* or *Genista.* It was hypothesized that leafless plants failed to shade the eggs of the beetle from the harmful insolation (Savastano 1911) or that the smell of the plants repelled the beetles (Balachowsky 1930). However, if the coccids which had fed on *Spartium* or *Genista* were offered to the ladybirds in isolation from the plants they were still rejected (Poutiers 1930). It may therefore be assumed that *Icerya* takes some substances from the plant which decrease its suitability as food for *Rodolia.* The unsuitable host-plants contain the yellow pigment genistein and the alkaloid spartein.

In contrast to some relative coccinellid species, *Chilocorus rubidus* refuses *Chionaspis salicis* and *Lepidosaphes ulmi* (Pantyukhov 1968b). *S. punctillum* fed not only on phytophagous tetranychid mites (*Metatetranychus ulmi*, *Tetranychus bimaculatus* and *Paratetranychus spp.*), but also on predaceous mites of the genus *Typhlodromus* whereas it does not feed on *Bryobia praetiosa* (Putman 1955).

6.1122 Accepted but inadequate prey

In addition to observations on the rejection of a particular prey, there is also evidence that food may be taken which, however, does not seem to be adequate. In such cases oviposition is prevented or reduced, and a varying percentage of larvae die without completing development.

This may occur when coccinellids, specialized to certain taxonomic groups of prey, are fed with food from other groups, e. g. other food than mites is fed to acarophagous species or only non-aphid food to aphidophagous species etc. Although both the adults and larvae of *Adalia bipunctata* were occasionally found feeding on tetranychid mites (Robinson 1951) and the gut of *A. bipunctata* and of three *Coccinella spp.* contained some remains of *Panonychus ulmi* (Putman 1964), these coccinellids could notdevtelop on this prey (Robinson 1951, Putman 1957). Conversely, the adults of the acarophagous *Stethorus punctillum* did not oviposit when fed on aphids, and the larvae cannoo complete their development (Putman 1955).

The aphido- and coccidophagous *Leis conformis*, in spite of its considerable polyphagy, has been reported not to be able to complete its development on some coccids and aphids (Moursi and Kamal 1946), while on *Aphis durantae* it not only oviposits but its larvae also develop.

Larvae of *Coccinella undecimpunctata aegyptiaca*, when provided with eggs or young larvae of *Prodenia litura*, or nymphs of the mealybugs *Pseudocococcus filamentosus* or *Phenacoccus hirsutus*, either refused to feed or fed for a very short time, but failed to complete their development (Ibrahim 1955a).

Not only the prey of other taxonomic groups is inadequate, but also other species of the same group.

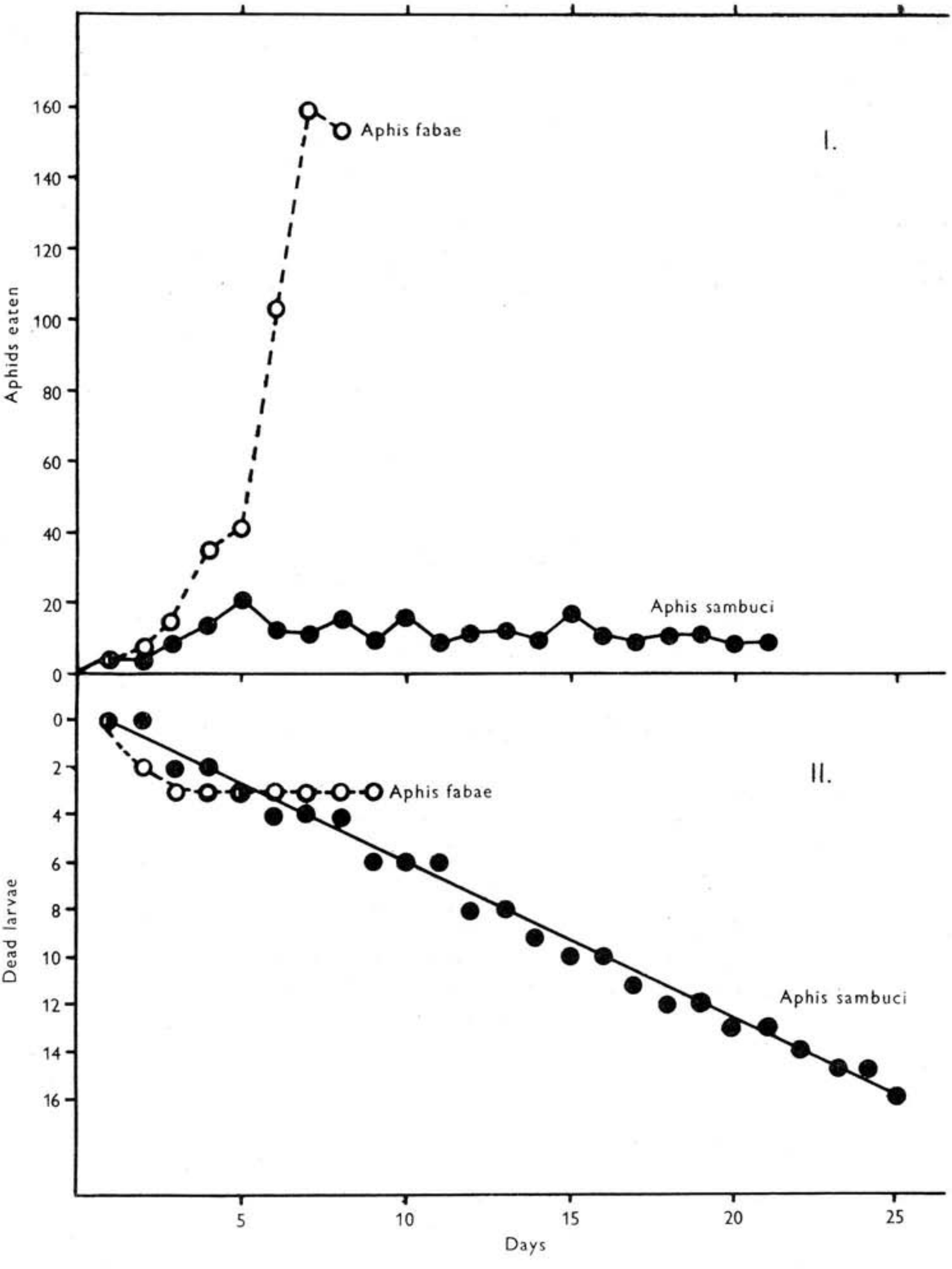


Fig. 6.01 Effect of *Aphis sambuci* on the larval development of *Coccinella septempunctata* (Hodek 1956). I. Daily feeding rate of larvae. II. Mortality of larvae.

Jöhnssen (1930) happened to observe a marked increase in feeding, when he changed the food of *Coccinella septempunctata* from *Aphis sambuci* to *A. hederae*. He did, however, not comment on this.

Dyadechko (1954) found *Aphis fabae* somewhat less suitable than *Toxoptera graminum* for *Coccinula quatuordecimpustulata*. The larvae fed less on *A. fabae* (the 4th-instar-larvae consumed 27 *A. fabae*, contrast 46 *T. graminum* per day) and the larval development was retarded (21 days on *A. fabae*, contrast 17 days on *T. graminum*).

Hodek (1956) found a rather low intake of *A. sambuci* (Fig. 6.01) by *C. septempunctata* and in a series of experiments showed that this aphid is inadequate food for both larvae and adults of *C. septempunctata*. The larvae could not complete their development and died within 25—26 days (Fig. 6.01). In the first experiment two thirds of larvae attained the 4th instar, whereas in the second experiment all but one died in the 3rd instar. This was consistent with the observed feeding rates in the two experiments. In the first experiment, the daily feeding rate after the 7th day exceeded 20 aphids, and later it ranged between 40—60 aphids. In contrast, in the second experiment the feeding rate remained consistently below 20 aphids.

This difference between the two experiments, carried out at naturally alternating temperatures, began to show on the 5th — 6th day. In the first experiment a large increase in temperature occurred at that time and the mean temperature then remained about 3 °C higher than in the second experiment. The effect may also have been caused by differences in the food. The chemical composition of aphids is probably different in early (first experiment, started 24. 6. 1953) and late summer (second experiment, started 22.7.) particularly as far as the presumed content of toxic substance is concerned (see later).

The adults, freshly emerged from the pupae, were sensitive to being fed on *A. sambuci* in the same way as the larvae. If, after emergence, they were fed only with this food, they died on average after 17.5 days. The control adults, fed on *Aphis fabae* or on *Uromelan aeneus* had at most a mortality of 16.6 %.

Overwintered adults fed on *A. sambuci* did not die more than those in the control culture, but did not lay eggs during the whole month of the experiment (Hodek 1957b). The ovaries, however, were found by dissection to be in the process of maturation. Not until suitable food had been fed for 9 days, did the adults begin to oviposit. In spring, adults of *C. septempunctata* are usually found on colonies of *A. sambuci* in the field, because the host-plant, *Sambucus nigra*, often grows at the hibernation quarters of this coccinellid.

As the feeding rate on *A. sambuci* is substantially lower than on the suitable food, *Aphis fabae* (Fig. 6.01), it might be assumed that the negative effect on the mortality of larvae is caused by insufficient intake of food which has little attraction. This possibility, however, can be discounted by following experiments which have shown (Hodek 1957a) that substantially reduced feeding rates on suitable food in the most voracious 4th instar did not cause any rise in mortality (Tab. 6.02). Of course, the reduction of the daily feeding rate to one-seventh prolonged the 4th instar by more than twice, but even so development was completed with about one-third of total food intake (in comparison with a surplus of aphids), and there was no increase in mortality.

If only the first three larval instars or only the fourth instar were fed with *A. sambuci* (Hodek 1957a), the majority of the larvae pupated; the mortality was respectively 32 and 24 %, (8 % in control) and larval development was prolonged to 9.2 and 11.2 days (in control 7.8 days).

The larvae of *Adalia bipunctata* were able to complete their development on *A. sambuci*, although at a somewhat slower rate than on *Aphis fabae* (Hodek 1957a). Perhaps an adaptation has evolved in this species, which breeds in central Europe in the same

Tab. 6.02 Larvae of *Coccinella septempunctata* fed on reduced daily rates of *Aphis fabae* (Hodek 1957a)

Daily feeding rate in 4th instar (number of aphids)	Duration of development (in days)					Mortality [%]	N
	Larval instars		Pre-pupa	Pupa	In total		
	1.+2.+3.	4.					
surplus (aver. consumed 70)	5.2	2.6	1.0	4.0	12.8	8	13
30	4.8	3.7	0.8	4.2	13.5	0	18
10	4.9	5.9	0.9	4.2	15.9	10	20

habitat as *A. sambuci*. In England *A. bipunctata* occurs abundantly on field crops (see 5.53).

On the basis of these observations and analogous concurrent findings on other coccinellids (Ibrahim 1955a, b, Putman 1955), criticism has been levied against the hitherto accepted way of evaluating the predator-prey relationship (Hodek 1959, 1962b). A warning was sounded that it is erroneous to judge this relationship by observing voracity, as this can confuse "acceptability" with "suitability". Such terms as stenophagy, polyphagy, etc., should not be improperly based on evidence of "acceptability" alone. Types of food can be divided into two main groups — essential and alternative. While essential foods ensure the completion of larval development and oviposition, alternative foods serve only as a source of energy and thus prolong survival in comparison with starvation. Naturally, there are transitions between both types; thus essential foods show varying degrees of favourability, etc.

In the last decade, a series of data have accumulated which confirm the validity of regarding food as "essential" or "alternative". *Semiadalia undecimnotata* can neither complete larval development nor oviposit when fed on *Aphis craccivora* (on *Vicia faba*) which is an essential food for *C. septempunctata* (Hodek 1960b). *Aulacorthum magnoliae* (on *Sambucus racemosa sieboldiana*) is detrimental to the larvae of *C. septempunctata bruckii* and *Harmonia axyridis*, while *A. craccivora* (on *Robinia pseudoacacia* as well as on *Vicia faba*) is only detrimental to the larvae of *H. axyridis* (Okamoto in Hodek 1966 p. 45). The same author (Okamoto 1961) found that *Brevicoryne brassicae* was less suitable for larvae of *C. septempunctata bruckii* than was *Rhopalosiphum prunifoliae*. He used pre-imaginal mortality, rate of development, resistance of resulting adults to starvation and their size as criteria of prey suitability.

Atwal and Sethi (1963) found that *Lipaphis erysimi* was more nutritious for larvae of *C. septempunctata* than were *Macrosiphum granarium* and *Aphis gossypii*, as both the larvae and resulting pupae were heavier and contained more dry matter.

Nine out of ten species of coccinellids (including the polyphagous *Coleomegilla maculata*) tested by Smith (1965a) failed to complete their larval development when fed on *Aphis fabae*. The tenth species, *Hippodamia tredecimpunctata*, reached the adult stage, but the beetles were smaller and their development time was significantly longer than when fed on *Acyrthosiphon pisum* or *Rhopalosiphum maidis*.

Chilocorus bipustulatus is unable to reproduce when feeding on *Saissetia oleae* (Huffaker and Doutt 1965.)

Chilocorus stigma has a markedly lower fecundity and survival and a prolonged pre-oviposition period if fed on *Lepidosaphes beckii* (Muma 1955b), whereas *Chrysomphalus aonidum* is a suitable prey.

If *Stethorus gilvifrons* preys on *Bryobia rubrioculus*, the adults do not oviposit and the larvae die in the 2nd and at the latest in the 3rd stage (Dosse 1967).

Aiolocaria mirabilis, a specialized predator on chrysomelids, has been reported as feeding both in the larval and adult stages on all pre-imaginal stages of several chrysomelids (Iwata 1932, 1965, Savoïskaya 1970b), but rejected *Agelastica coerulea* from *Alnus japonica* (Iwata 1965) and two central-Asiatic chrysomelids, mentioned only by their popular names (Savoïskaya 1970b). In Alma-Ata, its essential prey is *Melasoma populi*.

In a thorough study, Blackman (1965, 1967a) tested the suitability of several aphid foods for *Adalia bipunctata* and *C. septempunctata* (Table 6.03 and 6.04, Fig. 6.02 and 6.03). Although *Aphis fabae* and *A. sambuci* are natural prey for *A. bipunctata* in the field, they were found to be relatively unsuitable food for this coccinellid, as is shown by the longer larval development and the greater larval mortality. *A. bipunctata* had also a lower fecundity and fertility when fed on *A. fabae*. A preliminary observation suggested that *Brevicoryne brassicae* was even more unsuitable.

Tab. 6.03 Larval development and oviposition of *Adalia bipunctata* on different aphids (Blackman 1965, 1967a)1)

Aphid species	Larval development [days]	Larval mortality [%]	Weight of adult at emergence [mg]	Fecundity [total eggs laid]	Fertility [% of viable eggs]
Myzus persicae	10.4	17.8	11.8	676.2	89.4
Aulacorthum circumflexum	9.5	16.7	11.9		
Acyrthosiphon pisum	10.8	13.9	12.6		
Microlophium evansi	10.6	9.1	12.4		
Aphis fabae	13.0	27.6	7.9	249.6	55.9
Aphis sambuci	13.4	25.0	8.0		
*Brevicoryne brassicae*2)	21; 23	(66.7)	5.1; 6.1		

1) 20 °C const., 16hr light per 24 hr.
2) Only 2 out of 6 larvae completed development.

Tab. 6.04 Development of *Coccinella septempunctata* larvae on different aphids (Blackman 1965, 1967a)1)

Aphid species	Development [days]	Mortality [%]	Weight of adult at emergence [mg]
Myzus persicae	13.0	12.5	36.4
Aphis fabae	13.6	9.1	36.3
Acyrthosiphon pisum	13.3	18.6	37.2
Megoura viciae	14.8	13.4	33.5
Brevicoryne brassicae	16.1	26.1	30.9
*Aphis sambuci*2)	19.5	(50.0)	18.4

1) 20 °C const., 16 hr light per 24 hr.
2) Only 6 out of 12 larvae completed their development.

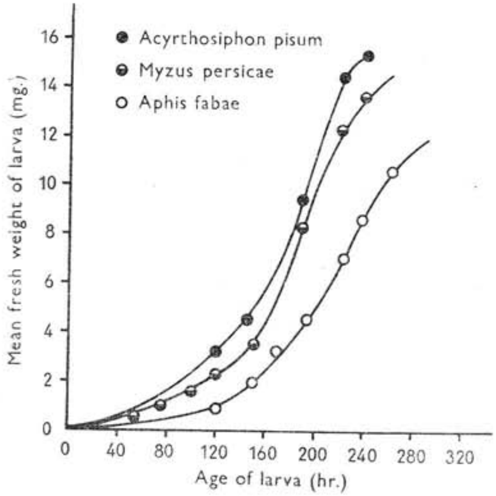


Fig. 6.02 Development of *Adalia bipunctata* larvae on different aphid foods (Blackman 1967a).

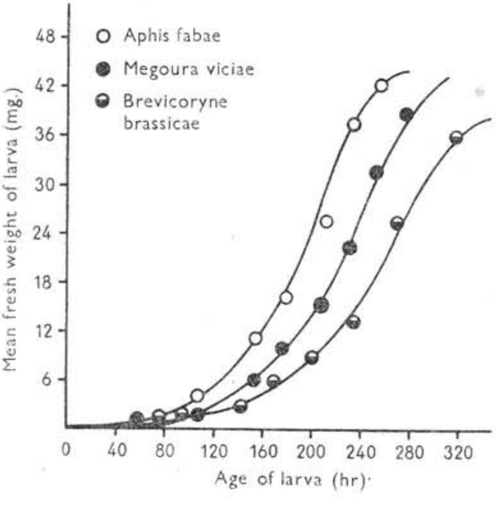


Fig. 6.03 Development of *Coccinella septempunctata* larvae on different aphid foods (Blackman 1967a).

In contrast to *A. bipunctata*, larvae of *C. septempunctata* were able to develop on *Aphis fabae* as successfully as on other favourable aphid foods. *Megoura viciae*, toxic for *A. bipunctata* (see 6.1123), was only slightly less suitable for *C. septempunctata* than other aphids. *A. sambuci*, although a very poor food, enabled half the specimens to develop to extremely small adults. Thus the effect of *A. sambuci* was less detrimental than in previous experiments with the same coccinellid, where mortality was complete (Hodek 1956).

A. fabae was shown to be a rather unsuitable food for *A. bipunctata* also by Hariri (1966a, b). When the larvae were fed on this aphid the emerged adults were lighter in weight, had less fat and glycogen content and their fecundity was halved (Tab. 6.05, Fig. 6.04). Iperti (1966) has also ascertained that *A. fabae* has an adverse effect on vitellogenesis in *A. bipunctata*, although it does not inhibit it entirely.

Hukusima and Kamei (1970) contributed to the understanding of food specificity in *Harmonia axyridis*. Three aphids out of ten (*Aphis pomi*, *Brevicoryne brassicae*, *Hyalopterus arundinis*) appeared slightly less suitable for the larvae, prolonging their development by approximately one-third compared with diets of the six more suitable species (Tab. 6.06). Larvae, however, succeeded in completing their development on these three relatively unsuitable aphid species. *Aphis craccivora* on most of its host-plants was an unsuitable food: larvae did not develop on this diet and died, and adults also died within 4—6 days. In contrast, *A. craccivora* on other host-plants (*Vicia sativa* or *Vigna catiang*) enabled larvae of *H. axyridis* to develop from the 2nd instar to adult. In contrast to *H. axyridis*, both larvae and adults of *Propylaea japonica* are resistant to the detrimental effect of *A. craccivora* from *Robinia pseudoacacia*.

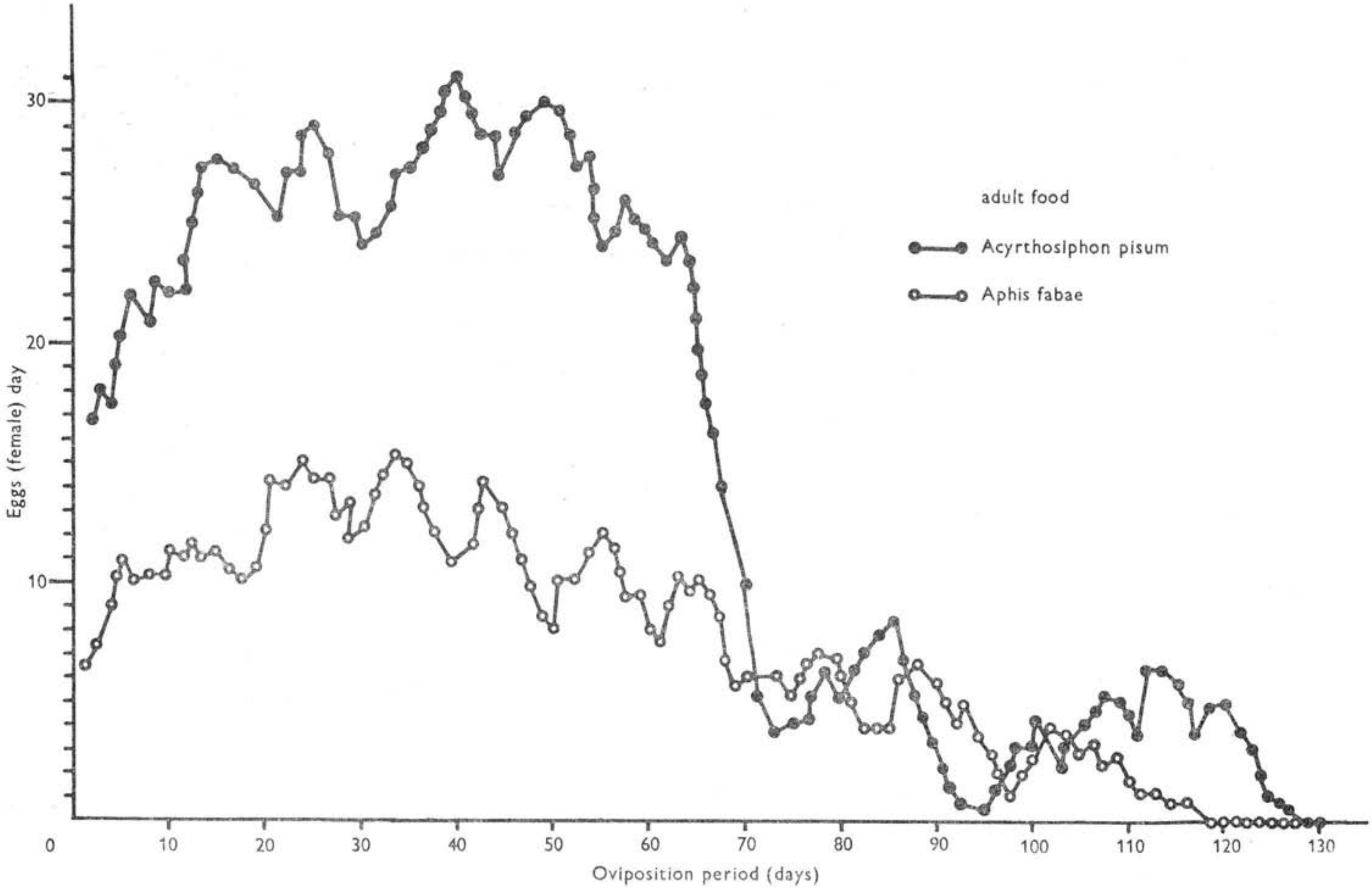


Fig. 6.04 Oviposition of *Adalia bipunctata* on different aphid foods (Hariri 1966a).

Tab. 6.05 Comparison of two aphid foods for *Adalia bipunctata* (Hariri 1966a, b)

Diet for		Newly emerged adult			Fecundity		Longevity [days]	
larvae	adult	live weight [mg]	fat content [mg]	glycogen content [µg]	total [eggs]	per day [eggs]	♂♂	♀♀
Acyrthosiphon pisum	—	14.2	0.7	26.1				
Aphis fabae	*Aphis fabae*	9.2	0.2	11.0	738	9.3	81.7	76.9
Microlophium evansi	*Acyrthosiphon pisum*				1535	20.4	77.1	79.4

Tab. 6.06 Various aphids as food for larvae of *Harmonia axyridis*[1] (Hukusima and Kamei 1970)

Aphid species	N	Total consumption [aphids]	N	Development [days]
Acyrthosiphon pisum	17	89	17	7.7
Aphis pomi	20	369	18	12.2
Amphorophora oleraceae	17	101	17	7.2
	15	123[2]	15	15.1[2]
	19	140[2]	19	15.4[2]
Brevicoryne brassicae	14	276	14	13.3
Hyalopterus arundinis	12	297	12	13.2
Macrosiphum rosae ibarae	41	156	41	7.9
Megoura viciae japonica	20	160	20	7.9
Myzus persicae	24	189[2]	24	15.9[2]
	8	211[2]	8	14.1[2]
	23	218	23	7.5
Periphyllus californensis	21	214	33	9.5

[1] At 30 °C.
[2] At 25 °C.

6.1123 Toxic prey

While a gradual poisoning is one of the possible explanations of the detrimental effect of some unsuitable aphids (as *Aphis sambuci* or *A. craccivora*) (see 6.1124), in some instances an acute toxic effect has been proved or at least strongly indicated.

Larvae of *Adalia decempunctata* attack and eat *Aphis fabae* and *Megoura viciae*, but after about two minutes the larvae frequently release the prey and regurgitate the gut contents. Six of twelve 4th-instar larvae provided with *M. viciae* died after a few days, although other aphids had then been offered as food (Dixon 1958).

The toxicity of *M. viciae* to *Adiaal bipunctata* has also been demonstrated (Blackman 1965, 1967 a). This aphid is lethal to all larval stages and to the adults. Neither

Tab. 6.07 Three aphids as food for adults of *Harmonia axyridis* (Hukusima and Kamei 1970)

Temperature	25 °C						30 °C					
Aphid species	Aver. daily consumption [aphids]		Longevity [days]		Eggs laid		Aver. daily consumption [aphids]		Longevity [days]		Eggs laid	
	♂	♀	♂	♀	total number	per day	♂	♀	♂	♀	total number	per day
Myzus persicae	22	65	92	98	2,310	27	30	64	57	50	778	22
Amphorophora oleraceae	15	45	152	170	3,819	25	18	40	101	86	945	14
Aphis craccivora												
on *Robinia pseudoacacia*	36	30	6	6								
on *Astragalus sinicus*	20	30	4	4								
on *Vicia hirsuta*	24	27	5	4								

larvae nor adults have the ability to avoid attacking this aphid when it is presented mixed with a suitable food. Even when fed on a mixture of *M. viciae* and *Acyrthosiphon pisum* in the ratio of 1 : 9, all of the larvae failed to reach the pupal stage. The lst-instar larvae perished more rapidly on this food than when starved. The 4th-instar larvae accepted *M. viciae* readily, but after about 4 min. of feeding they suddenly rejected their prey and vomited. When fed on this prey the adults all died within a week of emergence.

Aphis nerii from *Nerium oleander* is poisonous for most coccinellids tested (*Coccinella septempunctata*, *Semiadalia undecimnotata*, *Propylaea quatuordecimpunctata*, *Adalia bipunctata*) with the exception of *Adonia variegata*, which develops normally on this prey (Iperti 1966).

6.1124 Possible causes of unsuitability or harmfulness

The reasons why particular prey species are harmful for particular coccinellids are not yet clear. That death is caused simply by starvation, resulting from a very low feeding rate on unsuitable food, can be discounted since such reduced feeding rates repeated artificially with essential food do not cause a substantial rise in mortality (Hodek 1957a). There seem to be two other possibilities. Either the aphids contain some special substances (derived from the plants) poisonous for coccinellids, or the aphids are deficient in nutritive value.

For *Aphis sambuci* we can assume a passage of the glycoside sambunigrin1) (contained in the host plant *Sambucus nigra*) from the plant into the aphid. This glycoside may be split enzymatically into hydrocyanic acid in the body of the coccinellid, for enzymes which split glycosides have been identified in the body of *Coccinella spp.* (Kuznetsov 1948). The same explanation is possible for *Aulacorthum magnoliae*, where the host plant is *Sambucus racemosa* (Okamoto in Hodek 1966 p. 45).

The rapid response of *Adalia bipunctata* and *A. decempunctata* (obvious distress within two minutes) to *Megoura viciae* eliminated viral transmission or polypeptides as the factors responsible and makes it likely that a substance is obtained by the aphid from the host plant (Dixon 1958). Dixon et al. (1965) made a thorough analysis of the aphid, searching for physiologically active compounds. They could not, however, implicate any of the compounds found (aphin pigments, alkanes, fatty acid esters, amino-acids, peptides and two sugars D-glucose and D-ribose).

Similarly in *Macrosiphum aconitum*, which feeds on *Aconitum*, the presence of poisonous aconitin may be the reason why coccinellids reject this aphid, although Hawkes (1920) suspects the intensive colour. Also the rejection of *Icerya* from *Genista* or *Spartium* by *Rodolia cardinalis* may be explained by the yellow pigment genistein and the alkaloid spartein contained in the host plants (see 6.1121).

Hukusima and Kamei (1970) suggest the same explanation for the unsuitability of *Aphis craccivora* for *Harmonia axyridis* if the aphid was collected from one of seven host plants (*Robinia pseudoacacia*, *Astragalus sinicus*, *Vicia hirsuta*, *Capsella bursa-pastoris*, *Cardamine flexuosa*, *Rorippa palustris*, *Hemistepta carthamoides*). As *A. craccivora* was a favourable food when collected on *Vicia sativa* or *Vigna catiang* var. *sinensis*, the authors tried to explain the differential host plant effect by two-dimensional thin layer chromatography. They analysed the ninhydrine-positive compounds in *Aphis craccivora* collected from the different host plants. Aphids from *R. pseudoacacia* contained two extra aminoacids (glycine and arginine) and additionally three unidentified substances; aphids from *V. catiang* contained two additional unidentified substances.

---

1) The chemical structure of sambunigrin is D—cyanonitrileglukoside.

This influence of host plant on unsuitability of prey to some extent throws light on an earlier observation that the larvae of *Coccinella septempunctata bruckii* and *Propylaea japonica* die when fed on the aphid *Aphis craccivora* in the spring, but not in the summer (Takeda et al. 1964). Apparently different host plants were again involved, and the effect is not one of temperature or of other abiotic factors connected with the advanced season.

These findings provide a context for a brief note on some results from Central Asia. Ul'yanova (1956) reports unpublished observations of unnamed workers from the Tashkent Institute of Plant Protection concerning the deleterious effect of feeding "local coccinellids" on *Aphis craccivora* from *Robinia pseudoacacia*, whereas the same aphid from cotton or alfalfa was suitable. Ul'yanova, however, doubted these results, for she obtained apparently different results, i. e. complete larval development of *C. septempunctata* and *C. undecimpunctata* on *A. craccivora* collected from *R. pseudoacacia.*

Some authors attempt to explain the unsuitability of certain foods by the second possibility mentioned earlier, i. e. by nutritive deficiency.

Atwal and Sethi (1963) suggest that the higher protein content of *Rhopalosiphum* (*Lipaphis*) *erysimi* makes this aphid more favourable than *Aphis gossypii* for *C. septempunctata.* Hariri (1966b) similarly supposes that *Acyrthosiphon pisum* is more nutritious for *A. bipunctata* than is *Aphis fabae.* However, he states that the causes of the adverse effect of *A. fabae* are "still unexplained". For the same relationship, i. e. *A. fabae* unsuitable for larvae of *A. bipunctata*, Blackman (1967a) assumes two factors: difficulty in ingesting the food and low nutritive value. The two may be related; nutritive value may be low because some essential nutrient remains behind in the uningested part of the prey.

Mechanical defences of the aphid are further phenomena which may be harmful to the predator. Large aphids of the genus *Macrosiphum* can smear the mouthparts of *Hippodamia convergens* with a glue excreted from the cornicles and thus cause starvation of the coccinellid (Palmer 1914). This defence by the aphid seems successful only at low temperatures; at higher temperatures the coccinellids can ingest the glue. A similar defence mechanism of aphids has been observed in the relation between *Hyalopterus pruni* and *Adalia bipunctata* (Hawkes 1920).

6.113 Criteria of suitability

In the preceding text enough evidence has been gathered together to show that coccinellids in spite of their considerable polyphagy as to accepted food, are very specific as far as essential food is concerned. Thus it is necessary to define the prey-predator relationship in these terms and to assess the possible impact of a coccinellid against any given pest, by testing the range of essential prey of the predator under consideration. Different criteria of suitability have been used.

The old — and as we already know — invalid criterion of food suitability was its acceptability. Kanervo (1940) evaluates the type of prey (principal, secondary, substitutive) according to the degree of readiness at the food intake in the laboratory and according to observations in the open. A somewhat better idea of the relationship between coccinellid and host aphid might appear to be deducible from preferences for certain prey; but Blackman's (1967b) experiments with *Megoura viciae* have shown that even this criterion is not safe.

The presence of developmental stages of the predator on a particular prey is frequently considered to be good evidence for evaluating food specificity in the field. Such evidence may, however, often be misleading because the predator usually lives in any given habitat together with several insect species, any of which may serve as its prey.

There are isolated cases where the relation of a predator to a prey may be safely identified by another indirect method: that of systematic and long term observation. Eastop and Pope (1966, 1969) found 99 % of specimens of *Pullus auritus* on oaks infested with *Phylloxera glabra*. In the course of five years (1963—1968), they also observed a close coincidence between the abundance of the prey and the predator.

In most cases, only experimental evidence is adequately unequivocal and precise. Under experimental conditions, responses of coccinellids to different species of prey in terms such as rate of larval development, larval mortality, weight of larvae or pupae or emerging adults, feeding rate, longevity of adults and fecundity may be studied. Thus one can determine the essential foods which are those that ensure the completion of larval development and oviposition, and one can determine their relative suitability.

6.114 Essential foods

Mention of some essential foods has been scattered throughout the previous sections of chapter 6.11 as contrasts to unsuitable foods. For a better orientation, these examples as well as other essential foods are brought together in Tab. 6.08.

Tab. 6.08 Essential food of *Coccinellidae*

Adalia bipunctata		
	Acyrthosiphon pisum	Blackman 1965, 1967a, Hariri 1966a,b
	A. pisum (dry powdered)	Smith 1965a
	Appelia tragopogonis	Iperti 1965
	Aphis pomi	Iperti 1965, Sem'yanov 1970
	Aulacorthum circumflexum	Blackman 1965,1967a
	Brachycaudus subterranea	Iperti 1965
	Hyalopterus pruni	Sem'yanov 1970
	Microlophium evansi	Blackman 1965, 1967a, Hariri 1966a, b
	Myzus cerasi	Iperti 1965
	Myzus persicae	Blackman 1965, 1967a
	Rhopalosiphum maidis (dry powdered) (slightly slower development)	Smith 1965a
	Rhopalosiphum padi (lower oviposition)	Sem'yanov 1970
Adalia decempunctata		
	Aphis pomi	Iperti 1965
	Brachycaudus subterranea	Iperti 1965
	Cinara palestinensis	Bodenheimer and Neumark 1955
	Matsucoccus josephi	Bodenheimer and Neumark 1955
	Rhopalosiphum maidis	Iperti 1965
Adonia variegata		
	Aphis craccivora	Iperti 1965
	Aphis nerii	Iperti 1965
	Macrosiphoniella artemisiae	Iperti 1965
	Myzus persicae	Iperti 1965
Anatis mali		
	Acyrthosiphon pisum	Smith 1965a
	Rhopalosiphum maidis	Smith 1965a

Anatis ocellata	
Myzus persicae (less suitable)	Kesten 1969
Rhopalosiphum padi (less suitable)	Kesten 1969
Schizolachnus pineti	Kesten 1969
Anisolemnia (Caria) dilatata	
Oregma bambusicola	Puttarudriah and Channabasavanna 1952
Aphidecta obliterata	
Adelges cooleyi (lower fecundity)	Wylie 1958
Adelges nüsslini	Wylie 1958
Calvia quinquedecimguttata	
Melasoma aenea (pre-imag. stages)	Kanervo 1946
Chilocorus bipustulatus	
Chrysomphalus aonidum	Yinon 1969a
Chilocorus kuwanae	
Unaspis yanonensis	Nohara 1962a
Chilocorus rubidus	
Eulecanium caraganae (eggs for larvae, eggs and larvae for adults)	Pantyukhov 1968b
Chilocorus stigma (bivulnerus)	
Chrysomphalus aonidum	Muma 1955b
Coccinella septempunctata	
Acyrthosiphon pisum	Blackman 1965, 1967a
Aphis craccivora (= *Pergandeida medicaginis*)	Hodek 1960b, Iperti 1965
Aphis fabae	Hodek 1956, Blackman 1965, 1967a. Iperti 1965
Aphis gossypii	Iperti 1965
Aphis urticae	Iperti 1965
Hyalopterus pruni	Hodek 1960b
Lipaphis erysimi	Atwal and Sethi 1963, Sethi and Atwal 1964
Longiunguis donacis	Iperti 1965
Macrosiphoniella artemisiae	Iperti 1965
Megoura viciae (slightly less suitable)	Blackman 1965,1967a
Myzus persicae	Blackman 1965,1967a
Uromelan aeneus	Hodek 1960b
Coccinella septempunctata bruckii	
C. s. bruckii (eggs) (development prolonged)	Koide 1962
Macrosiphum granarium	Hukusima and Sakurai 1964
Myzus malisuctus	Hukusima and Sakurai 1964
Myzus persicae	Hukusima and Sakurai 1964
Neophyllaphis podocarpi	Maeta 1965
Rhopalosiphum prunifoliae	Okamoto 1961, in Hodek 1966
Vesiculaphis caricis	Takeda et al. 1964
Coccinella transversoguttata richardsoni	
Acyrthosiphon pisum (dry powdered)	Smith 1965a
Coccinella undecimpunctata	
Aphis pomi	Harpaz 1958
Coccinella undecimpunctata aegyptiaca	
Aphis durantae	Ibrahim 1955a
Aphis gossypii	Ibrahim 1955a
Aphis laburni	Ibrahim 1955a
Aphis maidis	Ibrahim 1955a
Aphis nerii	Ibrahim 1955a
Aphis pseudobrassicae	Ibrahim 1955a
Hyalopterus arundinis	Ibrahim 1955a
Macrosiphum sanborni	Ibrahim 1955a
Myzus persicae	Ibrahim 1955a
Coleomegilla maculata (ssp. *lengi* included)	
Acyrthosiphon pisum (also dry powdered)	Smith 1965c

C. maculata (eggs)	Warren and Tadic 1967
Hyphantria cunea (eggs)	Warren and Tadic 1967
Rhopalosiphum maidis (also dry powdered) (slightly less suitable)	Smith 1965c
Cycloneda limbifer	
Aphis craccivora	Zelený 1969
Cycloneda munda	
Acyrthosiphon pisum	Smith 1965a
Exochomus flavipes	
Dactylopius opuntiae	Geyer 1947
Matsucoccus josephi	Bodenheimer and Neumark 1955
Halyzia hauseri	
Podosphaera leucotricha (apple powdery mildew)	Liu 1950
Harmonia axyridis	
Acyrthosiphon pisum	Hukusima and Kamei 1970
Amphorophora oleraceae	Hukusima and Kamei 1970
Aphis craccivora	Mogi 1969
Aphis pomi	Hukusima and Kamei 1970
Brevicoryne brassicae (less suitable)	Hukusima and Kamei 1970
Hyalopterus arundinis (less suitable)	Hukusima and Kamei 1970
Macrosiphum rosae ibarae	Hukusima and Kamei 1970
Megoura viciae japonica	Hukusima and Kamei 1970
Myzus persicae	Hukusima and Kamei 1970
Neophyllaphis podocarpi	Maeta 1965
Periphyllus californensis	Hukusima and Kamei 1970
Rhopalosiphum prunifoliae	Okamoto in Hodek 1966
Hippodamia convergens	
Therioaphis maculata	Nielson and Curie 1960
Hippodamia parenthesis	
Acyrthosiphon pisum (dry powdered)	Smith 1965a
Hippodamia quinquesignata	
Macrosiphum pisi	Kaddou 1960
Hippodamia tredecimpunctata	
Acyrthosiphon pisum (dry powdered)	Smith 1965a
Rhopalosiphum maidis (dry powdered) (1/4 slower development)	Smith 1965a
Hyperaspis lateralis	
Pseudococcus aurilanatus	McKenzie 1932
Pseudococcus sequoiae (eggs and young larvae of both species are preferred)	McKenzie 1932
Leis conformis	
Aphis durantae	Moursi and Kamal 1946
Pharoscymnus numidicus	
Parlatoria blanchardi	Kehat 1968a
Prodenia litura (eggs)	Kehat 1968a
Pullus auritus	
Phylloxera glabra	Eastop and Pope 1966, 1969
Semiadalia undecimnotata	
Aphis fabae	Hodek 1960b, Iperti 1965
Stethorus gilvifrons	
Panonychus ulmi	Dosse 1967
Tetranychus cinnabarinus — complex (eggs)	Dosse 1967
Tetranychus urticae (eggs)	Dosse 1967
Stethorus punctillum	
Metatetranychus ulmi	Putman 1955
Tetranychus bimaculatus	Putman 1955
Synharmonia conglobata	
Aphis pomi	Iperti 1965
Brachycaudus subterranea	Iperti 1965

Cinara palestinensis	Bodenheimer and Neumark 1955
Galerucella lineola (preimag. stages)	Kanervo 1946
Matsucoccus josephi	Bodenheimer and Neumark 1955
Rhopalosiphum maidis	Iperti 1965
Synonycha grandis	
Oregma bambusicola	Puttarudriah and Channabasavanna 1952

6.12 Stenophagy and euryphagy

As has been stressed before, the well-known polyphagy of predaceous *Coccinellidae* only applies to their relation to accepted but inadequate foods; they in fact show a pronounced specificity with regard to their essential food, which is food that allows full development (both of larvae and ovaries). Profound studies evaluating the essential food of individual coccinellids are still so scarce that it is premature to try to compare the level of true stenophagy or polyphagy in individual species.

A very narrow range of prey nearing to monophagy may be presumed in stenotopic species, as e. g. *Coccinella hieroglyphica*, occurring on heather (*Calluna vulgaris*)(Table 6.11), but such cases are exceptional.

A good comparison of the polyphagy or stenophagy of several nearctic species has been obtained in the peach orchards of the Niagara Peninsula, Ontario (Putman 1957). Several of the common coccinellids were fed with either two tetranychid mites, crawlers of a coccid (Table 6.09) or eggs and larvae of the oriental fruit moth (*Grapholitha molesta*). A distinct polyphagy was revealed for *Coleomegilla maculata lengi*. The larval development of this species was not slowed down by feeding on *Tetranychus telarius* (compared with aphid food). All larvae completed their development, adult survival was very high and oviposition was not inhibited. *Metatetranychus ulmi* also appeared to be suitable food for larvae of *C. maculata*, and the adults fed much more on crawlers of *Pulvinaria vitis* than did the other coccinellids. In contrast to *C. maculata*, all three *Coccinella spp.* appeared to be rather stenophagous, and *Cycloneda* and *Adalia* were next in order in this respect. This experiment was, of course, designed to compare polyphagy among major taxonomic groups of prey.

It appears necessary that studies of this type should be taken further to assess polyphagy within individual groups of prey, i. e. the comparison of the relation of a series of coccinellids to several species of aphids or coccids etc. Some data in this direction have already been supplied for *Coccinella septempunctata* and *Adalia bipunctata* by Blackman (1967a, b) and for *Harmonia axyridis* and *C. s. bruckii* by some Japanese authors (Okamoto 1961, 1966, Hukusima and Sakurai 1964, Hukusima and Kamei 1970, Takeda et al. 1964).

Recently the value of several aphids has been compared in their effect on the fecundity of overwintered females of *Adalia bipunctata* (Tab. 6.10). *Rhopalosiphum padi* and *Acyrthosiphon caraganae* were found to be somewhat inferior to the other two species (Sem'yanov 1970). It was reported that, in spite of the different fecundities obtained, the rate of larval development was not significantly different when any of the first three species listed in the table were used as food.

The stenophagy of the *Coccinella spp.*, indicated by the findings of Putman (1957) (Tab. 6.09), seems confirmed by the failure of these coccinellids to complete their larval development on artificial diets (Smith 1965b) (see 6.14), and by the following results by this author involving natural foods.

Of three coccinellids tested on different plant pollens, *Coccinella trifasciata* gave the poorest results; only the 1st instar was completed (Smith 1961b). Two *Coccinella spp.*

Tab. 6.09 Effect of some prey on coccinellids of Ontario peach orchards (tabulated from data by

Prey species	*Rhopalosiphum rufomaculatum*		*Tetranychus telarius* (two-spotted spider mite)				
Type of response Coccinellid species	larval period [days]	initial number of beetles	larval period [days]	initial number of larvae	completion of larval development [%]	initial number of larvae	survival of adults at 20 days
Coleomegilla maculata	11.7	10	12.9	9	100	17	85
Hippodamia convergens	12.0	8	21.8	8	61	23	33
H. parenthesis					80	15	
H. tredecimpunctata					60	15	(50)[3]
Adalia bipunctata	14.3	10	26	10	31	16	(33)
Cycloneda munda [1]					15	13	0
Coccinella transverso-guttata					0	16	0
C. novemnotata					0	16	0
C. trifasciata					0	16	(17)
Anatis quindecimpunctata					0	8	

[1] In Putman 1957 *C. sanguinea:* in Putman 1964 corrected to *C. munda.*

[2] Enough mites were available to feed the larvae for 6 days only; infestations of *M. ulmi* dense could not be found on foliage free of toxic spray residues.

[3] Brackets indicate percentages which are considered unreliable because of the small number

Tab. 6.10 Fecundity of *Adalia bipunctata* on three aphids (Sem'yanov 1970)

Aphid species	Generation	Total number of eggs laid/female			Number of pairs
		max.	min.	average	
Aphis pomi	over-wintered (0).	298	230	264 ± 20.1	5
Hyalopterus pruni		262	215	241 ± 8.5	5
Rhopalosiphum padi		186	147	161 ± 6.8	5
Hyalopterus pruni	1.	98	86	94 ± 2.8	4
Acyrthosiphon caraganae		42	36	39 ± 1.3	4

(*C. novemnotata*, *C. trifasciata*) could not even complete their larval development on dry powdered aphids. *C. transversoguttata* succeeded at least on one of the three aphids tested (on dry *Acyrthosiphon pisum*) (Smith 1965a).

Coleomegilla maculata is exactly the opposite and is perhaps the most euryphagous coccinellid known. Its polyphagy, however, has one peculiar feature. The microhabitat preference (lower strata of a corn field) already discussed in 5.41 is apparently related to the pollinivory of this species (Ewert and Chiang, in Hodek 1966 p. 195). Laboratory tests have proved that plant pollen serves as essential food for *C. maculata*. The pollens of *Betula populifolia* and *Carpinus caroliniana* were found to be superior to pollen of *Zea mays*, *Cannabis sativa*, *Juglans cinerea* and *Typha latifolia*, but all these pollens

Putman 1957)

		Metatetranychus ulmi			*Pulvinaria vitis* (crawlers)			
initial number of beetles	cessation of oviposition	initial number of beetles	larval development within 6 days2)	initial number of larvae	number of beetles	number eating crawlers	number of crawlers eaten max.	aver.
13	no cessation	6	normal	10	11	9	123	24
12	in 6 days	5	50 % mortality	10	3	3	5	4
4	in 2 days	9						
6	in 6 days	11	100 % mortality	10	15	8	26	4
10								
6	in 6 days	14			10	3	13	7
3					5	2	5	1
6	in 6 days	7			10	6	36	11

enough to bring the larvae to maturity or to support the adults for an appreciable length of time

of individuals involved.

enabled the completion of larvae development in *C. maculata* (Smith 1960, 1961b). By contrast, the pollens of coniferous trees, also those of *Quercus rubra* and *Ambrosia artemisiifolia* were unsuitable (Smith 1960, 1961b). When Atallah and Newsom (1966a) used stamens of cotton as a source of pollen, *C. maculata* larvae failed to develop and died within 4 days. Although *C. maculata* can develop satisfactorily also on different artificial diets (see 6.14), on mites (Putman 1957), live aphids (Smith 1965a), and also on lepidopterous eggs (Szumkowski 1955, Warren and Tadić 1967), it in fact shows a distinct specificity for powdered food. Only 30 % of the larvae completed development if fed with live *Acyrthosiphon pisum*, and the resulted adults weighed only 8,5 mg; the same prey in a dry powdered state, however, gave a much higher survival (90 %) and heavier adults (12.0 mg). Larval and pupal development were only slightly prolonged on living aphids (17.5 vs. 16.4 days) (Smith 1965a). In the comparison of dry aphids and pollen for suitability as food, dry aphids appeared marginally more suitable, but this difference was not consistent (Smith 1965a).

A limit to the polyphagy of *C. maculata* was shown in experiments where both adults and larvae refused nymphal leafhoppers of several species which were, however, eaten by larvae of *Coccinella novemnotata* and adults of *C. trifasciata* (Yadava and Shaw 1968). The suitability of this prey for the latter two species was, however, not determined.

Synharmonia conglobata shows tendency towards polyphagy; both aphids and pre-imaginal stages of chrysomelids were found to be essential prey for this species by Kanervo (1940, 1946). The same author studied *Calvia quinquedecimguttata* and claimed that this species was a specialized feeder on chrysomelids and that aphids were accepted as merely alternative prey (Tab. 6.11).

Tab. 6.11 Chrysomelids accepted as food by coccinellid predators of *Melasoma aenea* (Kanervo 1946) [1] [2]

Coccinellid species	*Melasoma aenea*			*Phyllodecta atrovirens*	*Gastroidea polygoni*		*Phaeodon cochleariae*		*Plagiodera versicolora*			*Melasoma populi*			*Galerucella*							*Agelastica alni*		*Aphids psyllids* [3]
															sagitariae			*lineola*		*tenella*				
	E	L	P	L	E	L	E	L	E	L	P	E	L	P	E	L	P	E	L	E	L	E	L	
Hippodamia septemmaculata	(0)	(0)	(0)	—	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	principal
Adalia bipunctata	—	(0)	—	0	—	—	++	00	—	00	—	—	—	—	—	—	—	—	—	—	—	00		principal
Coccinella septempunctata	0	—	—	00	—	—	++	—	—	—	—	—	—	—	—	(0)	—	0	—	—	—	0	—	principal
C. quinquepunctata	⧻	++	0	00	principal 000	—	princ. ⧻	++	—	—	—	00	—	—	—	00	—	principal 000	00	—	—	—	—	principal
C. distincta	00	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—	00	—	—	—	000	—	principal
C. hieroglyphica	—	—	0	—	—	—	—	—	—	(0)	—	—	—	—	—	—	—	00	(0)	—	—	—	—	principal
Synharmonia conglobata	⧻	⧻	⧻	00	principal 000	00	—	—	—	000	—	00	—	—			—	principal ⧻	⧻	000	000	—	—	principal
Myrrha octodecimguttata	0	—	—	—	—	(0)	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	principal
Calvia quatuordecimguttata	(0)	(0)	0	—	—	(0)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	principal
C. quinquedecimguttata	principal ⧻	⧻	⧻	—	principal 000	000	(0)	0	principal											—	—	—	0	
Anatis ocellata	0	00	000	—	—	(0)	—	—	—	—	—	—	—	—	—	—	00	—	00	—	—	—	—	principal
Exochomus quadripustulatus	—	—	⧻	—	—	—	0	—	—	—	—	—	—	—	00	—	—	—	—	—	—	—	—	principal

[1] accepted — *000* and ⧻: in abundance; *00* and ++: rather amply; *0* and +: rarely; *(0)* very rarely; observed — *0* in laboratory; + also in the open.

[2] E — eggs, L — larvae, P — pupae.

[3] Principal food is marked for comparison. according to Kanervo (1940).

The strange finding that the larvae of *Coccinella undecimpunctata* can complete their development when fed solely on fresh manure (Hawkes and Marriner 1927) has been questioned by recent authors such as Benham and Muggleton (1970). They believe that in making the observation, Hawkes and Marriner overlooked cannibalism. Also with *C. undecimpunctata*, Harpaz (1958) in Israel achieved the completion of larval development on *Aphis pomi*.

6.13 Cannibalism

It is even possible for individuals of the same or of other coccinellid species to serve as alternative food in the absence of other prey. Mainly eggs or soft individuals which have just moulted are consumed. This habit has been observed in the majority of papers dealing with coccinellids and is one of the main obstacles preventing simple mass production of coccinellids. In order for cannibalism to be eliminated the larvae, as soon as they hatch, must be isolated and be cultured in isolation. A good and more practical alternative is to provide an increased travelling space in the cages by filling them with fluffed-up wood shavings ("excelsior") (Shands et al. 1970).

The value to newly hatched larvae of cannibalising other eggs of the same batch is discussed in 6.31. Cannibalism increases the chances of survival of the larvae only when there is a very low density of prey.

In general, cannibalism can be considered as having a selective value for the species; however, when late instar larvae feed on pupae of their own species, there is probably no such advantage to the species (Way in Hodek 1966 p. 91).

Koide (1962) obtained complete larval development of *C. septempunctata* on an exclusive diet of eggs of their own species. This diet was less favourable for the larvae than were aphids: the rate of development decreased by 38 % and the larvae were 15 to 25 % smaller. *Coleomegilla maculata* larvae can also develop when reared on eggs of their own species, and consume on average 76.3 eggs during the whole development. The duration of larval plus pupal development (21.1 days at 26.7°) was slightly longer than when the larvae were fed on pig's liver (20.6 days) and increased markedly compared with that of larval feeding on *Hyphantria cunea* eggs (18.2 days) (Warren and Tadić 1967). In contrast to these two findings is the older observation on the coccidophagous species *Exochomus flavipes*. The larvae generally developed in a shorter time when fed on the eggs of their own species than when fed on their normal food, *Dactylopius opuntiae* (Geyer 1947).

6.14 Artificial diets

As the prey can be collected in the field only for part of the season and as the breeding of aphids or coccids requires a large investment in both space and man power, attempts have been made to feed predaceous coccinellids on substances other than live prey.

The first attempts were rather primitive. Hawkes (1920), for example attempted to rear the larvae of *Adalia bipunctata* on cooked or raw hens' eggs and on pounded dates. Considerable progress has since been achieved, even though successfull breeding, especially on chemically defined diets, is still rather a rarity.

The simplest way to compensate for a shortage of aphids from the field is to use them dried (Smith 1965a) or frozen (Shands et al. 1966). Smith (1965a) succeeded in rearing *Anatis mali*, *Adalia bipunctata*, *Hippodamia tredecimpunctata* and *Coleomegilla maculata* on dry powdered aphids, but failed with *Coccinella spp*. When fed quick--frozen aphids, development of larvae and adults of *Coccinella septempunctata* was the same as when fed living aphids (Shands et al. 1966). Similar evidence is quoted by Hagen (1962) for *Hippodamia convergens.*

There are two approaches for developing artificial foods for insects. The by far more complicated method is to prepare a mixture of chemically defined substances (holidic diet). This has been achieved with only a few insects, as the demands of the insect on its food are very complex and are not yet completely understood. Not only must the diet contain all necessary nutrients, but also the food must have the correct mechanical properties to enable the intake of food to occur (e. g. sufficiently small particles for 1st instar coccinellid larvae — Smith 1960) and furthermore gustatory properties to induce feeding. In many insects the complex nature of feeding behaviour must also be considered as e. g. in the development of artificial food for the curculionid *Anthonomus grandis* (Vanderzant and Davich 1961), where the boll weevil will only accept food at the tip of a vertical stick.

Usually, however, an easier technique for preparing artificial foods for insects is to mix different natural substances (meridic diets). Substances such as honey, yeast, royal jelly, are known to be rich in most of the necessary nutrients, including carbohydrates, proteins, essential aminoacids, minerals, lipids and sterols. In some cases, some of these nutrients may need to be added in the chemically pure form. As yet, all attempts to breed coccinellids artificially have been based on meridic diets.

When it is necessary to transport coccinellids, droplets of honey mixed with agar have often been successfully used to increase survival. The task of composing an artificial diet, which can completely substitute for the essential food, is much more difficult. The best results have been achieved with *Coleomegilla maculata.* This is probably a reflection of the extensive polyphagy or rather pollinivory of this species (see 6.111 and 6.12). Several authors have succeeded in rearing this ladybird on laboratory diets. Szumkowski (1952) successfully (93 % development) used mammalian liver enriched with vitamin C for rearing this species. Later he found that a mixture of minced liver with an added 30—50 % honey solution was the best diet for oviposition, but the results were also satisfactory if liver was substituted by meat or fish and the honey by sugar. A mixture of protein hydrolysates and sugar solution was not so successful, and caused an increase in mortality of the beetles and a reduced oviposition (Szumkowski 1961a). For larval development, however, a mixture of fresh yeast (30—60 %) with 2—10 % glucose or sucrose solution was superior to the liver diet. Warren and Tadić (1967) used Szumkowski's first method (pig's liver with 1 or 2 drops of a liquid vitamin mixture — Deca-Vi-Sol) with success for ovipositing *C. maculata* females.

These diets although they had proved satisfactory for *C. maculata*, failed to support oviposition of females and development of larvae in *Cycloneda sanguinea* and *Hippodamia convergens* (Szumkowski 1961b). Hukusima and Sakurai (1963) tested a series of diets of which the least unsuccessful was quite a simple diet. This simple diet was composed of: grasshoppers (1 g), yeast (0.3 g). agar (0.7 g). honey (3 g) and sugar (8 g). This concentrate was made up with a mixture of water (25 cc) and milk (25 cc) with vitamins added in the form of a multivitamin preparation (0.3 g). When second instar-larvae of *Coccinella septempunctata bruckii* were fed on this food, about 10 % completed larval development and became adults. When 1st instar larvae were put on the diet, they died in the 3rd instar.

Similar lack of success with a series of 25 diets is reported by Tanaka and Maeta (1965). The diets had value only as alternative food for all three species tested (*Harmonia axyridis, C. septempunctata bruckii* and *Chilocorus kuwanae*). The females could not mature or oviposit, and the larvae could not develop from 1st instar to adult.

Smith (1965a, b) tested several meridic, mostly powdered diets. A diet based on brewer's yeast and sucrose, with other growth factors added (Tab. 6.12), enabled a higher percentage of *C. maculata* larvae to complete larval development (86 %) and at a higher developmental rate (21.3 days) than if they were reared on corn pollen (52 %, 22.9 days) (Smith 1965a). This diet was, however, not satisfactory for oviposition by adults; for this purpose, the yeast had to be replaced by a liver preparation (Smith 1965a). The diets were prepared by dehydrating an aqueous mixture of the ingredients and grinding the residue to a fine powder. Three other similar dry foods and a banana diet were tested for adults of 13 species (Smith 1965b). All species accepted at least some of the diets tested, but only 8 species oviposited (Tab 6.13). In these latter tests, Smith did not compare fecundity on artificial foods with that on natural foods as he had done for *C. maculata* in his earlier tests (Smith 1965a). For the remaining 5 species, among them all three *Coccinella spp.*, the mixtures served only as alternative food, and merely increased longevity without promoting oviposition. On three diets oviposition by *Hippodamia convergens* was achieved. Hagen (1962, in de Bach, 1964) also obtained some eggs from *Hippodamia convergens* adults that had overwintered, after feeding them with a fluid consisting of water, fructose, enzymatic protein hydrolysate of yeast, choline chloride, cholesterol, vitamins and standard nutritional salt mixture.

Atallah and Newson (1966) formulated and tested 16 experimental diets, based on chemical analysis of aphids and calf liver, for rearing *Coleomegilla maculata.* Six diets were satisfactory for larval development and oviposition. The final and most satisfactory of the diets[1]) (Tab. 6.12, No. 16) differed from all the others in two respects. Double the amount of liver preparation was included, but a more important addition was an extract from 50 cotton leaves (carotenoids and sterols). Beetle copulation was increased when the diet also included 0.2 ml vitamin E. Eight generations were reared on diet no. 16 without any reduction in viability after the 2nd generation. The diet failed, however, to support other coccinellids tested (*Coccinella novemnotata*, *Cycloneda spp.*, *Hippodamia convergens*, *Olla abdominalis*).

The above paragraphs tell a story of little success in rearing species other than *C. maculata* on artificial diets, and no complete successes with *Coccinella spp.* Good results were reported by two authors who added a small amount of natural food to their artificial diets; these achievements could not, however, be repeated by other authors (Tanaka and Maeta 1965, Iperti pers. comm.). Smirnoff (1958) claimed good results with 18 species (aphido-, coccido-, acaro-, and mycophagous); he added a small amount of pulverized dry prey to a medium otherwise made from water, agar, cane sugar, honey, alfalfa flour, yeast, and royal jelly. He believed that royal jelly was essential to the formula because of its content of growth stimulating factors and aseptic qualities. This diet was reported as excellent for adults, and was supplemented with beef jelly for larvae. Both rate of development and longevity were even higher than obtained on natural food, fecundity was not recorded. Another medium with added prey has been reported very successful in the rearing of *Cryptolaemus montrouzieri* by Chumakova (1962). The medium was composed of water, agar, sucrose, honey, casein, peptone, corn oil, vitamin E, cystine, yeast autolysate, and cotton oil. She even achieved an increased oviposition on a similar diet; no coccids were added, and peptone was replaced by nucleic acid. The larvae were reared on a more complicated diet, but, nevertheless suffered from a high mortality.

---

[1]) The technique for preparing the diet:

1. Half the amount of water was mixed thoroughly for 3—4 min. with all the ingredients except agar.
2. The other half of the water was heated to boiling, then the agar was added and carefully dissolved. The agar solution was then added to the mixture and blended at high speed for 1,5 min.
3. The diet was poured while still hot into the containers, where it solidified.

Tab. 6.12 Artificial diets for *Coccinellidae*

	Smith 1965a[1])		Smith 1965b[2]) for adults				Atallah and Newsom 1966[3]) for both larvae and adults		
	for larvae	for adults	banana diet	dry diet 1	dry diet 2	dry diet 3	diet 13	diet 14	diet 16
water	—	—					150 ml	200 ml	200 ml
salt mixture	1.5 %	1.5 %							
Wesson' s salt							1.25 g	1.25 g	1.25 g
brewer's yeast	40 %			30 %	10 %	10 %		1.0 g	1.0 g
Difco egg-meat				40 %					
Difco liver		40 %				40 %			
liver extract 1—20								3.0 g	3.0 g
liver fraction L							3.0 g		3.0 g
fresh banana			90 %						
pollen							3.0 g		
casein			9 %		40 %		7.0 g	6.0 g	6.0 g
soybean hydrolysate							3.0 g	3.0 g	3.0 g
sucrose	55.0 %	55.0 %		30 %	50 %	50 %	3.0 g	2.0 g	3.0 g
dextrose								1.0 g	1.0 g
glycogen							2.1 g	2.0 g	2.0 g
cholesterol	0.3 %	0.3 %							
butter fat							2.5 g	2.0 g	2.0 g
ribonucleic acid	1.5 %	1.5 %							
corn oil							2.5 ml	2.0 ml	2.0 ml
wheat germ oil	1.5 %	1.5 %	0.9 %						
wheat germ							4.0 g	4.0 g	4.0 g
choline chloride	< 0.1 %	< 0.1 %							
inositol chloride	< 0.1 %	< 0.1 %							
sorbic acid							0.1 g	0.1 g	0.2 g
ascorbic acid							0.4 g	0.4 g	0.5 g
carotenoids + sterols extr. from cotton leaves									from 50 leaves
vitamin solution[5])							3.0 ml[5])	2.0 ml[5])	3.0 ml[5])
B-vitamins[4])	[4])	[4])	c. 0.1 %						
tegosept (methyl p-hydroxybenzoate)							0.1 g	0.2 g	0.2 g
aureomycin							0.06 g	0.06 g	0.06 g
agar							5.0 g	4.0 g	4.0 g

1) 2) For results with these diets see Tab. 6.13.

4) All three diets enable both larval development and egg laying in *Coleomegilla maculata;* No. 16 is the most satisfactory.

3) B-vitamins, for each 10 g of diet approx.:

niacinamide	5.0 mg
Ca-pantothenate	2.5 mg
thiamine-HCl	1.5 mg
riboflavin	1.2 mg
pyridoxine-HCl	1.2 mg
folic acid	0.1 mg
biotin	0.02 mg
vitamin B 12	0.002 mg

5) Vitamin solution:

distilled water	100 ml
niacinamide-HCl	100 mg
Ca-pantothenate	100 mg
thiamine-HCl	25 mg
riboflavin	50 mg
pyridoxine-HCl	25 mg
folic acid (crystal.)	25 mg
biotin (crystal.)	2 mg
vitamin B 12	0.2 mg

Tab. 6.13 Laboratory diets (table 6.12) tested on several *Coccinellidae* (Smith 1965 b) (A — accepted, O — promoted oviposition)

Coccinellid species	Diet					Longevity
	fresh liver	banana diet	dry diet 1	dry diet 2	dry diet 3	
Adalia bipunctata	A	O	A		O	66.4 (55 — 88)
A. frigida		A	A	O	A	121.4 (45 — 173)
Anatis mali	O	O	A	A	O	52.6 (26 — 87)
Coccinella novemnotata		A				21.8 (17 — 36)
C. trifasciata perplexa	A	A	A	A	A	55.1 (43 — 72)
C. transversoguttata richardsoni		A				66.8 (27 — 112)
Coleomegilla maculata lengi	O	O	O	A	O	
Cycloneda munda	A	O				53.7 (33 — 126)
Hippodamia convergens	O	O	A	O		134.3 (76 — 167)
H. glacialis		O	A			120.6 (78 — 198)
H. parenthesis	A	A	A	A	A	40.8 (29 — 75)
H. tredecimpunctata tibialis	A	O	A	A	A	55.3 (36 — 108)
Mulsantina sp.		A		A	A	134.3 (106 — 191)

In view of the current position that artificial foods for the majority of typically carnivorous coccinellids have proved comparative failures, it is understandable that a number of experimenters have endeavoured to use as food insects which are easier to rear than are the typical prey (like aphids, coccids, mites). Thus Sundby (1966) succeeded in rearing *C. septempunctata* on eggs of *Ephestia kuehniella* and Kesten (1969) alternated *Musca* larvae with bananas daily, and frequently achieved a completion of larval development and pupation in *Anatis ocellata*. The adults, however, died in the process of emerging from the pupa or shortly afterwards. Surprisingly enough, the females oviposited for months if fed only on bananas by which they were strongly attracted. A claim that is very interesting is that continuous breeding of *Harmonia axyridis* has been achieved on frozen or lyophilized larvae or young pupae of drone honey-bees (Okada 1970). Ten generations were bred without any apparent decrease in vitality. If this food proves as 'essential' also for other species — particularly for the difficult *Coccinella spp.* — there may here be an important step forward in the study and utilization of coccinellids. The lack of a suitably practicable food is a barrier not only to making mass rearing of coccinellids for release an economic proposition, but also to providing sufficient specimens for experiments so that significant results can be obtained. It is no exaggeration to claim that the discovery of such food is a prerequisite for further qualitative progress in coccinellid studies.

In the event that this aim cannot be reached through some fortunate discovery involving a natural substitution (as mentioned above this discovery may already be with us), it will be necessary to search for it systematically by analysing natural food and by elimination experiments; a process which has already been carried out for a series of phytophagous insects. The study by Atallah and Killebrew (1967) of the amino-acid requirements of adult *Coleomegilla maculata* is perhaps the only work of this kind as yet done with coccinellids. Instead of eliminating the individual acids from the diet, the authors used a faster and more elegant method with labelled compounds. They fed the beetles with a metabolic precursor, ^{14}C-labelled sodium acetate. After 4 hr, the beetles were homogenized and the activity of the individual amino-acids (separated chromatographically) was measured. Since non-essential amino-acids can by definition be synthesized by the animal, the labelled precursor will be incorporated in them. Glycine, serine, aspartic acid, glutamic acid, proline and lysine showed high activity. These must therefore be synthetized in vivo and thus are non-essential. In contrast, threonine, phenylalanine, isoleucine and valine had a negligible activity, and are therefore apparently essential or derived from essential precursors.

6.15 Food of phytophagous Coccinellidae

Food specificity has also been described in phytophagous coccinellids. In Japan, *Epilachna vigintioctomaculata* prefers potato plants and its larvae cannot develop on eggplant, in contrast to *E. sparsa orientalis* for which evidently both plants are essential food (Iwao 1954). For *E. pustulosa*, which some workers regard as only a biological race of *E. vigintioctomaculata*, thistle (*Cirsium spp.*) is the normal food. However, a certain proportion of the beetles, which differs in various localities, accept potato as food. Within any one population the individual specimens even show a variable and apparently inherited response to potato. Tab. 6.14 shows a positive correlation between the acceptance of potato by parent females and the ability of their larval progeny to develop on this food. Moreover, the acceptance of potato by the young adults is related to the food they receive as larvae; only 31.3 % of individuals which

Tab. 6.14 Development of *Epilachna pustulosa* on thistle (*Cirsium microspicatum* var. *kiotoense*) and potato (Iwao and Machida 1961)

		Larval progeny		
Parent female	Food	Completion of development [%]	Duration of larval development [days][1])	N
rejected potato (even in absence of other food)	thistle	69.0	18.2	58
	potato	43.1	16.0	65
accepted potato (only in absence of other food)	thistle	75.3	18.5	89
	potato	50.5	17.2	97
accepted potato (in presence of thistle)	thistle	73.7	18.2	57
	potato	60.0	16.6	60

[1]) 27 °C 16 hr light.

had developed on thistle accepted potato as adults while 74.2 % of those which had developed on potato did so. However it is not certain, whether this was due to pre-imaginal "conditioning" or to negative selection, i. e. there may have been a high larval mortality of those individuals which have a low ability to sustain themselves on potato. The percentage of beetles which accept potato, can be markedly increased in another way; they can be "conditioned" in the first days of adult life (Iwao and Machida 1961).

Klausnitzer (1965) failed to obtain eggs from *Epilachna argus* which had been collected on *Bryonia alba* and subsequently fed on *Bryonia dioica*. Dissection of dead females revealed an abundance of matured eggs.

Epilachna vigintioctopunctata, which feeds on *Luffa aegyptiaca* in India, prefers to feed on the corolla of the flower of this cucurbitaceous plant if under illumination, but makes no distinction between flowers and leaves in the dark (Sinha and Krishna 1969). A pest of cucurbits, *Henosepilachna elaterii* (= *Epilachna chrysomelina*) has been recorded also feeding on aphids (El Khidir 1969).

As well as the above species (all *Epilachninae*) which feed on vegetative parts of plants, there is an isolated genus *Bulaea* in the *Coccinellinae* which has obviously specialised on a different form of phytophagy. Capra (1947) reported that *B. lichatschovi* and other closely related species of the genus were "predominantly if not exclusively" pollinivorous both as larvae and adults, with a preference for *Chenopodiaceae*. *B. lichatschovi* is also considered as phytophagous by other authors (Dyadechko 1954, Bielawski 1959, Savoïskaya 1966, 1970a) and in the two last mentioned papers pollinivory is reported from Kazakhstan on various plants (*Euphorbia*, *Artemisia*, *Eurotia*, *Atriplex*, *Nitraria*, *Tamarix*, *Clematis*). In the last mentioned paper, various types of phytophagy are reported for this species from central Asia: feeding on pollen (*Tamarix*, *Euphorbia*, *Artemisia*, *Eurotia ceratoides*, *Atriplex*), on nectar (*Nitraria*, *Clematis*) and on leaves (sugar-beet, young apple trees).

There is much less information on the genus *Verania* for which pollinivory has also been reported (quoted by Goidanich 1943). Pollinivory in *Coleomegilla maculata* has already been discussed in 6.111 and 6.12.

6.16 Food of mycophagous Coccinellidae

The coccinellids comprising the mycophagous genera *Halyzia*, *Vibidia* and *Thea* have long been mistakenly considered as carnivorous. This mistaken idea is evident both in observations listed by Schilder and Schilder (1928), Börner and Heinze (1957), Fulmek (1957), and from the taxonomic placing of these three genera as subgenera of the genus *Halyzia* together with the other subgenera of this genus (*Sospita*, *Calvia*, *Myrrha*, *Propylaea*) in spite of the fact that morphologically they are very clearly distinguishable by the shape of their mandibles (see 1.1/Head). The history of how the ecological and morphological differentiation of the members of the tribus *Psylloborini* (=*Halyziini* sensu Bielawski 1959) came to be realised and the consequences for taxonomy were discussed by Strouhal (1926) who also gave a detailed comparison of adult and larval mouthparts in the different species and a survey of observations on mycophagy to that date.

Since then the members of the three genera mentioned above as well as of other genera of this tribe (for example *Illeis*/Liu 1950/) have been reported as feeding on lower fungi, particularly the powdery mildews (*Erysiphaceae*); no experimental work has yet been done on their food. Strouhal's (1926) original concepts remained basically unchanged in later discussions of the topic by Goidanich (1943) and Capra (1945) who added further observations.

Tytthaspis sedecimpunctata is classified into the tribe *Coccinellini* and is usually reported as aphidophagous (Dyadechko 1954, Sem'yanov 1965a, Klausnitzer 1966), although Dauguet already in 1949 wrote: "serait mycophage". No precise information on its food had been published until Turian (1969) reported on observations and preliminary experiments demonstrating that *T. sedecimpunctata* feeds also on *Erysiphaceae*, like the *Halyziini*. According to Turian, *T. sedecimpunctata* adults have no specificity as to various species of mildew but this has only been established with respect to food intake. Turian observed *Thea vigintiduopunctata* larvae and adults also feeding on various *Erysiphaceae* and suggests the term micromycetophagy to describe feeding on lower fungi (*Micromycetes*).

6.2 Food consumption

A great deal has been published about the amount of food consumed by larvae and adults of individual coccinellid species. It does not seem particularly helpful to list here all the accumulated numerical data since they can hardly be adequately compared. Even within a group with the same prey-relations (aphidophagous, coccidophagous, acarophagous) the individual findings are based on different species and developmental stages of prey and have been obtained under a variety of physical conditions. Thus, for any one coccinellid species, figures quoted for the amount of food vary enormously.

Moreover, there are several different ways of measuring food consumption. The base-line mortality of prey may be checked in cages identical to experimental ones, with the same amount of prey but without predators. The base-line value thus obtained is subtracted from the number of dead aphids in the experimental cages, using the formula (Hodek 1956)

$$f = n - (s_{24} + m_{24})$$

where f is the daily feeding rate; n is the daily supply of prey, s_{24} is number of prey survived after 24 hr, m_{24} is mortality of aphids within 24 hr in the check cages (base-line mortality). Alternatively, Kaddou's method (1960) may be used. He felt it possible to identify the aphids which have died from natural causes and eliminate them from the calculations. Each prey killed is then classified arbitrarily by the proportion of it which has been consumed, and these fractions are summed up. Kaddou quotes as separate figures the number of prey killed and the units consumed. Most authors have not specified how they obtained their measure of feeding rate. A promising approach for collecting data in a more defined and more easily comparable way, is to express the quantity of prey consumed in terms of biomass, i. e. in weight units (Blackman 1967a). However, this approach requires the precaution that changes in weight by evaporation must be taken into account.

To give some idea of the variability in figures quoted for food intake, Tab. 6.15 presents some data for *Coccinella septempunctata*. In aphidophagous *Coccinellidae* the daily feeding rate of adults usually amounts to about 100 aphids (the females, particularly if ovipositing, feed more than males) and the larvae consume several hundreds of aphids (mostly 200—600) during their entire development. Usually, about 60—70 % of the total food intake is consumed during the 4th instar (Tab. 6.16). Naturally, the smaller coccinellids take less food than the larger ones.

Tab. 6.15 Feeding rate of *Coccinella septempunctata* (Hodek and al. 1965)

Author	Food intake (in number of aphids)		Aphid species
	by larvae during the whole larval development	by adults (daily average)	
Smee	305	—	*Microlophium urticae*
Moroshkina	—	243	*Schizaphis graminum*
Jöhnssen	624: 846	—	*Aphis fabae* *Brevicoryne brassicae* *Acyrthosiphon pisum* *Hyalopterus pruni*
Bodenheimer	629: 1930	—	*Aphis frangulae* *A. asclepiadis*
Volkov	200		*Dactynotus sonchi*
	297		*Rhopalosiphon padi*
	316		*Brevicoryne brassicae*
	373		*Schizaphis graminum*
Dunn	100		*Macrosiphum euphorbiae*
Blattný	up to 1000	92	
Dyadechko	665 (max. 668)	—	
Hodek	216: 275 const. temp.	—	*Aphis fabae*
	506 fluct. temp.	—	*Aphis fabae*
Weismann. Valló	239; 229; 339 const. temp.	—	*Aphis fabae*

6.21 Effect of physical factors on feeding rate

Naturally, the daily feeding rate both of larvae and adults increases with temperature within the favourable range. There is, however, a certain discrepancy between the data of individual authors (Tab. 6.17) concerning the effect of temperature on total food

Tab. 6.16 Proportion of food intake in individual larval stages

Coccinellid species (conditions)	Author	Food intake in larval instars [%]				
		I	II	III	IV	V[1]
Coccinella undecimpunctata	Ibrahim	6.4	12.1	16.7	64.6	
aegyptiaca	1955b	6.1	11.8	19.8	62.3	
Coccinella septempunctata	Asgari 1966					
(15° C/darkness)		4.5	17.0	29.2	49.3	
(20° C/darkness)		3.2	6.5	9.6	80.6	
(20° C/8 hr light)		4.2	13.3	25.5	57.0	
(20° C/12 hr light)		5.3	13.4	24.2	57.1	
(20° C/16 hr light)		4.1	10.4	31.7	53.5	
(25° C/darkness)		5.8	7.8	9.7	76.7	
Coccinella septempunctata bruckii	Koide 1961	8.0	5.6	14.5	71.9	
Adalia bipunctata						
(*Aphis pomi*)	Sem'yanov	8.2	26.8	29.2	45.7	
(*Hyalopterus pruni*)	1970	7.3	15.3	29.6	47.8	
Cycloneda limbifer	Zelený 1969	1.1.	4.7	23.5	70.6	
Leis conformis	Moursi, Kamal 1946	4.9	7.0	18.5	69.6	
Chilocorus bipustulatus	Yinon	10.8	15.6	28.6	44.7	
	1969	6.2	8.9	16.3	25.5	43.0
Exochomus flavipes (own eggs)	Geyer 1947a	4.0	5.6	16.9	73.5	

[1]) Some proportion of laboratory cultured larvae of *C. bipustulatus* revealed 5 instars see 4. 11.

consumption during the entire larval development. Whereas Hodek (1957b), Kaddou (1960 — only his data for the lower temperature range below 27 °C) and Sundby (1966) found a slight increase of total consumption with increased temperature. Kaddou (1960 — at temperatures above 27 °C), Asgari (1966), Ellingsen (1969a), Gurney and Hussey (1970) reported the reverse. With the exception of the data of Gurney and Hussey (1970), however, the differences are rather small, so that the general impression is that the total larval food consumption of *Coccinellidae* is more or less stable irrespective of temperature. Kehat (1968a) reported that the total feeding capacity of larvae of *Pharoscymnus numidicus* was not affected by temperature. This would be in accordance with Rubner's hypothesis and with results obtained with other insects [Rubner 1908 (in Allee et al. 1949)].

The inconsistent food consumptions referred to above may have been subject to various inaccuracies arising from the methodological difficulties discussed earlier. That this is so is partly indicated by the rather great inconsistencies in data obtained at the same temperature but in different photoperiods (Asgari 1966 — Tab. 6.17).

While the total larval food consumption seems to be similar at different constant temperatures, it was found to be doubled when larvae of *C. septempunctata* were kept under naturally fluctuating temperatures in summer (Hodek 1957b). When Sundby (1966) alternated two constant temperatures, 16 and 21 °C, food consumption remained unaffected by the alternation. In *Adalia bipunctata*, Ellingsen (1969b) found an increase (though only by 10.6 %) of total larval food consumption if the larvae were reared under an artificial diurnal cycle of temperature ranging between 8 and 28 °C with

Tab. 6.17 Total food consumption of larvae in relation to temperature

Author	Prey species	Coccinellid species	Temperatures [°C]																				
			15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	44	35
Jöhnssen 1930	several	*Coccinella septempunctata*							846	624													
Bodenheimer 1943	several	*Coccinella septempunctata*	(629¹)				(1930)¹)																
Hodek 1957b	*Aphis fabae*	*Coccinella septempunctata*				216 (const. light)								276 (const. light)									
Kaddou 1960	*Macrosiphum pisi*	*Hippodamia quinquesignata*		190											241			216		158			
Sundby 1966	*Myzus persicae*	*Coccinella septempunctata*		399						420													
Asgari 1966	*Aphidula pomi*	*Coccinella septempuncatata*	1550 (dark?)					1236 (dark) 1063 (8hr light) 1465 (12hr light) 991 (16hr light)					1010 (dark?)										
Ellingsen 1969a	*Myzus persicae*	*Adalia bipuncatta*				188										168							
Gurney and Hussey 1970	*Myzus persicae*	*Coleomegilla maculata*		652					449			359											
		Cycloneda sanguinea		320					292			205											

¹) the data were achieved in different generations in the open and are here plotted according to the aver. of temperatures.

an average of 18 °C. That fluctuating temperatures have a stimulating effect is also indicated by the fact that pupae of *C. septempunctata* derived from larvae reared under the above mentioned artificial cycle were heavier (Sundby unpubl., in Ellingsen 1969b).

There are some indications (Hodek et al. 1965) which suggest that at lower relative air humidities food intake may be increased, particularly when the prey is aphid. As lower humidities are usually combined with higher temperatures, it is difficult to separate both effects. It seems quite probable, however, that at lower humidities the coccinellids may — in the absence of water — consume more of a prey with a high water content to make up for the decrease in water content they suffer from increased transpiration.

As far as the effect of light conditions on food consumption is concerned, only the results of Asgari (1966) are available, from which no consistent conclusions can be drawn.

6.22 Response to prey density

Within certain limits, food consumption seems to be positively correlated with the population density of the prey. This follows from the findings on adult *Coccinella septempunctata* (Popov 1960) (Tab. 6.18) and larvae of *Harmonia axyridis* (Mogi 1969) (Fig. 6.05). Thus, coccinellids can act as a density-dependent mortality factor for aphids, although such an application of the above laboratory results to the field may not be fully justified. To emphasize this latter point, field observations do not confirm for *Adalia bipunctata* the dependence ascertained in the laboratory for *Coccinella septempunctata*. The proportion of *Drepanosiphum platanoides* taken by *A. bipunctata* on sycamore trees did not increase as the prey population density rose. Thus *A. bipunctata* does not regulate populations of *D. platanoides* (Dixon 1970).

Tab. 6.18 Effect of prey density (*Aphis gossypii* and *A. fabae*) on feeding rate of *Coccinella septempunctata* adults (Popov 1960)

Number of aphids offered to 5 beetles	Daily average number of aphids consumed by 1 beetle
125	21.1
250	40.2
375	59.8

The increase in the number of aphids killed at high aphid density may be the result of two different phenomena operating simultaneously. Firstly it has been observed that hungry coccinellids completely devour the first few prey they tackle but exploit subsequent prey with a gradually decreasing efficiency. Thus, with an increase in prey population density, an increasing proportion of partially consumed prey may be left. Secondly, when prey is abundant, the larvae may also consume considerably more than the minimum required for their development (see below). An ability to adjust to variable resources of food is very important if predators are to have an effective impact on their prey.

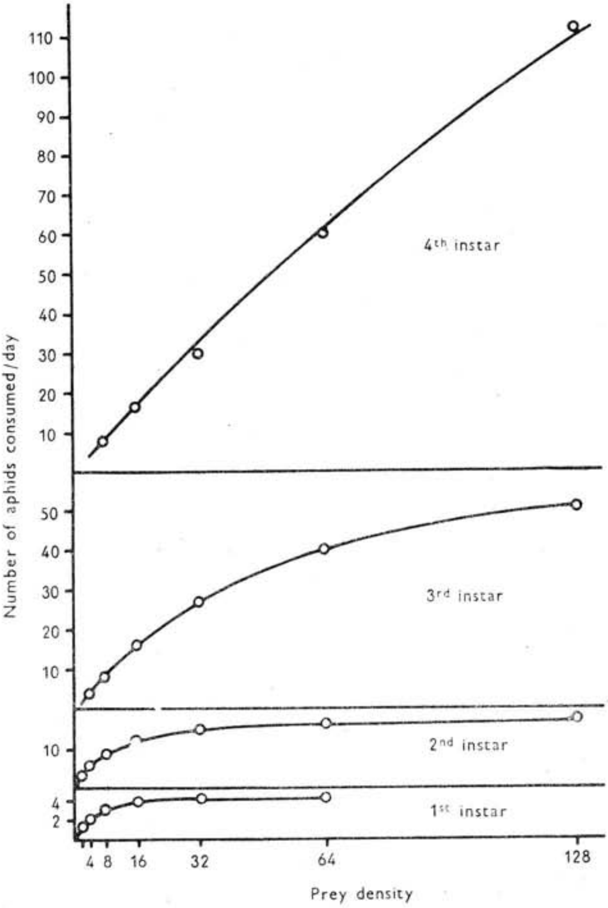


Fig. 6.05 Effect of prey density (*Aphis craccivora*) on the feeding rate of larvae of *Harmonia axyridis* (Mogi 1969).

6.23 Minimum food requirement

Larvae of *Coccinella septempunctata* complete their development even when their total food consumption is artificially reduced to 55 or even 40 per cent by limiting their daily supply in the 4th larval instar to 30 or even 10 aphids (*Aphis fabae*) (Tab. 6.02) (Hodek 1957a). Sundby (1966) verified this by showing that the larval period of *C. septempunctata* can be completed on only 7 aphids (*Myzus persicae*) per day. This feeding rate was only one-third of the normal value. Most of the larvae pupated, but the emergence of adults was low (only 3 out of 8). These adults were smaller and produced less eggs.

Similar observations have also been made with other coccinellids. The females of *Coccinella undecimpunctata aegyptiaca* began to oviposit with only 30 aphids per day and until 65 aphids were supplied per day there was a positive correlation between the consumption of food and egg-production. Longevity remained low up to 45 aphids per day (Fig. 6.06) (Ibrahim 1955b). The minimum supply on which larvae could complete their development was 15 *Aphis durantae* per day. An increase to 45 aphids per day shortened the duration of development and any further increase merely resulted in an increase in the size of adults produced (Ibrahim 1955b). Kaddou (1960) reported analogous results on larvae of *Hippodamia quinquesignata* (Tab. 6.19).

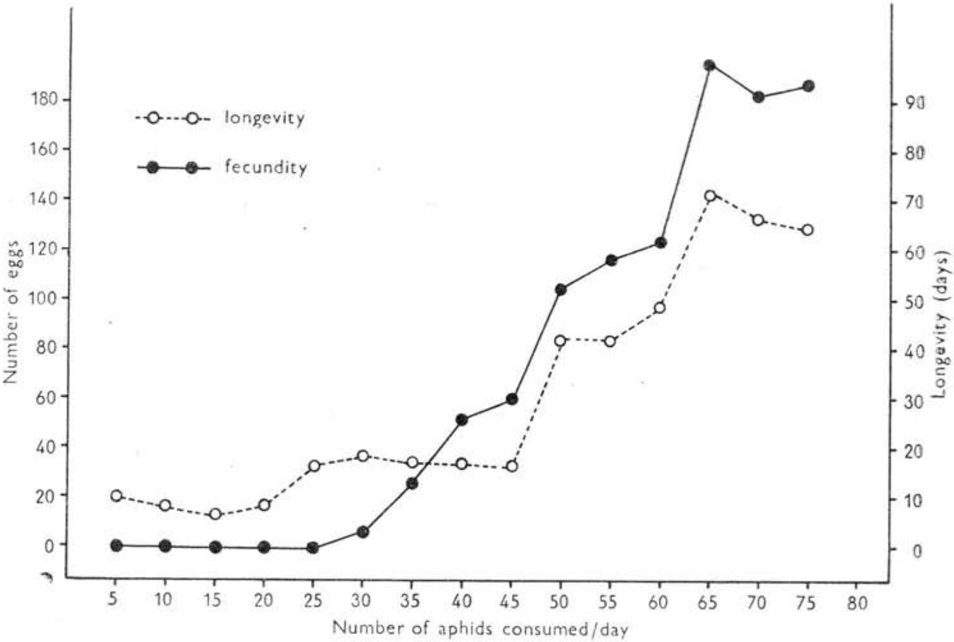


Fig. 6.06 Effect of daily feeding rate on the fecundity and longevity of *Coccinella undecimpunctata aegyptiaca* (Ibrahim 1955b).

Tab. 6.19 Effect of reduced feeding in larvae of *Hippodamia quinquesignata* (Kaddou 1960)[1])

Total larval aphid consumption [aphids][1])	Duration of stages larval [days]	pupal [days]	Weight of pupae [mg]	adults [mg]	N
32.3	27.0	4.0	5.4	4.5	3[2])
78.4	—	—	10.7	—	4[2])
131.7	8.5	4.0	17.6	14.1	8
191.8	8.2	3.8	20.5	16.6	5
215.6[3])	8.1	3.1	23.1	18.7	10

[1]) Food: 2nd instar larvae of *Macrosiphum pisi:* temperature: 30° C.

[2]) Only 3 and 4 larvae completed development out of an initial 32 and 11, resp. (in other replicates mortality is not given).

[3]) Check replicate supplied with surplus of aphids.

The minimum daily feeding rate for individual larval instars and its effect on oviposition (Tab. 6.20) have also been measured for the acarophagous *Stethorus bifidus* (Collyer 1964). Larvae of *Stethorus picipes* require a minimum of one fifth of their maximum diet in order to complete the life cycle successfully (Fleschner 1950).

Smith (1965c) expressed minimum food consumption in terms of prey weight. The dry weight and size of *Coleomegilla maculata lengi* adults increased with the quantity of larval food, but only up to about 10 mg of the prey (dried *Acyrthosiphon pisum*). Additional food consumed contributed nothing to the weight of the adult (Fig. 6.07). In *Anatis mali* an excess of larval food, unimportant for survival, nearly doubled adult weight (Tab. 6.21). When the food supply was increased, developmental time decreased significantly in *A. mali*, but remained unchanged in *C. maculata*. *A. mali* was more flexible than *C. maculata* in this ability to adjust developmental time and adult weight to changes of food available (Smith 1965c).

Tab. 6.20 Fecundity of *Stethorus bifidus* on different prey-density (*Panonychus ulmi*) (Collyer 1964)

Prey density (mites per day)	Fecundity	
	total number of eggs	daily number of eggs (av. per female)
40—60	308 333 438	6
20	24 64 67	2
10[1]	2 19 27 30 33	1

[1] Some of the females ceased oviposition prematurely, although they continued to live.

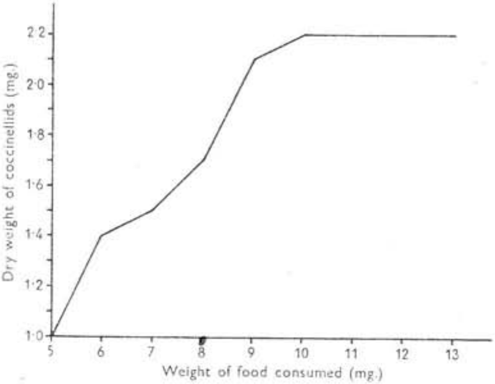


Fig. 6.07 Dependence of the adult size of *Coleomegilla maculata* on the amount of food consumed during larval life (Smith 1965c).

A similar flexibility is found in *Pharoscymnus numidicus*. The 4th instar larvae feeding under conditions of food scarcity showed a decreased rate of development and increased mortality; also small adults developed (Fig. 6.08). The larvae could complete their development on 1/7 of the normal food consumption. Thus *P. numidicus* has both a high tolerance to food scarcity and the ability to increase voracity when prey is abundant (Kehat 1968a).

Tab. 6.21 Effect of food intake (*Acyrthosiphon pisum* — dried) on *Anatis mali* (Smith 1965c

Amount of food [mg]	Length of development from egg to adult [days]	Survival [%]	Adult dry weight [mg]
5	—	0	—
15	24.7 ± 0.1	30	4.6 ± 0.3
30	19.2 ± 0.1	90	6.7 ± 0.4
45—55	20.9 ± 0.3	85	12.8 ± 0.3

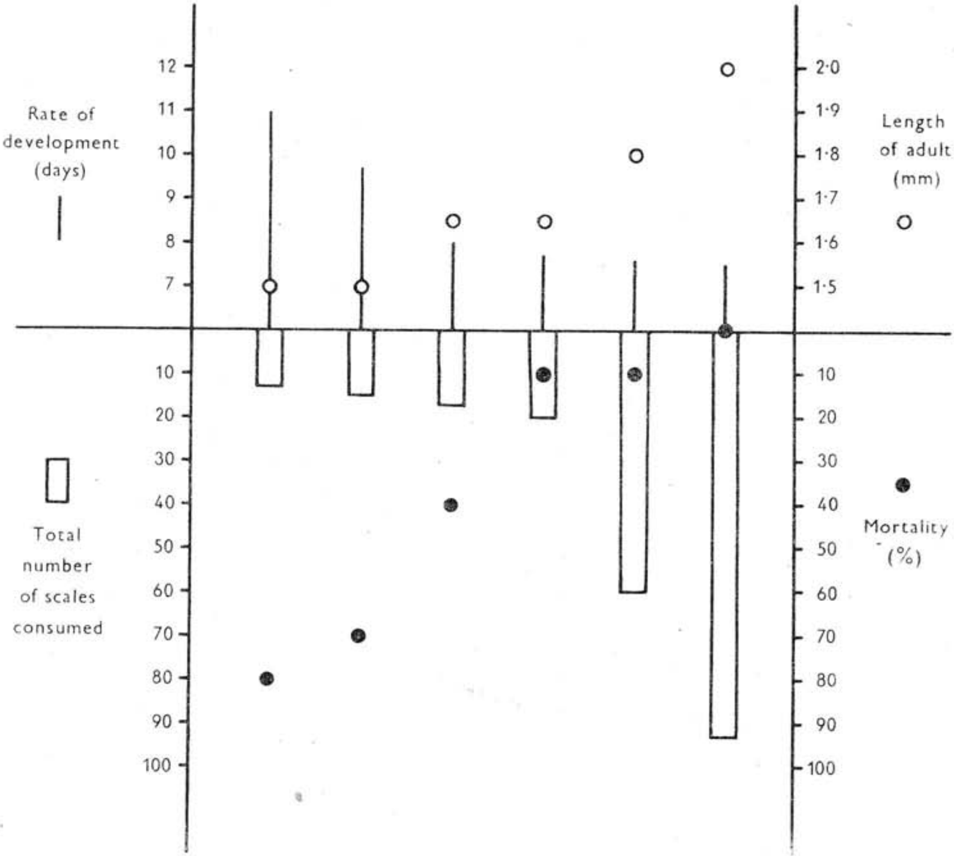


Fig. 6.08 Development and feeding of 4th instar larvae of *Pharoscymnus numidicus* under conditions of food scarcity (*Parlatoria* females as food) (Kehat 1968a).

6.3 Behaviour related to food

6.31 Searching behaviour

Thompson (1951) wrote that coccidophagous *Coccinellidae* "have a full complement of sense organs and there is no doubt that they can perceive their hosts at a distance". Further he believed that "certainly there seems no reason to think that insect predators are so casual in their food relations that their behaviour can be described in any sense as random action". This distinguished specialist on entomophagous insects made this statement on the basis of observation in the absence of experimental evidence, and now that such is available, these statements can no longer be regarded as valid, particularly for aphidophagous and acarophagous coccinellids.

Nearly all the experimental work on searching behaviour was published after Thompson wrote these words. Detailed experiments with acarophagous and aphidophagous coccinellids (also one coccidophagous species included) have now shown that neither optic nor olfactory orientation operates in prey searching behaviour (Fleschner 1950 — *Stethorus picipes*, Putman 1955 and Moter 1959 — *S. punctillum*, Banks 1954b, 1957 — *Coccinella septempunctata*, *Adalia bipunctata*, *Propylaea quatuordecimpunctata*, Dixon 1959 — *Adalia decempunctata*, Kaddou 1960 — *Hippodamia quinquesignata*, Bänsch 1964, in Hodek 1966 p. 123 — *C. septempunctata*, *A. bipunctata*, Kehat 1968a — *Pharoscymnus numidicus*, Kesten 1969 — *Anatis ocellata*).

No discovery of prey is made by the coccinellid until actual contact occurs. The prey may be missed if only a few millimeters away (Banks 1957), even when wind carries the smell to the coccinellids (Bänsch 1964, in Hodek 1966 p. 123, experiments on larvae). Fleschner (1950) quotes the value of 0.5 mm as the area of perception. Kesten (1969) found out that the maxillary palps are perhaps the most important sensory organs through which both adults and larvae of *Anatis ocellata* recognize the prey.

However, the movement of coccinellid larvae and adults is not completely haphazard. Certain regularities of behaviour, which make the encounter of predator and prey more probable, have been observed. (1) Such encounters are made more likely, at least between aphidophagous and acarophagous species and their prey, by a correspondence of tactic responses: like coccinellids, both mites and aphids show positive phototaxis and negative geotaxis (Fleschner 1950, Dixon 1959, Kesten 1969). (2) Searching efficiency may be increased further by the tendency of coccinellids to crawl along an edge or a raised surface. Thus on leaves, veins influence the direction of movements, and it is near veins that colonies of aphids occur most often (Banks 1957, Dixon 1959, Bänsch 1964, in Hodek 1966 p. 123). (3) In addition, the change in search pattern that the coccinellids show after finding prey has an advantage for predators of prey which forms colonies. After feeding, the larva increases the thoroughness of its subsequent searching by slower, winding movements in the vicinity, often turning frequently in a short distance (Banks 1957, Dixon 1959, Kaddou 1960, Kesten 1969) (Fig. 6.09).

Apart from these three regularities in behaviour, crawling is haphazard and the larvae revisit places already searched and neglect other areas. So, for example, a 1st-instar larva of *Propylaea quatuordecimpunctata*, moving for three hours on a clump of 14 bean stems spent 52 % of the time searching on leaves visited more than once and only 12 % on leaves visited only once (the rest of the time was spent on stems or stationary) (Banks 1957).

To study the movements of predators on the stem and twigs of plants, Bänsch (1964, in Hodek 1966 p. 123) used a model tree 50 cm high. When moving upwards on the

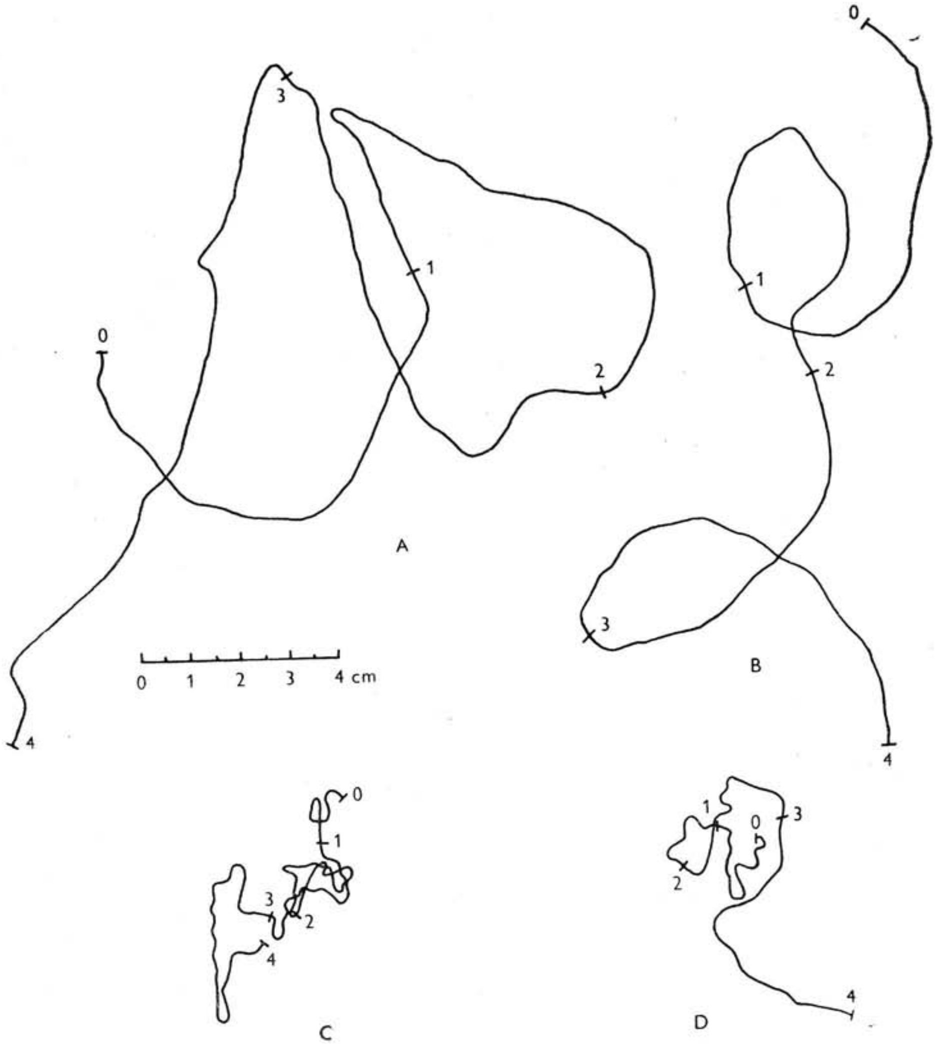


Fig. 6.09 Tracks of an unfed 4th instar larva of *Adalia bipunctata* on paper, before (A, B) and after (C, D) feeding on an aphid. (On the tracks there are indicated the passage of 4 successive intervals of 15sec.) (Banks 1957).

stem, coccinellids stop moving at bifurcations, but soon continue walking to follow the main axis. After an unsuccessful search at the top the larvae return down the stem, but their behaviour changes and they now follow each bifurcation. If also unsuccessful on a twig, they return to the stem and move to the top again. So, on the model tree, the larvae are more or less "trapped" between the apex and the tops of branches (Fig. 6.10). If the larvae eventually reach the ground, they do not move upwards again until they have covered a certain horizontal distance on the ground. Larvae of *C.*

septempunctata which have found aphid colonies remain close to them for long periods (e. g. 18 hr) (Banks 1957). The adults differ in their searching behaviour in that they soon fly away after an unsuccessful search.

In contradiction to all previous observations which have rejected the possibility of sense orientation by coccinellids towards their prey, Colburn and Asquith (1970) found that *Stethorus punctum* adults were attracted to their prey by smell in a special cage with four vials attached. Air was blown through the vials towards the beetles at the centre, but only some vials contained prey.

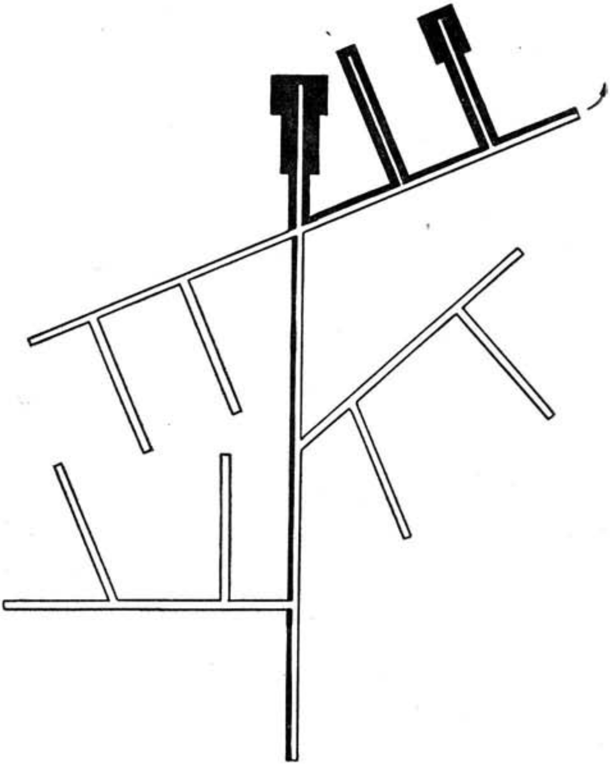


Fig. 6.10 Search pattern of one *Adalia bipunctata* adult on the model tree until flying away (arrow) after 23 min. (Bänsch 1964). The thickness of the line indicates the searching frequency of the predator.

Two behaviour studies which support Thompson's (1951) view have recently been reported and concern two large coccinellids preying on coleopterous and lepidopterous larvae. Savoïskaya (1970b) reports that the later instar larvae of *Aiolocaria mirabilis*, a specialized predator of chrysomelids, are very mobile and aggressive and actively pursue their prey. A similar behaviour is shown by the adults of the imported *Anatis ocellata*, which in Michigan preys on larvae of the tortricid *Choristoneura pinus*. Although the beetles search at random, they show a characteristic attack behaviour. "Within a distance of 1/2 — 3/4 in. (= 1.3 — 1.9 cm) from the prey . . . . the hungry adults stopped momentarily before moving forward and quickly snatching it in their mandibles". Physical contact was not required to arouse the attack and visual stimuli seemed to play a role (Allen et al. 1970).

From the point of view of economic impact of coccinellids, searching at random has its advantages and disadvantages. Such behaviour may improve the predator impact in particular situations (see 9.121).

However, random searching behaviour evidently markedly increases the mortality of newly hatched first instar larvae when prey density is low. According to Banks (1957) the first instar larvae of *Propylaea quatuordecimpunctata* spend 12—24 hours on the empty egg shells before they disperse and when food is absent then search actively for 25—35 hours. Activity then ceases, and death follows within 24—28 hours. They therefore need to find food within 1—1.5 days. During this time they can crawl for 75—300 cm. This distance is rather short for survival because, in searching randomly, the larvae may cover the same ground several times. Moreover, the movements of first instar larvae become impeded by honeydew and by hairs (Tab. 6.22). Therefore, when ladybird eggs are laid remote from aphid colonies, there is only a poor chance that the newly hatched larvae will find prey. The immature stages therefore suffer a high mortality (Banks 1954b). Laboratory observations of searching behaviour of *Adalia bipunctata* larvae agree with observations over 8 years in the field that under field conditions, the first instar larvae would be unable to survive unless the population density of young aphids on sycamore leaves exceeds 2 aphids per 100 cm^2 (Dixon 1970).

With first instar larva of *A. decempunctata* (and presumably generally), the chance of capturing prey increases once the first aphid has been eaten (Dixon 1959). Also cannibalism on eggs may prolong survival (see 6.13). Banks (1954b) found that the consumption of just a single egg nearly doubled the time a larva can survive and considered that the searching ability of newly hatched larvae was increased by feeding on eggs of the same egg batch. This has been queried by Pienkowski (1965), who found that cannibalism on eggs makes a larva disperse later from the egg batch and then be less active and even after 4 days of feeding on aphids less successful in finding prey (Tab. 6.23). As the larvae even feed on viable but more slowly developing eggs, the value of egg cannibalism for the impact of coccinellids on their prey seems rather doubtful. Cannibalism only increases the chance of survival of the larvae where there is a very low density of prey.

Tab. 6.22 Mean rates of movements (mm/min) of first instar larvae of *Propylaea quatuordecimpunctata* on various surfaces (Banks 1957)

	Paper	Clean bean leaf	Honey-dewed bean leaf	Hairy potato leaf
mm/min	151	154	104	54
m/1—1.5 day		225—300	150—200	75—100

Tab. 6.23 Influence of egg cannibalism on the predatory efficiency of first-instar larvae of *Coleomegilla maculata* (Pienkowski 1965)

Average number of eggs eaten per larva	0.3	0.1	0
larvae observed attacking aphids	34 %	36 %	51 %
larvae active after 3 days	20 %	34 %	46 %
larvae active after 4 days	38 %	44 %	67 %

6.32 Prey capture

Even when an encounter occurs, the coccinellid may fail to capture the prey and feed on it. This section of prey/predator relationships has been largely neglected, although it can be of paramount importance for the impact of the predator (Varley and Gradwell 1970).

Although aphids are generally considered to be completely "helpless" (Imms 1947), their defensive and escape mechanisms have been observed several times. Recently two authors have studied such responses of aphids towards two *Adalia spp.* (both larvae and adults of *Adalia decempunctata* — Dixon 1958, 1959, and larvae of *A. bipunctata* — Klingauf 1967). The aphids show various defence responses, as e. g. kicking movements, movements of the body, pulling free the appendage seized by the coccinellid and "waxing" the coccinellid with an oily liquid appearing on the tip of the siphunculi. Moreover, the aphids may escape by walking away or dropping off the plant (Fig. 6.11). The intensity of response varies with the size and stage of the predator. If an *A. decempunctata* adult approaches, the response of aphids (*Microlophium evansi*) is more intense than with coccinellid larvae; adult coccinellids induce escape rather than defence responses of aphids (Dixon 1959). The success or failure of a predator to capture the prey depends on their comparative size (Fig. 6.12).

Older larvae of *A. bipunctata* (9 mm long) succeed in capturing 90—100 % of first instar and about 60—70 % of adult *Myzus persicae* or *Neomyzus circumflexus*, but only 0—50 % of the much larger *Acyrthosiphon pisum* (Klingauf 1967). This finding agrees with the observation that aphids with long appendages were more difficult for *Hippodamia quinquesignata* larvae to capture than the more compact and tenacious aphids

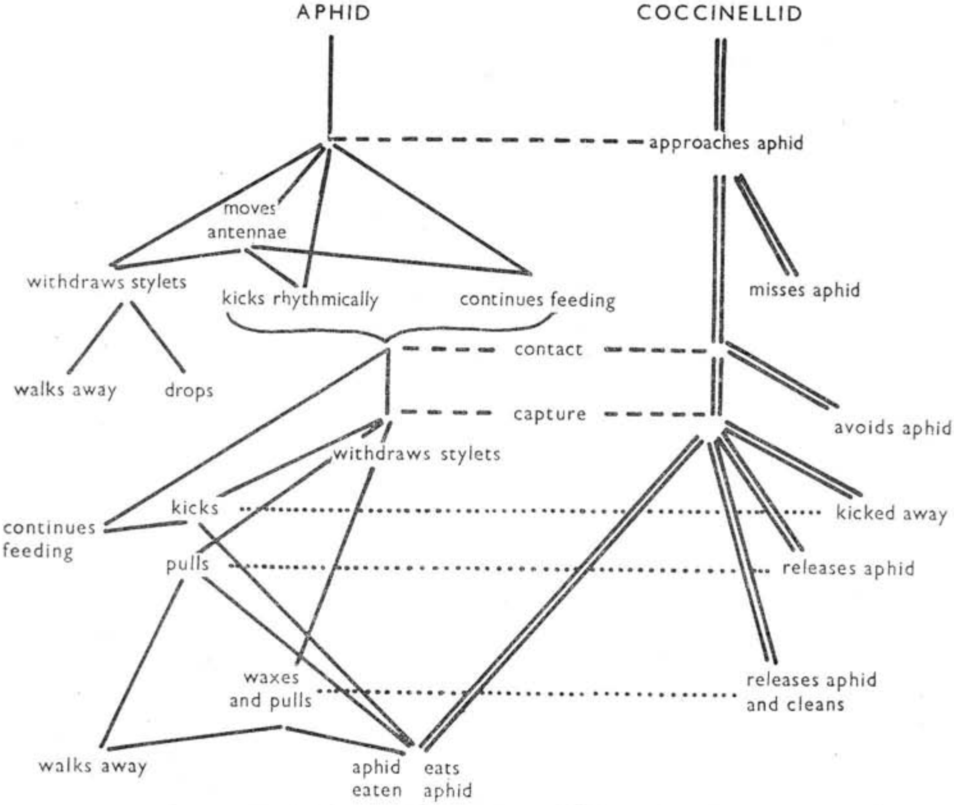
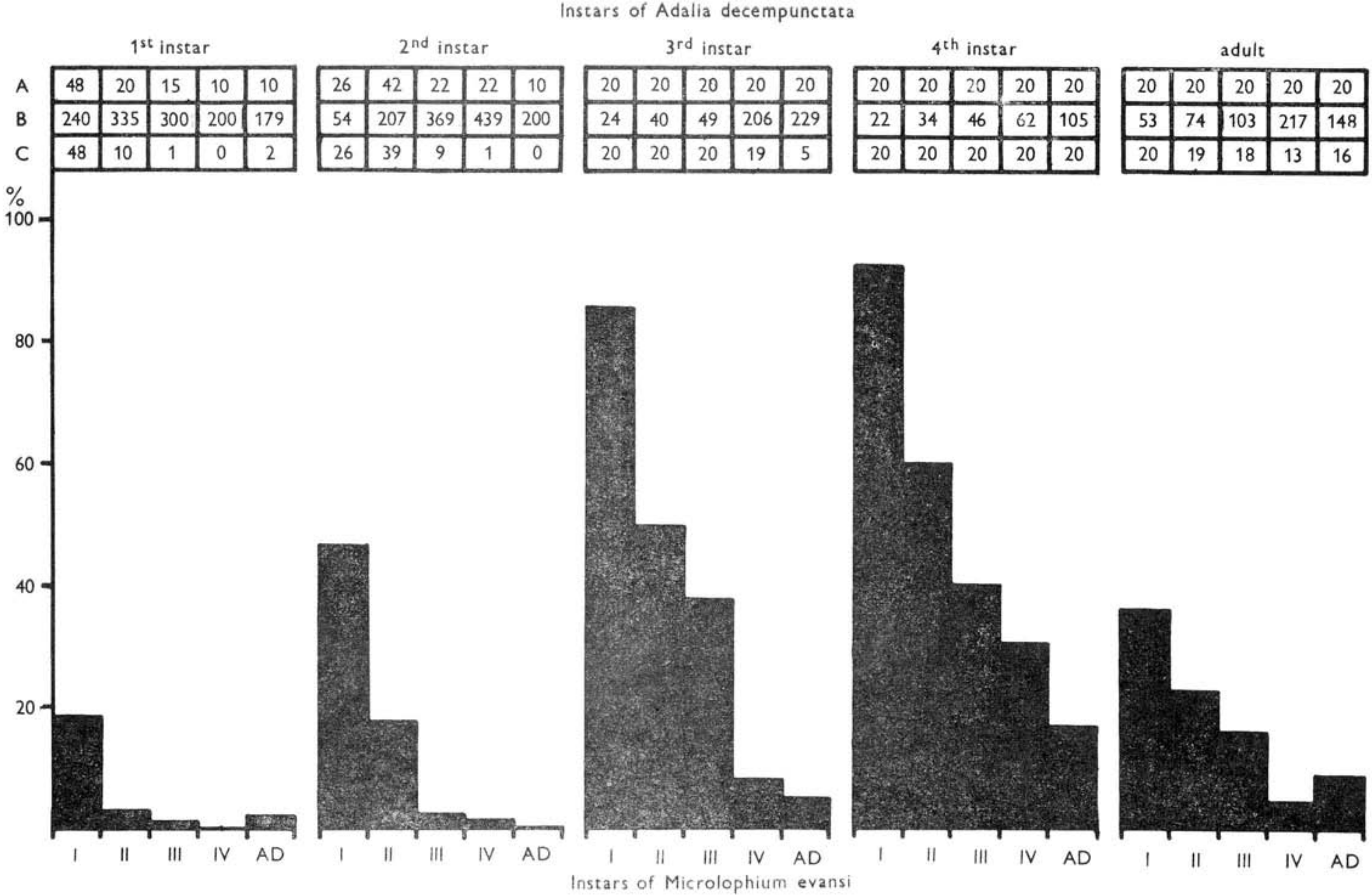


Fig. 6.11 Diagrammatic representation of the possible interactions between the behaviour patterns of *Microlophium evansi* and *Adalia decempunctata* during an encounter (Dixon 1958).



	1st instar					2nd instar					3rd instar					4th instar					adult				
	I	II	III	IV	AD	I	II	III	IV	AD	I	II	III	IV	AD	I	II	III	IV	AD	I	II	III	IV	AD
A	48	20	15	10	10	26	42	22	22	10	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
B	240	335	300	200	179	54	207	369	439	200	24	40	49	206	229	22	34	46	62	105	53	74	103	217	148
C	48	10	1	0	2	26	39	9	1	0	20	20	20	19	5	20	20	20	20	20	20	19	18	13	16

Fig. 6.12 The efficiency (% of encounters resulting in capture) of *Adalia decempunctata* in capturing *Microlophium evansi* (Dixon 1959). A, number of coccinellids tested; B, encounters observed; C, aphids captured.

with short appendages (Kaddou 1960). The aphids may apparently succeed in escape because they perceive the predator at a distance of several millimetres (*Acyrthosiphon pisum* at 4 mm, sometimes even at 10 mm — Klingauf 1967), while the predators perceive the prey only by contact. Thus the aphid attains a time advantage and may use this for escape. The aphid may also gain time when it is encountered by a small coccinellid larva which at first shows a fright response and only attacks the prey after a delay (Bänsch 1964). The intensity of the fright response depends on the size of the prey and is gradually suppressed once the predator has captured several prey (Bänsch 1964, Klingauf 1967).

Some aphids are protected against their predators by attendant ants (see 8.1). Some adult coccids are protected by their hard scale coverings to such an extent that only their larvae are preyed upon by coccinellids.

6.33 Food intake

The food of the *Epilachninae* consists of plant juices. The **phyllophagous** coccinellids scrape the parenchyma off the leaves and suck it, taking only fluid. The sucked parenchyma remains on the leaf leaving a characteristic feeding symptom (Butt 1951, Klausnitzer 1965).

The food of **aphidophagous** coccinellids consists not only of the sucked body fluid of aphids, but also of solid parts of the aphid body, e. g. legs, antennae, etc. (Butt 1951). The type of feeding evidently depends on the comparative size of prey and predator. When the prey is too large, it is merely sucked out and the skin with appendages is rejected (Butt 1951, Harpaz 1958, Hagen 1962¹), Kesten 1969). This type of feeding behaviour is normal in younger larvae (1st and 2nd instar). Older larvae and adults may consume smaller prey completely (Butt 1951, Hagen 1962¹), Kesten 1969).

Most coccinellids, particularly their larvae, show extra-intestinal digestion; they periodically regurgitate fluid from the gut into the chewed prey and suck back the pre-digested food. Some coccinellid larvae even perform extra-intestinal digestion through their perforated, sucking mandibles, like the larvae of *Dytiscus*, *Chrysopa*, etc. (Wigglesworth, 5th ed., 1953). This type of pre-digestion has been observed in larvae of *Stethorus spp.* (Blattný and Osvald 1949, Fleschner 1950, Putman 1955, Hagen 1962¹) and in the unusually shaped larvae (Plate XXXIV) of *Platynaspis luteorubra*. These larvae were repeatedly observed sucking aphids hollow merely via one of the aphid's appendages; during the process the body of the aphid was alternately deflated and inflated (Hodek unpubl.).

---

¹) A series of references, quoted by Hagen (1962) in his discussion of feeding behaviour, are not repeated here.