3 VARIABILITY AND GENETIC STUDIES

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3.1 Cytogenetic studies

The science of cytogenetics is concerned with the mechanisms of heredity and variability at the cellular level. Because of the crucial importance of chromosomal pattern, this pattern and its changes are of paramount interest.

3.11 Chromosomal complements and their variability

The chromosomal complements of many coccinellid species have been catalogued by Smith (1960). The number of $2n = 18$ autosomes and the XX (♀) : XY (♂) sex determining mechanism, which are both typical in beetles are also retained in many coccinellids, though some changes (reduction or multiplication of autosomes, disappearance of the Y chromosome) in both these features have been found in several species.

Variability in chromosomal complements has been investigated by Smith (1956, 1959) in North American *Chilocorus* species. In this genus and some related coccinellids, all the standard chromosomes are metacentric; one arm is entirely euchromatic and the other entirely heterochromatic. This condition permits a reduction of chromosome numbers by "centric fusion" i. e. translocation of euchromatic arms between non-homologous chromosomes. In this way chromosomes arise, in which both arms are euchromatic, while the two heterochromatic arms are lost from the chromosomal complement. Thus the total number of chromosomes decreases by one, each time one centric fusion occurs (Smith 1965). *Chilocorus stigma* which inhabits the eastern part of North America, exhibits chromosomal polymorphism (Fig. 3.01). A population with $2n = 26$ chromosomes inhabits Florida. As one moves northwest from Florida, three centric fusions appear to have been sequentially incorporated in the population; the first appears in Maine, the second in Ontario, the third in Manitoba. Thus within the Manitoba population, individuals are found with a chromosome number reduced to $2n = 20$ as the result of all three fusions being homozygous. A complex of *Chilocorus* species is found in the western part of North America. *C. fraternus* and *C. orbus* (both in California) have $2n = 22$, *C. tricyclus* (British Columbia and Washington) has $2n = 20$ and *C. hexacyclus* (Alberta, Saskatchewan) has $2n = 14$. All these species have a stable number of chromosomes. Crossing experiments have shown that they share a monophyletic origin. Each species underwent a characteristic number of centric fusions during its evolution. Smith (1959) suspects that the progressive increase in number of centric fusions which occurred both in *C. stigma* and the western *Chilocorus* complex confers some adaptive advantage during the recolonisation by these species of the northern regions after the glacial period.

Fig. 3.01 Proportion of centric fusions (dark) (maximum number per individual is six) in *Chilocorus stigma* populations (Smith 1956).

3.12 Interspecific crossing and sterility

Komai (1956) has sumarized the older data. Two field observations throw further light on this subject. In central Asia, near Tashkent, natural changes established contact between the distribution areas of *Chilocorus bipustulatus* and *C. geminus* (Zaslavskiï 1967). In the contact area (only 20—30 km wide) the F_1 hybrids are completely sterile. In both directions from this zone, only pure populations of one of the species occur. This sterility is the only isolating factor that isolates the populations, for the ecological conditions are similar on both sides of the contact zone and there is no geographical barrier. By contrast *Chilocorus tricyclus* has invaded the range of *C. hexacyclus* in Canada and succeeded in cross-breeding with the resident population (Smith 1966). The former species has the chromosome number $2n = 20$, and the latter one has $2n = 14$. Any hybrids therefore show chromosomal polymorphism and one part of population of hybrids is sterile for cytological reasons. Laboratory crossing is possible between all the North American species of *Chilocorus* but the percentage of viable eggs obtained is variable (Smith 1959).

3.2 Genetic studies

The only review is that of Komai (1956). It mainly stresses work with *Harmonia axyridis* from a number of Chinese and Japanese papers. The papers quoted by Komai are mostly omitted from our list of references.

3.21 Variability of colour patterns

The surface of most of coccinellids (particularly the elytra) has characteristic colour patterns, which show great variability within many species and have therefore been intensively studied.

Colour patterns are composed of a dark design on a light (brownish, yellowish, reddish or whitish) background. The dark pigment is melanin; the light pigments have been found to contain derivates of carotenoids (α—, and β— carotene and lycopene).

The basic unit of pattern is a 'spot'; the spots occur on exactly prescribed places on the elytra. The various aberrations are each characterized by the number of spots, by their position and by the number of their fusions. In this way, the variability of pattern is strongly discontinuous.

Variability can be classified in several alternative ways¹):

1) According to the degree of elytral pigmentation, i. e. how much of the surface is covered by the dark design.

2) Forms may be placed into 'eunomic series' which are each defined by the particular sequential development of one character (e. g. increase of number of spots or number of fusions). Each series is distinct and forms a separate progression. Two individuals which differ from one another by one unit of a character change (e. g. by one spot or by one fusion) are placed next to each other in the 'eunomic series' (Zarapkin 1930).

3) The "Variationsbild" of Schilder combines the advantages of both methods 1) and 2) (Fig. 3.02). The beetles are classified according to the number of spots or number of fusions (degree of melanisation), into horizontal series (analogous to method 1). The way in which one form is thought to be derived from another is indicated by vertical lines (eunomic series as in 2). Schilder's technique thus arranges the variability in two dimensions (Schilder and Schilder 1951—2, Schilder 1952—3).

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¹) Both sexes ought to be treated separately, as sexual dimorphism is often expressed. Statistical differences in proportion of various aberrations between both sexes have been found. In *Aphidecta obliterata* variability is limited mostly to female sex, while males are almost uniform (Eichhorn and Graf 1971).

4) This approach bears an illusory resemblance to classical taxonomy. From the most 'primitive' (basic) pattern for a species other patterns may be derived by fusing or by eliminating spots (Fig. 3.03). Similarly basic patterns for a genus can be derived by comparing the basic patterns of the species within this genus (Johnson 1910).

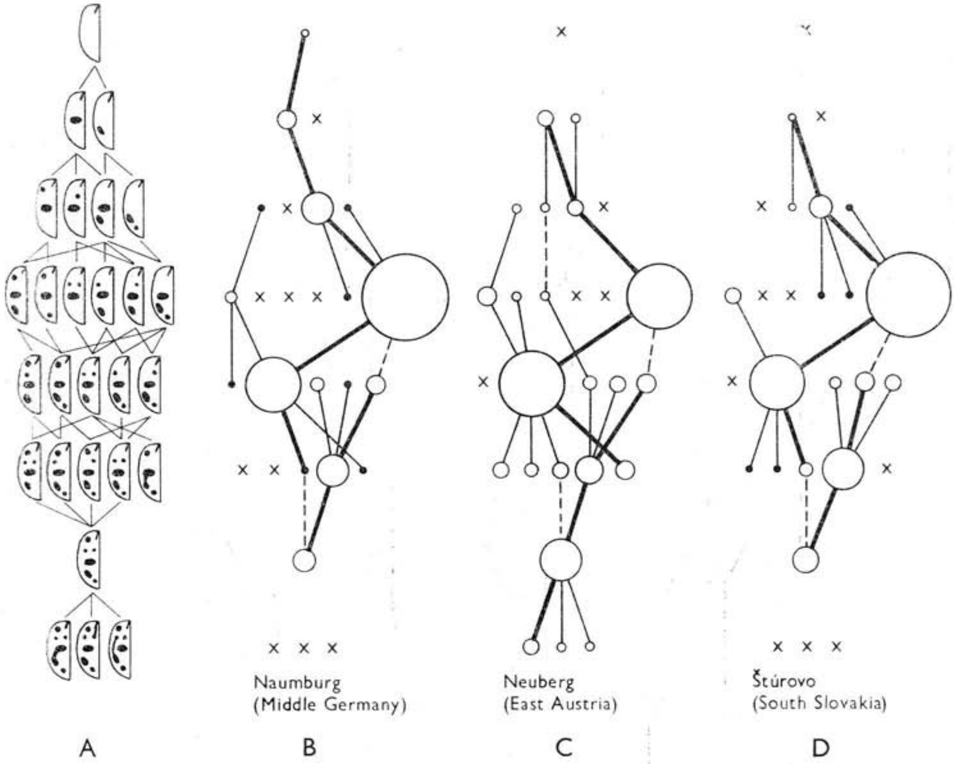

Fig. 3.02 Classification of variability in *Adonia variegata*. A — Schilder's „Variationsbild". B—D — Frequency of aberrations (indicated by diameters of circles) in three localities (Schilder 1951—2).

3.22 Ontogenetic manifestation of the genetic background

The genetic background of an organism is a kind of "blue-print" which materializes in the course of the ontogenesis of the animal, presumably by affecting the metabolism of the body structures. The end-point of the pathway of gene manifestation is a distinct morphological character. No more than a beginning has been made in elucidating the origin in colour patterns in coccinellids from this particular point of view.

Zarapkin (1938b) used statistics to study the colour patterns of coccinellid elytra. He found that the existing combinations of spot arrangement by no means exhausted the statistical possibilities. This indicates some biological restraint on randomness, a restraint which is probably genetical and physiological in origin. The action of the restraint can be well demonstrated in the ontogeny of colour pattern.

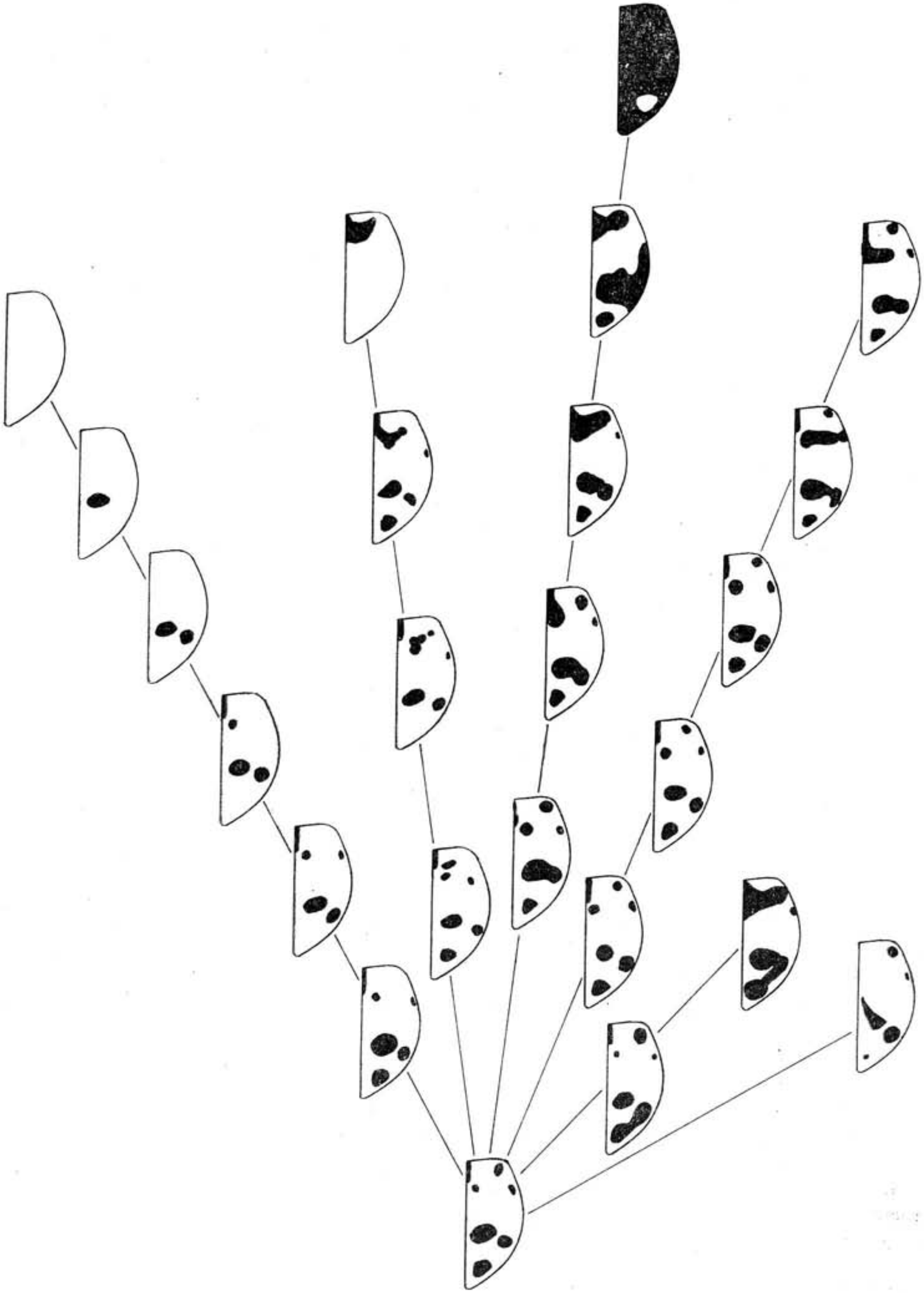

Fig. 3.03 Classification of variability (mode 4) in *Hippodamia convergens* (Johnson 1910).

It is well known that spots appear in a characteristic sequence in the course of several hours following the adult ecdysis. Zarapkin (1938a) described 7 different sequences in descendants of one pair of *Adalia decempunctata* (Fig. 3.04). In the population of descendants of the original pair, the various sequences were not equally represented

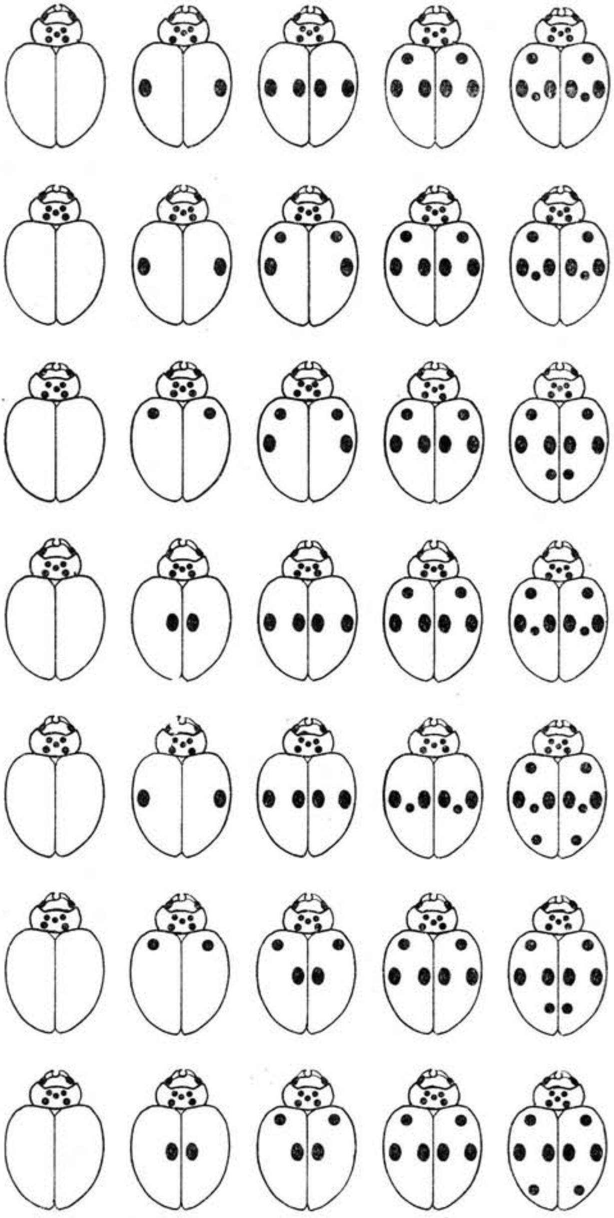

Fig. 3.04 Modes of ontogenetic development of colour patterns in *Adalia decempunctata* (Zarapkin 1938a).

in terms of numbers. Spots which formed earlier were larger than the later ones. The ontogenetic sequences of pigmentation development which Zarapkin established as most abundant in this laboratory-bred population were also the abundant eunomic sequences which can be found in the field.

3.23 Heredity of colour patterns

The heredity of colour patterns has been studied by the classical genetic methods, i. e. recording the ratios by which characters split after the first and the second generation etc. The most recent example of this type of work is that of Lusis (1971). Three forms of genus *Calvia* had been considered to be separate species according to their colour patterns (*C. punctata*, *C. obversepunctata*, *C. duplicipunctata*). However, Lusis ascertained that they were only forms of one polymorphic species, *C. punctata*. In the F_1 generation he obtained a typical Mendelian ratio, on the assumption that forms are genetically based on a series of three multiple alleles with the following sequence of dominancy:

$$c^d \text{ (punctata)} > c^o \text{ (obversepunctata)} > c^p \text{ (duplicipunctata)}$$

Individuals with all possible homo- and heterozygote combinations of alleles occure in the nature.

Similar polymorphism based on a series of multiple alleles has been found in *Adalia decempunctata*, *Coelophora inaequalis*, *Propylaea japonica*, *Harmonia axyridis* and *Hippodamia quinquesignata* (reviewed by Komai 1956).

Komai concludes that such series of multiple alleles determine the main colour types of elytra and ensure that the stable and distinct polymorphism within each species is maintained. The minor peculiarities of pattern, which undergo continual change are controlled by polygenes (modifiers). Ford (1964) considers it more likely that such a multiple allele effect as has been demonstrated in coccinellids is most likely caused by a sufficiently close juxtaposition of the loci of the genes so that crossing-over is most unlikely to separate them. Ford designates such a complex of loci as a 'supergene'.

Manifestation of genes may also be influenced by temperature, i. e. some characters may be produced either by hereditary or by somatic factors. In *Epilachna chrysomelina* the total area of spots decreases by 30—55 % (according to geographical origin of investigated population) when temperature increases from 20 to 35 °C. This variation in various geographic populations is due to differences in the rate of diminution of single spots; the shape of spots, however, remains constant (Timofeeff-Ressovsky 1941). The same increase in temperature also suppresses the melanisation of the ventral surface of the body (Zimmermann 1931). The critical stage for induction of colour changes by temperature is at the prepupa and early pupa. Other environmental agents (light, humidity) were without effect (Timofeeff - Ressovsky 1941). A similar temperature effect on gene manifestation has been found in *Harmonia axyridis*.

3.24 Geographic variability

The proportions of individuals with more or less pronounced pigmentation varies according to geographical position in a manner which is consistent among many coccinellid species (Dobzhansky 1933, Dobzhansky and Sivertzev-Dobzhansky 1927). The consistent variability of *Coccinella septempunctata*, *C. quinquepunctata*, *Adonia variegata*, *Synharmonia conglobata* is shown in figs. 3.05—3.08.

Another similar consistent trend in geographical variability occurs in the species *Anatis ocellata*, *Coccinella transversoguttata*, *Coccinula quatuordecimpustulata*, *Coccinella divaricata*, *Anisosticta novemdecimpunctata*, *Adalia bipunctata*.

Fig. 3.05 Geographical variability of the diameter of the macula discoldalis in *Coccinella septempunctata* (Dobzhansky and Sivertzev-Dobzhansky 1927).

For all the members of both 'groups' of species referred to, there exist centres with less pigmented populations and centres with more pigmented ones. Moreover, such centres for the different species roughly co-incide in geographical location.

The centre of light forms lies in Central Asia for the eastern hemisphere, and in California for the western hemisphere. A significant centre of dark forms is situated in the Old World in the Far East. However, the proportion of pigmented forms increases radially in all directions from each light centre, i. e. not only from Central Asia northeastwards to the dark centre in the Far East but also northwestwards to Europe and southwards to Africa as far as Assam in case of *C. septempunctata;* similarly in North America dark forms increase eastwards and northwards from California. Thus, in *Adonia variegata*, the most pigmented populations live simultaneously in Ethiopia and in the Far East. *Coccinella transversoguttata*, a Palaearctic and Nearctic species has similar duplicate geographical centres of light and dark forms in both regions.

The phenomenon of geographical variability parallel in several species (apparent also in other animal groups), is usually generalised by reference to various 'rules' (Allen's rule, Gloger's rule). Many workers have suggested that the individual biotypes are selected by different climatic factors (particularly temperature and humidity).

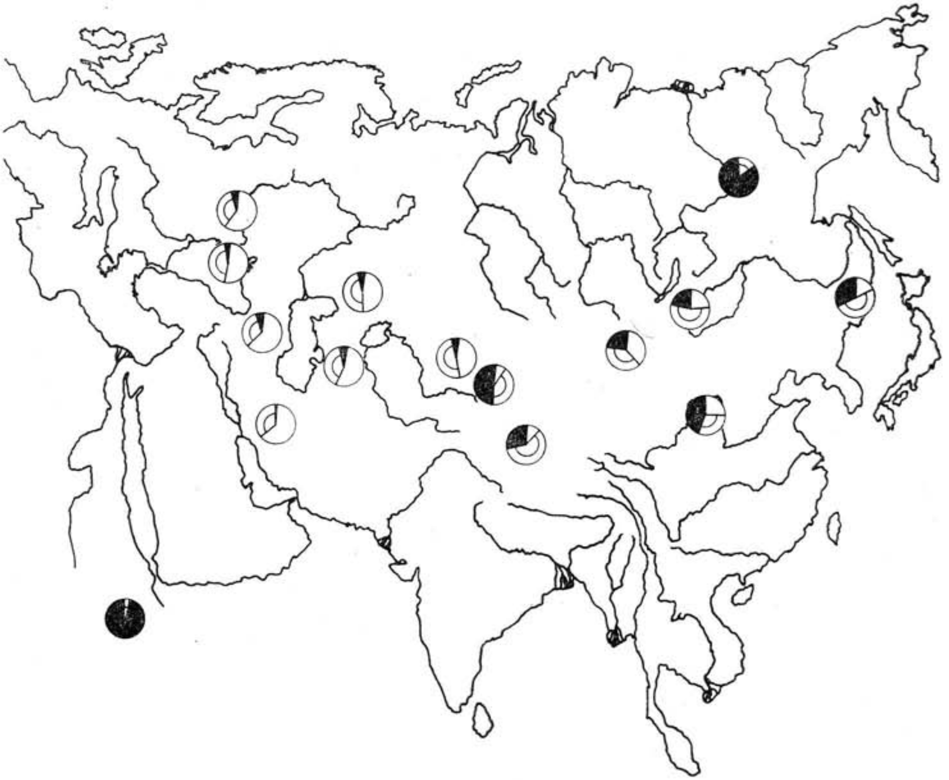

Fig. 3.06 Geographical variability by proportion of forms with 0 — 9 (white), 11 — 15 (white, with central stripe or 15 confluent (black) spots in *Adonia variegata* (Dobzhansky 1933).

The situation in coccinellids supports this suggestion only as far as humidity is concerned. The centres of light populations lie in arid areas, while pigmentation increases with the humidity of a region. The correlation between pigmentation and temperature of the respective regions is much less. For example, similar pigmentation is found in populations of *A. variegata* from Ethiopia (average temperature +30° C) and from Yakutsk (aver. temperature —10° C). Pigmentation is also similar in populations of *C. septempunctata* from Algeria or Italy (aver. temperature +15 to +20° C) and in those from the Far East (aver. temperature +5 to—5° C). Pigmentation itself need not have any selective value and may merely coincide with changes in the physiological processes of the organisms. On the other hand, it has been pointed out that the darker (i. e. more pigmented) species have an advantage in being able to make fuller use of insolation (Kryľcov 1956, see also *A. bipunctata*).

Differences in pigmentation of various forms have often been found to occur between closely adjacent local populations e. g. in *Adonia variegata* (Schilder and Schilder 1951—2) (Fig. 3.02). In principle, they can be explained by the above mentioned relationship between pigmentation and humidity. Kryľcov (1956) compared the pigmentation of coccinellids in two valleys in central Asia. These two valleys were relatively near to each other, but had a different climate, i. e. Chuiskaya valley had a dry continental climate and the Issyk-kul valley had a humid climate. Out of the 8 species studied 5 were darker in the more humid conditions (*Thea vigintiduopunctata, Bulaea lichatschovi, Propylaea quatuordecimpunctata, Adonia variegata, Hippodamia tredecimpunctata*), in 3 species (*Coccinella septempunctata, C. quatuordecimpunctata, C. sinuatomarginata*) no correlation between climate and pigmentation could be found and one (*Coccinula redimita*) showed the reverse tendency. Kryľcov claimed that the species which had a lighter background colouration were more likely to show local changes of melanisation.

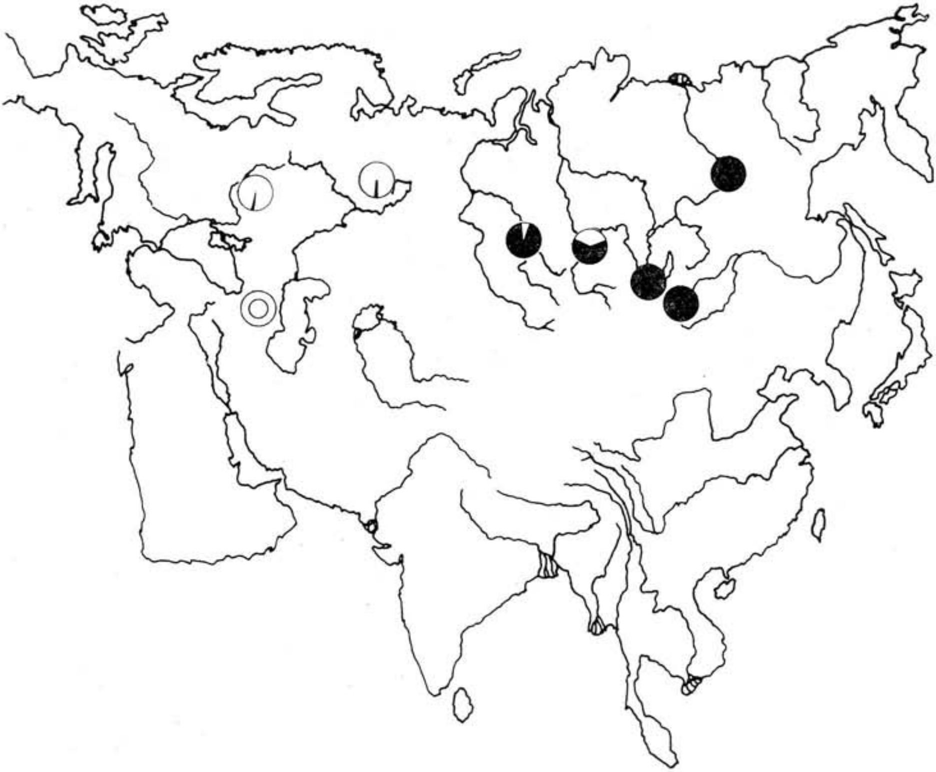

Fig. 3.07 Geographical variability by proportion of forms with 0 — 3 (white, with central stripe), 5 (white), 7 — 10 (black) spots in *Coccinella quinquepunctata* (Dobzhansky 1933).

Although the influence of humidity on pigmentation has been so often hypothetized, it has not yet been proved experimentally (see Chap. 3.23).

The species studied by Dobzhansky and mentioned earlier (see p. 62-64) provide

information on the question of the origin of geographical races (Dobzhansky 1933). They can be ranked on the basis of some contemporary theories, to illustrate the steps by which they are thought to have originated. (1) First there are the species which, over the whole distribution area, largely only differ in the proportion by which individual forms are represented (*Adonia variegata*, *Anatis ocellata*). This is sympatric

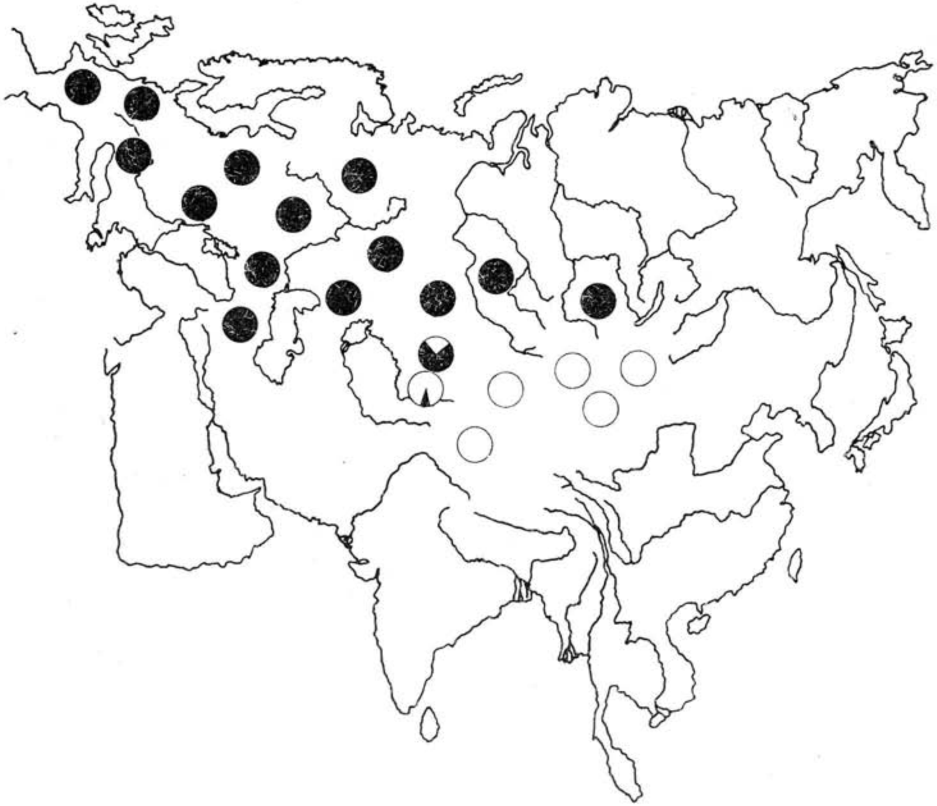

Fig. 3.08 Geographical distribution of the typical form of *Synharmonia conglobata* (black) and its v. *buphthalmus* (white) (Dobzhansky 1933).

polymorphism, and the various forms have the taxonomic status of aberrations or varieties. (2) The next rank contains species which again show sympatric polymorphism but in which there are centres with quite different populations at the extremes of the area. However, the variability shows complete overlap and transition, so it is only possible to observe proportional changes in the forms between adjacent localities. (3) The extreme rank is the formation of geographical races, i. e. biotypes with allopatric distribution; these show either minimum areas of transition (*Hippodamia tredecimpunctata*) or completely isolated populations (*Synharmonia conglobata*). *Harmonia axyridis* is the special case; in the western part of the distribution area a monomorphic race occurs (consisting alone of the form *axyridis*), while the eastern part is inhabited **by a mixture of forms (see also Komai 1956 for review of Japanese conditions).**

3.25 The case of Adalia bipunctata

Adalia bipunctata is an example where the whole complex of problems has been shown in a single species. *A. bipunctata* is a polymorphous species. In principle, part of the population has a predominantly dark design (dark forms), while the other part has a design consisting only of individual spots (light forms). It is of interest that the North America populations show a very limited variability and dark forms are rare.

The first experiments with crossing the most abundant light aberration (*f. typica*)

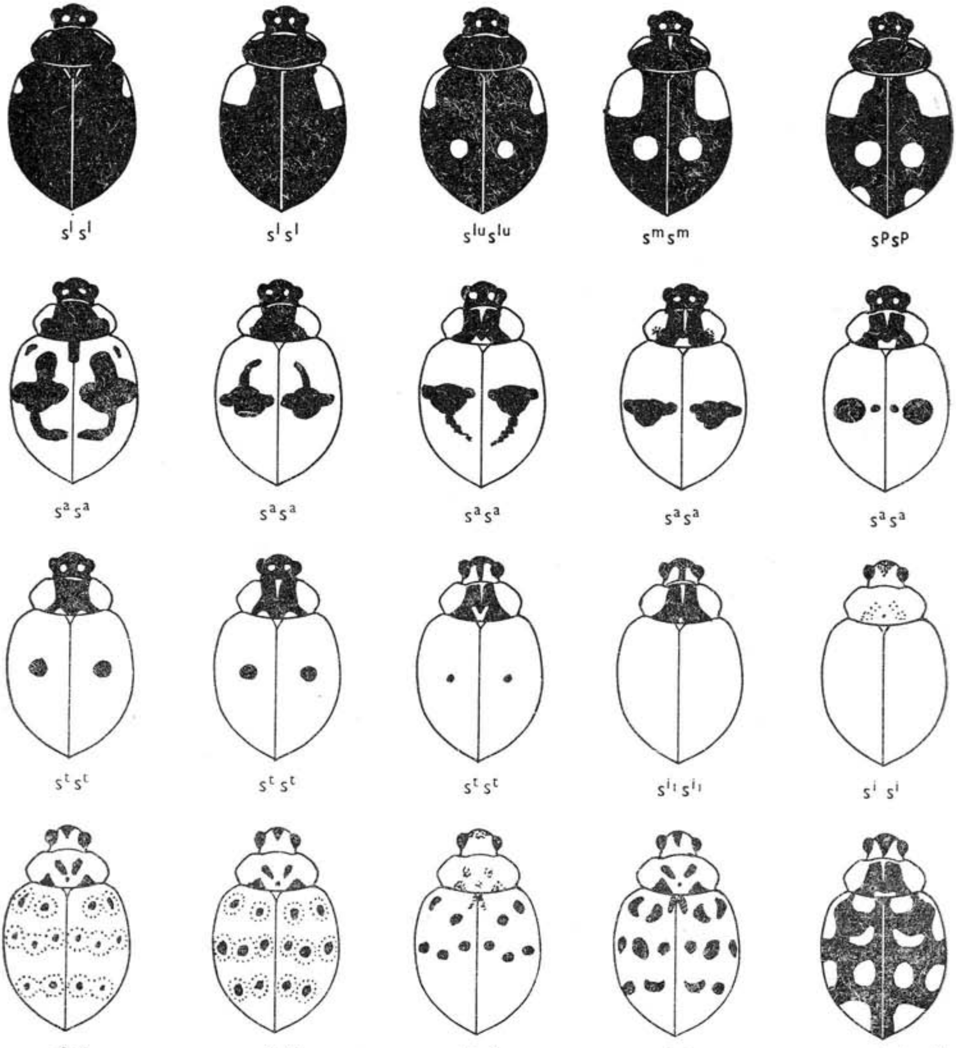

Fig. 3.09 Variability of *Adalia bipuncata*; homozygous forms (Lusis 1932)

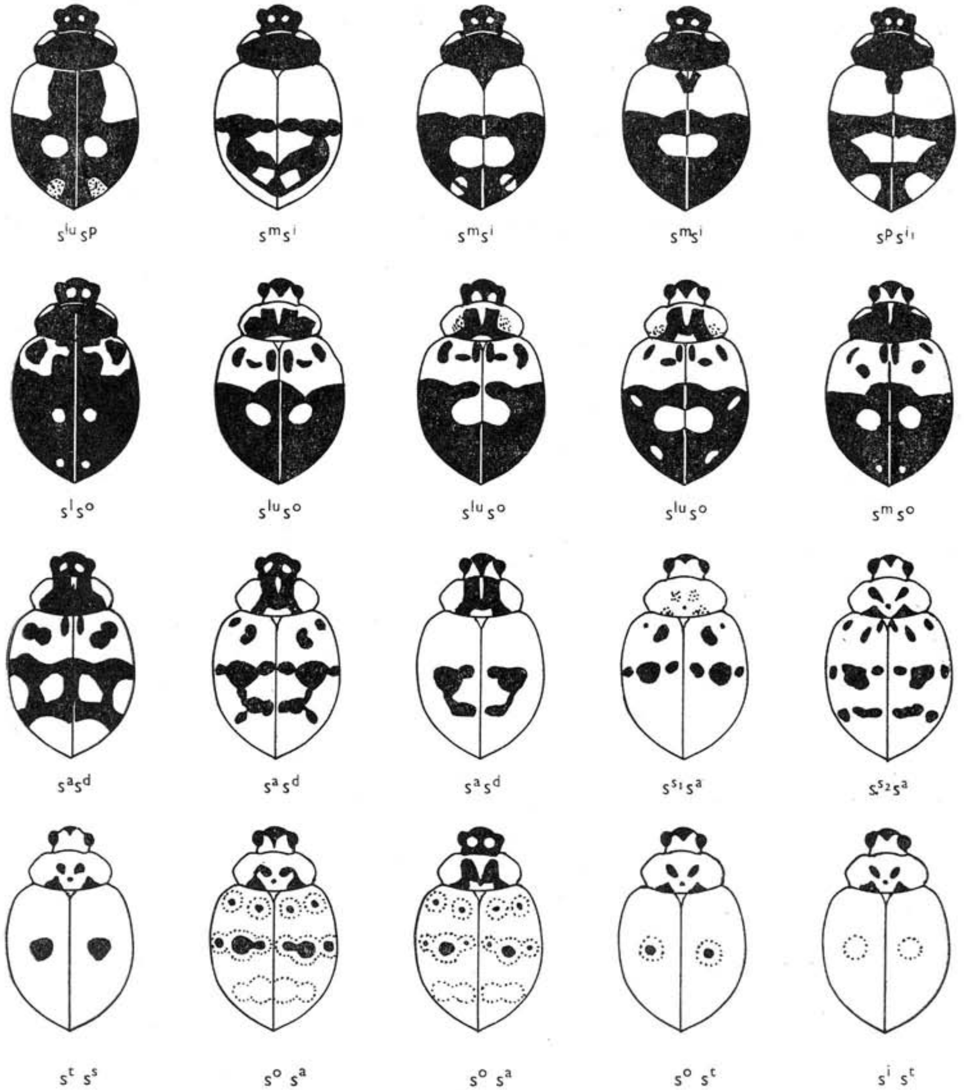

Fig. 3.09 Variability of *Adalia bipunctata;* heterozygous forms (Lusis 1932).

with two dark forms (*sexpustulata* and *quadrimaculata*) indicated that 'dark' is dominant over 'light'. This result however, cannot be generally applied to all forms. Lusis (1932) formed a series of twelve colour patterns on the basis of the homozygotous condition of twelve allelomorphic factors, (Fig. 3.09), and arranged allelomorphs according to dominancy:

s^{l} s^{lu} s^{m} s^{p} s^{i} s^{i1} s^{t} s^{o} s^{s1} s^{s2} s^{a} s^{d}

This does not correspond to the sequence by which the total amount of melanistic pigment decreases:

(dark) s^{l} s^{lu} s^{m} s^{p} s^{d} s^{a} s^{s1} s^{s2} s^{o} s^{t} s^{i1} s^{i} (light)

Because of incomplete dominance, the colour pattern of heterozygotous combinations is intermediate (Fig. 3.09).

The heterozygote having alleles s^l s^{lu} s^m s^p combined with each other, or with s^d s^{s1} s^{s2} s^a, tend to be dark. The combination of any allel with s^i and s^o considerably diminishes the quantity of deposited pigment. The homozygous combination *ocellata* (s^o s^o) is lethal.

Both geographical and temporal variability in the proportions of the various biotypes have been shown to occur in natural populations. Populations from Central Asia, for example, include 27 % of form *impunctata*, 41 % of f. *typica* and only 18 % of dark forms, in contrast, European populations (Kiev-USSR, Germany) include 0 % of f. *impunctata*, 53—69 % of f. *typica*, and 28,5—44 % of dark forms (Dobzhansky 1924). This corresponds to general rules of geographical variability in coccinellids. Moreover the percentage of dark forms is very variable in European population. Lusis (1961) suggests that a larger percentage of dark forms live in humid coastal areas and also in industrial areas. The occurence of temporal variability has been verified by several observations. Dark forms prevail in summer and autumn; in spring the number of light forms increases markedly.

Several factors, which in summer and winter select for opposite tendencies play a role in maintaining polymorphism. A possible explanation (Lusis 1961) may be presented: It has been found that, in natural populations, the sexual activity of dark forms is greater. Thus, with 2—3 generations a year and frequent copulations, the number of dark individuals considerably increases towards the autumn. On the other hand, the dark forms have a much higher mortality during hibernation and thus the relative proportions get into balance again every spring. The advantage of dark forms lies in their better utilization of insolation for the increase of body temperature. This significant advantage is particularly apparent at foggy coasts and smoky urban localities with intermittent insolation. In consequence the rise in the percentage of the dark forms is most noticeable in both such areas.

A. bipunctata also has other interesting adaptations (Lusis 1947a, b). It has been discovered that the concentration of recessive alleles, which are lethal when homozygous, is high in all populations (inbreeding causes a very rapid decline in viability); practically every individual carries 1—3, and even more such lethal alleles. Therefore high heterozygosity appears necessary if the population is to be maintained. This heterozygosity is achieved partly by the behaviour of the species (frequent copulations) and partly by the fact that there occur in natural populations females whose progeny is exclusively female (male zygotes perish). Such females must then out-cross. Not only has this the advantage of reducing breeding between related individuals, but also the large production of females enables exceptionally rapid breeding in the spring. The percentage of females with only female progeny is constant within a given population and is evidently geographically variable. These females are more abundant in northern populations, which suffer a high mortality during hibernation. The small populations which emerge from hibernation are very vulnerable to inbreeding and also need to build-up rapidly. The heredity of this feature is very complicated. It is very likely that a complex of several dominant autosomal lethal genes, whose action is limited to the male sex, exists and that the effects of these genes are modified by maternal factors.

4 LIFE HISTORY AND BIOLOGICAL PROPERTIES

4.1 Developmental stages

4.11 Characteristics of individual stages

Coccinellids are holometabolous, i. e. they have a "complete metamorphosis", and pass through the following stages: egg, 4 larval instars, prepupa, pupa, adult.

Egg. — Eggs are usually oval or spindle-shaped, vary in colour from yellowish to reddish orange and are mostly laid in clusters with each egg attached to the substrate by the narrow end. These clusters are laid on the underside of a leaf or in bark-crevices. Some species, however, lay their eggs singly; for example, females of *Chilocorus rubidus* lay one egg at a time under the scale of a coccid larva (Pantyukhov 1968b). Females of *Exochomus flavipes* have occasionally been observed laying their eggs into empty pupae of their own species from which insect parasites had emerged (Geyer 1947). A few days before hatching the eggs become greyish.

Larva. — After hatching from the eggs, the larvae stay on the egg shells for up to one day, and often eat unfertilized nonviable eggs or larvae from later hatching eggs. Then they crawl about in search of their normal food. Usually 3 larval ecdyses separate the 4 larval instars. Species with 5 larval instars are rare, but this instar number has been observed in *Callicaria superba* (= *Pseudosynonycha japonica*) (Iwata 1932, 1965), and in the laboratory, in a certain proportion of larvae of *Coleomegilla maculata* (Warren and Tadić 1967) and *Chilocorus bipustulatus* (Yinon 1969). The larva stops feeding before ecdysis, uses its "anal organ" to fix itself with its head down to a surface and sheds its skin. Larvae of the genus *Chilocorus* aggregate for ecdysis (Fomenko 1970, Fomenko and Zaslavskiĭ 1970). Larvae of the Japanese species *Pseudoscymnus sylvaticus* live confined inside a closed aphid-gall. The gall only opens again when the newly emerging adults are ready to escape (Sasaji, in press). For several days before ecdysis to pupa, the 4th instar larva remains immobile and does not feed. Some authors separate this stage ("prepupa") from the other larval instars.

Pupa. — Different groups in the family *Coccinellidae* have different types of pupa. Coccinellids in the subfamilies *Coccinellinae* and *Sticholotinae* have an uncovered pupa— at the ecdysis to pupa the larval skin is sloughed from the pupa right up to the point where the cauda is attached to the substrate. The pupae in the tribes *Chilocorini* and *Noviini* are partly covered; they remain within the larval skin which splits lengthwise dorsally but is not shed. *Hyperaspini* and *Scymnini* have pupae completely covered by the larval skin. The pupa is not entirely immobile; if irritated, the head region is raised several times by upward jerks of the body. The colouration of pupae is much influenced by the environmental conditions. For example, *Coccinella septempunctata* may have light orange pupae under conditions of high temperature and low humidity (35 °C, 55%), whereas under the reverse conditions (15 °C, 95%) dark brown pupae are produced (Hodek 1958).

Adult. — The elytra of the emerged adult are at first soft, matt, light in colour and without pattern; the hind wings protrude from under them (Photo 5—7). The elytra acquire their normal appearance only gradually; most changes occur in a matter of hours, but the red colour remains a lighter shade for weeks or even months. It is thus easy to distinguish overwintered adults from the new generation for a long time.

4.12 Effect of temperature on the developmental rate

In common with all other insects the speed of development of coccinellids is dependent on the ambient temperature. Within the favourable range the developmental rate of all stages increases with temperature. As the upper threshold of thermal tolerance is approached, further temperature increases produce only a slight increase and above a certain thermal limit there is even a decrease in developmental rate.

Empirical values for the length of individual stages in coccinellids at different temperatures have mostly been presented only in the form of tables, and only values for embryonic development have been plotted as graphs.

A detailed survey of the efforts at a mathematical formulation of the dependence on temperature of developmental rate in poikilotherms can be found in an early review by Uvarov (1931) and in a series of physiological and ecological compendia, e. g. Wigglesworth (5th edition 1953), Allee et al. (1949), Andrewartha and Birch (1954), Schwerdtfeger (1963).

The simple classic formula suggested by Sanderson and Peairs (1913), Blunck (1914) and Peairs (1914) has been widely used by many workers, including Bodenheimer (1943) and Bodenheimer and Neumark (1955) for several coccinellids. The formula is based on the classic theory, originally produced by botanists, that the completion of any given stage in development requires the accumulation of a definite amount of heat energy. Because it is difficult to measure energy, the effective temperature (i. e. the temperature above the development threshold) is accumulated as day-degrees. The theoretical assumption, that the product of the effective temperature and time is always a constant, may be written as a formula: $D\,(T - a) = C$
where D is the duration of the developmental stage at temperature T, a is the development threshold, and C is the thermal constant. This is the equation of an equilateral hyperbola, which — if calculated from two experimental results — is in agreement with the empirical data.

The reciprocal of development time, the speed of development, is expressed by the reciprocal of the hyperbola, i. e. by a straight line. This line crosses the temperature axis at the point "a" which is the theoretical lower development threshold.

The values of the development threshold and the thermal constant (for the periods of pre-imaginal development plus pre-oviposition period) for *Coccinella septempunctata* are 12.8 °C and 297 day-degrees (Bodenheimer 1943), for *Synharmonia conglobata* 12.4 °C and 323 day-degrees, for *Adalia decempunctata* 9.1 °C and 390 day-degrees and for *Chilocorus bipustulatus* 10.6°C and 697 day-degrees (Bodenheimer and Neumark 1955).

The linear relationship between temperature and the speed of development only holds for the middle range of temperatures; at either end of the favourable range the relationship is far from linear. The line expressing speed of development is in fact not straight but sigmoid. To get a close fit between the lines derived from the equations and empirical data over a greater proportion of the temperature range, other equations have been proposed (see the literature quoted above). Davidson (1942, 1944) found out

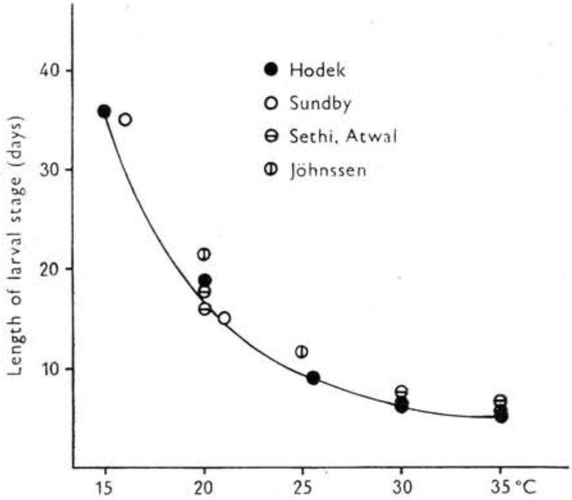

Fig. 4.01 Influence of temperature on the duration of larval development in *Coccinella septempunctata* (see also Tab. 4.01) (Hodek 1958).

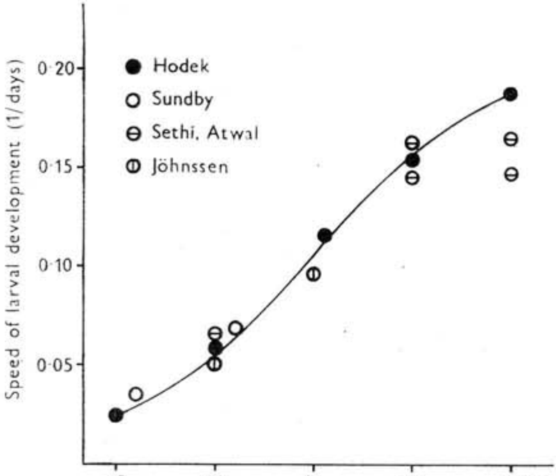

Fig. 4.02 Influence of temperature on the rate of larval development in *Coccinella septempunctata* (Hodek 1958).

that Verhulst's logistic curve si the most adequate description of the observed speed of development of insects, and the curve can be calculated directly from the empirical data.

The logistic equation may be written:

$$\frac{1}{y} = \frac{K}{1+e^{\,a-bx}}$$

where y represents the duration of development at temperature x (in °C), and a, b and K are constants. "K defines the upper asymptote toward which the curve is trending; b defines the slope of the curve and a relative to b fixes its position along the x axis. This may be more easily comprehended by considering that the logistic curve is a bi-symmetrical sigmoid curve having a point of inflection whose coordinates are $1/y = K/2$ and $x = a/b$" (Andrewartha and Birch 1954).

Hodek (1958) found the logistic curve consistent with the empirical data for the preimaginal development of *Coccinella septempunctata* in the temperature range of 15—35 °C (Fig. 4.01 — 4.04).

One might expect that the relation to temperature varies, within one species, between populations separated very widely geographically. However, at least as far as the effect of the ambient temperature on the rate of development is concerned, this is not so even in the ecologically extremely plastic species *C. septempunctata*. The data for areas as far apart as Norway, central Europe and Punjab (India) are almost constant (Tab. 4.01).

This is even more striking when we take notice of the considerably different numbers found for central Europe at, for example, 25 °C by Jöhnssen (1930) and Hodek (1958). By contrast, only small differences between central Europe and Punjab have been reported by Hodek (1958) and Sethi and Atwal (1964).

Thus in central Europe (Hodek 1958) the rate of development was 1.8 days higher at 35 °C than at 30 °C (although the increase per degree was reduced in comparison with the central temperature range), whereas in the Punjab (Sethi and Atwal 1964) the total duration of pre-imaginal development was practically the same at both temperatures. As the upper limit of temperature tolerance is close to 35 °C, it is not surprising that some variability is evidenced.

The data of Ogloblin (1913) from Russia and Bodenheimer (1943) from Israel cannot be included in the comparison or the table, as the authors did not rear the coccinellids at constant temperatures.

Any differences between distant populations might be more likely to show themselves in survival near the upper temperature limit than in developmental rate. However, no data are available for such an interesting comparison.

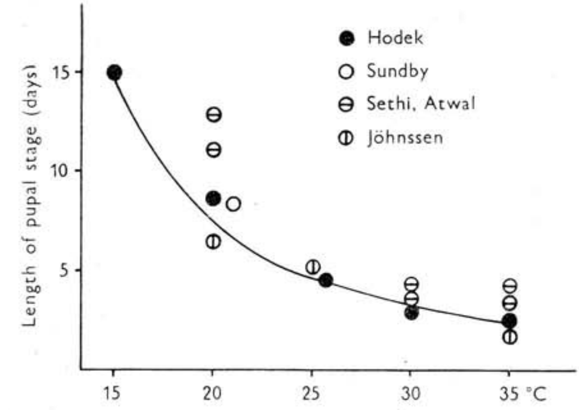

Fig. 4.03 Influence of temperature on the duration of pupal development in *Coccinella septempunctata* (see also Tab. 4.01) (Hodek 1958).

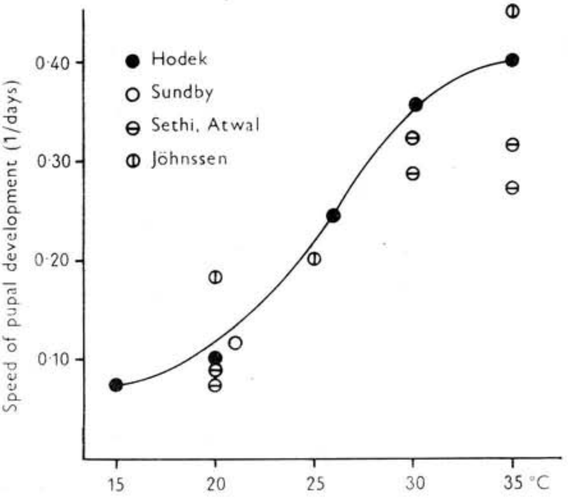

Fig. 4.04 Influence of temperature on the rate of pupal development of *Coccinella septempunctata* (Hodek 1958).

The east Asian race of *Coccinella septempunctata*, *C. septempunctata bruckii*, however, seems to be strikingly different from the nominate race in the dependence of developmental rate on temperature (Koide 1962). The curve for the dependence of the duration of larval plus pupal development on temperature is much more "recurved" than that of the nominate race (Fig. 4.05). The curves for the two races approach each other in the medium temperature range between 20 ° and 25 °C (and would identify between about 22 ° and 23 °C), but they separate from each other at both temperature extremes. The whole post-embryonal pre-imaginal development of *C. s. bruckii* is significantly slowed by 39 days when temperature decreases from 20 °C by 5° . At the other temperature extreme, development already slows from 30 °C so that at 33 ° it is 3 days longer than at 20 °. If the data can be repeated, this race would be strikingly more stenothermic than the nominate race.

The contrast between the ecophysiological constancy of the nominate race over such a large area of the world and the striking difference of the east Asian form has an analogy in the variability of colour patterns. Indian specimens from the Himalayas and Punjab

Tab. 4.01 Speed of pre-imaginal development of *Coccinella septempunctata* in relation to ambient temperature (Jöhnssen 1930, Hodek 1958—central Europe. Sethi and Atwal 1964 — northern India, Sundby 1966 — northern Europe)

Author	Relative humidity [%]	Constant temperature [°C]	Duration of pre-imaginal stages (days)					N
			egg	larva	pupa	larva+pupa	all	
Hodek	(90)	15 (14.5—16.3)[1]	10.3	35.5	15.0	50.5	60.8	5[2]
Sundby		16		35.0			60.4	30
Jöhnssen		20	5.0	19—22	6		30—33	
Hodek	80	20 (± 1.3)	5.0	18.6	8.4	27.0	32.0	19[2]
Sethi, Atwal	40	20	5.0	17.5	13.3	30.8	35.8	20
	70	20	4.8	17.2	12.9	30.1	34.9	20
	90	20	4.0	15.8	11.1	26.9	30.9	20
Sundby		21 (± 1)	5.0	15.0	8.5	23.5	28.5	67
Jöhnssen		22—23	3.5—4	16—20	4—6		25—29	
Jöhnssen		25	3—3.5	10—11	4—5		20—21	
Hodek	60 70	25.6 (±0.4)	(2.6)	8.7	4.0	12.7	15.3	12[2]
Hodek	60—90	30 (±2)	1.9	6.7	2.9	9.6	11.5	18[2]
Sethi, Atwal	40	30	2.0	6.5	3.0	9.5	11.5	20
	70	30	2.0	6.6	3.4	10.0	12.0	20
	90	30	1.7	7.3	3.7	11.0	12.7	20
Jöhnssen		32—33	2	7—9	2.5—3		12—14	
Hodek	60—90	35 (± 1.8)	1.8	5.4	2.5	7.9	9.7	14[2]
Sethi, Atwal	40	35	1.7	6.0	3.7	9.7	11.4	20
	70	35	2.0	7.1	3.1	10.2	12.2	20
	90	35	2.0	6.2	3.9	10.1	12.1	20

[1] The temperature gradually increased during the two months of the experiment.

[2] Number of adults hatched.

cannot be distinguished from the European specimens by the conspicuous enlargement of spots which is typical for the east Asian race (*C. s. bruckii*) from Japan and Korea (Günther 1958).

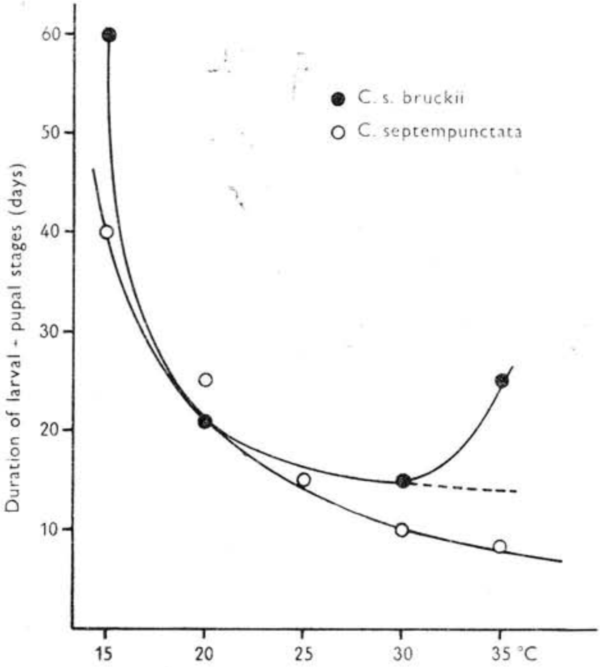

Fig. 4.05 Comparison of the effect of temperature on the postembryonal development of *Coccinella septempunctata* (Hodek 1958) and *C. s. bruckii* (Koide 1962).

4.2 Biological activities and properties of adults

Copulation. — Coccinellids copulate in the manner which is normal in beetles, i. e., the male uses its legs to hold itself onto the elytra of the female and is carried by her. Lim Sook Ming (1971) observed that newly emerged females (less than 1.5 — 2 days old) rejected the attempts of males to copulate: they moved rapidly away from the male, kicked the extended aedeagus with their legs and curved the last abdominal segments. The copulation posture may last as long as several days, as described by Iwata (1932) for *Aiolocaria mirabilis.*

The first copulation takes place a few days after emergence and is usually repeated several times during adult life, even though for most species (except for *Stethorus punctillum* which lacks a spermatheca (Moter 1959, Putman 1955), one copulation is generally reported as sufficient for permanent fertility of the female. Ellingsen (1969a) questions this assumption because a dying out of males was correlated with a decrease in the viability of eggs in *Adalia bipunctata.* In *A. bipunctata*, Sem'yanov (1970) proved that copulation had a stimulatory effect on the number of eggs laid. The maximum number of eggs was laid after the first copulation, oviposition then decreased but increased again following each copulation.

Diapausing coccinellids mate partly prior to diapause (when, apparently, some of the males die), but mainly at the end of hibernation before the aggregations disperse. The bringing together of the two sexes from different sites for hibernation probably has the adaptive advantages of preventing inbreeding in relatively common species and raising the probability that the sexes of rare species meet.

Oviposition. — Eggs are laid in the vicinity of prey, apparently because coccinellids oviposit where they have been feeding on essential prey. Other stimuli appear to be of minor value (Iperti 1965, Iperti in Hodek 1966, p. 121, Putman 1955). The close vicinity of the prey is not essential in the same way as it is for the oviposition of most syrphids. This feature causes a fairly high mortality of the first instar coccinellid larvae (see 6.31). Females bred on artificial diets do not lay eggs in Petri dishes, but only in cages containing parts of plants (Smirnoff 1958). There is considerable variability in the fecundity and size of egg batches of individual females.

Longevity. — The life span of coccinellids is also quite variable; in species with a long period of inactive life, longevity is about one year. There are, however, records of a second hibernation in *Calvia quinquedecimguttata* (Kanervo 1946), in *Propylaea quatuordecimpunctata* (El-Hariri 1966b), in *Stethorus punctillum* (Putman 1955) and in *Aiolocaria mirabilis* (Iwata 1932, Savoïskaya 1970b, d). Savoïskaya (1970b, d) ascertained that in *Harmonia axyridis* the longevity may reach three years in about 15—20 % of population. Females even oviposited in the third year, after the species was imported to the foot hills of Zailiïskiï Alatau from the Far East.

5 DISTRIBUTION IN HABITATS

5.1 Terminology

Throughout this chapter, the word habitat is used frequently. Some information should therefore be given about this term, which is so often used but so poorly defined. Such explanation is necessary to make the chapter comprehensible in the context of the various different ecological terminologies.

In the German ecological literature a strict hierarchy for different types of "living space" (Lebensraum) has been established, the basic unit being the "Biotop" (as a living-place of a "Biocenosis", or "Zootop" for "Zoocenosis"), "Monotop", or "Demotop" (as a living-place of an animal or of a population). Smaller units than "Biotop" are "Stratum", a horizontal layer of a Biotop (e. g. in a forest: strata of tree crowns, of shrubs, of herbaceous plants, of surface of soil), or "Biochore" (point of concentration of individuals of a species) or "Merotop" (place where the conditions differ only slightly from the surroundings e. g. a slightly depressed or elevated place). A broader term is "Bioregion" (a living place for a "Biom", see Schwerdtfeger 1963).

Only the last two terms are used in the English ecological literature with the same meaning as in the German, although sometimes the words "biotic zone" are used instead of "bioregion'' for the living-place of a "biome" (e. g. tundra, taiga, steppe etc.). The word "habitat" is used to include all German terms for lower categories, (i. e. all words with the ending "top") expanded by the prefixes "micro" and "macro". This seems a very useful device, as a classification precise enough to express the extremely complex structure of a "living-place" can really never be devised. The word "habitat" will be used in this book following Odum's (1953) definition: "habitat of an organism is the place where it lives". This use ignores the suggestion by Clements and Shelford (1939) that the word should be restricted to refer to "the physical and chemical factors that operate upon the community", and also Andrewartha and Birch (1954) who suggested the word should be replaced by the phrase "a place in which to live", which is cumbersome. In many standard textbooks and reviews the word is used in the sense defined by Odum, and for our purpose it is very useful that plants are also included in a habitat as a living-place for animals. The reader, accustomed to the German usage of terms, should replace the word "habitat" by the terms "Monotop" or "Zönotop" (Schwerdtfeger 1963), which appear to have a very similar meaning.

It seems, however, that the word "Monotop" also includes some aspects of the English term "ecological niche". As this latter term is often misinterpreted by non-English ecologists, it is worth quoting Odum's (1953) definition: "The ecological niche, on the other hand, is the position or status of an organism within its community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behaviour. . . . . it may be said that the habitat is the organism's "address", and the niche is its "profession", biologically speaking."

The word eurytopic will be used to denote species which occur in many types of habitat (euryoecious species), and the word stenotopic will be used for the stenoecious species. Species will also be divided very roughly into xerophilous (inhabiting dry places), hygrophilous (humid places) and mesophilous (intermediate), according to their humidity requirements.

5.2 Typical habitat

Coccinellids show a wide range from stenotopic to eurytopic species. Many species of coccinellids are known to be firmly restricted to a certain, more or less strictly defined habitat. Among the common species, for example, the hygrophilous *Anisosticta novemdecimpunctata* is bound to vegetation of paludinous habitats (as marshes, fens and moist meadows), *Adalia conglomerata* to coniferous forests with preference for *Picea*, *Synharmonia conglobata* to deciduous trees, and the xero- and thermophilous species *Coccinula sinuatomarginata* to steppes and dry meadows. Only exceptionally is stenotopy so extreme, that the species is limited to one or a few plants in an extremely strictly defined habitat, e. g. *Coccinella hieroglyphica* is limited to forest peat bogs with *Calluna vulgaris*. By contrast, some species are very eurytopic and nearly ubiquitous, e. g. *Coccinella septempunctata* or *Propylaea quatuordecimpunctata*, although even these (esp. the former) breed preferentially in the herbaceous stratum of the various habitats they utilize.

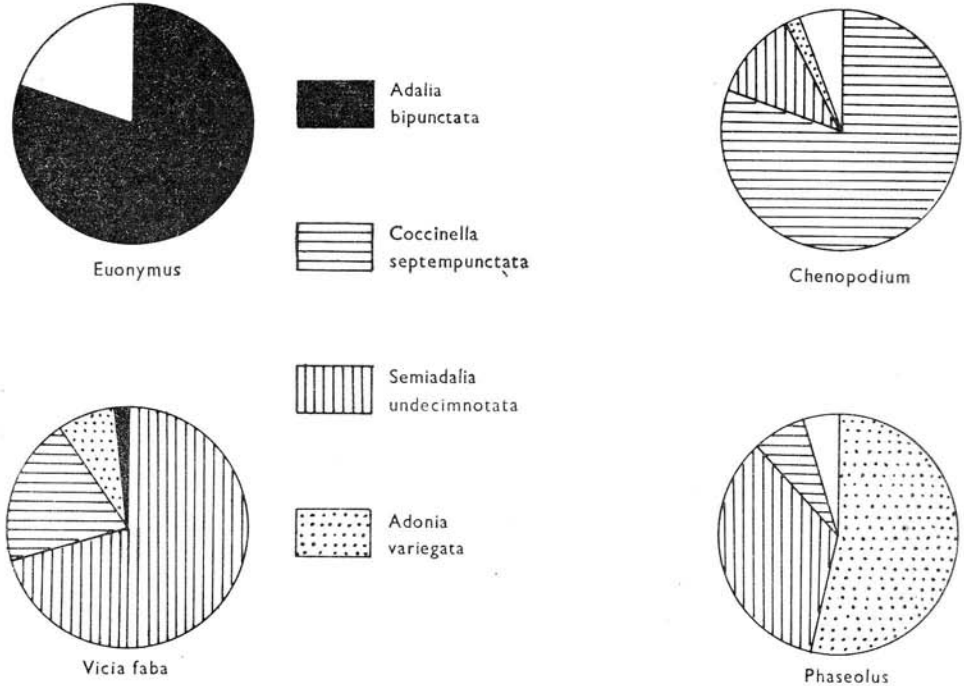

Fig. 5.01 Distribution of coccinellid larvae on host-plants of *Aphis fabae* in south-eastern France (Iperti, in Hodek 1966, p. 31).

The dependence of any species on a given habitat is mainly determined by the occurrence of essential prey and the physical conditions of the environment. In fact, for no coccinellid species is the interrelationship and differential importance of these two features of the habitat precisely known. There are some indications that for a number of species the microclimatic conditions may be of primary importance. Certain strata of vegetation are preferred by certain coccinellid species. Iperti (1965) has reported that in south-eastern France (1) *C. septempunctata* and *Semiadalia undecimnotata* prefer plants lower than 0.5 m; (2) *P. quatuordecimpunctata* and *Adonia variegata* prefer shrubs (0.5 — 2 m); (3) *Adalia bipunctata* and *Synharmonia conglobata* prefer trees (above 2 m). That this difference in distribution need not be a reflection of prey preference, is demonstrated by the different distribution of coccinellids on different plants infested with *Aphis fabae* (Iperti, in Hodek 1966, p. 31) (Fig. 5.01).

5.21 Criteria of the typical habitat

The usual criterion for considering a habitat typical for a particular species is that the latter will breed there (Tischler 1949). The adults of many coccinellids are not firmly restricted to a single habitat because of their great mobility and because they often visit non-typical sites while roving in search of food. The other criterion used for judging the relation of a species to a habitat is the abundance of adults present there. Often these two criteria will both apply in a given habitat.

In Karnevo's (1940) samples from *Alnus incana* (Hirvensalmi and Ruovesi, Finland), larvae were found whenever adults were abundant in four species: *Calvia quatuordecimguttata*, *C. quinquedecimguttata*, *Synharmonia conglobata* and *Propylaea quatuordecimpunctata*. The situation was different with two other species. In 1938 in Hirvensalmi, adults of *Coccinella distincta* were scarce, but were accompanied by larvae. On the other hand, *Halyzia sedecimguttata*, although the fourth commonest species in 1939 in Ruovesi, was present only as adults.

In North Dakota, *Hippodamia tredecimpunctata* and *H. convergens* were the most abundant species (76 and 18%) of all adult coccinellids (N = 617)[1] on sweetcorn. All mature larvae found belonged to one of these two species (Havnvik and Frye 1969).

In the peach orchards of the Niagara peninsula (Ontario, Canada), Putman (1957, 1964) found ten species of "larger aphidophagous coccinellids". 46% of the adults were *Adalia bipunctata*, 22 % *Coccinella trifasciata perplexa*, 12 % *Coleomegilla maculata lengi* and 8 % *Coccinella transversoguttata richardsoni* (N = 888). 69 % of the larvae (N = 93) were *A. bipunctata*, other species present as larvae included *Coleomegilla maculata lengi*, and four others which only represented small fractions (1—4 %) among the adults found. Surprisingly no larvae of *C. t. perplexa*, the second most abundant species as adult, were found and no larvae of any other *Coccinella spp.* All fourth-instar larvae collected were *A. bipunctata;* this suggests that only this species completes its whole life-history in the peach orchards. The case of *C. t. perplexa* demonstrates that the abundance of adults is not a decisive criterion for evaluating the relationship of a species to a habitat.

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[1] Throughout this chaper, when percentage are quoted, the total number of coccinellids, of all species is given the form N = ...

In 1949 and 1950 *Adonia variegata*, which became very abundant in the Ukraine, was found everywhere, including forests; the larvae, however, continued developing only in the fields. Of the numerous species found in the Ukrainian fields of cereals, only *C. septempunctata*, *A. variegata*, *C. divaricata* and less frequently *Coccinula quatuordecimpustulata* and *Hippodamia tredecimpunctata* produced larvae there (Dyadechko 1954).

The suitability of a habitat is also determined by reasons other than the presence of food or an adequate climate. Some plants may exert a mechanically deleterious effect on coccinellids. Putman (1955) found that the hooked trichomes on the foliage of scarlet runner bean, *Phaseolus coccineus*, tore the integument of *Stethorus punctillum;* the larvae were quickly killed and the longevity of adults was shortened by a laceration of the delicate membranes of the terminal abdominal segment. While studying the efficiency of *S. punctillum* as a predator of *Tetranychus cinnabarinus* in Israel, Plaut (1965) found that the coccinellid reproduced in several habitats (apple orchards, cotton, watermelon and sugar-beet fields), but on bush beans only adults without any larvae could be found. He supposed, similarly to Putman (1955), that the hooked trichomes on bush beans were deleterious for the larvae.

5.22 Adaptations to the typical habitat

In the stenotopic species, the continuing relationship with a particular habitat may be (and often is) reflected in specific morphological, physiological and ethological adaptations. These characteristics have seldom been studied experimentally and thus the causal relationship involved in the distributions of coccinellids remain almost completely hidden.

Climatic preference. — Ewert and Chiang, (in Hodek 1966, p. 195) tried to analyse the factors which might be responsible for the distribution of coccinellids among different microhabitats in corn fields. Apart from food relationship (see 5.41), distribution was governed by responses to physical factors. It was found that *Coleomegilla maculata* was brought to the lower strata of plants by a negative photoresponse and a positive response to high relative humidity, further increased after dehydration. The presence of *Hippodamia convergens*, which is tolerant to dessication, in the higher stratum of corn field (Fig. 5.02) was caused by its positive photoresponse and insensitivity to air moisture gradients. We may expect that strictly stenotopic species may show even more pronounced differences of this kind, e. g. a contrast between xerophilous and hygrophilous spp.

Changes in mobility. — In certain habitats flight can be an activity unfavourable for the survival of the species. The classic example is the fauna of small islands. Another example is given by *Spiladelpha barovskii kiritschenkoi* and *Coccinella reitteri* which live in exposed situations at high altitudes in the Zailiĭskiĭ Alatau (Kazakh SSR). Both species rarely fly, although they have normally developed wings (Savoĭskaya 1970a).

Adaptations to arboreal life. — A combination of morphological and ethological adaptations has evolved in arboreal species of coccinellids. Whereas the coccinellids which live on herbaceous plants usually fall from the plant very easily if disturbed, the arboreal species, particularly their larvae, stick to the surface. This is made possible both by morphological characters such as the form of the body and the pronounced adhesive organ on the 10th abdominal segment of the larvae (in *Adalia bipunctata* —

Putman 1964 or in *Anatis ocellata* — Kesten 1969), and by differences in behaviour. "The stout, short-legged larvae of *Coccinella spp.* tend to curl up and drop when disturbed. The more slender, active larvae of *Coleomegilla maculata lengi* and *Hippodamia spp.* . . . . . . scramble about when disturbed and are easily dislodged. On the other hand, larvae of *A. bipunctata* cling tenaciously to leaves" (Putman 1964.)

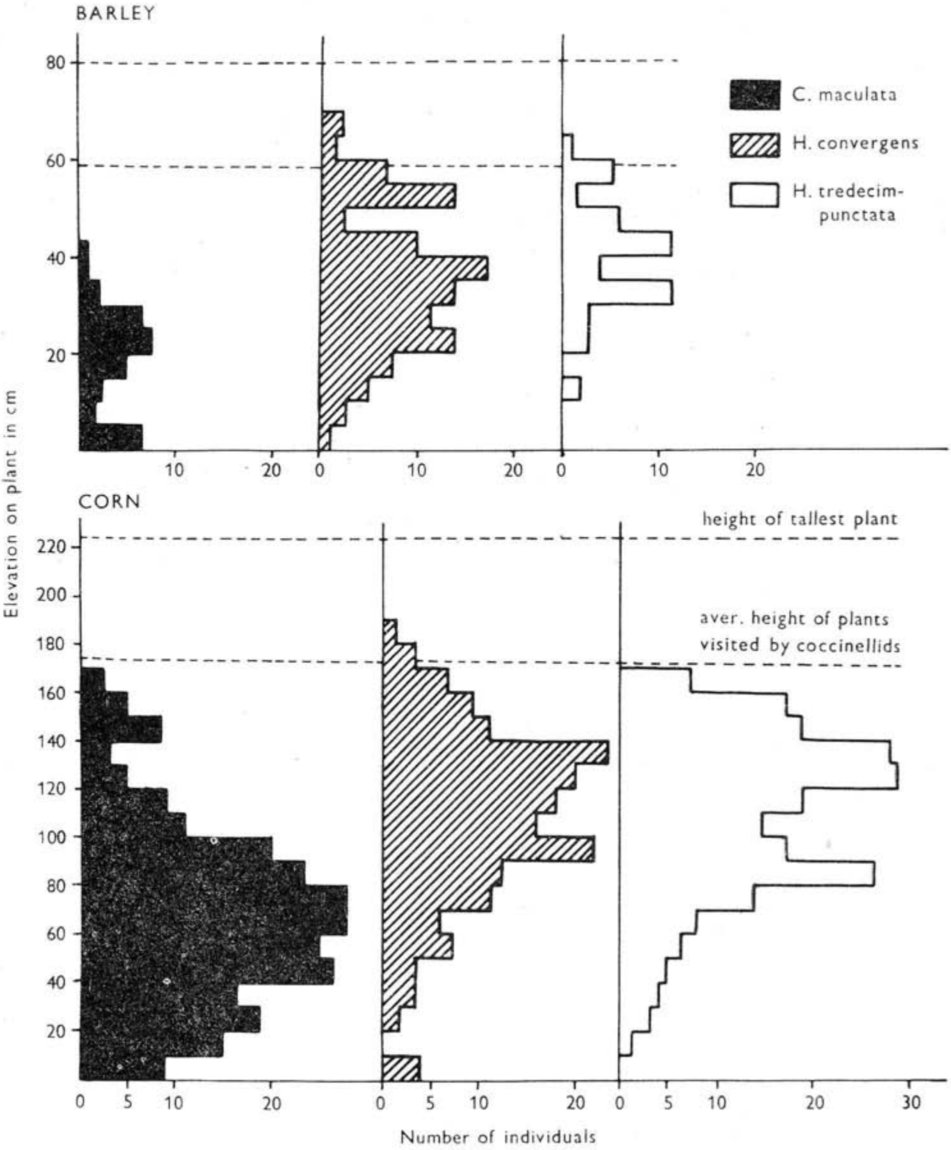

Fig. 5.02 Vertical distribution of three coccinellids on two crops (Ewert and Chiang 1966) (see also Fig. 5.04).

5.3 Changes of habitat with time

5.31 Sporadic migrations

It has long been well known that coccinellids sometimes occur in vast numbers. This phenomenon, which has often been a much discussed puzzle, has been partly explained by an understanding of the dormancy behaviour of *Coccinellidae* (see 7.3).

Some of the massive appearances of ladybirds, however, do not fit into a pattern of migration to or from dormancy sites or aggregation there. Such sporadic mass appearances have been convincingly explained by Hagen (1962). Favourable environmental conditions i. e. massive overpopulation of aphids and optimal weather may bring to realization the high potential fecundity of female coccinellids and lead to a large decrease in the mortality of larvae and pupae. When the young adults emerge (at an estimated density of e. g. about 54,000 individuals from one acre of alfalfa — Dickson et al. 1955) the aphids may be (and this has often been observed) disappearing from the habitat by the combined effect of their emigration as part of the normal seasonal life-cycle and the preying activity of the coccinellids. Due to a high competition for the remaining prey the mobility of the beetles increases tremendously upon emerggence; a hot day may bring them into the air in enormous numbers and the air currents will blow them far away. This highly probable chain of events may indeed explain the nonperiodic appearances of coccinellids, whether migrating (Marriner 1939) or aggregating, both on mountains and in plains, or washed up on the seashore or edges of large lakes (see references in Hodek 1960a, Hagen 1962 and recent observations by Savoïskaya in Hodek 1966 p. 139). Generally only the aphidophagous coccinellids appear in such great numbers because of the ephemeral abundance of their prey in most habitats; with phyto-, myco- or coccidophagous species the same phenomenon is almost unknown.

5.32 Regular seasonal movements

The chain of events described above with reference to mass appearance of coccinellids also regularly occur on a lesser scale with many aphidophagous coccinellids living on herbaceous plants. These species, specialised to such an ephemeral prey as aphids, have a much higher tendency to dispersal than more polyphagous coccinellids. Ewert and Chiang in Hodek (1966, p. 195) ascertained in several ways that two aphidophagous *Hippodamia* species (*H. convergens* and *H. tredecimpunctata*) were much more mobile (15 times or 9 times, resp.) than *Coleomegilla maculata*, which feeds preferentially on pollen (see 6.111 and 6.12). Also the mobile aphidophagous species occurred in the higher stratum of corn fields, but *C. maculata* in the lower (see also 5.2).

When the prey becomes too scarce in one habitat, the coccinellids leave and search for food in neighbouring habitats. They may thus switch between several habitats with suitable prey during one vegetational season, in addition to their hibernation quarters. Sometimes, they also feed at the dormancy sites, or in their close vicinity.

In England, all the three abundant species (*Coccinella septempunctata*, *Adalia bipunctata*, *Propylaea quatuordecimpunctata*) produced their first brood on *Microlophium evansi* (= *Macrosiphum urticae*) infesting nettles, which are the most frequented breeding habitat of the coccinellids after emergence from hibernation quarters. Both the overwintering adults (zero generation) and their offspring (lst generation) then moved to bean plots infested with *Aphis fabae* and also bred there (Banks 1955).

In early spring *C. septempunctata* adults feed on aphids on bushes near their hibernation habitats in the large plains. Usually neither oviposition nor development of larvae occurs there. This contrasts strongly with *A. bipunctata*, which is found on the bushes together with *C. septempunctata* but is, of course, breeding there in its typical habitat. Gradually the overwintering adults of *C. septempunctata* move to the fields (mostly to forage crops at first, later to other crops) and oviposit. The larvae often manage to complete their development there. In central Europe, however, the emergence of new adults more or less coincides with a decline in the aphid population in the fields. Hence the young adults rove in search of food, mostly to weeds and frequently to more humid places (Hodek et al. 1962, 1966). Some authors even suggest (Telenga 1948) that *C. septempunctata* is attracted to the tree and shrub habitats at the forest edges, and thus return to near their hibernation quarters in its search for food.

Lusis (1961) has followed a similar gradual change of habitat in *Adalia bipunctata* in three regions (Riga, Leningrad, Moscow). This species first appears on *Padus* and fruit-trees in parks and orchards, then on ornamental shrubs and trees (*Rosa*, *Philadelphus*, *Caragana*, *Ulmus*) and still later on other trees as *Tilia*, *Populus* or *Salix*. After the disappearance of aphids from trees, *A bipunctata* moves to weeds (*Lappa*, *Artemisia*, *Chenopodium*, *Atriplex*).

In the foothills of south-eastern Kazakhstan (USSR), *A. bipunctata* shows a pronounced spring and early summer preference for orchard aphids, whereas in midsummer and autumn, when the aphids have disappeared from the fruit-trees, the coccinellids are quite evenly distributed over both herbaceous plants and trees (Savoïskaya 1965). Right in the Zailiïskiï Alatau-mountains (S. E. Kazakhstan), in midsummer, a part of the abundant early summer population of this species migrates from deciduous to coniferous forests (Savoïskaya 1970a). In Georgia (USSR), *Adalia bipunctata* produces the first generation in peach orchards; afterwards the beetles move to *Prunus*, following the migration of *Myzus persicae* (Aleksidze 1970).

In early summer, *Propylaea quatuordecimpunctata* is the most abundant and economically most important coccinellid species in the stone-fruit orchards infested with *Hyalopterus pruni* and *Anuraphis persicae* in the mountains near Alma-Ata. In midsummer, *P. quatuordecimpunctata* moves from the fruit-trees to herbaceous plants and becomes very numerous on mountain meadows (Savoïskaya 1965, 1970a).

A similar change of habitat, due to shortage of food, is undertaken by two aphidophagous coccinellids in a neighbouring region of central Asia (USSR, Karakalpakistan) (Yakhontov in Hodek 1966 p. 35). In spring they live in the orchards; the larvae of *Synharmonia conglobata* mainly feed on *Hyalopterus arundinis* and *Myzus persicae*, and the larvae of *Coccinella undecimpunctata* on *Aphis pomi*. In mid-July the aphids almost completely disappear from the fruit-trees, some of them migrating to their secondary host-plants, e. g. *H. arundinis* to *Phragmites*. The search for food leads to massive migrations by the second generation of *S. conglobata* to herbaceous plants or to other trees infested with aphids e. g. to poplars with *Chaitophorus jaxarti* and to *Salix* with *C. shaposhnikovi* or *C. saliceti; C. undecimpunctata* disperses to cotton and alfalfa fields (with *Aphis gossypii* or *Acyrthosiphon gossypii* and *Therioaphis ononidis* or *Acyrthosiphon pisum*).

Also in south-east France, many coccinellids can only utilize those habitats which have the most favourable microclimatic conditions during the spring period, when plenty of aphids can be found on all plants. In summer, scarcity of aphids forces them to search for food in non-typical habitats (Iperti 1965). Sometimes they can only find alternative food there. Thus, for example, *Adalia bipunctata*, which reproduces in the spring on trees (mainly fruit-trees: cherry, plum, peach, apple, but also shrubs of rose), can be found on *Zea mais* and *Phragmites communis*, but only as adults. This alternation of habitats is similarly undertaken by *Adalia decempunctata* and *Synharmonia conglobata*.

Thus in *A. bipunctata* (and in ecologically similar species) a similar alternation of habitats occurs not only in regions which have similar seasonal changes of climate (French Riviera, the foothill zone in central Asia), but also in northern regions of the European USSR with both sea and continental climate. This similar habitat alternation in spite of differing climates demonstrates convincingly that the alternation of habitat by aphidophagous coccinellids results from the seasonal changes of host-plants used by their prey — aphids. As the coccinellids do not find their essential prey in many of the habitats they visited, they frequently occur only as adults (see also 5.21 and 6.113).

Coccinellids with typical habitats other than the fruit orchards also alternate their sites of active life throughout the vegetational season. Sometimes both sites may be typical habitats. Both adults and preimaginal stages of *Coccinella divaricata* occur on coniferous trees infested with aphids in late summer, while normally the species lives on herbaceous plants near rivers in the Zailiĭskiĭ Alatau-mountains (Savoĭskaya 1970a).

Coccinula quatuordecimpustulata and *C. sinuatomarginata* disappear from the mountain steppes in mid-summer. One part of the populations migrates down to the agricultural zone to alfalfa fields while the other part flies up to the herbaceous habitats of the forest zone (Savoĭskaya 1970a).

In the subtropical and tropical regions, low humidity due to high temperature can result in distributional changes of coccinellids.

In the Nile delta regular habitat change by *Coccinella undecimpunctata* has been observed (Wiesmann 1955) between "bersem" (a kind of *Trifolium*), cotton and maize. After a period of inactivity in their hibernation sites (XII — I) the coccinellids reproduce on "bersem" until mid-May, when irrigation of this crop ceases. The drying of "bersem" induces the migration of all insects including *C. undecimpunctata* to cotton where, however, no reproduction was observed in 1951. From mid-May to late August the predators migrate to maize where they reproduce. The drying of maize causes the predators to move to shelter. The migrations in Egypt of *C. undecimpunctata aegyptiaca* from cotton to maize are reported also by Ibrahim (1955a).

During the hot period of July — September when the temperatures exceed 40 °C, the distribution of *Chilocorus bipustulatus* var. *iranensis* (introduced from Iran to Mauretania, W. Africa — Iperti et al. 1970, Laudého et al. 1970) becomes reduced to the relatively more humid places near permanent water.

Brown (1969) observed that in the Orange Free State coccinellids dispersed to other crops (such as sorghum, radish, maize, peaches, garden ornamentals) in order to survive periodic disruption of the habitat of wheat crop by harvest. The most abundant species *Lioadalia flavomaculata* was able to breed continuously for 8—10 generations per year because of its regular seasonal movements to its most important winter habitat (Japanese radish, *Raphanus sativus*) in late summer.

Bielawski (1961, p. 514) assumes that the "oversaturation" ("przesycenie") of the habitat by populations of different coccinellid species is the reason why they alternate habitats. In this connection he also refers to a "waiting-period" ("okres wyczekiwania") in the life-cycle of *Adalia bipunctata*, *A. decempunctata*, *Coccinula quatuordecimpustulata* and *Subcoccinella vigintiquatuorpunctata*. In both *Adalia spp.* a "waiting-period" of about one month has been observed, when the beetles remain on young pines until the time of the formation of leaves on oaks (*Quer-*

cus), usually in the course of April. They are thus "waiting" actively (feeding, copulating) in the habitat where they hibernated. The other two species "wait" before hibernation at the same dormancy habitat, sitting inactively among needles of young pines under which they will hibernate in the litter until the first frosts. The "waiting" period of *C. quatuordecimpustulata* and *S. vigintiquatuorpunctata* is, however, connected more with the onset of diapause than with any "oversaturation of the habitat" where they spend their active life.

5.33 Influence of adjacent habitats

The mobility of some coccinellid species is rather great, and is increased markedly by high ambient temperature, so that often very distant habitats may be reached not only in migrations connected with dormancy, but also in dispersal during search for food (see the previous chapter 5.31 and 5.32). The larvae are of course much less mobile,[1] and also the dispersion of adults may be delayed and slowed down, if they find food nearby, e. g. after emergence from hibernation quarters, particularly if the temperature is low. Hence the occurrence of coccinellids in a given habitat may be influenced to a great extent by the neighbouring habitats.

The proximity of the hibernation sites — whether these be forest edges (Fenjves 1945, Galecka 1966) or hedgerows (van Emden 1965a, b, c) — have a fundamental effect on the occurrence of coccinellids on agricultural areas. With low aphid infestations of potato fields (Galecka 1966) or brussels sprouts (van Emden 1965c), there was an increase in the population density of aphids and a decrease in coccinellid numbers toward the centre of the field away from the adjacent shelter. At high aphid populations, this correlation becomes obscured by the dependence of coccinellids on the population density of aphids.

In England, the population density of coccinellids on three bean plots infested with *Aphis fabae* has been shown to be dependent on the distance between the plots and both grass, which appeared to be the hibernation site of *Coccinella septempunctata* (Fig. 5.03, I, II) and patches of nettles (Fig. 5.03, a, b, c) where overwintered adults of *Adalia bipunctata* and *C. septempunctata* first concentrated. The shelter afforded by trees and buildings hindered the access of the beetles to the beans in plot A. Plot C always had a high population of coccinellids; this was attributed to its situation between the two nettle sites rich in coccinellids (Tab. 5.01, 5.02) (Banks 1955).

Galecka (1966) studied aphids and their predators on four potato fields in Poland for two seasons. In two fields, situated 0.5 km from each other in an unwooded region near Warsaw, there were both less species and specimens of coccinellids than in the two other fields situated in the forest area of Kampinos; one was at the forest edge and the other 1.5 km from the forest on the bank of the river Vistula. In the two fields of the unwooded region about 40 and 60 coccinellids were collected, belonging to three eurytopic species: *Coccinella septempunctata*, *C. quinquepunctata* and *Propylaea quatuordecimpunctata*. In the forest area, the field situated near the river yielded 90 specimens, and apart from the above three species, three more were found. The presence of the hygrophilous *Hippodamia tredecimpunctata* is explained by the vicinity of the river. The field at the forest edge had greatest numbers of coccinellids, as 120 were collected. As well as three eurytopic species, *Adalia bipunctata* was also present and reflected the neighbourhood of the tree-habitat. The two fields in the wooded region were inhabited also by two inhabitants of drier herbaceous habitats: *Coccinula quatuordecimpustulata* and *Adonia variegata*. This enrichment of the coccinellid fauna of potato fields by steppe species in the forest region is rather

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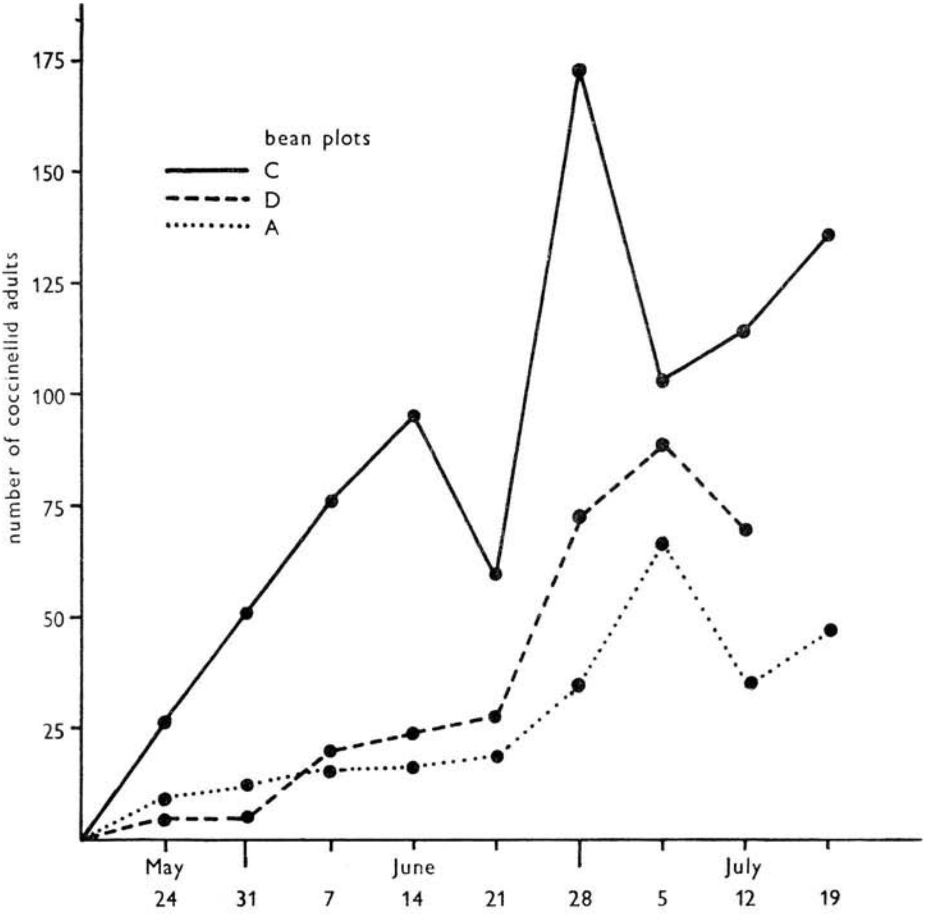
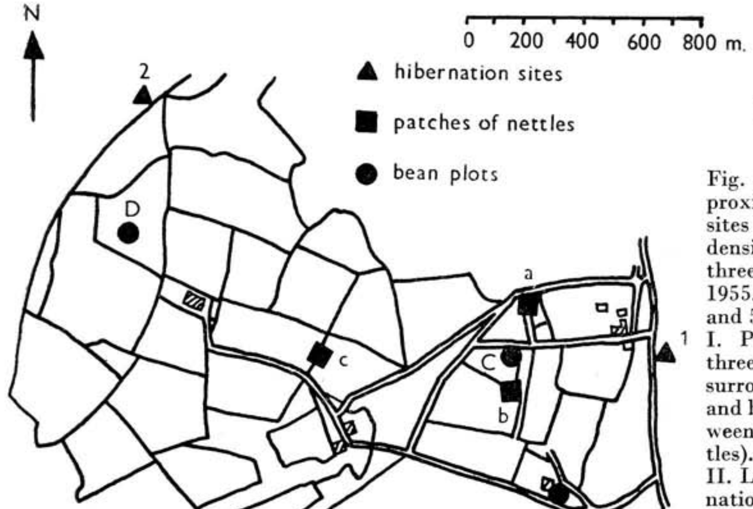
[1]) A rather high mobility of coccinellid larvae has been demonstrated by the capture in pitfall traps of large numbers of larvae of *Anatis ocellata*, *Adalia conglomerata* and *Neomysia oblongoguttata* under an old spruce stand with no ground vegetation (Klausnitzer and Bellmann 1969; see also 5. 51).





II.

Fig. 5.03 Effect of the proximity of hibernation sites on the population density of coccinellids on three bean plots (Banks 1955, see also Tab. 5.01 and 5.02).
I. Population density on three bean plots (plot A surrounded by tall trees and buildings, plot C between two patches of nettles).
II. Location of the hibernation sites (▲), patches of nettles (■) and the three bean plots (●).

surprising. As there does not seem to be a difference in climate between the two regions, the presence of these two species may be assumed to be caused by provision of suitable quarter for hibernation in the nearby forest. Both species are known to hibernate in the litter of the forest edges in eastern Europe (Dyadechko 1954, Bielawski 1961).

Tab. 5.01 Maximum numbers of overwintered coccinellids at Rothamsted counted during April and May 1952 (Banks 1955)

Locality	Habitat	No.	*C. septempunctata*	*A. bipunctata*	*P. quatuordecimp.*	*C. undecimpunctata*	Total
Harpenden Common	grass	1	111	0	0	12	123
West Barnfield	grass	2	40	0	0	0	40
Great Field III	nettles	a	37	218	13	0	268
Great Field II	nettles	b	27	60	9	0	96
Broadbalk	nettles	c	108	137	47	0	292

Apart from providing hibernation shelter, adjacent uncultivated land may serve both as a source of prey, when the pest species have become scarce in the field, and as a source of re-inforcement of active natural enemies after the outbreak of the pest on crop. Uncultivated land may, therefore, enable beneficial insects to bridge failures in their synchronization to pest species (van Emden 1965a).

Adjacent parts of a crop may also have a similar function. Thus van den Bosch et al. (1959) report that adult coccinellids, moving from adjoining parts of the same crop, invaded those alfalfa plants where a quick build-up of aphids had occurred. This finding led to the idea of "strip cutting" of alfalfa (Schlinger and Dietrick 1960, see below and 9.225). By contrast, Skuhravý and Novák (in Hodek 1966 p. 167) could not show a similar movement of coccinellids when alfalfa was cut adjacent to aphid infested sugar-beet in central Bohemia. They failed to find an invasion of coccinellids from the mown alfalfa rich in coccinellid beetles, when a 300 m wide edge strip of the sugar beet field was sampled 3 and 8 days after the alfalfa had been mown. They believed that, even after the mowing of the alfalfa field, the coccinellids still found enough food there.

Uncultivated land is important in determining the effectivity of coccinellids and other natural enemies on crops. Van Emden (1965a) has raised the question whether pest problems in Great Britain are so much less than those in the United States for the very reason that in England crop fields are normally islands surrounded by large areas of less cultivated land. The study of these hitherto little known interrelations could lead to new methods of integrated control. The evaluation of the function of the adjoining crops (or the adjacent part of the same crop) as the source of mobile natural enemies — which include the vast majority of coccinellids — has already led to the introduction of strip-cutting, or strip-treating with pesticides; both methods seem very promising for integrated control (see 9.225).

Tab. 5.02 Total numbers of *Coccinellidae* of all species counted weekly on the bean plots A, C and D (Banks 1955)

Plot	Week		Adults					Eggs	Larvae	Pupae
	no.	4th day	*A. bipuncta-ta*	*P. quatuor-decimp.*	*C. septem-punctata*	Others	Total			
A	7	24.5.	4	5	0	0	9	154	0	0
	8	31.5.	2	10	0	0	12	327	13	0
	9	7.6.	12	4	0	0	16	232	26	0
	10	14.6.	13	3	0	0	16	571	51	0
	11	21.6.	17	0	0	0	17	270	92	0
	12	28.6.	25	4	3	0	32	1293	162	26
	13	5.7.	47	10	3	5	65	979	276	70
	14	12.7.	20	9	0	2	31	538	281	31
	15	19.7.	29	4	10	1	44	21	146	32
Totals			169	49	16	8	242	4385	1047	159
C	7	24.5.	13	13	1	0	27	456	0	0
	8	31.5.	31	17	3	0	51	537	29	0
	9	7.6.	61	12	3	0	76	1392	28	0
	10	14.6.	76	6	11	0	93	2444	261	0
	11	21.6.	49	2	4	4	59	1883	330	4
	12	28.6.	115	23	34	1	173	3527	687	85
	13	5.7.	53	31	15	3	102	1193	445	328
	14	12.7.	83	28	6	2	119	215	402	130
	15	19.7.	96	2	32	2	132	6	103	63
Totals			577	134	109	12	832	11653	2285	610
D	7	24.5.	0	4	2	0	6	249	13	0
	8	31.5.	4	1	0	0	5	180	15	0
	9	7.6.	11	8	0	0	19	324	51	0
	10	14.6.	20	3	0	1	24	616	39	0
	11	21.6.	20	3	3	1	27	527	99	1
	12	28.6.	46	16	7	2	71	2922	270	58
	13	5.7.	61	10	12	5	88	1794	249	112
	14	12.7.	38	27	1	2	68	323	348	105
Totals			200	72	25	11	308	6935	1084	276

5.34 Succession of species as a habitat ages

Changes in the condition of annual plants (and herbaceous plants generally) are so quick that it is virtually impossible to study their direct effect on the spectrum of coccinellid species, and moreover such effects would certainly be masked by changes in aphid infestation. The succession could be more easily followed on trees, but even so scarcely any such studies have been undertaken.

In central Europe, only the young stands of pines have usually been sampled for coccinellids (Bielawski 1961, Klausnitzer 1967), and the larvae of *Myrrha octodecimguttata* have never been found; Bielawski did not even find any adults during the vegetation season. Still this species, which hibernates in bark crevices at the base of large pines (Bielawski 1961, Pulliainen 1966) (see 7.324), has been supposed to be typical for stands of pines. Klausnitzer (1968) investigated samples of pine crowns of mature trees and found a much higher incidence of *M. octodecimguttata* adults (27 %) (N = 188) than on young pines (1 %). He believes that the species breeds in the crowns of older pines and considers that the stratum of crowns in old pines[1] is a typical habitat for *M. octodecimguttata*. *Scymnus nigrinus*, the second most abundant species in a young Pinetum, but which also occurs in other habitats such as deciduous forests, meadows and fields (see 5.5), is extremely scarce in crowns (Tab. 5.03). However, total number of individuals of both *Scymnus spp.* in young pine trees and crowns is remarkably similar. The near absence of *S. nigrinus* in crowns is compensated by a very high incidence of *S. suturalis*. The fauna of pine crowns is also characterized by a complete absence of the other eurytopic species, *Coccinella quinquepunctata*, *Chilocorus bipustulatus* and *Propylaea quatuordecimpunctata*. The first of these species is apparently a more or less incidental visitor of young pines, while the last has been reported as breeding (Bielawski 1961) in this habitat. The rather eurytopic *C. bipustulatus* seems to prefer the deciduous shrubs and trees (according to the survey of faunistical data from eastern Europe) (see 5.51). The hypothetical assumption that *C. bipustulatus* breeds in pine crowns (Bielawski 1961) has been disproved by its absence there (Klausnitzer 1968). The coccinellid fauna of pine crowns also differs from that of young pines by the lower occurrence of *Exochomus quadripustulatus*. Other differences may be incidental (N = 188).

Gumoś and Wiśniewski (1960) also compared young (about 10 years old) and old (about 40 years old) pine stands. They apparently did not sample Scymnini and included autumn samples. They thus obtained high numbers of *C. septempunctata* in the young stand (70 %). Their results are interesting, for they show large catches of *Anatis ocellata*, four times higher in the old forest (81 %), and the presence of *Halyzia sedecimguttata*.

We may conclude that in central Europe the fauna of young pines basically contains more species with a broader ecological range than does that of the crowns of old pines which are inhabited by less species, bound more strictly to the Pinetum and rather stenotopic.

The succession of coccinellid species (Tab. 5.04) in the course of ageing of red pine stands infested with *Schizolachnus piniradiatae* in central Ontario, Canada, is apparently brought about by a gradual decrease in prey density (Gagné and Martin 1968). *Cocci-*

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[1])Placing the discussion of the effect of the tree age is somewhat arbitrary as it could equally well be discussed in 5.41 as a difference between strata. However stands of older pines do not usually have young pines growing among them — thus, strictly speaking, young pines form rather a habitat more distinct from old pines than applies with young and older trees in a mixed deciduous woodland.

Tab. 5.03 Coccinellids on pines [in %]

Coccinellid species	Poland (15 km N. E. of Poznan) Gumos and Wisniewski 1960		Poland (Warszawa-Bielany) Bielawski 1961	German Dem. Republic Klausnitzer 1967b, 1968a	
	9—11 years old 3 m high	37—41 years old 16 m high	cca 15 years old[1])	young pines[1]) N = 1465	crowns of old pines N = 188
Subcoccinella vigintiquatuorpunctata			1.6		
Stethorus punctillum			1.0		
Scymnus auritus			2.1		
S. suturalis			23.7	33.5	60.2
S. nigrinus			22.6	29.0	0.5
S. frontalis			1.0		
Aphidecta obliterata			1.6		
Adalia decempunctata			2.1		
A. bipunctata			1.3		
Coccinella septempunctata	70	4	5.2	4.8	2.1
C. quinquepunctata	2		1.6	5.3	
Coccinula quatuordecimpustulata	4		1.6		
Synharmonia conglobata			0.3		
Harmonia quadripunctata			2.3	4.4	1.6
Myrrha octodecimguttata				1.0	27.1
Propylaea quatuordecimpunctata			27.3	6.2	
Neomysia oblongoguttata		2			
Anatis ocellata	20	81		1.7	4.3
Halyzia sedecimguttata	2	11			
Chilocorus bipustulatus				2.7	
Exochomus quadripustulatus			4.4	9.2	1.1
Other species	2	2		2.2	3.1

[1]) Only the samples from May — July included, to exclude the coccinellids for which the habitat served as a dormancy site only.

Tab. 5.04 Occurrence of *Coccinellidae* in red pine stands of different age [1]) (Gagne and Martin 1968)

Species	Age of the stand				
	newly planted	5 years	15 years	26 years	36 year
Hippodamia parenthesis	—[2])	+[2])	—	—	—
Coccinella novemnotata	—	+	(+)[2])	—	—
C. transversoguttata	—	+	+	—	—
C. trifasciata	—	+	+	(+)	(+)
Scymnus lacustris	—	+	+	(+)	(+)
Anatis mali	—	(+)	+	+	+
Mulsantina picta	—	(+)	+	+	+
Cycloneda munda	—	—	(+)	+	+
Hippodamia convergens	—	—	+	—	—

[1]) Only species breeding at least at one age are included.
[2]) — absent, + present and breeding, (+) present.

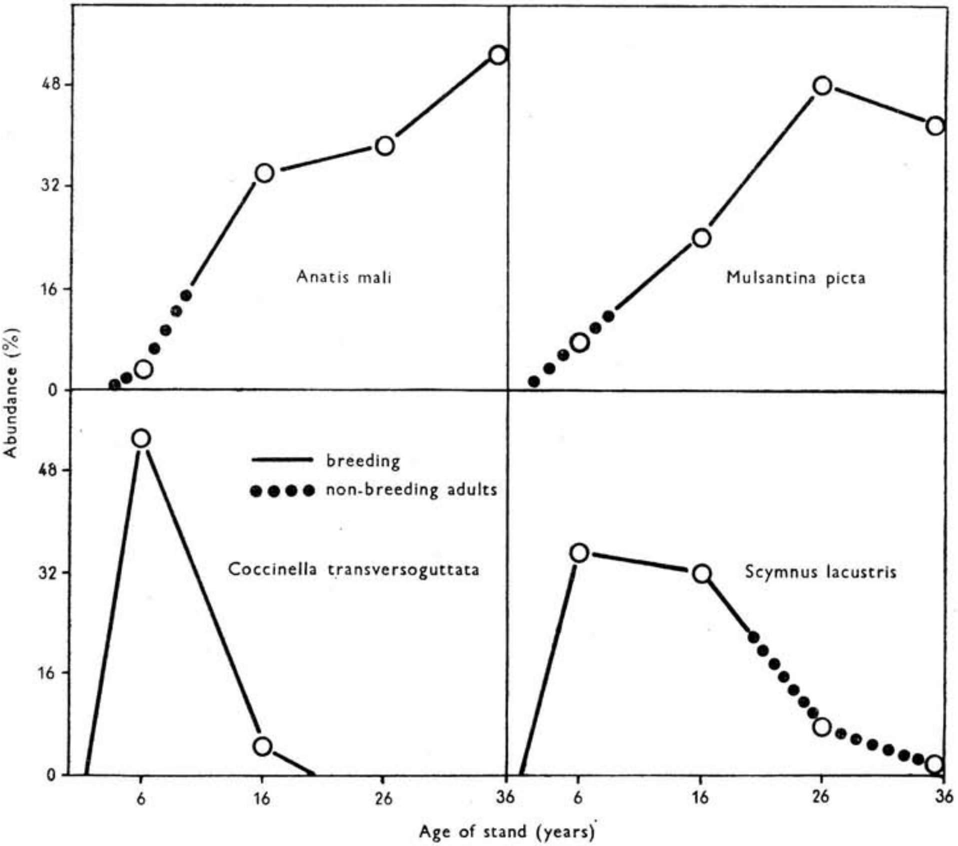

Fig. 5.04 Changes in relative abundance of coccinellids in red pine plantations of different age (Gagné and Martin 1968).

nella transversoguttata and *Scymnus lacustris* appear dominant in younger stands (Fig. 5.04), whereas *Mulsantina picta* and *Anatis mali* are the most common species in the older plantations. Survival of a coccinellid species in older stands with a lower prey density seems to require a greater searching capacity and mobility of the larvae. In fact, the larvae of *M. picta* and *A. mali* can be observed searching rapidly, while the larvae of *S. lacustris* are "slow moving and practically sedentary".

In Israel, the population level of *Chilocorus bipustulatus* appears considerably higher in mature citrus groves (23—30 years), than in young ones (7—9 years) throughout the year (Rosen and Gerson 1965). The same preference for older, more shaded groves has been found in date palm plantations (Kehat 1967a, 1968b). This feature, the depression of the population in summer, and the absence of *C. bipustulatus* in the warmer and drier regions of southern Israel (see 5.42), all are apparently related to the low resistance of the species to high temperature and/or low humidity.

5.4 Spatial differences

5.41 Differences between strata within a habitat

There is a great need for data on this subject. An isolated study has been undertaken by Ewert and Chiang (in Hodek 1966 p. 195). They found that the three dominant species of coccinellids were unevenly distributed at different heights in crops in Minnesota, USA. The difference in distribution was significant in corn and barley. Whereas *Hippodamia convergens* and *H. tredecimpunctata* occurred on higher portions in corn and barley, *Coleomegilla maculata* was distributed predominantly in the lower stratum of these crops (Tab. 5.05, Fig. 5.02).

The authors tried to reveal the causes underlying the differential distribution and

Tab. 5.05 Vertical distribution of adult *Coccinellidae* in four crops (Ewert and Chiang in Hodek, 1966)

Crop		Coccinellids	
Name	Average height of plants [1] [cm]	N	Average elevation on plants [cm]
		Hippodamia tredecimpunctata	
corn	172	242	112
barley	62	260	45
sorghum	87	148	64
alfalfa	42	105	30
		Hippodamia convergens	
corn	172	230	114
barley	58	430	38
sorghum	86	175	57
alfalfa	44	66	34
		Coleomegilla maculata	
corn	173	221	73[2]
barley	59	83	26[2]
sorghum	87	162	43
alfalfa	42	28	26

[1] Plants infested with coccinellids.

[2] Significantly different from *Hippodamia spp.* at the 0.01 level of probability.

they succeeded in finding several, at least for *H. convergens* and *C. maculata*. The aphidophagous *Hippodamia spp.* meet their prey in the higher stratum of the plants, while plant pollen, the preferred food of *C. maculata* (see 6.111 and 6.12) usually accumulates on the lower parts of plants. *H. convergens* and *C. maculata* also show opposite responses to physical factors (light, humidity) (see 5.22) and a contrasting resistance to desiccation. *H. convergens* is resistant, and *C. maculata* is sensitive to desiccation. This is in full accord with other factors and with their distribution in the crop strata. In *H. tredecimpunctata* the situation is more complicated. This species must search for its prey in the upper stratum and is directed in this respect by appropriate behavioural responses (negative geotaxis, positive phototaxis). The species is, however, not adapted to this microhabitat as it is sensitive to desiccation in the same way as *C. maculata* (Fig. 5.05). This is apparently related to its limited circumboreal distribution: the other two species occur in temperate and tropical zones.

As further evidence, it has recently been found that the coccinellids react differently to changes in the microclimate of corn plants as influenced by plant density (Smith 1971). *Coleomegilla maculata and Hippodamia tredecimpunctata* were most abundant at a density of 3.2 plants per m^2 (i. e. 9000 plants per acre) and two *Coccinella spp.* (*C. novemnotata* and *C. transversoguttata*) on even less dense plants (1.6 plants per m^2). The temperature was lower in the denser stand; the mean and range of differences were 2.1 (0.5—8.6) °C for the densities 1.6 vs. 11.4 plants per m^2.

Differences in the occurrence of coccinellids between the young trees and crowns of pines were discussed as age differences in chapter 5.34, as was the preference of *Chilocorus bipustulatus* for older groves of citrus trees and date palms in Israel. The same preference has been found for *C. b. iranensis*, introduced to Mauretania (W. Africa). Within the traditional stands of date palms with an undergrowth of younger palms, the coccinellid shows a clear preference for the upper crowns (Laudého et al. 1970).

Wylie (1958) reported that *Aphidecta obliterata* shows preference for a twig rather than a stem habitat on firs, which indicates its adaptation to *Adelges nüsslini* rather than *A. piceae*.

Hukusima (1949b, 1950, 1951a, b, 1955) systematically studied the effect of slight deviations in cultivation of potatoes on the temperature of the microhabitat and the consequent changes in the occurrence of, and the damage by the phytophagous *Epilachna vigintioctomaculata*. The temperature among the potato leaves increases and hence the feeding activity of the coccinellid decreases, if:

- the potatoes are planted more thinly, in furrows 75 cm apart (contrast 60 cm) (Hukusima 1949b);
- the plants are cultivated on higher ridges (20 or at least 15 cm, contrast 10 cm) (Hukusima 1950);
- the ridges run from east to west (Hukusima 1951a);
- intercropping or fencing cultivation of potatoes is used (Hukusima 1951b). These relationships are, naturally, only valid for the region studied. In different climatic conditions they would certainly be modified.

5.42 Differences between similar habitats in different biotic zones

The relation of coccinellid species to their habitats can vary in different regions of their distribution area. This may be due to the presence of different prey; but even if food conditions are the same or similar, the different temperature and/or humidity condi-

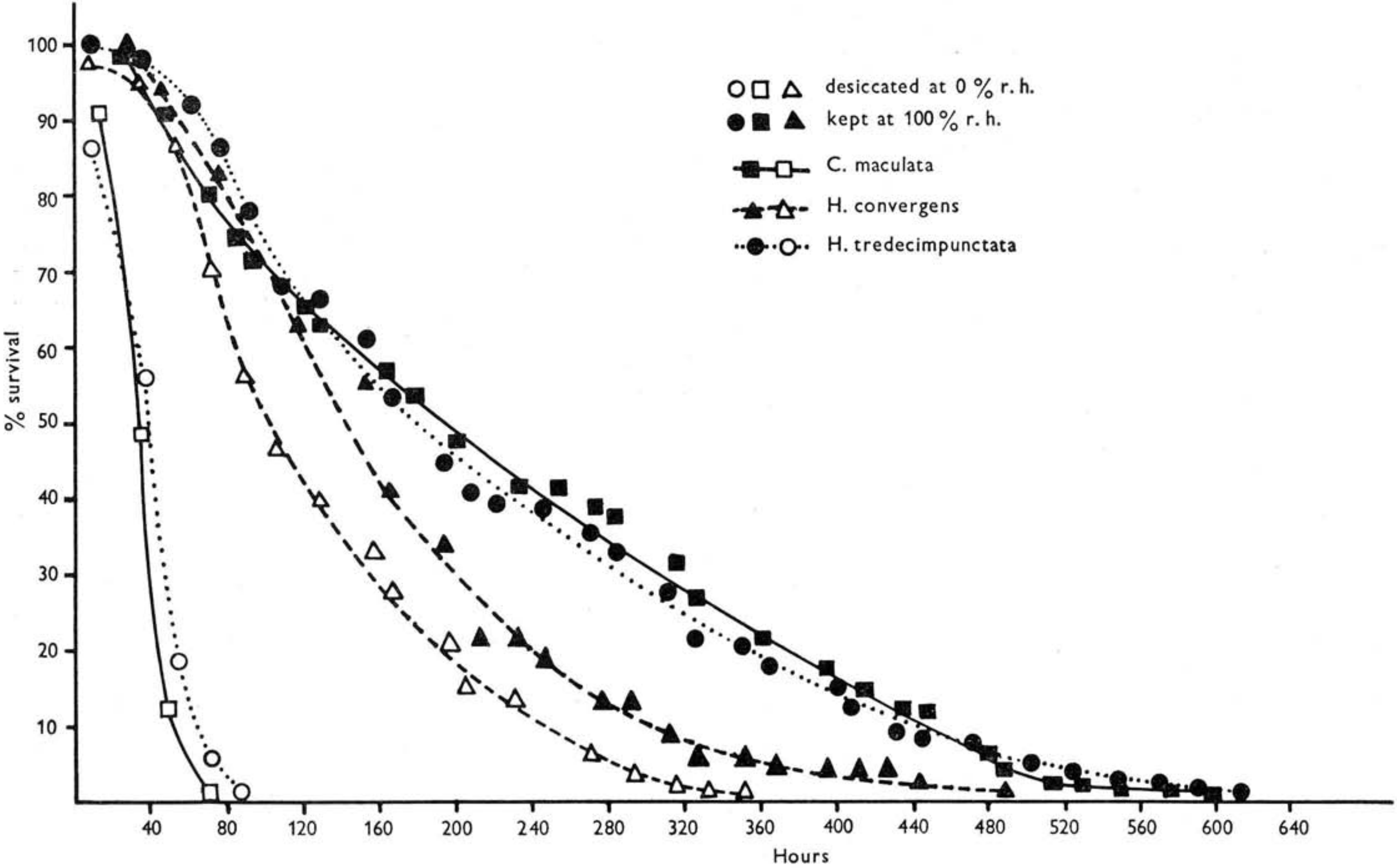

Fig. 5.05 Survival at 30 °C of three coccinellid species at different relative humidities (Ewert and Chiang 1966) (see also Fig. 5.02).

tions in another climatic zone may so drastically change the microclimate of a particular habitat that it becomes favourable for other coccinellid species.

Evidence that such differences exist is rather limited because only in rare cases has the fauna of coccinellids of the same habitat in different zones of one zoogeographical region been studied.

The material collected by Dyadechko (1954) in the Ukraine provides a possibility of seeking such a comparison. The area, except for a small part in the zone of mixed forests, belongs to the zone of the forest-steppe and the steppe zone.

Often the same typical coccinellid species occur in a certain type of habitat (see 5.5) regardless of the zone in which the habitat lies, but the zone may substantially influence relative proportions of the species. For example, in deciduous forests of the forest-steppe zone (Tab. 5.06), the most abundant species apart from *Stethorus punctillum* (33 %) were: *Synharmonia conglobata* (11 %), *Vibidia duodecimguttata* (10 %) and *Halyzia sedecimguttata* (10 %). In deciduous forests of the steppe zone, however, besides the similarly abundant *S. punctillum* (32 %), the most abundant species were: *Exochomus quadripustulatus* (16 %), *Propylaea quatuordecimpunctata* (16 %), *Scymnus (Pullus) subvillosus* (11 %) and *Hyperaspis reppensis* (9 %).

Tab. 5.06 Coccinellids in the mixed deciduous forests in the Ukraine (Dyadechko 1954)[1]

Coccinellid species	Forest-steppe zone (Chernovcy, Kiev, Sumy) N = 1279	Steppe zone (Nikolaev, Odesa Kharkov) N = 1205
Stethorus punctillum	32,8	32,4
Scymnus (Pullus) subvillosus	5,5	11,3
Hyperaspis campestris	3,7	6,0
Hyperaspis reppensis	1,1	9,4
Adalia bipunctata	2,1	2,6
Synharmonia conglobata	10,6	2,0
Calvia decemguttata	5,6	0,9
C. quatuordecimguttata	6,3	1,0
Propylaea quatuordecimpunctata	7,3	15,6
Halyzia sedecimguttata	9,9	0,9
Vibidia duodecimguttata	10,2	1,5
Exochomus quadripustulatus	5,0	16,4

[1]) In each zone at each of the three localities 400 sweepings were made (11. 6.—18. 7.).

Kehat (1967a) found a distinct difference in the occurrence of coccinellids in date palm plantations between the northern (Bet Shean, Jordan) and southern (Dead Sea, Elat — Arava) regions of Israel. Four species (*Pharoscymnus pharoides*, *Chilocorus bipustulatus*, *Rhizobius (Lindorus) lophantae* and *Scymnus (Nephus) bipunctatus* were absent in Arava, though they occurred in both northern regions. By contrast *Pharoscymnus setulosus* was evenly distributed. Two *Pharoscymnus* species had darker forms in the North and lighter ones in the South (Fig. 5.06) (see 3.24).

5.5 The coccinellid fauna of some diverse habitats

This chapter simply consists of an annotated list of coccinellid species in several habitats which have been chosen more or less arbitrarily, although emphasis has been put on habitats of economic importance. The chapter nevertheless includes most of the available data, particularly data suitable for comparison between habitats. Not many types of habitat have been studied sufficiently widely and most authors report the data of one single area. It is, of course, necessary to study the fauna of a certain habitat at several localities in the same region and over a long period to give a clear picture which excludes incidental effects such as adjacent habitats, climatic conditions in a particular season, etc.

The presence of larvae and pupae of a species is a sign that the habitat is typical for that species (see chapter 5.21).

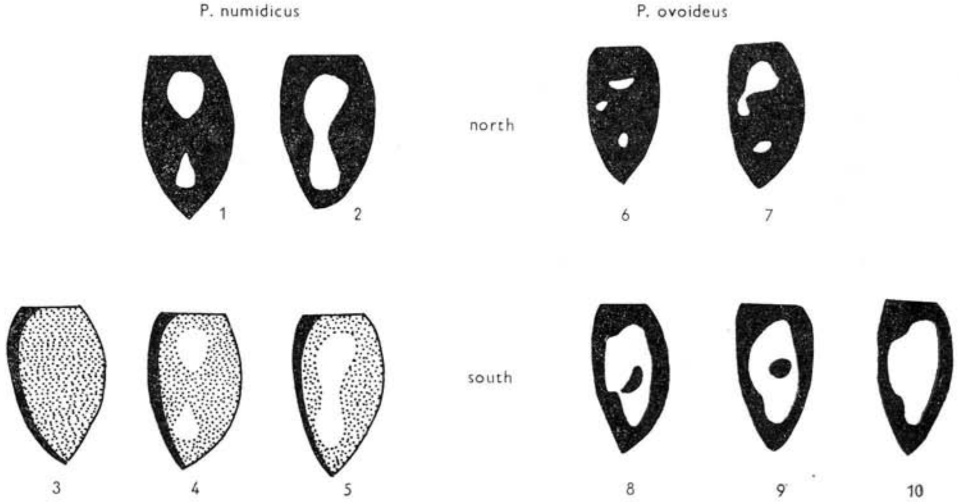

Fig. 5.06 Distribution of darker and lighter forms of two *Pharoscymnus spp.* in northern and southern Israel (Kehat 1967a).
1, 2, *P. numidicus* (nominate form); 3, *P. n. f. unicolor;* 4, 5, *P. n. f. junctus;* 6, *P. ovoideus f. guttatus;* 7, *P. o. f. hamifer;* 8—10 *P. ovoideus* (nominate form).

5.51 Forests

Pine. — This habitat is thoroughly discussed with respect to middle or eastern Europe and Canada in chapter 5.34.

Spruce. — A good picture of the coccinellid fauna of an old stand (110 years) in Eastern Germany (Tharandt near Dresden) was achieved surprisingly using pitfall traps (Barber traps) by Klausnitzer and Bellmann (1969). About one sixth of all *Coleoptera* larvae were the larvae of 8 coccinellid species (N = 1080). Most abundant was *Anatis ocellata* (55 %), which like *Neomysia oblongoguttata* (13 %) is not as typical of coniferous trees, as some of the other species which follow. *Adalia conglomerata*, which is the most typical inhabitant of spruce forests, accounted for 23 % of all larvae, and *Aphidecta obliterata*, which perhaps also prefers spruce, formed only 5.5 %. The rather eurytopic *Exochomus quadripustulatus* accounted for nearly 3 %. Three remaining species were apparently caught accidentally and together formed less than 1 %.

Alder. — (see 5.21).

5.52 Orchards, groves

Apple. — Palaearctic region. — Data on apple orchards are relatively abundant (Tab. 5.07), especially from western Germany: from near Hamburg (N = 739) (Speyer 1935), from near Köln (Redenz-Rüsch 1959), and from near Stuttgart (Asgari 1966). A striking difference between the data of Speyer and Redenz-Rüsch is the abundance of *Adonia variegata* (27.5 %) in the apple orchards near Hamburg. This typical inhabitant of herbaceous plants in drier places is absent in the samples of all other authors even in other countries. The only likely explanation is that during the sampling, which was in late season (VIII.—IX. 1934), the coccinellids temporarily invaded the orchard from adjacent fields, in which the crop had been harvested or was lacking aphids. Speyer's other aberrant result is a low incidence of *Propylaea quatuordecimpunctata* (1.7 %) which is usually quite abundant in orchards. The high incidences of *Adalia bipunctata* (38.5 %), *Coccinella septempunctata* (15.5.%) and *C. quinquepunctata* (14.5 %) are quite typical, although Redenz-Rüsch (1959) gives a much lower incidence of *C. quinquepunctata* (+) in comparison with *C. septempunctata* (+++). There are also variations in the incidence of *Adalia decempunctata*, rather abundant near Köln (++) and rare near Hamburg (1.3 %). *Stethorus punctillum* is absent in both places, Redenz-Rüsch (1959) reports rather high numbers of *Scymnus bipunctatus* (++). The rich occurrence of *Calvia quatuordecimguttata* near Köln is apparently caused by the proximity of forest (see below — Novák unpubl.).

Asgari (1966) listed natural enemies of *Aphidula pomi* in apple orchards around Stuttgart — Hohenheim without stating their abundance. His list contains seven likely species (*Coccinella septempunctata*, *Adalia bipunctata*, *A. decempunctata*, *Propylaea quatuordecimpunctata*, *Harmonia quadripunctata*, *Coccinula quatuordecimpustulata* and *Calvia quatuordecimguttata* but also seven non-existent species (*Coccinella 12-punctata*, *C. 12-maculata*, *C. quadrimaculata*, *C. 10-maculata*, *C. bimaculata*, *C. 6-punctata*, *C. 10-pustulata)* ! (The last three are presumably aberrations of *Adalia decempunctata*). Therefore even his statement that *Coccinella septempunctata* is the most abundant as well as the most voracious coccinellid preying on *A. pomi* must be questioned, especially as it is unsupported by any numerical data.

That *A. bipunctata* and *C. septempunctata* are present in apple orchards is confirmed by other workers in northern, southern and western Europe, but from their papers certain contrasts also emerge. Kanervo (1962) failed to find *P. quatuordecimpunctata* in Finland, and reported a relatively high occurrence of *Calvia quatuordecimguttata* (++) and *Coccinella quinquepunctata* (++). In orchards near Ferrara in Italy and in the Netherlands near Wageningen, *P. quatuordecimpunctata* was present (Principi et al. 1967, Evenhuis 1968). Both in Italy and in the Netherlands *C. quinquepunctata* was absent.

Novák (unpubl.) sampled the coccinellids in apple orchards at two localities in northern Bohemia, Czechoslovakia (N = 3345) for three years. At Holovousy, a mixed deciduous forest was adjacent to the orchards, whereas at Podsedice the orchard was situated in an open area.

The difference in the setting of the orchards is clearly reflected in the high incidence in the Holovousy orchards (11.5 %, contrast 0.1 % at Podsedice) of *Calvia quatuordecimguttata*, a typical inhabitant of deciduous forests. The less open surroundings caused the orchard at Holovousy to be understandably more visited by *Adalia bipunctata* (30.2 %, contrast 4.5 %) and *A. decempunctata* (4.6 %, contrast 0.4 %). The tenfold higher abundance of *Coccinella quinquepunctata* in Holovousy can be related to the neighbouring forest providing a dormancy site of this species, which often hibernates in the litter at forest edges. At Podsedice, by the far most numerous species was *Stet-*

Tab. 5.07 Coccinellids in apple orchards (and the average from five fruit-orchards in the Ukraine)

Coccinellid species	Germany			Finland	Italy	Holand	Czechoslovakia		Ukraine (USSR)
	Speyer 1935 N = 739	Redenz-Rüsch 1959	Asgari 1966	Kanervo 1962	Principi et al. 1967	Even-huis 1968	Novák Holo-vousy 1968—69 N=1637	(unpubl.) Podse-dice 1969—70 N=1708	Dyadech-ko 1954 N=1081
Subcoccinella vigintiquatuorpunctata								2.3	
Stethorus punctillum				++			5.4	61.2	17.2
Scymnus (Pullus) subvillosus									8.5
Scymnus (Nephus) bipunctatus		++							
Hyperaspis campestris									5.1
H. reppensis									1.3
Hippodamia septemmaculata		+							
Adonia variegata	27.5							0.1	1.9
Semiadalia undecimnotata									9.6
Adalia decempunctata	1.3	++	+			+	4.6	0.4	7.1
A. bipunctata	38.5	+++	+	++	+	+	30.2	4.5	24.4
Coccinella septempunctata	15.5	+++	+	+++	+	+	8.1	3.9	0.6
C. quinquepunctata	14.5	+		++			33.5	3.0	
Coccinula quatuordecimpustulata		+	+						
Synharmonia conglobata						+	0.7	0.2	
Calvia quatuordecimguttata		++	+	++			11.5	0.1	
Propylaea quatuordecimpunctata	1.7	++	+		+	+	4.2	20.4	1.8
Anatis ocellata								0.2	
Thea vigintiduopunctata								1.3	
Chilocorus renipustulatus									5.4
C. bipustulatus									1.5
Exochomus quadripustulatus		+				+			13.9
E. flavipes									1.6
Other species	1.0						1.8	2.2	

horus punctillum (61.2 %) which was ten times less abundant at Holovousy (5.4 %), although the occurrence of *Panonychus ulmi* was approximately the same at both localities. The second dominant species at Podsedice was *Propylaea quatuordecimpunctata* (20.4 %) and all other species were far less abundant.

The fivefold difference in the occurrence of *P. quatuordecimpunctata* at the two localities is apparently due to some hitherto unknown microclimatic preference of this species, which is commonly considered as eurytopic (Dyadechko 1954) or ubiquitous (Horion 1961). Its somewhat higher incidence in more humid localities, mentioned by Bielawski (1959), seems to receive support from Dyadechko's (1954) data. In his samplings from the Ukrainian SSR, *P. quatuordecimpunctata* was completely missing in field habitats, was rare in orchards (1.8 %, in 3 out of 5 orchards missing completely) but rather abundant in deciduous forests (occurring, however, more frequently in the steppe-zone — 16 %, than in the forest-steppe zone — 7 %). It cannot be excluded that in an area with both forests and orchards it may be more abundant in the forests because these are the more humid environment, whereas in an area with no forests at all, it may prefer orchards as more humid than fields. These considerations again stress how necessary it is to study the incidence of such mobile insects as coccinellids in neighbouring habitats also. As the food ecology of *P. quatuordecimpunctata* has not been sufficiently studied, there is the possibility that it is able to maintain itself on psyllids in the absence of aphids better than the other coccinellid species.

Dyadechko (1954) reported on the occurrence of coccinellids in Ukrainian orchards of all kinds. From a general picture produced by five samples from four localities (Kiev, Chernovcy, Odessa, Kherson) on different dates (5.6.—3.8.), three species appear prevalent: *Adalia bipunctata* (24 %), *Stethorus punctillum* (17 %) and *Exochomus quadripustulatus* (14 %). Dyadechko (1954) further lists those species he regards as typical for orchards: *Adalia decempunctata* (7 %), *Scymnus* (*Pullus*) *subvillosus* (8.5 %), *Chilocorus bipustulatus* (1.5 %), *Hyperaspis reppensis* (1 %) and *H. campestris* (5 %). Although he caught quite a number of *Semiadalia undecimnotata* (10 %), he si certainly quite right not to include this species into his list of typical inhabitants of orchards.

The data of Hukusima (1963a, b, 1966a, b) on the influence of various pesticides on the fauna of orchards give some idea about coccinellids on apple trees in Japan. He collected more than 1500 coccinellids, about 300 of them in unsprayed controls. The three dominant species were *Chilocorus kuwanae* (28 % and 26 %[1]), *Stethorus japonicus* (26 % and 11 %) and *Propylaea japonica* (21 % and 32 %). *Harmonia axyridis*, which accounted for only 11 % in the total catch, was relatively much more abundant in the unsprayed plots (21 %). *Scymnus hilaris* accounted for 10 and 9 %, while *Coccinella septempunctata bruckii* was very rare (2 and 1 %).

Nearctic region. — In the apple orchards of Canada the Holarctic *Adalia bipunctata* is accompanied by several Nearctic species: *Coccinella transversoguttata quinquenotata*, *C. novemnotata*, *C. trifasciata perplexa* and *Hippodamia parenthesis* have been found in the Belleville area of Ontario (Smith 1958). Evenhuis (1960) mentioned only two species from Nova Scotia, *C. transversoguttata quinquenotata* and *A. bipunctata*.

Peach. — Putman (1964) reported ten species from the peach orchards of the Niagara Peninsula (Ontario, Canada). *Adalia bipunctata* was by far the most abundant (46 %), the next frequent were: *Coccinella trifasciata perplexa* (22 %), *Coleomegilla maculata lengi* (12 %), *Coccinella transversoguttata richardsoni* (8 %), *Hippodamia tredecimpunctata tibialis* and *Coccinella novemnotata* (3 %). Thus the coccinellid fauna of peach orchards

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[1] Two percentages are given, the one from the sprayed plots, followed by that of the unsprayed plots.

differs from apple orchards, as reported by Smith (1958), only by the presence of *C. m. lengi* and *H. t. tibialis*.

Pear. — Thirteen species of *Coccinellidae* were collected in southern Oregon in pear orchards infested with *Psylla pyricola* (Westigard et al. 1968). Six species accounted for the majority taken: *Coccinella transversoguttata richardsoni*, *Scymnus marginicoelis*, *Hippodamia convergens*, *Olla abdominalis*, *Cycloneda polita* and *Stethorus picipes*. Only the first species is in common with the coccinellid fauna of East Canadian orchards (apple, peach).

Walnut. — *Hippodamia convergens* (42 %) and *Olla abdominalis* (53 %) were the most abundant (N =905) coccinellid species in walnut orchards in northern California infested by *Chromaphis juglandicola* (Sluss 1967). Both breed in the orchards. *Adalia bipunctata* adults were much less abundant (4 %) and its larvae were never found on the trees, although some pupae were present. *Hippodamia quinquesignata punctulata* was very rare. *O. abdominalis* was reported from the same habitat and prey by Essig (1912).

Citrus groves. — Palaearctic region. — Both sets of data available from Japan come from the isle of Honshu. Nakao (1962, 1964) found nine predatory coccinellids in citrus groves near Fukuoka, where three important pests were present: *Aphis citricidus*, the coccid *Unaspis yanonensis* and the mite *Panonychus citri*. The most abundant predators were *Scymnus hareja*, *Telsimia nigra* and *Chilocorus kuwanae*. The prey-predator relations are depicted in Fig. 5.07. Other predatory coccinellids present but less abundant were: *Scymnus hilaris*, *S. dorcatomoides*, *Stethorus japonicus*, *Hyperaspis japonica*, *Rodolia cardinalis* and *Propylaea japonica*.

In the citrus groves of the Yamaguchi Prefecture, Nohara (1963) found 23 species of *Coccinellidae;* all were entomophagous with the exception of the apparently mycophagous *Thea cincta*. Eight species were important predators: *Scymnus hilaris* and *Hyperaspis japonica* reported as aphidophagous, *Propylaea japonica* both aphidophagous and coccidophagous, *Stethorus japonicus* both coccido- and acarophagous, and four other species coccidophagous (*Rodolia cardinalis*, *Scymnus hareja*, *Telsimia nigra*, *Chilocorus kuwanae*). The coccid pest *Unaspis yanonensis* was reported as being controlled by the coccinellids though apparently aphids and mites were also present. Although the prey-predator relationships differ, the lists of coccinellid species given by Nohara and Nakao are identical, with the exception that *S. dorcatomoides* is not mentioned by Nohara.

In Israel the most important predator of citrus scale insects is *Chilocorus bipustulatus* (Rosen and Gerson 1965, Ben Dov and Rosen 1969).

Nearctic region. — In Florida, USA, Muma (1953—1955) found a number of predaceous coccinellids in citrus groves. Their predator/prey relations are given in Fig. 5.08. Apart from the species included there, some others were collected which were less abundant. The introduced *Cryptolaemus montrouzieri*, feeding on mealybugs was not common on citrus. *Delphastus pallidus* a predator of *Aleyrodidae* could be found in relatively large numbers, though only for a short time. *Scymnillodes subtropicus* which also feeds on white flies was rare together with an incidental predator of scale insects and white flies, *Scymnillus aterrimus*. *Decadiomus bahamicus* which feeds on mealybugs was found only in one region, as was the aphidophagous *Leis dimitata quinquespilota*, introduced from California in 1925. The aphidophagous *Scymnus partitus*, once common, has apparently decreased in numbers and was found only in late summer and early autumn.

Neotropic region. — From southern Brazil, Wille (1926) reported *Curinus (Orcus) zonatus* as the most important coccidophagous species.

In **date palm** plantations in Israel (Kehat 1967a), four *Pharoscymnus spp.* (*numidicus, setulosus, ovoideus, pharoides*), *Chilocorus bipustulatus, Rhizobius* (*Lindorus*) *lophantae* and *Scymnus* (*Nephus*) *bipunctatus* were found reproducing. Three other coccinellids were found frequently as adults only (*Exochomus flavipes, Scymnus* (*Pullus*) *pallidivestis, Stethorus punctillum* and 15 occasionally.

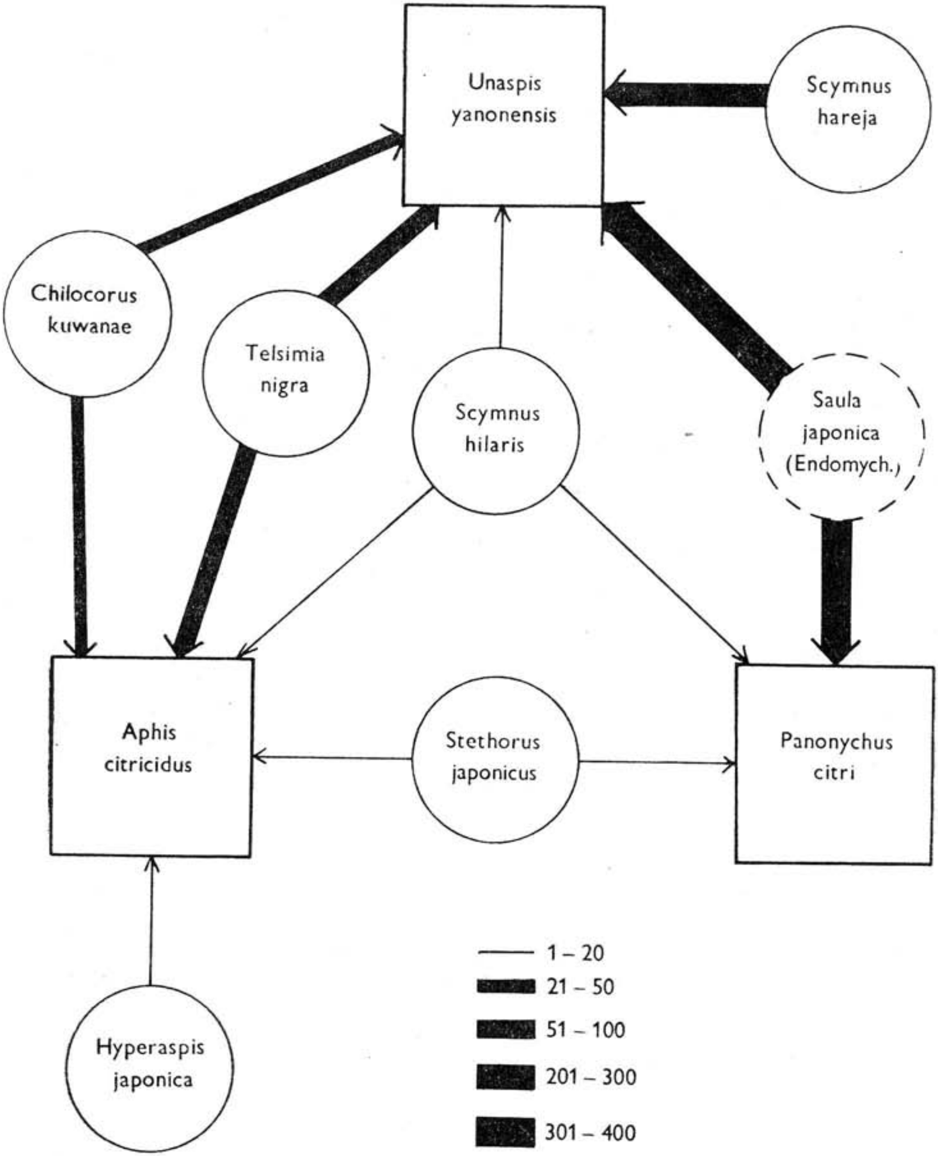

Fig. 5.07 Coccinellid predators (○) of the three most important pests (□) of citrus in Japan (Nakao 1964). The width of arrows shows the numbers of adult predators in Tachibana.

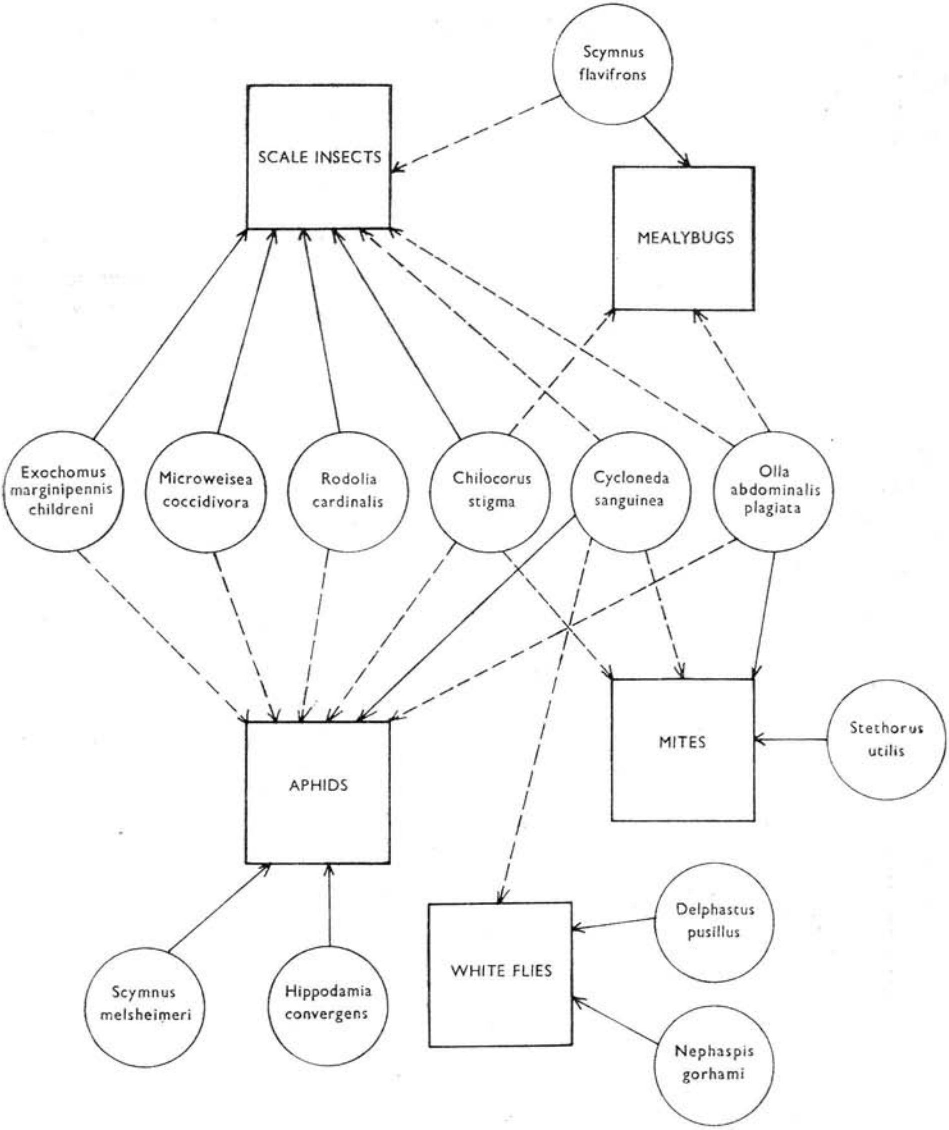

Fig. 5.08 Coccinellids and their common (———) and incidental prey (— — —) in citrus groves of Florida (after data by Muma 1953–54, 1955a).

5.53 Field crops

Cereal crops. — Palaearctic region. — In the Ukraine, *Adonia variegata* and *Coccinella septempunctata* are the typical species of cereal fields (Dyadechko 1954). In the steppe zone *C. quinquepunctata* seems to be absent in cereal crops and to be replaced by the south-palaearctic *Semiadalia undecimnotata* (Tab. 5.08).

Nearctic region. — In the USA, the most important species on corn and other cereals are *Hippodamia convergens*, *H. tredecimpunctata* and *Coleomegilla maculata* (Tab. 5.09). Their abundance varies significantly, as is shown by the data from corn in two neighbouring states (Minnesota, North Dakota). In the area of Belleville, Ontario, Canada, two *Coccinella spp.*, forming almost half of the specimens collected, were found in addition to the range of species observed in the USA, while *Hippodamia convergens* was only scarce (Smith 1971).

Tab. 5.08 Coccinellids on cereal crops in the Ukraine (USSR) (Dyadechko 1954)

Coccinellid species	corn Odessa (July) N = 135[1] [%]		oats Sumy region (July) N = 166[1] [%]		winter wheat Kiev (June) N = 180[1] [%]	
Scymnus frontalis					10.6	—
S. apetzi	16.3	+				
Hippodamia tredecimpunctata					6.1	—
Adonia variegata	30.4	+	21.1	+	55.0	+
Semiadalia undecimnotata	23.0	+				
Coccinella septempunctata	10.4	+	40.4	+	11.7	+
C. quinquepunctata			21.7	+	9.4	?
C. divaricata	11.9	—	16.9	+	2.8	—
Coccinula quatuordecimpustulata	8.1	—			4.4	+

[1] + denotes presence, — absence of larvae.

Tab. 5.09 Coccinellids on cereals (Nearctic region)

Coccinellid species	corn Smith 1958 Ontario	corn Schiefelbein & Chiang 1966 Minnesota [%]	sweet-corn Havnvik & Frye 1969 N. Dakota N = 617 [%]	corn Smith 1971 Ontario [%]	cereal crops Kieckhefer & Miller 1967 S. Dakota	oats Shade et al. 1970 North Indiana
Coleomegilla maculata	+	31.0	0.2	17[5]		+++
Hippodamia convergens	—	62.0	18.0	<1	+[1]	+++
H. glacialis				<1	+[3]	
H. parenthesis	—		0.8	2	+[2]	+
H. tredecimpunctata	+	6.7	76.0	32[5]		+
Cycloneda munda						
Anatis mali				<1		
Coccinella novemnotata	+			20[5]		+
C. nivicola			2.5			
C. trifasciata	+			5		
C. transversoguttata	+			24[5]		
Adalia bipunctata	—		2.5	<1	+[4]	

[1] [2] [3] [4] — The numbers denote the approximate order of numerical importance.
[5] — Reproducing on the corn field infested with *Rhopalosiphum maidis*.

Alfalfa. — Palaearctic region. — In eastern European fields of *Medicago*, which coccinellid species are dominant, is apparently related to air humidity (Tab. 5.10). Whereas *Propylaea quatuordecimpunctata* is by far the most abundant species in the zone of deciduous forests in Poland (Ruszkowski 1961), the species disappears completely in the alfalfa fields in both the forest-steppe and steppe zones of Ukraine (similarly as *C. quinquepunctata*) and the dominant position is taken over by the two south-palaearctic *Coccinula spp.*, which have a clear preference for dry environments (Dyadechko 1954).

Nearctic region. — The commonest coccinellid on alfalfa all over the USA is *Hippodamia convergens* (Tab. 5.11). Only in rather older records from Utah (Knowlton et al. 1938) are other three species similarly abundant.

Potato. — Palaearctic region. — Four common species form the bulk of the coccinellid fauna in potato fields in Czechoslovakia and Poland (Tab. 5.12): *Adonia variegata*, *Coccinella septempunctata*, *C. quinquepunctata* and *Propylaea quatuordecimpunctata.*

Sugar-beet. — Palaearctic region. — In Central Europe, the same four species are most abundant in sugar-beet (Tab. 5.13). In a dry and warm region (near Louny), however, *P. quatuordecimpunctata* is replaced by the south-palaearctic *Semiadalia undecimnotata.* In the Ukraine, there is apparently a similar climatic variation as occurs on alfalfa. In the moist oceanic climate of southern England *C. septempunctata* disappears and the dominant position is taken over by *Adalia bipunctata* which in continental Europe is a typical inhabitant of orchards, parks or edges of deciduous forests.

A general abundance of *A. bipunctata* in field crops has also been reported by Banks (1955) from beans in Hertfordshire and by Dunn (1960) from lettuce in Warwickshire. The distinct changes in habitat preferences between regions with different climate (e. g. typical continental climate of the Ukraine, the transition climate of central Europe, the oceanic climate of England) apparently reflect a distinct preference for particularly microclimatic conditions (most probably for different relative air humidity). As has already been stressed in chapter 5.22, there is a great lack of exactly that type of study which could elevate the subject of habitat preferences of individual species to a level of cause and effect.

Tab. 5.10 Coccinellids in the alfalfa fields (Palaearctic region)

Coccinellid species	Ukraine (USSR)		Poland (Lublin Poznan)
	steppe (Kherson) N = 147 Dyadechko 1954 [%]	forest-steppe (Chernovcy) N = 150	N = 128 Ruszkowski 1961 [%]
Subcoccinella vigintiquatuorpunctata		4.7	
Scymnus frontalis	6.1	22.7	
Hippodamia tredecimpunctata			4
Adonia variegata	18.4	19.3	
Adalia bipunctata			1
Coccinella septempunctata	15.0	8.7	21
Coccinella quinquepunctata			8
Coccinula quatuordecimpustulata	50.0	42.0	11
Coccinula sinuatomarginata	10.9	2.7	
Propylaea quatuordecimpunctata			55

Tab. 5.11 Coccinellids on alfalfa fields (Nearctic region)

Coccinellid species	Utah				Kansas	California	South. California	Ontario	Massachussetts
	1937			Delta 1956	Manhattan 1958	Imperial Valley 1954—55		Belleville	
	Knowlton et al. 1938 [1] [%]	Knowlton 1939 [1]	Knowlton & Goodarzy 1956	Goodarzy & Davis 1958 [%]	Simpson & Burkhardt 1960 [%]	Dickson et al. 1955 [%]	V. d. Bosch et al. 1959	Smith 1958	Yadava & Shaw 1968
Coleomegilla maculata lengi					11.2			+	+
Ceratomegilla vittigera	5.5	+							
Cycloneda munda	4.8	+			1.7				
C. sanguinea						14.9		+	
Hippodamia convergens	13.0	+	+	54.9	82.0	85.1	+	—	+
H. glacialis glacialis					0.6				
H. parenthesis	4.3	+	+	9.4	3.9		+	+	+
H. sinuata disjuncta			+	17.4			+		
H. americana	14.0	+							
H. apicalis	13.0	+	+						
H. lecontei	7.2	+							
H. quinquesignata	7.1						+		
H. tredecimpunctata	3.3	+						+	
H. pleuralis			+						
Olla abdominalis			+						
Coccinella novemnotata	3.3	+	+	3.8				+	+
C. transversoguttata	15.5	+	+	6.1				+	+
C. trifasciata perplexa								+	+
Adalia bipunctata		+							
Other species				8.5					

[1] Pea and alfalfa fields infested with *Macrosiphum pisi*.

Tab. 5.12 Coccinellids in potato fields

Coccinellid species	England Dunn 1949	Czechoslovakia		Poland Galecka 1966	
		western Bohemia Skuhravý & Novák 1957 N = 461	western Slovakia Korbel unpubl. N = 260	unwooded area	near forests
Hippodamia redecimpunctata			0.4		+
Adonia variegata		23.2	26.5		+
Adalia bipunctata	±	1.3			+
Coccinella septempunctata	+	5.4	54.2	+	+
Coccinella quinquepunctata		12.8	0.4	+	+
Coccinella undecimpunctata			1.9		
Coccinula quatuordecimpustulata			1.5		+
Propylaea quatuordecimpunctata		57.2	15.0	+	+

Tab. 5.13 Coccinellids in sugar-beet fields

Coccinellid species	W. Germany (Göttingen) seed sugarbeet Sol 1961	Czechoslovakia			Ukraine (USSR) (Rostov)	S. England
		central Bohemia	northern Bohemia	Bohemia + Slovakia	Minoranskiĭ 1966	Heathcote 1969
		Hodek et al. 1966				
	N = 57	N = 126 [%]	N = 69 [%]		1)	2) [%]
Adonia variegata		0.8	2.9	+	+	
Semiadalia undecimnotata			46.3	+		
Adalia bipunctata	+			—		50
A. decempunctata	+			—		6
Coccinella septempunctata	+	46.8	30.4	+++	+	1
C. quinquepunctata		47.6	20.2	++		
Propylaea quatuordecimpunctata	+	4.8		++		26

1) The aphid pest was not *Aphis fabae*, as in other cases. but *Pemphigus fuscicornis*.
2) Coccinellids were caught in traps 1.5 m above the ground (not on plants).