7 DORMANCY

7.1 The adaptive function of diapause

On most land surfaces, periods which are favourable for growth and morphogenesis alternate with unfavourable periods. In insects (as in other animals and plants) this has led to the evolution of appropriate annual life - cycles. The period of favourable environmental conditions (i. e. sufficient food and suitable physical factors) must be utilized for active life, i. e. for growth and development (of preimaginal stages and adults) made possible by adequate feeding. It is advantageous for a species to bridge the unfavourable period in a more or less inactive state in a stage which in some way has an increased survival potential. The presence of reserves and a reduced metabolic rate makes survival possible over a long period without feeding; different adaptations increase resistance to unfavourable physical conditions.

At first, workers mainly considered only the aspects concerned with resistance to drastic changes in climatic factors, especially the cold winter period in temperate climates. This is indicated by the introduction of general terms for hibernation and hibernation quarters in all languages (zimovka; overwintering; Überwinterung. Winterschlaf; l'hivernation). These terms are often misleading because they are commonly used for dormancy, which begins in late summer and ends in spring. Some coccinellid species, however, already enter their 'hibernation' quarters in late July! In this connection an assumption also arose that the main aim of diapause is to increase **frost-resistance**, This assumption has largely been abandoned. It appears in fact that gradual cooling gradually increases cold resistance, and that a series of arctic insects survive the winter successfully in a simple quiescence without entering diapause (Downes 1965).

Only more recently has there been a stronger emphasis on the need for a **synchronization** of the occurrence of the feeding stages with periods of sufficient food, although resistance to adverse conditions is a necessary corollary. This is the substantial purpose of diapause "during which the resistance to adverse climatic conditions is increased by physiological and sometimes morphological features fitting together into an 'adaptation syndrome' varying from species to species" (De Wilde 1970). Diapause is necessary so that morphogenesis (i. e. the maturation of ovaries in coccinellids, which almost always only have an imaginal diapause) shall be arrested in time, before there is a lack of food: diapause is therefore most necessary for the period during which climatic conditions alone would in fact allow morphogenesis to continue. In this sense the function of diapause is finished, for example, in temperate climates once the temperature has fallen below the level necessary for development and reproduction. In general, in those insects where this problem has been investigated, diapause has been found to be terminated in December or January.

By and large, the timely inhibition of morphogenesis (prevention of maturation in adults) in insects is governed by a series of signals from the environment. Decrease in temperature or the physiological ageing of host-plants is not repeated with such regularity year after year as are changes in day-length. Therefore, it is photoperiod¹) which most often serves as the signal, often called 'seasonal token'.

7.2 Anatomical and chemical changes in dormant Coccinellidae

7.21 Anatomical changes

A greatly enlarged **fat body** is a conspicuous feature of diapausing coccinellids of both sexes, and this has been reported in all species observed, as well as the fact that the digestive tract becomes emptied of food. The **mid-guts** of adults of *Coccinella novemnotata* that were feeding on aphids were distended, thin walled, semitransparent, and packed with green aphid parts. In contrast, the mid-guts of beetles that had attained the stage of dormancy were reduced to whitish, opaque, thick-walled tube that contained a brown fluid (Mc Mullen 1967a).

The **ovaries** which in most cases do not develop beyond the stage of mere germaria, stop developing in diapausing females (Photos 17, 18). Such a situation has been recorded in *Coccinella septempunctata* (Hodek and Čerkasov 1961, Hodek 1962a, Hariri 1966), in *Semiadalia undecimnotata* (Hodek and Landa 1971), in *Adalia bipunctata* and *Propylaea quatuordecimpunctata* (Hariri 1966), in *Coccinella novemnotata* (McMullen 1967a) and *Hippodamia convergens*. The situation in the genus *Chilocorus* is rather different. For *C. renipustulatus*, Pantyukhov (1965, 1968a) describes that the majority of females diapause with ovaries in which development was blocked at quite an early stage (this condition is not defined); in about 7 % of the females development is stopped even earlier and follicles are completely missing. The females with no follicles have a substantially longer longevity, by 1 — 2 months in the laboratory, than those where some development has occurred. The situation is probably similar in *C. bipustulatus* and *C. geminus*. Zaslavskiï and Bogdanova (1965) report that in some diapausing females of these two species, the development of the ovarioles is inhibited at the stage where only one follicle is formed. The diameter of this follicle is, however, not larger than the diameter of the germarium, although yolk is deposited in the oocyte.

It is at the end of dormancy in spring, often still at dormancy sites while no food is taken, that previtellogenesis and the formation of the first oocyte occurs, e. g. in *A. bipunctata* (Hariri 1966) and in *S. undecimnotata* (Tab. 7.01) (Hodek and Landa 1971). In *C. septempunctata* and *P. quatuordecimpunctata*, Hariri (1966) states that this stage can only be reached after the beetles have emerged from hibernation and have fed on aphids.

The females of *Stethorus punctillum* often live for 2 years and enter a second dormancy. The mature ovaries are largely resorbed and the metabolic reserves are re-accumulated in the enlarged fat body. This resorption of ovaries even occurs during the first hibernation of those females which have emerged from pupae early in the season (before late July) and have already oviposited in that season (Putman 1955). This latter

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¹) Duration of light period = photophase and dark phase = scotophase within 24 hours.

Tab. 7.01 Gonads in dormant *Semiadalia undecimnotata* (Hodek and Landa 1971)

Date of sampling¹)	Ovaria		Spermatheca		Testes²) spermatocytes in testicular follicles	
	without egg chambers	with one oocyte	without sperm	with sperm	absent	present
23.10.57	20	—	(17)	(3)	20	—
16.12.57	20	—	20	—	20	—
11.2.58	20	—	20	—	20	—
8.4.58	30	—	30	—	20	—
23.4.58	20	—	18	2	11	9
29.4.58	20	—	12	8	7	13
5.5.58	20	—	4	16	—	20
13. 5.58	10	10	—	20	—	20
19. 5.58	7	13	—	20	—	20

¹) All samples collected in Louny-hills (northern Bohemia).
²) Vesiculae seminales always full of sperm.

situation may be expected to apply in every polyvoltine cycle (or at least partly bivoltine), as occurs in *C. septempunctata* (Hodek 1962a). It is also unlikely that a second hibernation is an exceptional event; it has been proved to occur in *P. quatuordecimpunctata* by Hariri (1966) in England, in *C. septempunctata* by Sundby (1968) in Norway, and in two species (*Harmonia axyridis* and *Aiolocaria mirabilis*) introduced to central Asia from the Far East (Savoiskaya 1970b, d).

In males, the activity of the follicular tissue in the **testes** already starts in the pupa, and, moreover, does not stop in diapausing individuals. In *S. undecimnotata* (Hodek and Landa 1971) both spermatogenesis and spermateliosis proceed during the first, warmer period of dormancy (Tab. 7.01) (Photos 19—22). Only during the cold period (November — March) are the testicular follicles mostly empty and there is only a cluster of spermatogonies ("apical cells") at their distal tip and there is a mass of sperm bundles (spermatodesms) in the proximal third of their lumen. In April, spermatogenesis is resumed. In the seminal vesicles, the viable spermatozoids are permanently stored. Copulation takes place before the beetles emerge from the dormancy sites, so that all females disperse with a reserve of spermatozoids in their spermathecae.

This process, although it has not been studied in detail in other species, seems to be similar in *C. septempunctata* (Hodek and Čerkasov 1961, Hodek and Landa 1971) and in *A. bipunctata* (Hariri 1966) where its passage is indicated by changes of dimensions: the diameter of testes is least during the winter months and increases in the spring. Mating activity just prior to dispersing from aggregation has also been reported in California for *Hippodamia quinquesignata punctulata, H. sinuata*, and *H. parenthesis* (Hagen 1962). Well developed testes in *Hippodamia convergens* in dormancy sites have been reported by Stewart et al. (1967).

For *Chilocorus bipustulatus* and *C. geminus*, Zaslavskiĭ and Bogdanova (1965) similarly did not ascertain any effect of conditions inducing diapause on the state of testes. Gametogenesis evidently ceases very early in the life of both these species because it was very difficult to find mitotic divisions in active or diapausing males older than 7—10 days.

The presence of spermatozoa in the spermathecae of some *C. septempunctata* females in autumn (Hodek and Čerkasov 1961) and particularly the fertilization of females by males kept under diapause conditions, observed in *C. septempunctata* by Bonnemaison (1964) and in *S. punctillum* by Putman (1955), both would suggest that the activity of the male accessory glands is also independent of diapause.

It has been proved experimentally in *S. undecimnotata* and *C. septempunctata* that the activity of the testicular follicles depends on the ambient temperature; under favourable temperature conditions it may be continued or resumed, at least if alternative food (e. g. honey solution) is provided. At a temperature around +12 °C the males can embark on a normal and gradual decrease in gonad activity (Hodek and Landa 1971).

7.22 Changes in chemical composition

7.221 Lipids

Diapausing insects typically show an increased fat content (Lees 1955, Hodek and Čerkasov 1963, Beck 1968). Their survival during dormancy largely depends on the amount of metabolic reserves they can accumulate before diapause.

In many coccinellids the deposition of reserves in the fat body is quite extensive. A hypertrophied fat body is always mentioned in diapausing coccinellids. Numerical estimates based on biochemical analysis of the amount of fat accumulated are, however, given only for 6 coccinellid species (Tab. 7.02).

The data for *C. septempunctata* indicate that in the laboratory slightly less fat is accumulated than in the field (Hodek and Čerkasov 1961). Females, sampled in the hibernation sites in early October, when an important proportion of the reserves must already have been utilized, still had 0.205 mg of lipids per mg total weight. Females, in which an "artificial" diapause had been induced (by 12 hrs light and a constant 18 °C) had 20 % less lipids — 0.164 mg.

The usual way in which lipid contents are stated as a percentage of dry weight is not very suitable for following changes during dormancy. It is better to express fat content (and also other components) in absolute values of weight per specimen. In this way, changes in individual components become mutually independent.

We can compare both these ways of expression in Tab. 7.02. While the fat content in *S. undecimnotata* in reality decreased substantially from late August to late October, e. g. in males from 6.4 to 3.6 mg, i. e. by 44 %, this decrease is hardly reflected in the relative expression: the initial 41 % fat of dry weight only fallsot 38 % dry weight over the same period. The substantial decrease of fats is masked by the decrease of other components of dry weight.

All aphidophagous coccinellids that have been studied enter hibernation with considerable amounts of fat. In *Semiadalia undecimnotata* 6 — 7 mg of fat per beetle were recovered, i. e. about 40 % of dry weight (Hodek and Čerkasov 1963). As the first sample for analysis was taken as late as one month after the arrival of the beetles in the winter quarters, it may be supposed that the initial fat content, especially before migration, was even substantially higher. The comparison of our results with those in the literature shows that *S. undecimnotata* has the highest relative fat content of all the insects which have been analysed. Hariri (1966c) ascertained similarly high values in 3 further species of aphidophagous coccinellids: 5 — 9 mg fat in *Coccinella septempunctata*, 1 — 3 mg in *Adalia bipunctata* and 1—2 mg in *Propylaea quatuordecimpunctata*. The fat content of these three species ranged from 37 to 48 % dry weight at the beginning of diapause. On the other hand, the coccidophagous *Chilocorus rubidus* only has 26.5 % fat of dry weight at the beginning of hibernation (Pantyukhov 1968b) and

Tab. 7.02 Fat content in dormant and active *Coccinellidae*

Coccinellid species	Amount of fat in	Dormant beetles										Active beetles							Reference
		Origin of sample	Changes in fat content									Origin of sample	Changes in fat content						
Coccinella septempunctata	mg/mg of total weight	natural hibernacula N. Bohemia	Date	10/10	9/5														Hodek and Čerkasov (1961)
			♂	0.21	0.11														
			♀	0.21	0.11														
		labor. culture (12hr, 18°)	♀	0.16								labor. culture (18hr, 18°)	♀ 0.07						
	mg/beetle	artificial hibernacula S. England	Date	17/9	17/11	2/3	5/5					feeding on aphids	Date	12/6					Hariri (1966c)
			♂	5.3	4.4	3.3	2.7						♂	1.8					
			♀	9.4	7.6	5.8	3.7						♀	2.5					
Semiadalia undecimnotata	mg/beetle	natural hibernacula N. Bohemia	♂	6.4	5.7	4.2	3.6	2.2	1.6	1.5	1.2								Hodek and Čerkasov (1963)
			♀	7.2	6.1	5.4	4.1	2.9	1.9	2.4	1.7								
	% of dry weight		Date	29/8	11/9	25/9	22/10	2/4	16/4	29/4	9/5								
			♂	41	47	36	38	30	25	21	17								
			♀	38	51	44	37	34	25	27	18								
Adalia bipunctata	mg/beetle	artificial hibernacula S. England	Date	15/8	14/9	13/11	9/2	7/4	4/5			feeding on aphids	Date	May					Hariri (1966c)
			♂	2.0	1.4	1.2	0.9	0.7	0.5				♂	0.7—0.9					
			♀	3.1	2.1	1.5	1.2	0.9	0.4				♀	0.8—1.1					
		natural hibernacula S. England	Date	16/10	22/12	28/3	23/4												
			♂	1.9	1.0	0.8	0.4												
			♀	2.1	1.8	1.1	0.9												
Propylaea quatuordecimpunctata	mg/beetle	artificial hibernacula S. England	Date	17/9	17/11	2/3	15/5					feeding on aphids	Date	10/6	8/8				Hariri (1966c)
			♂	1.4	1.1	0.9	0.4						♂	0.7	1.6				
			♀	2.0	1.5	1.2	0.8						♀	0.8	2.0				
Chilocorus renipustulatus	% of dry weight	labor. beetles in artificial hibernacula	Maikop	20	18	17	17	16	15	13		labor. culture	Maikop	10	16	19	11		Pantyukhov
			Date	30/10	28/11	30/12	30/1	28/2	28/3	29/4			Age [days]	1	15	40	75		
			Leningr.	20	19	17	16	16	15	13			Leningr.	10	16	19	9		(1965)
		labor. culture	Age [days]	21	30	40	50	75											
				23	24	25	24	21											(1968a)
Chilocorus rubidus	% of dry weight	natural hibernacula (Leningrad)	Date	15/9	30/10	30/11	30/12	28/2	30/3	20/4		labor. culture	Age [days]	1	15	30	45	60	Pantyukhov (1968b)
				27	25	24	23	22	21	18				12	18	20	27	27	

C. renipustulatus 25 % (Pantyukhov 1968a). The latter results come from individuals reared in the laboratory. Earlier experiments with this species yielded even less fat (20 %) (Pantyukhov 1965).

Rate of decrease. — The decrease in the substantial fat reserves during hibernation is also substantial: during the eight months of dormancy the absolute amount of fat decreases to a mere quarter in *S. undecimnotata*. The decrease is half as great in the pentatomid bug *Eurygaster integriceps* and a quarter as great in the chrysomelid *Leptinotarsa decemlineata*, which are both dormant in the soil and thus partly isolated from temperature changes. The proportions of the initial fat content consumed throughout the whole hibernation period in *C. septempunctata*, *A. bipunctata* and *P. quatuordecimpunctata* were, for males and females respectively, as follows: 49 and 61, 75 and 87, and 71 and 60 %. Therefore, except in *P. quatuordecimpunctata*, males consumed a greater proportion of their fat than did females (Hariri 1966c). *Chilocorus rubidus* decomposed 32 % of the initial amount of fat during dormancy.

The rate of decrease in fat reserves in *S. undecimnotata* is evidently related to the effect of ambient temperature on locomotion and metabolism. The rapid decrease in fat content commences in late summer and early autumn. In September 1957 the average decrease in absolute weight amounted to 0.082 mg of lipids per day, in October 1958 the decrease was reduced to 0.022 mg per day. During the cold period of November till March the decrease of fat was 0.009 mg per day in both seasons studied. In April and early May the utilization of fat reserves again increased, and varied in the three springs studied due to different temperatures: the decrease of fat in *S. undecimnotata* males amounted to 0.018 mg, 0.045 mg and 0.027 mg per day in 1957, 1958 and 1959, respectively (Hodek and Čerkasov 1963).

Hariri's findings (1966c) completely agree with the above. He calculated a close positive correlation between the rate of fat consumption and temperature (the regression coefficient was 0.002 ± 0.0004 mg of fat per day per °C ($P = 0.02$). Also in coccidophagous coccinellids of the genus *Chilocorus* (*C. rubidus*, *C. renipustulatus*) it was found that the metabolism of fats was at a low level during the winter months (Pantyukhov 1968a, b).

By keeping *A. bipunctata* and *C. septempunctata* for six months at temperatures below zero (—1 to —3 ° or —2 to —10 °C) Hariri found out that negligible amounts of fat, but considerable amounts of glycogen, were consumed. At these temperatures glycogen is probably used directly as an energy source.

In Hariri's experiments, the coccinellids were stored in artificial hibernacula (zinc cages with dead leaves and pieces of corrugated cardboard, covered with polythene sheeting to keep out rain). Here they consumed fat, but not glycogen, much faster than those hibernating in the field.

Just before emerging from hibernation, *S. undecimnotata* males contained 17 — 19 % and females 18 — 22 % fat of dry weight (Hodek and Čerkasov 1963), *A. bipunctata* 14 %, *P. quatuordecimpunctata* 19 % and *C. septempunctata* 23 % fat of dry weight (Hariri 1966c).

Sexual differences. — On most occasions, *S. undecimnotata* (Hodek and Čerkasov 1963) females had a higher absolute fat content (by 0.1 — 1.2 mg) than males. Taking the amount of fat in males as 100 %, the amount of fat in females on ten occasions then represented 100 — 120 %, on twelve occasions 120 — 150 %, and on two occasions 150 — 160 %. Values less than 120 % were more common in the first period of dormancy, the higher values occurred in the second period and particularly at the end of dormancy. In the three species studied by Hariri (1966c), females contained 1.4 to 1.7 times more fat than males at the start of hibernation, but as the females consumed fat faster, both sexes contained about the same amount towards the end of hibernation. This differs from the findings for *S. undecimnotata*.

In addition to recording changes in fat content, Pantyukhov (1968b) also observed changes of the iodine number in the course of hibernation of *C. rubidus*. Although the iodine number before the onset of frosts in September and October amounted to 88 — 89, and to 86 at the end of March, in January and February this index of the proportion of fatty acids in fat which are unsaturated rose to 93 — 94. As the unsaturated acids have a lower freezing point than the saturated ones, their rise may increase cold resistance. In *C. renipustulatus* (Pantyukhov 1965) similar changes in the iodine number can be observed: there is an increase in winter from 59 — 60 to 62 — 64 and a decrease in spring to 58 — 59.

7.222 Glycogen

Like lipids, glycogen reserves are also accumulated during prediapause. Glycogen is unstable in comparison with the more stable fat, thus both absolute and relative glycogen content have been found greatly to fluctuate in the course of dormancy in *S. undecimnotata* (Hodek and Čerkasov 1963). Also a comparison of glycogen content during similar periods in different years revealed marked differences[1]).

The amount of glycogen in dormant coccinellids was roughly ten times less than the amount of fat (Tab. 7.03). In late August *S. undecimnotata* adults had about 0.4 mg of glycogen per beetle which represented about 2—3 % of dry weight. Moreover the amount of glycogen presumably decreased due to migration and a one-month stay in the dormancy site (Hodek and Čerkasov 1963). Values ascertained by Hariri (1966c) for *Adalia bipunctata* in mid-October are one tenth of those for *S. undecimnotata* — 0.04 mg of glycogen per beetle. The relative glycogen content is also substantially less, ranging from 0.4 to 1.2 % of dry weight. On the other hand, coccidophagous coccinellids of the genus *Chilocorus* appear to contain much more glycogen (10—12 % of dry weight) at the beginning of diapause (Pantyukhov 1965, 1968b).

Rate of decrease. — In all coccinellid species studied, a decrease in glycogen during dormancy has been observed. In *S. undecimnotata* the rate of decrease (as for fat content also) depended on temperature. In late summer and early autumn the decrease was very steep so that the daily decrease averaged 2.5 and 2.8 γ in males and females respectively. During the winter and early spring (November — March) the decrease was slow — 0.8 and 0.7 γ per day. In the last 37 days in the dormancy site the fall was about the same in males as during winter (0.9 γ per day), but became much steeper in females (2.0 γ per day). In a second year, when the emergence from winter quarters was more delayed, the decrease was much steeper in males (1.7 γ per day). In the females, however, the amount of glycogen increased within the last week before dispersion, and so the total average decrease was only 1.2 γ per day. On the whole, therefore, during the 8 months of dormancy in *S. undecimnotata*, glycogen decreased in males to about 1/5 (22 %) and in females to 1/4 of the initial amount (Hodek and Čerkasov 1963).

Hariri's (1966c) data for *C. septempunctata*, *A. bipunctata* and *P. quatuordecimpunctata* show that, at the end of hibernation the insects contained 11 to 35 % of the amounts of glycogen they had contained initially. In overwintering *C. septempunctata* and *A. bipunctata* which had been kept experimentally for 6 months in glass vials at subzero

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[1]) The amount of glycogen is reported in different works, even for one species of insect, on the basis of different methods of analysis or in different units (surveyed by Hodek and Čerkasov 1963). It is possible that the variability of the results is to some extent due to such differences.

Tab. 7.03 Glycogen content in dormant *Coccinellidae*

Coccinellid psecies	Amount of glycogen in	Origin of sample	Changes in amount of glycogen content									Reference
Semiadalia undecimnotata	mg/beetle	natural hibernacula (N. Bohemia)	♂	0.388	0.310	0.302	0.252	0.120	0.095	0.096	0.085	Hodek and Čerkasov (1963)
			♀	0.432	0.357	0.378	0.283	0.176	0.135	0.131	0.104	
			Date	29/8	11/9	25/9	22/10	2/4	16/4	29/4	9/5	
	% of dry weight		♂	2.5	2.5	2.6	2.7	1.6	1.5	1.4	1.2	
			♀	2.3	3.0	3.1	2.6	2.1	1.8	1.5	1.1	
Adalia bipunctata	mg/beetle	natural hibernacula (S. England)	Date					16/10	22/12	28/3	23/4	Hariri (1966c)
			♂					0.043	0.016	0.014	0.008	
			♀					0.045	0.042	0.019	0.007	
Chilocorus renipustulatus	% of dry weight	laboratory beetles in artificial hibernacula	Maikop		11.7	10.5	9.9	9.2	8.0	7.4	6.2	Pantyukhov (1965)
			Date		30/10	28/11	30/12	30/1	28/2	28/3	29/4	
			Leningrad		11.5	10.7	9.8	9.3	8.5	7.8	6.9	
Chilocorus rubidus	% of dry weight	natural hibernacula (Leningrad)	Date	15/9	30/10	30/11	30/12	30/1	28/2	30/3	20/4	Pantyukhov (1968b)
				9.6	9.1	7.9	8.3	6.8	5.0	5.3	6.5	

temperatures, Hariri (1966) found that negligible amounts of fat, but considerable amounts of glycogen, had been consumed. In the field, however, the results for these species paralleled those of Hodek and Čerkasov (1963): glycogen content decreased faster during the autumn and spring, and more slowly during the winter.

Before emergence from the dormancy site, *S. undecimnotata* contained 50 — 85 γ and 90 — 105 γ of glycogen in males and females respectively which equalled 0.7 — 1.3 % of dry weight. In *A. bipunctata* it was 5 — 8 γ in males and 6 — 9 γ in females and equalled about 0.2 % of dry weight.

Sexual differences. — A markedly higher absolute glycogen content was found in the females of *S. undecimnotata*. If the content in males is taken as 100 %, then in 7 cases the amount of glycogen in females represented 100 — 120 %, in 14 cases between 121 — 180 %, in 2 cases 181 — 200 % and 2 exceeded 200 % (Hodek and Čerkasov 1963). At the start of hibernation, *C. septempunctata* females contained very much more glycogen, and *A. bipunctata* females considerably more glycogen than did the males. Males and females of *P. quatuordecimpunctata* contained almost equal amounts of glycogen initially. Later the differences were negligible in all three species (Hariri 1966c).

According to the concept that glycerol and other polyols are possibly responsible for frost resistance, both fat and glycogen must be considered not only as a source of energy, but also as precursors for polyols (see 7.24).

7.223 Water

Hagen (1962) found that the water content in monthly samples of *Hippodamia convergens* taken from Sierra Nevada aggregations remained remarkably constant. Also in *S. undecimnotata* there was no general tendency for a decrease or increase in absolute water content during the eight months dormancy (Hodek and Čerkasov 1963). The water content usually amounted to 10 — 12 mg per male and to 11 — 14 mg per female. The continual increase in the relative water content from about 50 — 55 % to about 60 — 63 % which has been observed during dormancy is simply caused by the fall in dry weight, particularly of fat.

In *Chilocorus renipustulatus* and *C. rubidus*, Pantyukhov (1965, 1968b) found a slight decrease in the relative water content from 58 — 59 to 54 — 55 % and from 62 to 59 %, respectively, from October to January, and again a further increase till April to 64 and 68 %.

The body water content may be increased by drinking or by the production of metabolic water when splitting fat. The loss of body water by transpiration is affected by air humidity. The possibility that the intensive splitting of fat contributes to the increase in water content has been supposed (Hariri 1966c). He kept the coccinellids (*C. septempunctata*, *A. bipunctata*, *P. quatuordecimpunctata*) in artificial hibernacula covered with polythene sheeting to keep out rain. As the beetles were not able to drink, he related the relative increase in water content to the production of metabolic water. However, no explanation really need to be searched for the increase in water relative to dry matter. Only in one sample of *A. bipunctata* was there a small increase of 0.9 or 0.8 mg (males and females) in absolute water weight. In a second season no increase at all was found in *A. bipunctata*, and in both *C. septempunctata* and *P. quatuordecimpunctata* there was a gradual decrease in absolute water content.

In our studies of *S. undecimnotata* increases in water content usually coincided — especially after a period of drought — with rainfall and high humidity of the air. In contrast, decreases in water content coincided with drought. Hagen (1962) assumes, for *H. convergens*, that the water balance is maintained by imbibing water. If the beetles from aggregations are kept in a refrigerator for a month or so, in the absence of litter, there is a distinct water loss. When these beetles are then exposed to water, they drink avidly.

7.23 Changes in metabolic rate

The onset of diapause is invariably associated with a striking fall in the level of metabolism (Lees 1955), e. g. in *Leptinotarsa decemlineata* a drop to 15 — 20 % of the normal respiratory rate was observed in dormant beetles (De Wilde 1969).

Although rarely measured, a decrease in oxygen consumption has also been demonstrated for diapausing coccinellids. When measuring the respiratory rate at 18 °C in diapausing *Hippodamia convergens*, Stewart et al. (1967) obtained the value of 12 μl 0_2*/*beetle*/*hr immediately after the arrival at the aestivation quarters in Pinnacle mountains (Arkansas, USA) in late June. Later the oxygen consumption decreased somewwhat further, so that during aestivo-hibernation, from July to February, it fluctuated between 5 and 9 μl. On the other hand, in reproducing beetles the oxygen consumption in the lowlands in March was 29 μl. Thus during diapause the level of metabolism was reduced to about 1/3 — 1/6.

Pantyukhov (1968a, b) measured a decrease to c. 1/8 of active rate in *Chilocorus rubidus* (1968b) and to c. 1/2 in *C. renipustulatus* (1968a) (see Tab. 7.04). Oxygen consumption by diapausing *C. bipustulatus* females reared in the laboratory was only a little more than half that of non-diapausing individuals (Tadmor and Applebaum 1971). In southern Japan (Aichi Prefecture), where *Coccinella septempunctata bruckii* Mulsant breeds during the winter but aestivates, Sakurai (1969) ascertained a decrease in respiration rate from 2 — 3 μl 0_2 /mg/hr in active beetles to 0.4 — 1.3 μl 0_2 during aestivation, i. e. a fall to 1/2 — 1/5 of the active rate (measured at 30 °C). Hibernating *Semiadalia undecimnotata* have a respiration rate around 0.8 μl/mg/hr (measured at 25 °C), but if re-activated in the laboratory the beetles show a doubled oxygen consumption, so that in ovipositing females it amounts to 1.6 (1.1 — 2.0) μl/mg/hr (Hodek and Čerkasov 1958, Hodek 1970).

Tab. 7.04 Oxygen consumption in coccinellids of the genus *Chilocorus* (μl 0_2/mg weight/hr)

Species	Reproducing adults		Diapausing adults	
	(30 days old)	(40 days old)	(40 or 45 days old)	(50 or 60 days old)
C. renipustulatus[1])	1.25	1.12	0.52	0.43
C. rubidus[1])	0.80	—	0.10	0.09
C. bipustulatus (females)[2])	2.04		1.22—1.25	

[1]) Measured at 25 °C — Pantyukhov (1968a, b).
[2]) Measured at 32 °C — Tadmor and Applebaum (1971).

7.24 Changes in cold-resistance

Studies concentrated on the effect of low temperatures are extremely rare in coccinellids, although such data are of utmost importance especially if a species is to be introduced to a different climate for biological control. The scarce data available add some evidence to the recent concept of frost-resistance. In contrast to the original idea that diapause and the correlated changes in chemical composition are primarily connected with increased frost tolerance or resistance, the recently accumulated evidence is convincing that frost-resistance is low at the beginning of diapause and that it then only gradually rises under the influence of decreasing temperature.

Further evidence for this latter idea comes from the considerable increase of cold-resistance in *Chilocorus rubidus* between September and January (Pantyukhov 1968b, Fig. 7.01). In spring the cold-resistance decreases again. Similar changes in resistance have been noticed in measurements of the super-cooling points (Table 7.05)[1]). The

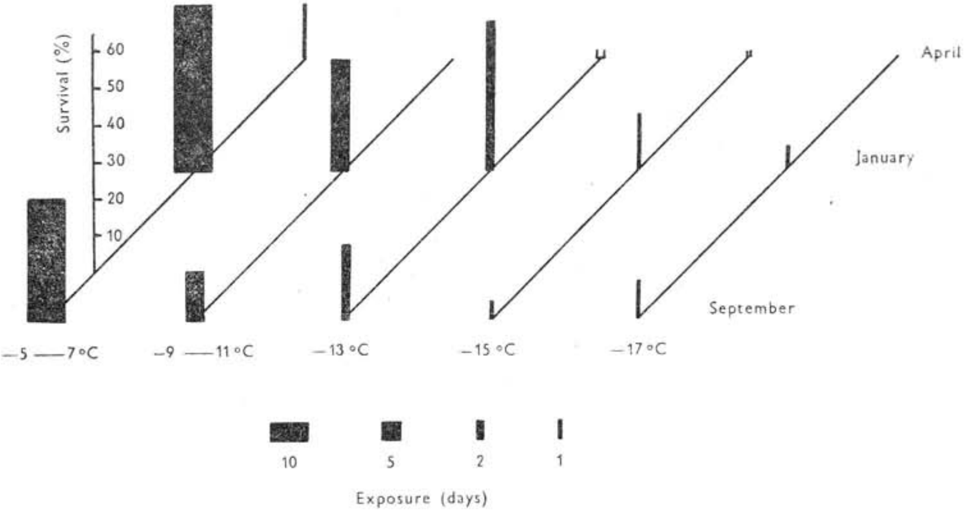

Fig. 7.01 Changes in frost-resistance during hibernation of *Chilocorus rubidus* (Pantyukhov 1968b). The width of columns indicates the length of exposure to cold.

Tab. 7.05 Supercooling point and freezing point in *Chilocorus rubidus* (Pantyukhov 1968b)

Months	N	Supercooling point [°C]			Freezing point [°C]		
		aver.	min.	max.	aver.	min.	max.
IX	41	− 8.2	−2.7	−14.2	−2.6	−0.4	−5.2
XII	57	−13.2	−4.9	−17.4	−3.2	−0.7	−6.8
I	50	−12.9	−4.3	−17.2	−3.2	−0.8	−6.7
II	40	−13.5	−5.6	−17.8	−3.4	−1.1	−6.9
IV	32	− 3.4	−0.2	− 5.5	−0.8	−0.1	−2.7

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[1]) As the temperature falls, supercooling occurs which is followed by freezing of the tissues accompanied by a rapid rise in internal temperature. The external temperature at which this occurs is defined as the supercooling point. For the general theory of frost-resistance and definitions of terms see Salt (1961, 1964).

lowest temperature that could still be survived in January by a considerable number of beetles (40 %) was —13.5 °C for 2 days. *C. rubidus* hibernates in the litter and if this is additionally covered by a sufficient layer of snow, the beetle is not exposed to extreme low temperatures. In the Leningrad region Pantyukhov (1968b) measured the minimum temperature on the earth under the snow; in the winter 1964/65 this was —2.5 °C and —7 °C in the winter 1965/66; the survival of the beetles was 67 — 82 % and 52 — 70 %, respectively. By contrast, in Alma-Ata where the minimum temperature (without snow) was —10 °C, only 12 % of the beetles survived due to alternations of temperature. In the Far East region the survival was 21 % in a microhabitat where the temperature was not measured (Pantyukhov 1968b).

The more common *C. bipustulatus* also has low cold-resistance: most individuals have their super-cooling point at —8 to —9 °C, the limit for survival being —10 to —12 °C (Pantyukhov 1965). A longlasting decrease of temperature down to —5 to —6 °C at the soil surface in the hibernation sites causes rather high mortality. Considerable mortality is only to be expected where there is a thin snow cover or where the spring temperature fluctuates.

The results achieved with coccinellids suggest conclusions valid for most insects. Resistance against temperatures below zero is rather high in the middle of dormancy, after 'hardening' due to the gradual decrease in temperature. Early or late frosts, however, can be very damaging.

The degree of resistance naturally varies in different species, in connection with their type of hibernation. Species which hibernate in litter are certainly more sensitive than the more exposed species which hibernate in crevices. This is indicated by a simple comparison of winter mortality in the species.

A much higher resistance to low moisture and larger extremes of temperature was found by Novák and Grenarová (1967) in *A. bipunctata* when compared with coccinellids hibernating in litter. When placed under the roof of an open hut or into the crown of *Picea*. *A. bipunctata* suffered only 13, 26 or 40 % mortality, while *C. septempunctata*, *C. quinquepunctata* and *Exochomus quadripustulatus* died out completely or by more than 90 % within 4.5 months (mid-October — early March). There were no differences, however, in the winter survival in the protected grass environment among the four species tested. The different tolerance of *A. bipunctata* is obviously connected with its hibernation in the drier habitat of bark crevices where it is not protected from ambient extremes.

H. convergens is obviously not very frost resistant, as Latta (1928) reported 100 % mortality caused by a sudden decrease in temperature from about —2 °C to —12 °C in December.

7.3 Behaviour patterns in dormant Coccinellidae

Coccinellids which have been induced to diapause change their behaviour to a greater or lesser extent. Some species make lengthy migratory flights, form large (dormancy) aggregations and exhibit a long dormancy. This behaviour is most pronounced in two *Hippodamiini* species from warm temperate and subtropical regions, *Hippodamia convergens* in America and *Semiadalia undecimnotata* in the Palaearctic region. In general, these features of flight, aggregation and dormancy developed as an adaptation in those species which depend on "ephemeral" prey. Consequently they very often occur in aphidophagous coccinellids of the tribes *Coccinellini*, *Hippodamiini* and *Anisostictini*. By contrast, they are missing or occur only rarely in coccinellids of the tribes *Hyperaspini*, *Scymnini*, *Psylloborini* and *Chilocorini*, which for the most part are coccidophagous or mycophagous.

Although ample literature exists on the behaviour of coccinellids, the causal relations remain by and large obscure. The vast majority of the literature only contains isolated observations accompanied with speculations based on insufficient evidence.

A complete review of the literature would therefore not be of much value and thus no such review is presented. What is required is a series of comparative observations of laboratory and field phenomena, the field observations carried out at a number of hibernation sites for several years. Unfortunately, such data are still extremely scarce.

There is the danger of providing misleading generalisations by basing them on the few well-documented experiments that have been carried out. This is especially because the behaviour of dormancy is very dissimilar in different species of coccinellids. Therefore the individual stages in the behaviour associated with dormancy will be briefly described, and then their specific variations in most common species discussed.

7.31 General account of the behaviour

7.311 Pre-diapause feeding

There is some controversy regarding pre-diapause feeding activity. Some coccinellids accumulate the reserves for hibernation as adults before the migration to hibernation quarters (*C. septempunctata*), other continue to feed after the main phase of migration (*H. convergens*) and in some it is even presumed, that the adults do not feed at all (*S. undecimnotata*).

In *C. septempunctata* it seems that the onset of diapause is determined in late pre--imaginal and early imaginal life (for details see chapter 7.411). The adults in which the "points" have been set in direction of diapause feed voraciously on aphids for a relatively short period. The ingested food is used for building of large metabolic reserves in the fat body instead of for reproduction; these reserves are mainly fat and glycogen, and serve as a source of energy during the long time without food that follows (see 7.22). It can be assumed that it is this accumulation of a sufficient amount of reserves that forms the stimulus for the beginning of migration.

In *Hippodamia convergens* it is presumed that diapause is induced mainly by food (Hagen 1962). When aphids are lacking, the coccinellids feed on alternative plant food (nectar of flowers or pollen — see 6.111) and this is why they accumulate reserves instead of reproducing. They migrate into the mountain forests, without having built up any great degree of fat. There they feed and deposit sufficient fat for aestivo-hibernation. Then they move to lower altitudes for the actual overwintering (*H. convergens* — Hagen 1962).

In *S. undecimnotata* the "switching of the points" apparently must already take place in the larva, for it is reported that the adults do not feed at all after they emerge from the pupa and manage during dormancy with the reserves accumulated by the larva (Yakhontov 1962).

It is possible that the controversy is to some extent the result of a difference in the way the various species have been studied and that further study will remove the difference which is currently thought to exist. Any comparison is at present made difficult by the fact that no publications with numerical data are available for *H. convergens* and *S. undecimnotata*.

Pre-diapause feeding of adults has been ascertained for many other species, e. g. *Chilocorus geminus* and *C. bipustulatus* (Zaslavskiĭ and Bogdanova 1965, Zaslavskiĭ 1970), and *Coccinella novemnotata* (Mc Mullen 1967a, b).

7.312 Migration

According to the latest concepts of migration (Johnson 1969) both the flights to and from the dormancy sites are migration. This type of displacement fully fits in migration class III., defined by Johnson as follows: "Some long-lived females fly, while sexually immature, from the site where they became adult to hibernate or aestivate at sites which may be either within or beyond the areas where climate limits seasonal breeding. The males may or may not accompany them. Next season, after diapause, they reinvade breeding places and oviposit there, at least some of them more or less retracing the emigration route".

Johnson's view is to some degree in disagreement with the Hagen's older conception of coccinellid migration. Hagen (1962) argues that the flight toward aggregational sites can be considered as migration since it is directional and under partial control of the beetle. The disbanding of aggregations is, however, a simple dispersal flight. Johnson (1969) counters that the direction of both displacements is greatly affected by wind. The contrasting ultimate results of migration (aggregation or dispersal) are not caused by differences in the flight behaviour during displacement, but by responses at the concluding phase of migration.

Although this disagreement might seem only semantic, it actually concerns the veritable crux of the problem of migration which is still quite unresolved: do coccinellids fly to hibernation sites by a directional flight, or are they brought there more or less passively by wind currents? No direct evidence is available to favour either of these possibilities. There is, however, some circumstantial evidence for both viewpoints.

The aggregations for dormancy are often formed at prominent features of the landscape. For those coccinellids that make lengthy migratory flights (*S. undecimnotata*) these may be peaks of hills, large rocks or posts on the slopes. There may, however, be a forest edge, a wave in the field, a shrub, a tree, or a post in a flat landscape for those coccinellids that aggregate within the breeding area but usually in a different habitat or microhabitat (*C. septempunctata*). These sites are the same year after year if the relief remains the same; but new sites are occupied if the relief is changed by the disappearance or formation of a prominent object. The creation or removal of triangulation posts, forest fences and huts has provided the author with "unintentional" experiments which show how often the aggregation sites of *S. undecimnotata* can change (Hodek unpubl.).

It seems improbable that coccinellids would always be transported passively to the same places or that wind currents would be so drastically changed, for example by a post of 15 cm or less in diameter, that the coccinellids are carried elsewhere. Also direct observations on the top of a hill (Raná in northern Bohemia or Kováčov-hills in southern Slovakia) have shown that *S. undecimnotata* landed actively e. g. on a shifting figure that constituted the most prominent object (Hodek unpubl.). Any air currents existing were too weak to be noticed by the observer.

Therefore an analogy has been sought between the aggregation of coccinellid at prominent objects and the swarming habits of pairing ants and other insects or the flight to the feeding sites in *Melolontha* hypsotactic orientation has been suspected (Hodek 1960a, Hagen 1962).

Some authors have observed that coccinellid adults move against the prevailing wind in the direction of mountain peaks (Mani 1962).

By contrast, coccinellids have also been observed to make use of air currents, especially in mountain valleys. Savoïskaya (1966) reported that in the Zailiĭskiĭ Alatau mountains (Kazakh. SSR) the coccinellids fly to their hibernation places up the valleys with the help of a steady breeze blowing upwards in the daytime. According to Hagen's hypothesis (1962, in Hodek p. 135, 1966) on the migratory flight behaviour of *Hippodamia convergens*, this species is also transported to the hibernation site and back by air currents.

It is possible that migration behaviour may be different in individual species. For instance Hagen (1962) clearly distinguishes 'hypsotactic' and 'climatotactic' aggregators. However, it seems more probable that for any one species (at least for most species) behavioural responses of both types apply (Hodek 1967), even if one type may dominate in certain species. Johnson (1969) judges that 'the hypothesis that postulates an appetence by a migrant for some perceived but far-distant habitat or hibernation site is at present unacceptable'.

In this context the mechanism for long distance migrations by coccinellids which Hagen (1962, in Hodek p. 135, 1966) hypothesized for *H. convergens* (see 7.324) seems most probable. It is only towards the end of the long migration that the hypsotactic response may be shown and that an optically oriented directional flight can guide the coccinellids to prominent features. This may even apply to the aggregations of *H. convergens* on mountain tops which have been reported many times (recently by Stewart et al. 1967), and the hypsotactic response may also be involved when coccinellids choose places of fairly large clearings on the slopes of hills for winter aggregation (Hagen 1962). Sem'yanov (1965b) states that the tendency to hibernate on at least slightly elevated ground may have the survival advantage that in some lowland regions extensive parts of the plains may be flooded. Many other authors have speculated on the adaptive significance of hibernation in the mountains and in aggregations (summarized in Hodek 1960a). It is quite possible that mass hibernation facilitates contact between beetles of the opposite sex which will be important for less abundant species and leads to crossings between those beetles which have developed under different climatic conditions. Hibernation in high mountains in areas with warm climates may retard the beginning of spring activity of the beetles till aphids have multiplied sufficiently. A similar function may be attributed to hibernation among the litter in plains, under mosses, and in other humid microhabitats where cooling is brought about by the evaporation of water.

7.313 Aggregations

The formation of aggregations or 'assemblages' in the sense of Mani (1962) and Kapur (1954), or the non-random distribution (Banks 1954) is a very specific behavioural feature connected with dormancy in many *Coccinellidae*.

The behavioural responses induce the coccinellids to aggregate in two ways. Some of the responses act **indirectly** — the beetles guided by them are passively brought to the same place. Hypsotactic responses (dealt with in 7.312) cause the beetles to concentrate on a larger spot, a portion of a habitat, as e. g. surrounding a post or a rock on a hill-slope, or in a clearing surrounded by high trees, etc. After arriving there, the beetles are influenced by their responses to physical factors (hygrotaxis, thermotaxis, phototaxis), and by geotaxis and thigmotaxis so that they hide into small places, in microhabitats, as e. g. the space under a stone, crevices in a rock, in a grass tussock, in tree bark, etc.

The beetles hibernating in the litter, for instance, have apparently been guided by negative phototaxis and positive geotaxis (possibly also positive hygrotaxis) to hide on or near the ground after a period of sitting on the plants. It can be assumed that during this period of 'waiting' the behavioural patterns gradually change from those which led the beetles to the hibernation habitat during migration.

As regards the hygrotactic responses, these are perhaps more specific for individual species. In *H. convergens* and *Coleomegilla maculata* moisture availability is an important requirement during hibernation (Hagen 1962), and in *Coccinella novemnotata* in aestivation (McMullen 1967a), whereas in *S. undecimnotata* and in other species with a similar type of hibernation ventilated crevices are preferred and seem to be the most favourable (Hodek 1960a, Yakhontov 1962, Iperti in Hodek 1966 p. 137,) as they apparently reduce the danger of mycosis (Iperti 1964, in Hodek 1966 p. 189).

Few experimental studies have investigated the reactions to light, temperature and moisture, also geotaxis. Pulliainen (1963, 1964) studied the responses of *Myrrha octodecimguttata* hibernating in bark crevices in the final period of dormancy, and reactivated by temperature in the laboratory. The beetles showed a strong hygronegative reaction, which only changed after a prolonged desiccation. They reacted indifferently to long-wave light and photonegatively to short-wave light. After desiccation, they became strongly photonegative to long-wave light also. The optimum relative humidity is about 30 — 40 %. Novák (1966) found that the georeaction was only very slightly positive in dormant adults of *Coccinella septempunctata* collected on trees during their 'waiting' period before they hid in the litter. In humid environments, the response changed to be slightly geonegative.

Surprisingly enough, although there are many indications (e. g. renewed dispersal in spring) that responses must change during dormancy, no studies on this have been carried out.

The **direct** stimuli which result in aggregation may — apart from thigmotaxis whose function in this context is unquestionable — also include chemotaxis i. e. attraction by a specific odour. The specific odour of coccinellids is penetratingly noticeable to man, and long ago speculations were published on its function both as a protective agent (see 8.2) and as an agent enabling the formation of aggregations. Unfortunately there is absolutely no experimental verification of this function and thus we must limit ourselves to mere hypotheses. Of recent works, particularly Savoïskaya (in Hodek 1966 p. 139) assumes an aggregative function for odour following her observations on the coccinellids of the genus *Adalia* (see 7.323); she reports that the odour is stronger during migration. It may be that the smell attracts the later migrants to those beetles which have arrived earlier. Yakhontov (1962) supposed that the dead bodies remaining from the previous hibernation had an attraction, but this has been denied by Iperti (pers. comm.), and Novák (1965) has proved experimentally that the dead beetles are more likely to act as a repellent.

Both monospecific and heterospecific aggregations of coccinellids may be formed. As a general rule, whenever several species spend their dormancy in the same habitat, they tend to form monospecific clusters (McMullen 1967a) though the presence of few adults of other species has been reported.

Rarely (in two cases) mixed clusters of *S. undecimnotata* with *A. bipunctata* have been observed. It is more usual to find heterospecific aggregations between *C. septempunctata* and *S. undecimnotata* in grass tussocks on the tops of hills (Hodek 1960a and unpubl.), especially where rocks are missing. Pulliainen (1966) has reported that *Scymnus suturalis* and *Aphidecta obliterata* were admixed to aggregations of *Myrrha octodecimguttata*.

7.314 Emergence from dormancy sites

During the closing stages of dormancy the beetles gradually change their behaviour in relation to changes in temperature in the converse way as happens in the introductory phase. The inactivity in the hiding places changes to slight mobility, sometimes already long before dispersion becomes noticeable. This closing stage is conspicuous and has often been observed in coccinellids hibernating in litter at the forest edges; such coccinellids stay for a prolonged period on the trees (esp. on young pines) in the dormancy site before dispersion (Bielawski 1961 etc. — see also 7.322).

In all species studied, dispersal from dormancy sites has been found to continue over a period of several weeks (Hodek 1960a, Bielawski 1961, Savoïskaya 1965, McMullen 1967a). The onset and progress of dispersal is regulated by the ambient temperature, as the second phase of dormancy has the characteristics of a simple quiescence (see 7.412). Usually a prolonged increase of average temperature over 10 °C induces the beetles to emerge (Hodek 1960a).

The different species of beetles, even if they have hibernated at the same site, do not disperse simultaneously. In Bohemia (Hodek 1960) *Adalia bipunctata* is the earliest species, followed by *Coccinella quinquepunctata*, *Propylaea quatuordecimpunctata* and *Tytthaspis sedecimpunctata*, then by *C. septempunctata* and *Adonia variegata*. *Semiadalia undecimnotata* seems to be very late. A similar, but not identical picture is reported by Bielawski (1961) at a hibernation quarter under young pines in Poland (Warszawa — Bielany). *A. bipunctata*, *A. decempunctata* and *C. quinquepunctata* leave about a month earlier than *C. septempunctata* and *P. quatuordecimpunctata*. Whereas these two observations agree that *A. bipunctata* is an early and *C. septempunctata* a late dispersor, Banks (1955) reports an opposite observation from England: *C. septempunctata* appeared on nettles one month earlier than *A. bipunctata* and *P. quatuordecimpunctata*.

7.32 Behaviour of individual species

7.321 Semiadalia undecimnotata

The migratory and aggregational behaviour of this species is suprisingly uniform in all the three regions, in which aestivo-hibernation has been studied although they differ in many respects; the three areas are: the typically continental central Asian region of the USSR (Dobzhansky 1925, Radzievskaya 1939, Yakhontov, in Hodek 1966, p. 107), Czechoslovakia at the northern limit of the distribution area (Hodek 1960a, 1967) and the maritime region of south-eastern France — Drome, Vaucluse and Basses-Alpes (Iperti in Hodek 1966, p. 137).

The dormancy sites are always situated on hills or mountains, (see photos 23—29, 36—42) at prominent features (large rocks, heaps of stones, shrubs or other plants, or artificial structures, such as posts, triangulation points, and only very rarely buildings or ruins of castles). It is assumed that such sites are chosen as the result of hypsotactic responses. Coccinellids prefer rock cracks, especially those exposed to wind, where their mortality is lower. They only hibernate in vegetation when there is an absence of suitable shelter among rocks on the hill; then a high percentage often die of mycosis. The petrography of the site is not crucial, hibernation quarters can be found both on limestone and on igneous rocks (e. g. basalt). The altitude of the site (above see level) is also in no way crucial, in central Asia it is naturally much higher (> 2000 m) than in Czechoslovakia (400 — 900 m) or in France (usually above 700 m). The great majority of dormancy sites are situated on the south-western upper slopes of the hills or mountains. According to Iperti (in Hodek 1966, p. 137) particular attractivity may be attributed to the afternoon insolation of these sites.

The coccinellids arrive at the hibernation places over a period of several weeks on warm calm days and leave again over the same period under similar conditions. At the onset and end of hibernation they creep around close to the shelter during the day, forming numerous small clusters during the night or colder spells. In the course of the central cold part of dormancy they are aggregated in one or a few large clusters.

Their spring emergence seems to be dependent on the ambient temperature. In the Louny-hills (northern Bohemia) emergence occurs after the mean temperature has remained above 12 — 14.5 °C for some time (Hodek 1960a). Yakhontov (1962) regards the relationship between emergence from hibernation quarters and temperature as secondary in that it influences the maturation of gonads; a certain degree of the gonad maturation then becomes the signal for emergence. This does not agree with the findings from Czechoslovakia, where females emerged at different times in different years depending on meteorological conditions, but with ovaries at different stages of maturation. When the females leave the hibernation sites early, they have not yet reached the onset of previtellogenesis (i. e. formation of the first oocyte). If they disperse later, this stage is already attained at the dormancy site (Hodek and Landa 1971). In males any dependence of emergence from hibernation quarters on the maturation of testes seems even more improbable for the tissue of the testicular follicles is fully active already 2 — 4 weeks before the emergence and the males fertilize the females (Hodek and Landa 1971).

Year after year *S. undecimnotata* uses the same dormancy sites if the silhouette of the hill has not changed.

The east Siberian *Harmonia axyridis* seems to have the same type of dormancy behaviour as *S. undecimnotata*, at least as far as the short description by Telenga and Bogunova (1936) is considered.

7.322 Coccinella septempunctata and other species dormant in the litter

Attention should be drawn to the fact that those references to hibernation of *C. septempunctata* in the literature which describe mass assemblages between rocks on mountain summits, most probably do not concern this species at all but refer to *S. undecimnotata*. (The seven spotted form of *S. undecimnotata* is often confused with *C. septempunctata*, even by professional entomologists.) Iperti (unpubl.) has verified that such confusion occurred in Fabre's data (1879) from Mont Ventoux and St. Amand. It is possible that the same confusion has occurred elsewhere: Poulton (1904) from Spain, Benner and Franz (1905) from Poland, Werner (1913) from Turkey, Semenov-Tyanshanskiĭ (1911) from Italy (Vesuvius), Reineck (1918) from Germany, Radzievskaya (1939) from central Asia, and Benkevich (1958) from Crimea.

Even if these observations are ignored, the dormancy behaviour of *C. septempunctata*, in contrast to that of *S. undecimnotata*, is extremely heterogeneous even within one geographical area. The only safe generalisation is that *C. septempunctata* always hibernates on the ground: under stones, in litter, in holes in the soil surface, near the base of plants, in grass tussocks [never in the cracks of tree bark or walls — contrast *A. bipunctata* (see 7.323)]. The species forms only small or medium size aggregations, not exceeding tens of beetles. *C. septempunctata* often hibernates near its breeding sites. If any higher area, however small, is to be found near the breeding habitats, the beetles prefer to hibernate there. In lowlands the usual dormancy sites are situated at forest edges, clearings, or in wind breaks. If no such site is close by, *C. septempunctata* hibernates near isolated shrubs or other plants, or on slight unevennesses of the terrain, as often occurs at the road, etc. The types of site mentioned above may be combined: the beetles are very often found at forest edges or clearings on the slopes of hills. No special differences seem to occur between individual countries in this rather wide choice of habitats and microhabitats used as dormancy sites by *C. septempunctata:* information is available from England (Banks 1954a), Germany (Klausnitzer 1967), Poland (Bielawski 1961), the Ukraine (Dobrzhanskiĭ 1922a,b, Telenga 1948, Dyadechko 1954), Belorussia and in the Leningrad region of the Soviet Union (Sem'yanov 1965a, b), also Czechoslovakia (Hodek 1960a).

Savoïskaya (1960, 1965.) who distinguishes 5 types of hibernation quarters of coccinellids in the Kazakh. SSR. states that *C. septempunctata* utilises no less than four. The most characteristic is hibernation under small stones in the mountains, both along the river beds in groups of about 50 individuals (up to 900 — 1400 m) and on the slopes in the alpine zone (2600 — 3300 m). Here they form groups of 2 — 5 up to 30 individuals under small stones. *Harmonia axyridis* and *Aiolocaria mirabilis* also hibernate in this way in the Far East region of the USSR (Telenga and Bogunova 1936, Savoïskaya 1970b). In the alpine zone, *C. septempunctata* also hibernates at the base of grass tussocks and shrubs, but in smaller numbers. In the lowland of Kazakhstan the dormancy sites of *C. septempunctata* do not differ from the microhabitats described for several countries above. Thus the species hibernates in the upper layers of the soil or in litter or holes at the base of plants. The latter sites are used also by *Propylaea quatuordecimpunctata.*

After their gradual arrival at the dormancy site the coccinellids remain clustered on the plants close to the hiding places (during August and September in Bohemia) and only hide by degrees as the air becomes cooler. They can very often be found at the ends of twigs of young pines (Hodek 1960a, Bielawski 1961, Sem'yanov 1965a, b, Klausnitzer 1967). In a similar way the coccinellids re-appear and stay on the vegetation near the hibernation site before their dispersal in spring.

Of the common coccinellids, *C. quinquepunctata* is another species with a hibernation behaviour similar to that of *C. septempunctata;* it is, howeverfar, more abundant than the latter on young pine trees at forest edges (Hodek 1960a, Bielawski 1961, Sem'yanov 1965a, b, Klausnitzer 1967). It can also be found among small stones on hills (e. g. Louny-hills in north Bohemia), used as hibernation quarters by *S. undecimnotata* and *C. septempunctata* (Hodek 1960 and unpubl.).

Some other species are usually present in similar hibernation sites in the plain (the litter or upper soil-layer at forest edges). Such species are *Coccinula quatuordecimpustulata, Propylaea quatuordecimpunctata, Adonia variegata* (in dry places), *Hippodamia spp.* (if moist habitats are near), the phytophagous *Subcoccinella vigintiquatuorpunctata,* the mycophagous *Thea vigintiduopunctata* (especially in rather moist places), and *Tytthaspis sedecimpunctata* (particularly in drier localities) (Hodek 1960a, Bielawski 1961, Sem'yanov 1965a, b, Klausnitzer 1967, Novák and Grenarová 1967). Litter also serves as the dormancy site for *Stethorus punctillum* (Putman 1955, Berker 1958), although some authors report its hibernation in the bark (Moter 1959).

Besides these species for which litter in the widest sense typically provides shelter, *Calvia quatuordecimguttata* and *Exochomus quadripustulatus* sometimes also occur there. These two species are equally abundant in bark crevices.

7.323 Adalia bipunctata

This coccinellid is well known for its frequent occurrence in buildings at the time of its dormancy, and appears in cracks in walls, in lofts, or behind windows and even in rooms (Hawkes 1920, Sem'yanov 1970). It can be assumed that the coccinellids are brought here by their hypsotactic behaviour. This behaviour is also indicated by the fact that a small aggregation of *A. bipunctata* (20 — 30 individuals) has been found close to a large aggregation of *S. undecimnotata* in a rock crevice on a hill-top (Hodek unpubl.).

However, a fair proportion of *A. bipunctata* apparently do not leave the habitats of orchards, parks or forests, and hibernate either in crevices of tree bark or in artificial objects on trees. Thus Speyer (1934) used to find *A. bipunctata* together with *Chilocorus bipustulatus* and *Stethorus punctillum* in grease bands.

Mass hibernation in the thick bark of old Tyan-shan spruces (*Picea schrenkiana*) is described by Savoïskaya (1965, in Hodek 1966, p. 139) from Kazakhstan (USSR). Every autumn, the beetles migrate in masses to the same trees in mountain valleys flying up the valley and a rate of 50 — 55 beetles per min. was observed in late September. It was noticed that they turned sharply back just behind the tree, swarmed in its shade and dropped rapidly onto the trunk. Up to 2000 beetles could be found on one tree. Similar sites on *Picea* are also used by *A. fasciatopunctata* and by *Synharmonia conglobata*. The latter species is most abundant up to 1500 m, while the two *Adalia* species prefer higher altitudes.

Large aggregations of up to 200 *A. bipunctata* adults have been observed by Smee (1922) on elm-trees *(Ulmus)* in England (as many as 1000 beetles on one tree). Smee was the first to succeed in attracting coccinellids to artificial hibernation quarters; he achieved colonisation by *A. bipunctata* of cages containing tree bark and arranged around the garden in mid-October.

A. bipunctata, being a polyvoltine species, is relatively late (in early October in Germany — Speyer 1934) to enter diapause and emerges very early in spring.

A. bipunctata is very often found together with *Chilocorus bipustulatus* (Speyer 1934, Bielawski 1961, Savoïskaya 1965).

7.324 Myrrha octodecimguttata and other forest species which hibernate in bark crevices

Not much is known about the hibernation of coccinellid species which are typical of forests (especially coniferous). According to recent observations, they do not seem to leave their breeding habitat.

Myrrha octodecimguttata which lives and breeds in the crowns of pine-trees (Klausnitzer 1968), hibernates in bark crevices of old pines; this has been established for Poland by Bielawski (1961) and for Finland by Pulliainen (1963, 1964, 1966). Pulliainen observed that the coccinellids preferred the lowest 10 cm of the trunk (93 %) and the south and east sides of the tree (62 %). On these sides tendency to aggregate is most pronounced; the aggregations were on average of 3.8 individuals, the largest one consisting of 14 individuals.

Bark crevices of old pines are used as dormancy sites by many other species, mostly by species also bound to the forest habitat for their breeding life: *Scymnus* (*Pullus*) *suturalis* (Pulliainen 1966; although Bielawski (1961) found this species more frequently in the bark crevices of deciduous trees), *Scymnus* (*Pullus*) *impexus* (Delucchi 1954), *Scymnus nigrinus* (Bielawski 1961), and *Aphidecta obliterata* (Pulliainen 1966). *Exochomus quadripustulatus* (Bielawski 1961) also uses bark crevices but utilizes crevices and litter as its dormancy site with about equal frequency (Klausnitzer 1967). Other conifers than pines may also be visited, e. g. cedar by *Hippodamia tredecimpunctata* (Thomas 1932). Some coccinellids prefer the crevices in the bark of deciduous trees, e. g. *Scymnus* (*Nephus*) *quadrimaculatus* prefers chestnuts (Bielawski 1961), and *Synharmonia conglobata* and *Harmonia quadripunctata* chestnut and poplar (Bielawski 1961, Hodek unpubl.).

7.325 Hippodamia convergens

The diapause of this species, which is one of the most common coccinellids in North America, has been thoroughly studied by Hagen (1962, in Hodek 1966, p. 131, 135) in northern California and three types of dormancy have been determined. The majority of the population in northern California has a univoltine cycle. This is the original pattern. as before irrigation was introduced, the species was dependent on spring-occurring aphids. The irrigated crops provide a later supply of food which enables exotic aphids to maintain themselves during the summer and autumn. *H. convergens* and some other *Hippodamia spp.* may react to this later abundance of aphids by summer reproduction and multivoltinism.

The multivoltine adults of *H. convergens* enter hibernation in the late autumn. Diapause is induced mainly by photoperiod and temperature. *H. convergens* often joins the other *Hippodamia spp.* in the valley aggregations.

Most univoltine *H. convergens* adults show a facultative diapause that appears to be largely nutritionally induced. In the laboratory, however, there were occasions when 10 — 20 % of the beetles entered diapause although the conditions were optimal and the beetles were supplied with an excess of essential aphid food. Some interaction of photoperiod and diapause has also been observed, but this is much less important than nutrition. The main factor inducing diapause is feeding upon non-insect food. The progeny of diapausing beetles emerge from pupae in early May. They do not rove much locally, but migrate long distances towards the mountains (in northern California to Sierra Nevada) if there are not enough aphids nearby.

Hagen (1962, in Hodek, 1966 p. 135) has proposed a hypothesis to explain the mechanism of migration, which is in harmony with the concepts of Johnson (1969). Migration is initiated by a take-off during the calm of morning; the subsequent vertical upward flight is apparently assisted by convection currents. This goes on until the temperature permits the beetles to fly. At about 11 — 13 °C flight is inhibited (Hagen calls this the temperature ceiling) and the beetles fall about 300 m to a warmer layer of air (13 — 18 °C) where flight is resumed. The beetles which are thought to undergo these vertical oscillations are simultaneously blown sideways (Fig. 7.02). Each day during the late morning in May and June, westerly winds develop which carry the beetles toward the mountains. The migration is terminated when the temperature ceiling for flight contacts the mountains.

If aphids are found near the landing place, the beetles produce eggs there. Usually, however, they feed on non-insect diet which is used for building up reserves. After a week or so the coccinellids exhibit secondary, directional flights near the ground, flying up and down mountain creeks in search of summer aggregation sites. In the summer aggregations the adults remain rather inactive until October, when they become mobile again, presumably disturbed by the first rains. The tertiary flight during warm periods usually leads them to lower parts of the creek where new, larger overwintering aggregations are found.

H. convergens adults are guided by a series of factors in their search for the aggregation sites. In contrast to *S. undecimnotata*, by and large they do not respond to prominent objects. Sometimes assemblages of *H. convergens* are indeed found at the top of mountains (Douglas 1930, Throne 1935, Sherman 1938, Stewart et al. 1967), but according to Hagen's (1962) hypothesis they would reach summits in a semi-passive way. Moisture and light are considered to be the most important factors influencing selection of aggregation sites. At first the coccinellids assemble on bushes and trees in large clearings on slopes near creeks. After several days they move closer to the creeks, and

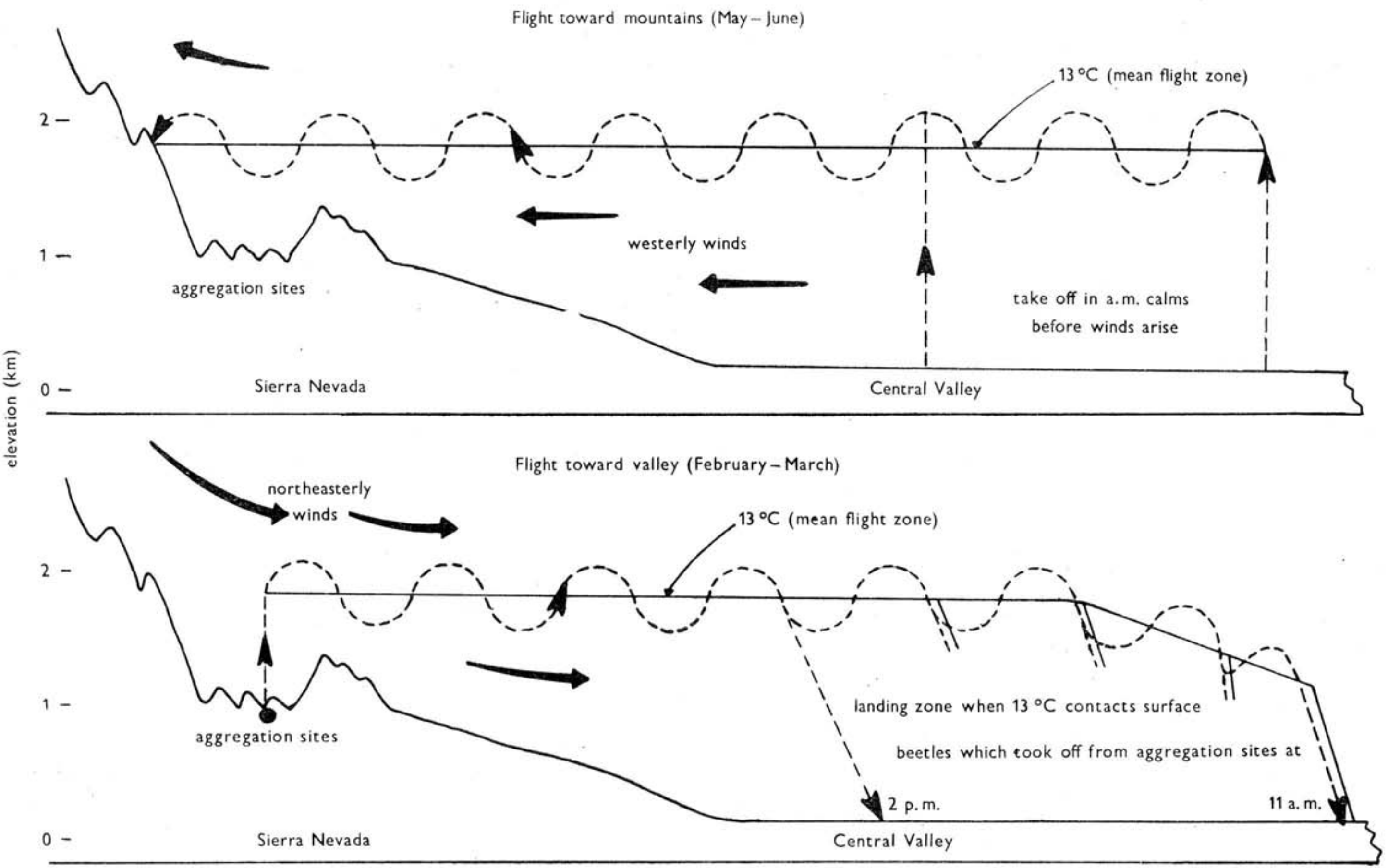

Fig. 7.02 Suspected temperature — controlled flight oscillations which *Hippodamia convergens* undergoes in its migratory flights (Hagen 1962).

settle down along the banks in the litter, often in spots exposed to the afternoon sunlight. As the beetles fly about, they concentrate in the sunlit spots until sunset. This may explain why the aggregations are formed in similar spots year after year. As new clearings are often selected, the assumption that dead beetles attract the aggregators (Yakhontov 1962) cannot apply here.

Hodson (1937) proved that the beetles exhibit a marked preference for litter with 20 % moisture. Hagen (1962) believes that *H. convergens* drinks water in order to maintain a constant water content and that a physiological requirement for free water may be the basic characteristic of "climatotactic" aggregators (*H. convergens*, *Coleomegilla maculata*), in contrast to "hypsotactic" species such as *S. undecimnotata*.

The large winter colonies (from one, about 40 million beetles have been collected) are formed by many non-contiguous small aggregations under leaves, at the bases of bushes, and on tree trunks. Snow often covers *H. convergens* aggregations for about three months at the higher altitudes. The majority, however, hibernate near the snow line in the Sierra Nevada, and during most of the winter they are not covered with snow.

Because the beetles aggregate in canyons, they are in the wind shadow. When they become heated to above 14 °C in the early spring, they take off vertically and are eventually caught up by the winds aloft (blowing in the opposite direction to that in summer) which "carry" them over ridges that lie to the west between the aggregation sites and the plains. The fall in air temperature in the evening forces the beetles to the ground, terminating the flight. Not all coccinellids, however, get so far. The beetles that aggregate during winter on the highest peaks of the Sierra are found after dispersal only to have reached the mountain valleys just below these peaks.

7.326 Mycophagous and phytophagous species

Hibernation in aggregations does not occur only in entomophagous coccinellids. Three mycophagous species have been reported hibernating in litter, one in large aggregations. In mid-April Ruscinsky (1933) found four large aggregations of *Vibidia duodecimguttata* among fallen leaves at the base of trees on top of a hill in erstwhile Rumania (Bessarabia). Each aggregation covered about 1 m^2 and consisted of some 2500 individuals. Evans (1936) found a dormancy aggregation of *Tytthaspis sedecimpunctata* on a wooden post in Berkshire, England in December; Legay and De Reggi (1962) found aggregations (50 — 150 individuals per 100 m^2) of the same species under litter at the base of trees on a small rise overtopping the surrounding fields by only 20 m. The beetles left this hibernation site near Lyon, France in mid-April. This same site contained aggregations which included 1 % of *Thea vigintiduopunctata*. This latter species was often found in litter at moist dormancy sites at forest edges visited by *C. septempunctata* and related species (Hodek 1960a, Bielawski 1961) (see 7.322).

Aggregations have even been observed in phytophagous coccinellids in the subfamily *Epilachninae*. In Africa, Poulton (1936) observed aestivation aggregations of *Epilachna dregei*, once in Bechuanaland and once in northern Uganda. Both observations were of aggregations of immobile adults on a prominent feature (a hill, a termite-hill) and were found in mid-July, i. e. in the middle of the dry season in Uganda. In February, Kapur (1954) found four aggregations of several thousand individuals of *Epilachna bisquadripunctata* at an altitude of about 400 m in India (Chota Nagpur, Bihar). The aggregations were at the base of grass ca. 70 cm high, in the vicinity of an almost dry brook. The fact that the coccinellids had empty guts, a large fat body and quite unripe ovaries is evidence that they were in diapause. In both *Epilachna spp.* observed, "hypsotactic" aggregation may have been involved. Ghabn (1951) mentions winter migrations of *Epilachna chrysomelina* from the fields into the surrounding desert in Egypt without, however, describing the hibernation sites.

7.4 Ecological mechanisms of diapause

7.41 Development and current state of the problem in insects in general

This problem has been discussed with reference to coccinellids in only a few papers, so that a review of such papers cannot provide a general picture. This introduction, therefore, will give an overall informative survey of the developments in this field based on the whole range of insects. Nevertheless, the rapid developments in this field require that substantial changes need to be made in earlier hypotheses still frequently held.[1])

The old differential definition of diapause and quiescence by Shelford (1929) and Roubaud (1930) suffered from a lack of experimental evidence. The term diapause (la diapause vraie) was restricted to those instances where development is arrested spontaneously, whereas an interruption of development by unfavourable conditions was considered to be quiescence (la pseudodiapause).[2])

In many cases diapause has been proved to be induced by environmental conditions, therefore, 25 years after its inception, Lees (1955) considered that the definition was inappropriate and modified it satisfactorily to that date. In general, however, he retained the concept that these two types of developmental arrest were opposed, though he recognized that no clear distinction could be made between them.

Lees considered quiescence (la pseudodiapause) was a state of direct inhibition of development, caused by the direct effect of ambient conditions (low temperature, lack of humidity), and was terminated immediately the conditions became favourable. Diapause (la diapause vraie) was thought to be caused by conditions which did not directly prevent development, but which were merely signals of seasonal changes ("seasonal tokens"). Thus diapause usually begins long before the onset of unfavourable environmental change.

Lees himself realised the limitations of these definitions and they indeed have recently lost some of their validity since photoperiodism has been more fully understood. The length of the photophase cannot be regarded as directly preventing development and thus these cases of diapause which are directly regulated by photoperiods were not really diapause in terms of the classical definitions. This dilemma has been circum-navigated by different approaches. It is possible to separate these problem cases from typical diapause (or eudiapause) by giving them different names: parapause, oligopause (Müller 1965, 1970). This solution has the advantage of emphasizing the existence of transitions between quiescence and diapause. A certain disadvantage lies in the fact

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[1]) The survey presented here can only be a simplified one. Students of diapause in coccinellids are recommended to refer to the literature cited.

[2]) Attention must be drawn to the fact that this concept, which may be misleading, has been retained by some authors and appears in the current literature. In some French papers (e. g. Bonnemaison 1964), the terms "la diapause vraie" in the sense of obligatory diapause and „la pseudodiapause" in the sense of facultative diapause are sometimes used.

that this system of terms and definitions, due to a relative shortage of facts, cannot yet be sufficiently elaborated to encompass all the striking complexity of the mechanisms involved. There are species of insects where the same individual contains the potential for alternative ways in which arrest or resumption of development can be affected; this is clearly seen in the coccinellid *Chilocorus bipustulatus* (Zaslavskiĭ 1970) (see 7.422).

Therefore many authors still retain the term diapause in a broad sense for any adaptive arrest of development which is accompanied by behavioural, structural and biochemical changes in the insects (Danilevskiĭ 1961, Fuzeau-Braesch 1961, Way 1963, Hodek 1965). Beck (1968) defines diapause as "a genetically determined state of suppressed development, the manifestation of which may be induced by environmental factors".

Not only do these terminological difficulties exist, but also all authors are aware of the variability of the ecological mechanisms which govern the induction, maintenance and termination of diapause, and accept as the only common feature the adaptive function of diapause which is (1) to synchronize the development of active stages with favourable conditions and (2) to enhance the survival potential during unfavourable periods. It is, however, to be expected that the underlying physiological mechanisms will, at least in principle, be the same for any one developmental stage (e. g. adult) in different insects.

It is difficult to imagine that simple quiescence in the sense of unadaptive torpor (whether caused by cold or heat) could enable a long survival under temperatures above zero.

Whereas the word 'dormancy' is used by most authors (and also throughout this book) as a more general term for any developmental arrest (comprising both quiescence and diapause), some authors use it in a restricted sense to designate 'quiescence', as e. g. Beck (1968): "simple dormancy, such as heat — and cold torpor . . .".

Just as with quiescence and diapause, so there is contradiction in the definition of the two basic types of diapause. If the potentialities for diapause are not realized in each generation, diapause is termed 'facultative'. The onset of such developmental arrest can be induced or prevented by environmental conditions. By contrast, obligatory diapause is entered by virtually every individual in each generation regardless of the environment (Lees 1955). Somewhat later it became emphasized that obligatory diapause is not essentially distinct from facultative diapause but is its marginal case (Fuzeau-Braesch 1961).

Recently the strict definition of obligatory diapause has been weakened by experiments involving the alternation of photoperiods in studies on the ecological mechanism of diapause. Some insects cease development under steady conditions, whether long or short-day, and require an alternation characteristic for the species. Müller (1958) ascertained that the requisite for a complete vitellogenesis in the delphacid *Stenocranus minutus* was a period of short days followed by a period of long days. Thiele (1966) found the same alternation was necessary for the carabid *Pterostichus nigrita*, and recently Zaslavskiĭ (1970) has shown the same for *Chilocorus bipustulatus*.

In some insects the situation is less marked, the succesion of long days following on short days leads only to a substantially increased percentage of females ovipositing (in the carabid *Agonum assimile* — Thiele 1966 and in the pentatomid *Aelia acuminata* — Hodek and Honěk unpubl.).

A different procedure was successful for preventing the diapause of the deutostage in *Gryllus campestris* where this effect was achieved by slowing down the development of larval stages (Fuzeau-Braesch 1966). Alternation of different photoperiodic regimes has as yet been very rarely tried; we can expect that many diapauses regarded as "obligatory" could be eliminated from the life cycle by analogous procedures. It is therefore advisable not to restrict oneself to the use of constant photoperiods when studying the induction of diapause in coccinellids.

The ideas concerning the **termination of diapause** have also changed substantially during the short history of the study of diapause. As diapause had long been connected with hibernation, the classical concept assumed that the prerequisite for the termination of diapause was a certain period of chilling. This concept had two variations. The earlier variation contained the assumption that the inhibition of development was "broken" by the exposure to cold, whereas in the second variation Andrewartha (1952) hypothesized that at low temperature a gradual "diapause development" must be completed before normal development can be resumed. Obviously, "diapause development" is made possible by temperatures differing from those which enable normal development; most often the effective range is +5 — +10 °C.

This concept is retained in Müller's (1970) definition of eudiapause: "The further development is established not by the inducing factor, photoperiod, but by a completely different factor, temperature". When later on, instances of summer diapause — aestivation — were recorded, the necessity of "chilling" for the resumption of development began to be questioned.

Recently, however, photoperiodic termination has been achieved in many insects and examples are listed by Beck (1968), Danilevskiï (ed.) (1968), and Hodek (1971b). It is significant that photoperiodic and "chilling" termination may operate in the same insect species, and in a single population of a given species diapause may be terminated in either of the two ways. In temperate zones diapause usually covers only the first period of hibernation or aestivo-hibernation. In mid-winter, and in some insects already in autumn, the potential for resumption of development is recovered. Then, during post-diapause, development is inhibited only environmentally, and may be resumed in the laboratory if favourable conditions (including essential food) are provided. This period may be, therefore, considered a mere quiescence.

An important shortcoming in the study of termination of diapause by cold has been that any effect of mere passage of time has never been separated. While analysing the factors which cause the termination of diapause in some bugs (Hodek, unpubl.), it became evident that both factors — elapsing of time and the need for a cold period were combined and further complicated by the "shock" effect of an increase in temperature. It seems that imaginal diapause which is apparently less immutable than diapause in other stages (Norris 1964) responds especially easily to changes in the environment. Some preliminary results suggesting this have been achieved by Strübing (1963) in *Homoptera*.

As well as increase in temperature and prolongation of photophase, also disturbance and injury can both terminate diapause or at least accelerate its termination (Hodek unpubl.).

As is emphasized by Beck (1968), there is no explanation of how such different agencies (such as exposure to various ecological factors, their abrupt changes, simple time lapses or surgical and chemical treatments) can trigger events on a physiological level in the same way. Presumably, all these stimuli, in different ways (some by exteroreceptors, some by proprioreceptors), influence the neurosecretory cells of the brain which now appear to be the prime movers of the neuroendocrine system (see chapter 7.5).

It would therefore be very dangerous to adhere to the rather generally used and oversimple concepts of diapause termination when studying dormancy in *Coccinellidae*, and to underestimate the complex nature of the mechanisms involved.

7.42 Induction, maintenance and termination of diapause in coccinellids

Before any experiments to analyse the effect of factors regulating diapause were carried out, some hypotheses had been published based on mere observation. These hypotheses in so far as they were justifiable deductions from detailed observations are useful if only as working hypotheses.

Two short studies by Th. Dobzhansky (Dobrzhanskiĭ 1922a, b) have a special position among such hypotheses; they are surprising for their clear-sightedness and show, for that time, a modern attitude. For the first time, imaginal diapause in *Coccinellidae* was recognized and its adaptive significance for survival realized, i. e. that beetles in diapause can withstand a long period of aphid scarcity or absence. Around Kiev (the Ukraine SSR) Dobzhansky ascertained that *Coccinella septempunctcta* had a bivoltine developmental cycle. The adults of the first generation emerge from the pupae between mid-June and mid-July and start ovipositing at the latest within two weeks. The females of the second generation, emerging from mid-July to September at the time of greatest heat, do not mature in the same year in spite of sufficient food, but only do so after hibernation. Having experimentally achieved the development of ovaries in the females of the first generation in spite of combined cold (13 °C) and starvation, the author came to the conclusion that maturation of ovaries is not influenced by external factors, but that a genetically fixed alternation of a generation with normal development with a generation entering diapause is involved. He confirmed this opinion by observing an anomalous situation in the year 1921 when overwintering females matured very late, in early July. In these unusual circumstances, the adults of the first generation emerged from pupae in August and early September — i. e. at a time when normally the second generation would have emerged. If diapause were caused by external conditions, it should then have been induced in the first generation in that particular year. However, it was not so, even so late the ovaries of the first generation females matured and oviposition took place. The emerged larvae then died in large numbers because of lack of food and later due to frost. (Surprisingly in the next March two live pupae were found which had successfully hibernated.) This data from the anomalous development of the beetles in 1921 seems to exclude the possibility that in a normal year diapause of the second generation could be induced by light conditions which Dobzhansky had not taken into consideration. At the same time he did not exclude high temperature (above optimum) as a potential inducing factor.

In over 30 other coccinellid species, where he found undeveloped ovaries during hibernation, he admits that environmental factors had influenced the induction of diapause.

In his paper of the same year, Smee (1922) wrongly states a 3 — 4 generation cycle of *C. septempunctata* in England, with the adults supposedly emerging from pupae in mid-May, early June, late July and in October!

In contrast to Dobzhansky's conclusions many later authors who merely speculated about diapause inducing factors (and did not quote his paper) emphasized the action of biotic or abiotic factors of the environment. Balduf (1935) did not actually hypothesize about diapause inducing factors in *Coccinellidae*, but about "causes of gregariousness" or of "flight from the place of their development". He mentioned three possibilities: high temperature, shortage of food or "state of obesity and satiety" due to the increase of fat content in the body. Yakhontov (1940) believes that shortage of food induces diapause in *Semiadalia undecimnotata* (which migrates without feeding after emerging from the pupa), whereas Telenga (1948) considers that a combination of low humidity and high temperature is the diapause inducing factor in *C. septempunctata*. Bodenheimer (1943) recognizes both biotic and physical factors in *C. septempunctata*.

Telenga and Bogunova (1936) drew attention to the fact that only those adults of *Harmonia axyridis* which emerge from pupae before mid-August can oviposit in the same season in East Siberia. Ul'yanova (1956) imported this coccinellid to a different climate of central Asia (Tashkent) where the beetles already emerged from hibernation in mid-February. The first adults of the first generation emerged from pupae in April, the second generation in June, the third in July, and the fourth in August. In the lst generation all females were reproductive, in the second a few females entered diapause, while in the third and fourth generations most females were diapausing. In both of these two papers there were not even guesses at causal relations made. Neither in the work on coccinellids of the Ukraine SSR (Dyadechko 1954), although very comprehensive as far as food ecology and distribution in habitats are concerned, is there included more than a simple statement of voltinism: "In the Ukraine, nearly all aphidophagous coccinellids reveal one complete and one incomplete generation".

7.421 Coccinella septempunctata

7.4211 Induction of diapause

Surprisingly enough, the diapause of *C. septempunctata* remained experimentally neglected for about 40 years after the preliminary experiments by Dobzhansky. In a thorough ecological study of *C. septempunctata*, Jöhnssen (1930) records the univoltine cycle in central Europe; the acceleration by temperature of the development of all stages led him to admit the possibility of a 2nd generation under especially favourable climatic conditions. He expected this second generation to die out as eggs or larvae. The only experiment that he carried out was to rear adults emerged from pupae in August indoors on food, until their oviposition in early March the next spring. As neither the physical conditions of the experiment nor the food are given, no definite conclusions can be drawn. If we assume that these rearings took place in a heated room (which seems very probable), the results suggest no more than that "chilling" is not obligatory for the spring maturation of the females.

We tried to go a little further in understanding the factors which induce diapause in *C. septempunctata*. This species or at least its populations in Czechoslovakia proved to be complicated in this respect.

Although in some years aggregations of dormant *C. septempunctata* of both sexes may be found in their hibernation quarters from early August onwards, we can also find actively feeding coccinellids on vegetation with aphids (especially often on different weeds as *Carduus spp.* and *Umbelliferrae*) for the whole September and in early October. This agrees with observations by Telenga (1948) who also used to find, at the same period of time, that the population of *C. septempunctata* was partly dormant and partly feeding. We compared the physiological condition of our coccinellids by dissection and rearing (Hodek 1962a). Whereas the alimentary canal in dormant beetles is empty of food and there are no traces of vitellinization in the ovaries, we found that the digestive tract is full of food in more than half of the active adults and that 13 — 20 % of females possess one or more vitellinized oocytes or even eggs. The difference in the amount of fat body is not very great (Table 7.06). The difference between the dormant and active fractions of the population is much more striking, if the beetles of both fractions are reared for three weeks under long-day conditions, with a relatively high

Tab. 7,06 Differences between two fractions of autumnal adults of *C. septempunctata* (Hodek 1962)

Date collected 1) 2)	Condition	N	Dissection 3)	Digestive tract		Fat body			Ovarioles with	
				empty	full of food	+	++	+++	germaria only	at least one vitellinized oocyte
18.9.1) 27.9.2)	active active	30 20	after sampling	4 9	26 11	3 5	8 3	19 12	26 16	4 4
18.9.1)	active	18	after rearing3)	—	—	—	—	—	2	16
8.8., 6.9.1)	dormant	17	after sampling	17	0	2	5	10	17	0
8.8.1)	dormant dormant	29 25	after rearing3)	— —	— —	— —	— —	— —	26 21	3 4

1) Collected in northern Bohemia, near Louny.

2) Collected in southeastern Slovakia, near Kráľ. Chlmec.

3) Reared for 3 weeks in long days, 19—22.5° C, fed with plenty of essential aphids.

temperature (19 — 22.5 °C) and are fed on plentiful essential aphid food. About 85 — 90 % of dormant females remain without any vitellinization, while about 90 % of the females collected on plants now possess vitellinized oocytes.

The summer dissections (mid-July) of females about a fortnight after emergence from the pupae indicated a strong tendency to univoltinism. and in the sugar-beet fields in central Bohemia about 84 — 93 % of females entered diapause. The incidence of diapause was still fairly high (about 65 — 80 %) when the coccinellids were reared indoors under conditions approaching those in the field (except for extremes) and with the natural light conditions of late June and early July. Similarly. an apparently very low percentage of ovipositing females was present in a simultaneous massive culture of more than 200 adults. as only 1 or 2 egg batches were found daily. In another simultaneous culture of 100 pairs most adults formed aggregations in corners of the cage from mid-July. only 5 — 10 beetles moving about. although the aggregation was disturbed purposefully every day from early August onwards. Plenty of essential food was supplied (field collected *Uromelan aeneus* and *Aphis fabae*). and the cage was heated with a lamp during colder days (during natural day-light only). Under these conditions only 1 or 2 egg batches were obtained per day. and by the end of October 75 males and 83 females still remained alive. Adults from the second generation. reared from the first batches. emerged from pupae from 17.8. onwards; they remained very active and feeding for about three weeks. and aggregated after four weeks (Hodek 1962).

By these crude experiments we proved that *C. septempunctata* adults feed before they enter diapause (in contrast to Yakhontov's (1962) finding for *S. undecimnotata*) and that the onset of diapause is not prevented by essential food being available (in contrast to Hagen's (1962) findings for *Hippodamia convergens*). The data showed no evidence of a possible diapause inducing function of decreasing day length because in some replicates the beetles entered diapause in spite of having emerged under the longest possible day length. The slight difference between the outdoor and indoor results indicated the possibility that temperature extremes may play some part in inducing diapause.

We tried to use a premature development of the 1st generation (the adults emerged from pupae as early as mid-May in spring 1968) to assess the potential for multivoltinism (or bivoltinism) of the species in a very warm region of Czechoslovakia — in southern Slovakia (Zohor near Bratislava). We reared the beetles in almost natural condititons. (except for extremes) by transferring them on cold days to the glass-house. or even to a constant 25 °C into the laboratory. into shadow during strong sunshine and indoors for the night. Diapausing females (i. e. females with ovarioles only consisting of germaria without any trace of vitellinization) ranged between 66 and 90 %. with the average of 79 % (N = 184) (Hodek unpubl.)

Notwithstanding the abnormally favourable conditions (a warm spring. a warm region) the tendency to a univoltine cycle persisted in a rather high percentage of *C. septempunctata* females in Czechoslovakia. As the last beetles were dissected on 21 June and therefore had lived through a period of still increasing daylength. the possibility that diapause was induced by the shortening of what were still long days was excluded in this experiment.

The next series of experiments was carried out under controlled light and temperature conditions (Hodek and Čerkasov 1960a, 1961, Hodek 1962a). Cultures were started in five successive seasons (1956—60) with beetles collected from the field after hibernation. As the eggs were collected at the end of the normally short pre-oviposition period. the eggs of any female with a delayed oviposition would have been excluded and thus a selection against the tendency to diapause was made. In this way. a gradual decrease in diapause incidence was achieved (Tab. 7.07). In spite of favourable conditions [i. e. long-day conditions (16 hr or 18 hr photophase in a 24 hr photoperiod). a constant 25 °C, an excess of essential aphid food]. the incidence of diapause remained rather high in the 1st generation, and usually fluctuated between 60 and 90 %. These fluctua-

Tab. 7.07 Incidence of diapause in *C. septempunctata* in five laboratory cultures of successive generations1) (Hodek and Čerkasov 1961a, b, Hodek 1962)

Culture (No. and year of its onset)	Generation	Percentage2) of diapausing females		N	Emergence of adults (lst day)
		average	min.—max. (in replicates)		
I 1956	1	86		22	3. 7.
	2	64		11	10. 8.
	3	11		9	30. 9.
	4	0		9	6.11.
	5	0		17	9.12.
	6	0		10	21. 1.
	7	0		10	3. 3.
	10	0		14	25. 7.
	12	10		10	27.10.
II 1957	1	63		27	12. 7.
	3	14		14	26.10.
	4	16		19	3.12.
	5	7		30	20. 2.
	6	17		18	15. 4.
	8	45		11	18. 6.
	9	10		58	30.7.
III 1958	1	67	—	18	25. 6.
	2	38	(20 — 50)	24	7. 8.
	3	18	—	11	11. 9.
	4	33	(13 — 48)	39	20.10.
	5	6	—	16	24.12.
	6	14	(5 — 32)	56	20. 1.
	7	8	—	13	23. 2.
	8	8	(8 — 9)	24	31. 3.
	9	5	(0 — 11)	21	22. 4.
IV 1959	1	32	(30 — 33)	22	16. 6.
	2	9	(0 — 20)	11	14. 7.
	5	4	(0 — 14)	50	26.11.
	6	5	(0 — 9)	22	1.12.
	8	6	(0 — 17)	36	29. 1.
	9	10	—	10	22. 2.
V 1960	1	81	(46 —100)	137	7. 3.

1) 25° C ± 3° const.; long-day conditions (photophase 16 hr, from October 1958, 18 hr); essential food (*Aphis craccivora*).
2) Females with ovaries consisting of germaria only.

tions were perhaps related to varying conditions: e. g. the number of specimens used to start a culture, the locality where the beetles had been collected, the age of the females at the time of laying the eggs from which the next generation originated and the age of dissected females. In the subsequent generations a progressive decrease was sometimes obtained as in 1956 or in 1958 within the first three generations, or a trend of decreasing diapause with fluctuations.

To achieve incidences of diapause approaching or reaching zero in generations higher than the fourth or fifth it is essential that the rearings remain in perfect order (a steady excess of food, cleanliness, and a population density not exceeding 25 pairs in a cage of about 8 l). Otherwise, the percentage of diapause increases (Tab. 7.07 : 1957 8th gen., 1958 4th gen.). In the course of laboratory breeding under constant conditions the vitality of the beetles decreases (Tab. 7.08).

Tab. 7.08 Decrease in fecundity and longevity in generations three, four and six in the culture II (1957) of *C. septempunctata* (Hodek and Čerkasov 1961a, b)[1])

Generation	No. of days on which oviposition occurred	Average longevity (days) females	Average longevity (days) males	Number females	Number males
3	20.6	59.4	71.3	26	27
4	13.3	62.9	60.5	29	30
6	7.7	47.6	46.9	23	30

[1]) Kept as isolated pairs; the oviposition and the mortality in each cage were recorded daily.

That diapause incidence decreases in the course of culturing subsequent generations indicates the progress of a selection against a tendency for obligatory onset of diapause under long day conditions. The results for *C. septempunctata* are not exceptional in the literature on diapause (Hodek and Honěk 1970). It is assumed that multiple genes control the diapause tendencies.

In the later generations (beyond the 4th or the 5th), all or nearly all the beetles could oviposit under long-day conditions. Thus the way was opened for environmental factors to induce diapause and for this to be studied (Hodek and Čerkasov 1961). This was done gradually, with coccinellids obtained from different generations and cultures (Tab. 7.09). Up to the time that the larvae were transferred to the experimental conditions, they had been reared under the normal breeding conditions used for the negative selection of the diapause tendency. Although the material used was not the same in all experiments, the results are surprisingly consistent, with only one value (for III/7 at 12 hr) slightly discrepant. Two factors were operating in conjunction for the induction of diapause in these artificial conditions, i. e. photoperiod and temperature. The importance of photoperiod was dominant: diapause was prevented by long-day conditions (19 hr per 24 hr) even at low temperatures of 18 or 18.5 °C in respectively 87 — 96 % of females.

The constant temperature of 18 °C caused a high mortality of the larvae, particularly if they were transferred there at the early age of 2 — 3 days. One of the factors contributing to this high mortality was the evaporation of water from parts of the vegetation which carried the aphids; this produced excess of humidity in the incubator.

The response of diapause to short-day conditions was considerably modified by temperature (Tab. 7.09). At lower temperatures, corresponding to those used in the long-day experiments, the incidence of diapause reached about 90 % (with one exception, when it was only 50 %). An increase in temperature (within optimum) led to a marked decrease of diapause incidence so that at temperatures fluctuating between 24 — 25 °C (night) and 27 — 28 °C (day) it amounted to 10 % only. No significant differences were found between different lengths of photophase within the range of 'long' or 'short' day or between the exposure of younger or older larvae or of pupae to

Tab. 7.09 The proportion of *C. septempunctata* females entering diapause under different conditions of temperature and daylength (Hodek and Čerkasov 1961a, b)[1])

Material culture/generation	Age of larvae at experiment onset[1]) [days]	Temperature [°C]	Photophase [hr/24hr]	Age at dissection [days]	N	Diapausing females [%]
I/7	3	17—18 (D)/20—22 (L)	12	42 — 51	15	94
I/7	pupae	17—18 (D)/20—22 (L)	12	56 — 62	15	87
I/9	5 — 8	17—18 (D)/20—21 (L)	12	24 — 41	30	87
III/4. 5	2 — 3	18 ± 0.5	12	26 — 43	20	85
III/7	6 — 7	18.5 ± 0.7	12	20 — 37	38	50
I/9	5 — 7	22 ± 0.5	8	33 — 35	10	70
II/4	4 — 5	22 ± 1.0	12	24 — 34	42	60
I/9	3 — 7	25 ± 0.5	12	30 — 33	40	33
I/6	eggs	24—25 (D)/27—28 (L)	8	24 — 26	20	10
III/4, 5	2 — 3	18 ± 0.5	19	26 — 43	24	13
III/7	6 — 7	18.5 ± 0.7	19	20 — 37	46	4

[1]) before the transfer to experimental conditions the insects were reared at 25°, 16 or 18 hr photophase; both before and during the experiment an excess of essential food was supplied

the experimental conditions. The critical photoperiod was not ascertained; it lay between 12 and 16 hr photophase.

These results obtained with beetles which had been cultured for several generations under a strong selective pressure against the diapause tendency, strikingly contradict the results using the progeny of hibernated beetles, i. e. the first generation. A possible explanation is that the central European population of *C. septempunctata* is very heterogeneous (Hodek 1962a). As this species is reported as univoltine in England and Norway (Banks 1954a, Sundby 1968) and obligatorily (Dobrzhanskiï 1922a, b,) or facultatively bivoltine in the Ukraine (Dyadechko 1954), it seems quite probable that Czechoslovakia lies in a transition zone (in the sense of Bodenheimer and Vermes 1957) between the distribution areas of uni-and multivoltine populations (Tab. 7.10).

Tab. 7.10 Hypothetical condition of *C. septempunctata* in early autumn (Hodek 1962)

Activity	Ovaria	Voltinism	Type of diapause	Generation	Origin
Dormant at hibernation quarters	without vitellinization	univoltine	obligatory	1.	(early batches)
Active (feeding) on plants	without vitellinization (primarily or retrogressed)	univoltine	obligatory	1.	(later batches or slower development)
		multivoltine	facultative	1. 2.	(later batches or slower development)
				0.	(overwintered adults. not yet dead)
	reproductive	multivoltine	facultative	1.	(early batches)

This apparently holds for central Europe in general, for Jöhnssen (1930) mentions the possibility that extremely favourable conditions may increase the number of generations per year from the normal one to two. This assumption is supported by the experiments both under natural and almost natural conditions described above. Other explanations, however, have not yet been excluded by experimental evidence. Norris (1964), for instance, argues that environmental effects on the parents during hibernation may be responsible for the high tendency to diapause in the first generation. This possibility, however, though still open for *C. septempunctata*, has been excluded for the pentatomid bug *Aelia acuminata* by comparing the incidence of diapause in the progeny of adults collected before and after hibernation (Hodek and Honěk 1970). The Czechoslovakian results on *C. septempunctata* also leave room for another possibility that the induction of diapause has been partly influenced by the change from long to short day during larval life. This possibility is, however, rendered less likely by two replicates where the transfer was carried out very early in larval life (2 — 3 days old) and the incidence of diapause was nevertheless high (85 and 94 %).

There remains the very real possibility that obligatory univoltinism is induced by the absence of a special alternation of environmental conditions, e. g. the succession fo long-day conditions after short-day conditions (as has been found in some insects, see 7.41) which is a prerequisite for the complete maturation and oviposition.Then the change in response of the later generations could have been caused by the gradual negative selection for this requirement. This idea, however, is not in essence differing from our original interpretation.

Although the climate around Paris (Ile-de-France) is substantially different from that of central Europe, the results of a study of diapause of *C. septempunctata* in this region are fully consistent with ours (Bonnemaison 1964). 85 — 95 % of the progeny of hibernants enter diapause in spite of favourable conditions (long day of 16 or 18 hr, 22 °C, excess of aphids, Tab. 7.11) under which selection proceeds from 85 % by steps of 40, 20, 5 and 5 % diapausing individuals for the first 5 generations to a culture consisting solely of non-diapausing coccinellids by the sixth generation. Already by the second generation a substantially different percentage of diapause could be achieved with an unfavourable photoperiod: whereas 35 — 40 % diapaused with an 18 hr photophase and excess of food, the figure rose to 85 % with 12 hr light or a shortage of food with long day illumination. Bonnemaison also ascertained a considerable variability in diapause incidence and accepts the hypothesis of a mixture of uni- and multivoltine races. He considers that air movements and human transport regularly bring univoltines from colder regions and multivoltines from the meridional zone to the Paris area. The development of a 2nd generation near Paris is considered impossible by Bonnemaison, except during exceptional conditions. He considers that temperature and lack of aphids in late July and in August are limiting.

Tab. 7.11 Incidence of diapause in the progeny of hibernating *C. septempunctata* in Paris region (Bonnemaison 1964)

Photophase1) [hr/24 hr]		Type of culture	Food	Diapausing females2) [%]
larvae	adults			
16	16	group	excess	85
16	18	group	limited	95
16	18	group	excess	85
16	16	isolated	excess	90
16	12	isolated	excess	95
12	18	group	excess	85
12	16	group	excess	85
12	12	group	excess	95
12	14	group	excess	95

1) 22 °C.
2) dissected at the age of 50 days; in all replicates N = 20.

The tendency to a univoltine cycle seems equally pronounced in the French Riviera (Cote d'Azur) (Iperti pers. comm.). Iperti (1966) recognizes *C. septempunctata* as univoltine or partly multivoltine. The situation is apparently similar in Israel according to Bodenheimer (1943). In the French Riviera the first generation only oviposits under exceptional conditions (the peninsula of Giens) after an aestivation period and thus forms a second generation.

When rearing the introduced *C. septempunctata* for releases in potato fields, Shands et al. (1970) found that "food in the larval stage and quality of light in the adult stage" are important for diapause induction.

7.4212 Completion of diapause

Only preliminary experiments have been conducted on the completion or termination of diapause in *C. septempunctata;* our ideas about the regulating mechanism involved are therefore still rather nebulous. "Artificial" diapause has been found to proceed to termination rather quickly; chilling is apparently not a prerequisite for further development (Hodek and Čerkasov 1961; Tab. 7.12).

Neither does "natural" diapause seem to be too firmly established (Tab. 7.13). After about three months of dormancy (17.11), all females can be activated within three weeks. Comparing this with the poor results obtained when activating the August samples (even when the beetles were exposed to a sufficiently high temperature of 24 °C for 8 weeks), indicates that the inhibition of maturation was lifted in the course of September, October (and early November) (Hodek 1962a). It was, however, not clear, whether merely some "time-keeping" factor is involved (as supposed by Hinton 1957

Tab. 7.12 Spontaneous termination of „artificial" diapause in *C. septempunctata* (Hodek and Čerkasov 1961)

12 hr, 22° / 5 weeks — 70 % diap. (N = 10) — 12 hr, 22° / 5 weeks — 36 % diap. (N = 39)

12 hr, 17.5° — 20.5° / 3.5 — 6 weeks — 87 % diap. (N = 30) — 12 hr, 17.5 — 20.5° 5 weeks dark, + 4.5° — (N = 7)

12 hr, 25° 3 weeks — 0 % diap. (N = 11)

Tab. 7.13 Attempts to terminate the „natural" diapause in *C. septempunctata* by transfer to the laboratory (Hodek 1962)

Sample[1]	Breeding[2]		Diapausing females [%][3]	N
	Duration [days]	Temperature [°C]		
8. 8. 61	22	17 ± 1/19.5 ± 0.5	90	29
30. 8. 61	18	20 ± 1.5	84	25
25. 8. 59	54	24 ± 1	78	18
4. 11. 60)[4]	20	24 ± 1	12	17
17. 11. 59	23	24 ± 1	0	23

[1] Sampled at the dormancy sites.
[2] Long day and excess of food.
[3] Dissection before breeding revealed immature ovaria possessing germaria only.
[4] Collected 18 Oct., stored in cold until 4 Nov.

and other authors) or whether the low autumn temperatures were effective, as is generally supposed to apply in insects.

A preliminary experiment with beetles collected in late August (i. e. after a maximum of 5 weeks in the dormancy sites) has not indicated any effect of low temperatures above zero: the highest temperature used (+ 12 °C const.) was most efficient in activation (Tab. 7.14). Zero was substantially less effective than other temperatures, even though the exposure lasted 9 weeks. At other temperatures, the activation rate was related to the duration of exposure (Hodek 1970). Thus diapause could be terminated in 60 — 100 % of the beetles after only about 14 weeks.

Tab. 7.14 Attempts to terminate the "natural" diapause in *C. septempunctata* by exposure to cold (Hodek 1970)1)

Exposure to cold2)		Diapausing females [%]	N
Duration [weeks]	Temperature [°C]		
3	12	45	11
6		0	8
3	+ 5/123)	67	21
6		40	20
3	+ 5	67	30
6		11	9
9	0	80	30

1) Sampled in late August.
2) After cold exposure the beetles were reared for 3 weeks (long day, excess of food, 18 ° — D/23 ° — L)
3) One increase and one decrease in temperature per 24 hr.

Near Paris, Bonnemaison (1964) found that diapause lasted 3 — 6 months in *C. septempunctata* females which had emerged from pupae in early August and were kept at 20 — 22 °C and a natural photoperiod. He failed to reactivate the diapausing females (collected in late July or early September) by an exposure to 8 ° (or 5 °) for 5, 9 and 13 weeks and by subsequent rearing at 20° and 16 hr for 15, 11 and 7 weeks to make a total of 20 weeks for each batch. His findings on the onset of previtellogenesis in females in the field from late September onwards (Tab. 7.15) indicate — very similarly

Tab. 7.15 Development of ovaries in *C. septempunctata* in the field (Paris region — Bonnemaison, 1964)

Sample	Females possesssing ovarioles with		Length of ovarioles		
	germarium only	one oocyte	average	min.	max.
21. 8.	100	0	575	510	620
11. 9.	100	0	610	530	660
30. 9.	96	4	600	480	672
11. 10.	16	84	730	640	870
19. 10.	30	70	660	465	800
27. 11.	25	75	590	460	750

to our results — some kind of lifting of the diapause inhibition in autumn. In contrast to Czechoslovakia, however, the apparently higher temperature of the Parisian region enabled the first stage of maturation to proceed in the field and to be identified directly by the dissection of field samples, whereas in central Europe the potential for maturation can only be revealed by laboratory breeding (Tab. 7.06).

When summarized, these fragmentary results indicate clearly enough that diapause in *C. septempunctata* usually lasts about 3 — 4 months (both in Czechoslovakia and in the region of Paris) and that "chilling" is not necessary for its completion. This is also confirmed by findings of Iperti (in Hodek 1966 p. 105) with populations from the Cote d'Azur. The high autumnal temperature together with the resurgence of aphids after summer drought may, under exceptional conditions (e. g. peninsula of Giens), enable the establishment of a 2nd generation. We may, however, expect important variations of this scheme in a species with such ecological plasticity as is a feature of *C. septempunctata.*

7.4213 Diapause in males

As explained earlier (part 7.2) diapause in coccinellids is not connected with inactivity of the tissue of the testicular follicles. From knowledge of other insects, one might however expect inhibitory changes in the accessory glands and in the copulatory aptitude of males. When Bonnemaison (1964) reared emerged males of the fourth selected generation under 12 hr light and 14° or 18 °C for 15 or 25 days, he could not even find these symptoms of diapause. After transfer to favourable conditions where females were being reared (16 hr, 20 °C), the males copulated after 2 — 7 days, and the females laid apparently viable eggs (not specified) after 3 — 23 days.

7.422 Chilocorus spp.

C. rubidus. — A species of eastern Siberia is strictly univoltine. The dormancy lasts between late August to mid September and late April, while diapause (which is marked by a trough in oxygen consumption ends as early as late December to early January. The rest of dormancy is spent in mere quiescence ("spyachka" — sleep) during which it is possible to obtain oviposition by transferring the beetles to a higher temperature. Pantyukhov (1968b) found that neither "chilling", nor any particular photoperiod was necessary for the termination of diapause, but the passage of 3.5 — 4 months under any conditions (25°, 20°, 5—8° and field conditions were tested) was alone sufficient.

C. renipustulatus. — In contrast to *C. rubidus* diapause in the majority of *C. renipustulatus* individuals can be prevented in both the populations that have been studied. Thus only 12 % of beetles from Maïkop (southern Ukraine) entered diapause in spite of long days, whereas in the population from Leningrad the figure was 38 %.

The critical photoperiod is insensitive to temperature (within the range 20—25 °C) and is 2 hr longer in the beetles from Leningrad than in the Maïkop strain (Pantyukhov 1968) (Fig. 7.03).

C. bipustulatus. — Of *Chilocorus spp.* most attention has been paid to *C. bipustulatus*, whose distributional area comprises a large part of the Palaearctic region. Whereas in Central Asia (Tashkent) this typical multivoltine species has a simple type of facultative diapause which can be prevented or terminated by long-day conditions (Zaslavskiï and Bogdanova 1965, Zaslavskiï 1970), the annual cycle of the northern populations (Leningrad) is regulated in a more complex way.

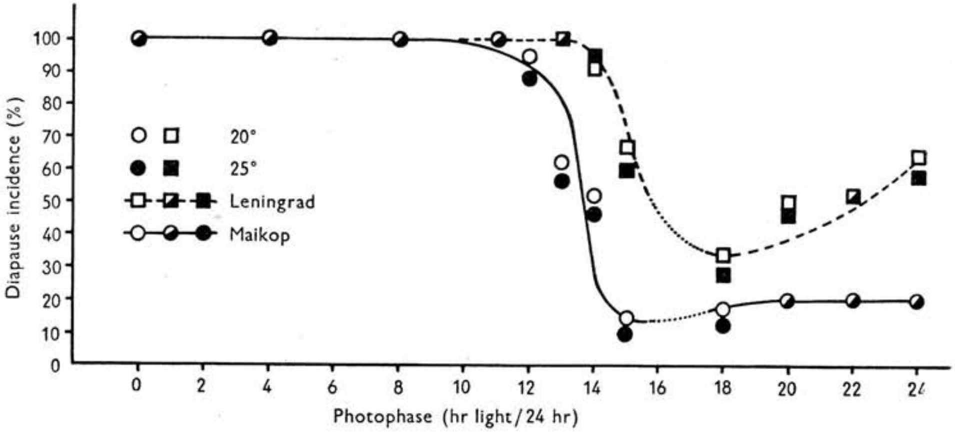

Fig. 7.03 The effect of photoperiod on the incidence of diapause in two strains of *Chilocorus renipustulatus* (Pantyukhov 1968a).

In *C. bipustulatus* from **Central Asia** (40 — 41° northern latitude) diapause is induced by a photophase shorter than 15 hr, and at 20 °C 100 % beetles enter diapause. At 24 °C, however, diapause is completely prevented in all females in spite of the short day (9 or 11hr). Under temperatures near 20° spontaneous termination of diapause does not occur providing that the beetles are maintained at diapause conditions. On the other hand, either an increase in temperature or a prolongation of photophase beyond the above-mentioned thresholds terminates diapause very quickly — oviposition takes place within a few days. It is equally easy to terminate diapause 7 — 10 days after its induction as it is after 3 months. By contrast, transfer of the ovipositing beetles from long day to diapause conditions gradually suppresses oviposition, while a return to long days restores it. Alternatively, diapause may be terminated by "chilling". After an exposure to + 8 °C for 30 — 40 days the beetles mature even in short days. Thus, sensitivity to photoperiod could be nullified by an exposure to cold.

The completion of adult diapause in *Pyrrhocoris apterus* (*Heteroptera*) closely resembles that of *C. bipustulatus* (Hodek 1968).

C. geminus — In the central Asian populations (Tashkent) of this closely related species (40 — 41 ° northern latitude) induction and termination of diapause is very similar to that in *C. bipustulatus*. The only difference is a higher temperature threshold — as much as 26 °C is needed to prevent diapause in short-days (Zaslavskiĭ and Bogdanova 1965).

C. bipustulatus from **Leningrad** (60° northern latitude). — The beetles of the northern population do not mature and do not lay eggs, if the larvae, pupae and adults are reared continuously in long days (20 hr) (Zaslavskiĭ 1970). Short-day conditions (9 hr) for at least 3 weeks before the transfer to long day are a prerequisite for normal reproductive activity. The short day treatment is equally effective when given to the larvae. The alternative way to induce oviposition is "chilling" for about a month at +7 °C followed by a transfer to long days or otherwise to "chilling" for at least 3 months before transfer even to short days. If the beetles are constantly left in long days diapause ends spontaneously after about 2 — 4 months. However, the beetles gradually cease ovipositing in continuous long days after about 1.5 — 2 months of egg laying and have to be reactivated from this "secondary" diapause by a new passage of about 25 days in short days.

The critical photoperiod for the beetles from Leningrad is 2 hr longer (17 hr) than for the central Asian population (Fig. 7.04). It does not change with temperature within the range of 20 — 27 °C.

The results of Zaslavskiĭ (1970) are of extreme importance, as they confirm for *Coccinellidae* that a number of alternative pathways lead to the triggering of the neuroendocrine system and its control of oviposition. The failure to oviposit in long days would normally place the diapause of the Leningrad strain of *C. bipustulatus* into the category of obligatory diapause.

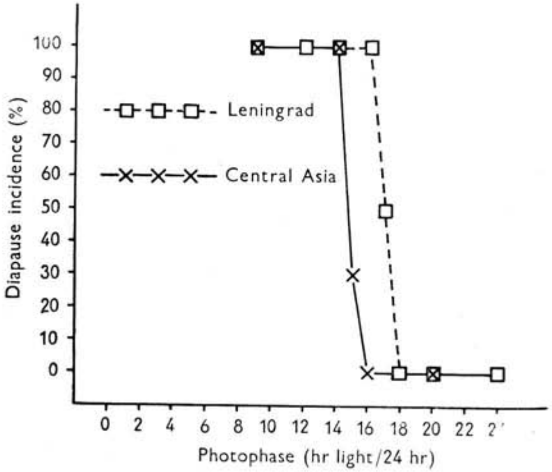

Fig. 7.04 The effect of photoperiod on the incidence of diapause in two strains of *Chilocorus bipustulatus* (Zaslavskiĭ 1970).

C. bipustulatus in **Israel** (32—33° northern latitude). — The populations from the eastern Mediterranean area (Israel) differ from those of central Asia in their threshold both for photoperiod and temperature (Tadmor and Applebaum 1971). A photophase of 14 hr (per 24 hr photoperiod) prevents diapause, whereas a shorter photophase (10 hr) tends to induce it (Tab. 7.16). Thus, consistent with the findings of Danilevskiĭ (ed.) (1968), the critical photoperiod is about 2 hr shorter in Israel than in the central — Asian strain. The effect of the short photophase is modified by temperature — at 22° it is completely nullified so that all females lay eggs. A cumulative sensitivity to diapause induction is exhibited both in the preimaginal stages and in the adults.

There is contradiction between early and more recent reports about the summer occurrence and efficiency of *C. bipustulatus* in Israel. Early reports concluded that

Tab. 7.16 Effect of photoperiod and temperature on oviposition in *Chilocorus bipustulatus* in Israel (Tadmor and Applebaum 1971)

Photophase [hr/24 hr] and temperature [°C]				Ovipositing females [%]	Mean pre-oviposition period [days]	Number of replicates
larva and pupa		adult				
24	28°	10	8°/20°[1]	46	21	11
24	28°	10	18°	60	17	10
10	18°	10	18°	1	21	11
24	28°	10	22°	100	10	7
24	28°	14	18°	93	14	14

[1] 8° during scotophase, 20° during photophase.

C. bipustulatus was common only in spring and extremely scarce in summer, and was therefore an inefficient predator of scale insects (Hecht 1936, Bodenheimer 1951). The high mortality in summer is supposed to have been caused by the 'chamsin' — a dry hot wind from the desert. The more recent findings show, however, that *C. bipustulatus* is rather abundant in the summer (some authors even report the population peak in early summer) and plays an important role in retarding the build-up of scales in this period (Nadel and Biron 1964, Avidov and Rosen 1965, Rosen and Gerson 1965, Kehat 1968b, Ben-Dov and Rosen 1969). In the summer, however, the females produce many fewer eggs and in this way determine the decrease in adult numbers later on. This has led to speculation that the difference in recent years has perhaps resulted from the improved physical conditions brought about by the introduction of irrigation (Hodek 1967) as the same difference also exists between older (Bodenheimer 1951) and more recent reports (Plaut 1965) on the abundance of *Stethorus punctillum*. Kehat et al. (1971 in print) attempted to analyse the factors which inhibit the reproductive activity of *C. bipustulatus* in late summer and winter. In citrus groves they found a considerable decline in numbers of females with well-developed ovaries during July, and October — December. Transferred to the laboratory (28 °C) and provided with coccids, the non-reproductive females matured at both these times of year. The failure by these authors to induce diapause at 16 combinations of light conditions was apparently due to too high a temperature of 28 ° and 20 ° (cf. Tadmor and Applebaum 1971). Very high temperature (35 °C) additionally, decreases oviposition and survival.

7.423 Coccinella novemnotata

The bivoltine *C. novemnotata* (McMullen 1967a, b) undergoes diapause twice during the annual cycle. The adults of the spring generation pass the hot, dry summer months in diapause and lay eggs in the early autumn. The adults of the autumn generation pass the winter in diapause and reproduce in the early spring. In the spring, the teneral adults are subjected to a photophase which increases from 17 hr 30' to 18 hr and in the autumn decreases from about 14 hr to 13 hr. In the field, diapause in this species is induced both by "long" and "short" days. This specific need is fulfilled by photoperiodic reaction which differs from the commonly described reactions of "long-day" or "short-day" insects, but has been verified experimentally. While in some insects diapause is prevented by long photoperiods and in others by short, in *C. novemnotata* diapause is induced both by short days of 10 hr, 12 hr and (even though less) 14 hr, and by long days of 18 hr (Fig. 7.05). As well as photoperiod, temperature and the amount of prey are also involved. Particularly low temperature contributes to the induction of diapause in the autumn generation. The intermediate photoperiod of

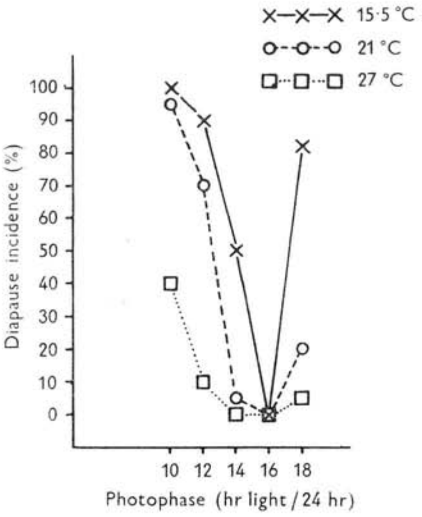

Fig. 7.05 Modification of the photoperiodic reaction by temperature in *Coccinella novemnotata* (McMullen 1967b).

16 hr consistently determines non-diapause development in 90 — 100 % of coccinellids, even when feeding rates are reduced to one-fourth and the whole temperature range of 15.5 — 32 °C is used.

Sensitive stage. — Experiments made with *C. novemnotata* (McMullen 1967b) are the only studies on *Coccinellidae* which are thorough with respect to the determination of the stage sensitive to diapause induction (Fig. 7.06). The author's conclusion that it is the young adult between the ages of 1 and 7 days which is sensitive is, however, rather questionable because the percentage of diapause was judged by the dissection of females at only 14 days of age (at 21 °C), i. e. only 4 days after transfer of adults 10 days old and 7 days after transfer of adults 7 days old. In such a short time the processes controlling the maturation or regression of ovaries could not be complete (see 7.5). In order to exclude what seems indeed very probable, i. e. that adults aged more than 7 days are also responsive, it would be necessary to dissect females sufficiently far in time (at least 14 days) from the date of transfer.

The above-mentioned transfer experiments evidently did not exclude the possibility that, as in other insects with imaginal diapause (*Pyrrhocoris apterus*, *Leptinotarsa decemlineata* — Hodek 1971a), even the pre-imaginal stages are sensitive to the stimuli controlling the onset of diapause. This is known to be so in *Chilocorus bipustulatus* (Tab. 7.16) (Tadmor and Applebaum 1971). In *C. novemnotata* (Fig. 7.06) the sensitivity of preimaginal stages is indicated by retarded ovogenesis in females (marked with 2)

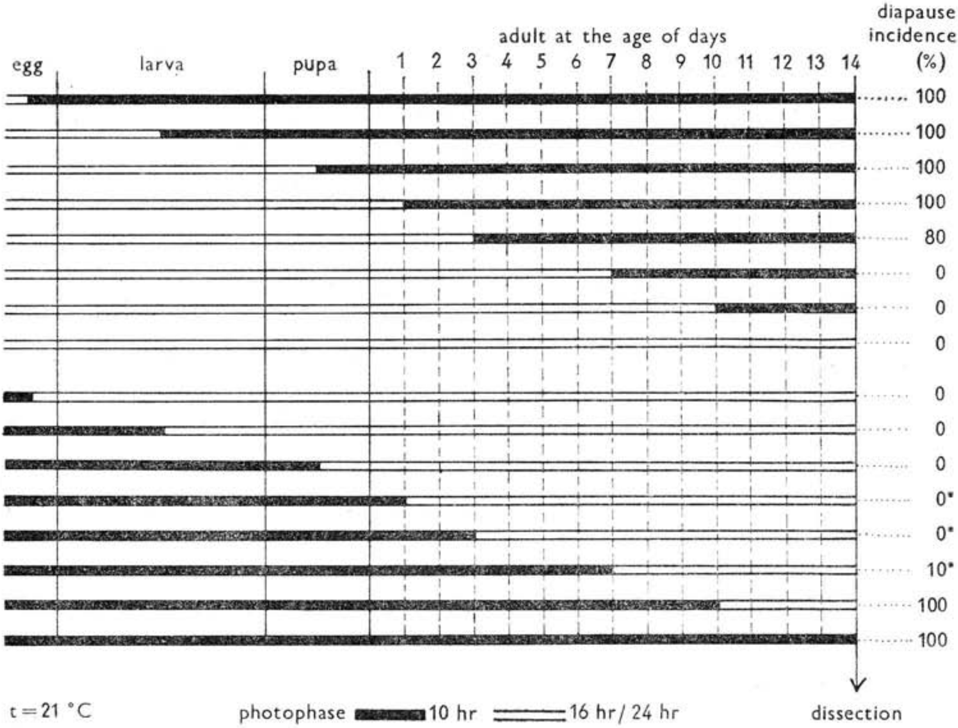

Fig. 7.06 The effect of change in photoperiod on the incidence of diapause in *Coccinella novemnotata*. Females were dissected at the age of 14 days. Under the treatments marked by * , ovogenesis in non-diapausing individuals was retarded (compared with the controls).

which were transferred to a non-diapause photoperiod as teneral or young adults.

The sensitivity of earlier stages may be masked when later stages are influenced by the reverse stimuli; the effect may thus be reversed. The sensitivity of the preimaginal stages may be distinguished when the adults are kept under neutral conditions. We do not usually search for a specific sensitive stage, but rather for the stage of development in which we can still succeed in completely preventing oviposition (i. e. to reverse the former opposite effect) by a transfer from non-diapause to diapause-inducing conditions. A suitable criterion for the sensitivity of larvae may be the length of the pre-oviposition period in females kept as larvae for different periods of time under diapause conditions (Hodek 1971a).

7.5 Physiological mechanisms of adult diapause

This chapter is included, although this book is written by an ecologist for ecologists. In the study of ecological causal relations which govern the onset and maintenance of diapause it appears to be helpful to have at least a general idea of the physiological pathways which regulate these phenomena.

The function of the neuro-endocrine system has not been studied very long, and so there is comparatively little knowledge about it and the findings from individual species are often contradictory. This brief survey will, therefore, suffer from oversimplification and will very soon become dated. The reader is referred to recent reviews (Engelmann 1968, De Wilde 1970) and reviews sure to appear in the future in publications such as Advances in Physiology, Annual Review of Entomology, Annual Review of Physiology, proceedings of various conferences, etc.

The following sequence of events seems to be relatively certain and common in insects. The information concerning the ambient physical or biotic conditions (token stimuli or seasonal tokens) or of endogenous information arrives at the brain. This information affects the neurosecretory cells of the pars intercerebralis of the protocerebrum which produces the brain hormone or activation hormone (AH) of which the chemical nature is still unknown. The corpora cardiaca have the function of a release organ for this neurosecretory material which apparently activates the corpora allata. (It is also thought to regulate protein metabolism.) The hormone (or hormones) liberated by the corpora allata (the juvenile hormone — JH) may have several functions. It promotes the incorporation of proteinaceous and lipid yolk into the growing oocytes, i. e. vitellogenesis in oocytes, probably via the ovarian follicular cells. (The JH is also supposed simultaneously to control various phases of metabolism, as, for example, the protein metabolism associated with egg maturation and fat metabolism.) This whole sequence of events accounts for a certain delay in the reproductive reaction of adults to a change in conditions. Because of that delay, the young females start laying eggs even when during the pre-oviposition period the conditions have changed from favourable to inhibitory. The oviposition then only ceases later on. The process initiated by the earlier stimulating conditions continues, and apparently cannot be affected by ambient "tokens" in later phases. Not until the JH disappears from the haemolymph, are vitellogenesis and ovulation arrested.

The above scheme does not apply to some insects or group of insects. In *Phasmida* and *Lepidoptera*, the extirpation of the corpora allata apparently does not prevent egg maturation and oviposition. In *Leucophaea* (*Blattaria*), in *Rhodnius* (*Heteroptera*) and in *Pieris* (*Lepidoptera*), neurosecretion from the pars intercerebralis does not control the function of the corpora allata (Engelmann 1968, De Wilde 1970).

The evidence for yet more chains of events is, however, still lacking or controversial. Above all, it is not at all certain whether the failure of ovaries to ripen during diapause is caused only by lack of JH or additionally by the presence of an inhibitory factor. Further there is the question of whether the connection between the brain and the corpora allata is only humoral, through the medium of corpora cardiaca and the haemolymph, or also nervous.

It can be assumed that the above mentioned organs also have a feed-back mechanism, e. g. that the corpora allata are somehow influenced by the maturation of ovaries, etc. No such feed-back, however, has as yet been proved (with the exception of viviparous *Blattaria* — Engelman 1968).

Another range of questions, very little studied till now, concerns the mechanism by which the whole system is affected when essential food is taken in. Some results indicate a possible direct connection between the receptors which detect food intake and the corpora allata, without the mediation of the brain. It is certain that it is not only sufficiency or lack of necessary material for the vitellogenesis which is involved. It seems that mating stimuli also activate the corpora allata.