Studies of the physiology of hibernating Coccinellidae (Coleoptera): changes in the metabolic reserves and gonads

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Synopsis

An account is given of changes in the fat and glycogen reserves and of the gonads of three species of aphidophagous Coccinellids during hibernation in southern England.

Introduction

Most predacious Coccinellidae in temperate climates hibernate as adults (Hagen, 1962). Their survival during hibernation and in times of scarcity of food must largely depend on the amount of metabolic reserves that they can accumulate before hibernating.

This study describes changes in the fat and glycogen reserves and of the gonads of three species of Coccinellidae in southern England, *Coccinella septempunctata* L., *Adalia bipunctata* (L.) and *Propylea quatuordecimpunctata* (L.), during hibernation and after emergence in the spring.

Materials and Methods

As overwintering Coccinellids are often difficult to find in the field in sufficient numbers for analysis, the following methods were used. Newly emerged young adults, and larvae and pupae of *C. septempunctata*, *A. bipunctata* and *P. quatuordecimpunctata* were collected from broad beans (*Vicia faba* L.) infested with *Aphis fabae* Scopoli and from nettles (*Urtica dioica* L.) infested with *Microlophium evansii* Theobald, during the late summers of 1963 and 1964, and were fed on aphids for three to five weeks in large cages in an insectary.

In late August, when about to hibernate, the adults were transferred to perforated zinc cages (15 cm. diameter, 15 cm. high) containing dead leaves of bean plants and nettles and pieces of corrugated cardboard, in which the insects could hide. The cages, each containing 50 to 150 adults, were placed on a patch of grass under trees where overwintering Coccinellids had been found in earlier years. The cages were covered with polythene sheeting to keep out rain and prevent flooding, but otherwise the insects were exposed to natural extremes of temperature and humidity.

Samples of the insects in these artificial hibernacula were taken every one to three months during the autumn, winter and spring to determine live and dry weights, and contents of water, fat and glycogen. Temperatures close to the cages were recorded on a weekly-recording thermograph. Other adults, which had started egg laying in the field during spring, were similarly analysed.

Other Coccinellids overwintering under natural conditions were occasionally found and analysed for comparison with those from the artificial hibernacula. About 150 *A. bipunctata*, hibernating in a house in Surrey, were collected and analysed in early March and April, 1964, and others of the same species hibernating in the roof of a laboratory at Rothamsted were sampled at intervals during the hibernation period in 1964–65. Except for a small sample of *C. undecimpunctata* L. collected in October 1964 from the folds of muslin sleeve bags used in an experiment on a plot of field beans at Rothamsted, no other naturally hibernating Coccinellid species could be found in suffiicent numbers for analysis.

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Proc. R. ent. Soc. Lond. (A). **41** (10–12). Pp. 133–144, 6 figs. 1966.

Each insect of a periodic random sample from the artificial and natural hibernacula was weighed alive, killed and re-weighed after drying. The fat and glycogen content of each dried insect was then determined by methods already described (Hariri, 1966). In the early stages of hibernation, the glycogen content of each insect was estimated, but in the late stages, when glycogen reserves were small, two to four insects were analysed together, and their mean glycogen content estimated.

Fat and glycogen are presented as percentages of the dry weight. When samples were taken for analysis of water, fat and glycogen contents, others were dissected and the following records made: the number and length of the ovarioles and the stage of development of the ovaries, the presence or absence of food in the gut, and the diameter of the testes and length of vesiculae seminalis. The insects were dissected in 0·75 per cent. saline solution, and ovaries and testes were stained by Goto's method, as described by Lewis (1959). At least four ovarioles in each ovary were measured, the terminal filament being excluded. Testes and vesiculae seminalis were measured in the saline solution.

Results

Adults of all three species entered hibernation with empty guts, immature ovaries and large fat bodies; testes were mature.

Mortality

The initial numbers of *Coccinella*, *Adalia* and *Propylea* in the artificial hibernacula were 137, 487 and 126, respectively.

Mortality in the hibernacula was recorded during 1963–64 for *Coccinella* and *Propylea* and during 1964–65 for *Adalia*.

In each species, mortality was high in the autumn (September–October) and low during mid-winter (December–February), and increased sharply during early spring (March–May) (fig. 1), possibly because of the onset of warmer weather. *Adalia* suffered the greatest mortality in the autumn (nearly 50 per cent. of the insects died during November 1964), and about 20 per cent. of *Coccinella* died during the late autumn of 1963; very few (2 per cent.) *Propylea* died at this time, and the greatest mortality of this species was in the spring.

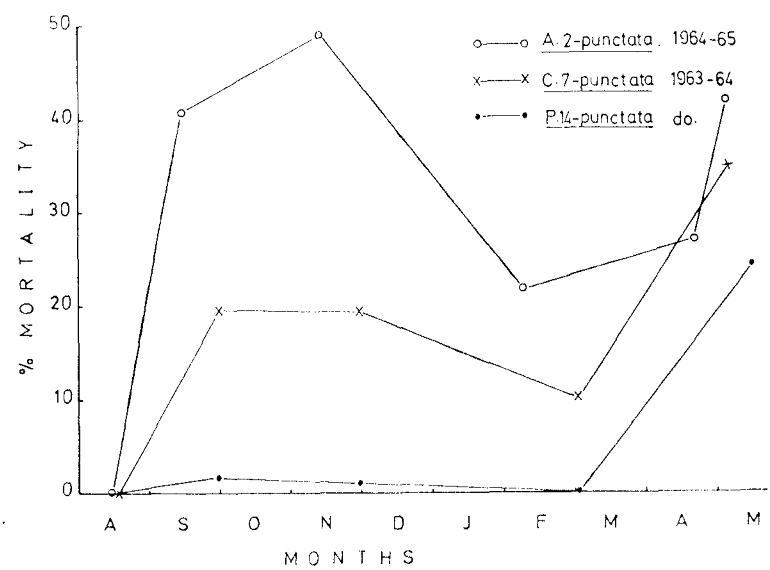

Fig. 1.—Mortality rates of hibernating Coccinellids in the artificial hibernacula, as percentages of the numbers of insects remaining after each sampling.

Changes in weight and water content

Insects of all three species lost 12 to 33 per cent. of their live weight and 9 to 48 per cent. of their dry weight during eight months of hibernation. At the start of hibernation, females were usually heavier than males, but the difference became less towards the end of the hibernation period because females then consumed their metabolic reserves faster. Adult *Adalia* kept in the artificial hibernacula in September, 1964, were heavier than hibernating insects found in the field but were of about the same weight as those kept in artificial hibernacula in September, 1963 (Tables I and II).

TABLE I.—*Mean water, fat and glycogen contents (with standard errors) of overwintering Coccinellids in artificial hibernacula*

Date	n.	Live weight (mg.)	Dry weight (mg.)	Water (mg.)	Fat (mg.)	Glycogen (μg.)
			C. septempunctata			
17.9.63	♂ (10)	29·8±1·2	13·9±0·9	15·9±0·5	5·3±0·7	58·6±13·2
	♀ (10)	42·5±1·1	21·5±0·9	21·1±0·5	9·4±0·7	159·2±31·1
17.11.63	♂ (9)	30·3±1·3	14·4±0·8	15·9±0·7	4·4±0·4	40·3±5·1
	♀ (7)	39·3±1·9	20·3±1·6	19·0±0·9	7·6±1·5	58·6±10·7
2.3.64	♂ (9)	25·9±1·6	12·4±0·9	13·5±0·8	3·3±0·3	34·4±6·3
	♀ (18)	34·8±1·0	17·6±0·7	17·2±0·5	5·8±0·4	34·5±3·3
5.5.64	♂ (9)	26·4±1·4	12·6±0·6	13·8±0·9	2·7±0·4	20·7±1·9
	♀ (3)	29·6±0·5	14·4±0·5	15·2±0·3	3·7±0·7	20·8±1·5
			A. bipunctata			
22.9.63	♂ (5)	9·0±0·2	3·1±0·1	5·9±0·3	0·9±0·1	22·5±5·9
	♀ (11)	12·0±0·5	4·6±0·2	7·4±0·2	1·5±0·1	36·0±8·1
14.2.64	♂ (10)	8·1±0·5	3·1±0·1	5·0±0·1	0·6±0·3	9·3±1·6
	♀ (10)	10·4±0·4	4·1±0·2	6·3±0·2	0·8±0·2	8·3±0·9
18.3.64	♂ (7)	8·0±0·3	3·2±0·2	4·8±0·2	0·5±0·1	10·0±4·3
	♀ (13)	10·2±0·3	4·4±0·2	5·8±0·2	1·1±0·1	17·2±2·3
23.4.64	♂ (7)	8·9±0·5	3·2±0·2	5·7±0·3	0·3±0·08	10·5±1·3
	♀ (13)	10·5±0·4	3·9±0·1	6·6±0·3	0·5±0·07	12·0±1·4
15.8.64	♂ (8)	10·8±0·4	4·9±0·3	5·9±0·2	2·0±0·2	42·3±4·7
	♀ (13)	14·6±0·4	6·9±0·3	7·7±0·2	3·1±0·1	55·3±4·7
14.9.64	♂ (7)	10·2±0·6	4·4±0·3	5·8±0·4	1·4±0·2	40·5±6·1
	♀ (17)	12·3±0·2	5·7±0·2	6·6±0·2	2·1±0·1	47·0±2·8
13.11.64	♂ (7)	10·4±0·4	4·4±0·2	6·0±0·3	1·2±0·2	21·2±3·4
	♀ (10)	12·4±0·4	5·3±0·3	7·1±0·3	1·5±0·2	39·4±3·5
9.2.65	♂ (4)	9·9±0·3	4·1±0·2	5·8±0·3	0·9±0·1	12·8±0·8
	♀ (13)	12·1±0·3	4·9±0·1	7·2±0·2	1·2±0·1	21·5±1·8
7.4.65	♂ (7)	9·6±0·4	3·7±0·2	5·9±0·3	0·7±0·1	14·1±1·1
	♀ (14)	11·5±0·5	4·4±0·2	7·1±0·3	0·9±0·1	16·8±1·8
4.5.65	♂ (8)	9·4±0·4	3·5±0·2	5·9±0·2	0·5±0·09	10·0±1·6
	♀ (10)	9·8±0·5	3·6±0·2	6·2±0·3	0·4±0·09	8·9±2·6
			P. quatuordecimpunctata			
17.9.63	♂ (10)	6·7±0·4	3·0±0·3	3·7±0·2	1·4±0·2	35·7±6·2
	♀ (10)	9·2±0·3	4·2±0·2	4·9±0·2	2·0±0·1	35·4±6·8
17.11.63	♂ (7)	6·9±0·4	3·2±0·2	3·7±0·3	1·1±0·2	23·4±2·1
	♀ (7)	9·0±0·4	4·4±0·2	4·6±0·2	1·5±0·2	21·1±2·8
2.3.64	♂ (7)	6·2±0·2	3·2±0·1	3·0±0·1	0·9±0·1	13·4±1·4
	♀ (10)	8·0±0·2	4·0±0·2	4·0±0·1	1·2±0·1	7·5±0·4
15.5.64	♂ (10)	5·3±0·4	2·6±0·1	2·7±0·1	0·4±0·1	4·1±0·9
	♀ (10)	6·8±0·2	3·5±0·1	3·3±0·1	0·8±0·1	7·0±0·7

After emergence from hibernation in the spring and after having fed on aphids, adults of all three species from hibernacula increased in live and dry weight (Table I). Males of *Coccinella*, *Adalia* and *Propylea* increased their live weights by 36, 13 and 32 per cent., respectively, but the corresponding increases for females (103,

TABLE II.—*Mean water, fat and glycogen contents (with standard errors) of overwintering Coccinellids in natural hibernacula*

Date	Place	n.	Live weight (mg.)	Dry weight (mg.)	Water (mg.)	Fat (mg.)	Glycogen (μg.)
			A. bipunctata				
3.3.64	Surrey	♂ (10)	8·0±0·2	3·5±0·1	4·5±0·2	0·8±0·1	9·1±1·5
		♀ (10)	10·9±0·4	4·9±0·2	6·0±0·3	1·3±0·1	16·2±1·7
19.3.64	,,	♂ (9)	6·8±0·4	3·1±0·2	3·7±0·2	0·7±0·1	9·3±3·3
		♀ (11)	9·7±0·3	4·2±0·2	5·5±0·2	1·0±0·1	15·4±1·7
8.4.64	,,	♂ (7)	8·0±0·6	3·5±0·3	4·5±0·3	0·8±0·2	10·5±1·0
		♀ (11)	9·0±0·7	4·0±0·3	5·0±0·4	1·1±0·2	14·7±0·2
29.4.64	,,	♂ (8)	7·7±0·2	2·8±0·1	4·9±0·1	0·3±0·1	5·9±1·2
		♀ (12)	8·5±0·2	3·4±0·1	5·1±0·1	0·7±0·1	6·3±1·1
26.4.64	Rothamsted	♂ (5)	7·7±0·4	3·0±0·3	4·7±0·2	0·3±0·2	5·0±2·5
		♀ (9)	9·3±0·6	3·6±0·2	5·7±0·5	0·5±0·1	8·9±1·1
16.10.64	,,	♂ (3)	9·8±0·4	4·9±0·3	4·9±0·2	1·9±0·2	43·3±5·4
		♀ (10)	10·7±0·8	5·1±0·4	5·6±0·4	2·1±0·3	45·4±4·9
22.12.64	,,	♂ (5)	7·4±0·6	3·8±0·3	3·6±0·3	1·0±0·1	16·2±3·0
		♀ (5)	10·2±0·8	5·1±0·5	5·1±0·3	1·8±0·3	41·5±7·3
28.3.65	,,	♂ (9)	8·2±0·4	3·7±0·2	4·5±0·2	0·8±0·1	13·6±2·4
		♀ (15)	10·0±0·5	4·5±0·2	5·5±0·4	1·1±0·1	19·4±3·3
23.4.65	,,	♂ (3)	6·4±0·8	2·9±0·3	3·5±0·4	0·4±0·07	7·9 .
		♀ (13)	8·4±0·5	3·7±0·2	4·7±0·3	0·9±0·2	6·9±0·7
			C. undecimpunctata				
5.10.64	Rothamsted	♂ (6)	9·2±0·2	4·6±0·2	4·6±0·2	2·0±0·1	47·1±3·9
		♀ (10)	9·8±0·2	4·7±0·1	5·1±0·2	2·0±0·1	40·6±2·0

41 and 54 per cent.) were much larger because they became gravid after feeding. Corresponding figures for the dry weights of hibernated insects from the field were: males—3, 20 and 8 per cent.; females—42, 36 and 14 per cent. (Table III).

In the artificial hibernacula *Adalia* entered hibernation in 1963 with more water (mean, 64 per cent.) than *Coccinella* (52 per cent.) and *Propylea* (56 per cent.), but in 1964 they contained on average 54 per cent. water on entering hibernation (Table I). *Coccinella* and *Propylea* gradually lost water during hibernation, but the proportion of water in *Adalia* (whether from the artificial hibernacula or collected from the field) increased during the spring of 1964 and again in the spring of 1965.

After emergence and feeding on aphids, the water content of male *Coccinella*, *Adalia* and *Propylea* increased respectively by 66, 9 and 56 per cent., but the corresponding increases in females were much larger (161, 44 and 97 per cent.) (Tables I and III).

Changes in fat and glycogen reserves

The adults entered hibernation in the artificial hibernacula with considerable amounts of fat (Table I). The largest, *Coccinella*, contained most fat and the smallest, *Propylea*, the least. The fat content of all species ranged initially from 37 to 48 per cent. of the dry weight (mean, 43 per cent.), although in a sample of five *Adalia*, taken in the autumn of 1963, an average of only 27 per cent. fat was found.

Females contained 1·4 to 1·7 times more fat than did males at the start of hibernation, but, as they consumed fat faster, both sexes contained about the same amount towards the end of hibernation (Tables I and II). The proportions of the initial fat contents consumed throughout the whole hibernation period in *Coccinella*, *Adalia* and *Propylea* were, for males and females, respectively: 49 and 61, 75 and 87, and 71 and 60 per cent.; that is, except for *Propylea*, males consumed a greater proportion of their fat than did females.

Fat was consumed fastest during the autumn, when the weather was warm

TABLE III.—*Mean water, fat and glycogen contents (with standard errors) of overwintered Coccinellids after emergence from hibernation and feeding on aphids*

Date	Place	n.	Live weight (mg.)	Dry weight (mg.)	Water (mg.)	Fat (mg.)	Glycogen (μg.)
			C. septempunctata				
12.6.63 .	Rothamsted	♂ (12)	35·9±0·9	13·0±0·4	22·9±0·6	1·8±0·1	.
	Broad beans	♀ (22)	60·2±1·6	20·5±0·5	39·7±1·2	2·5±0·1	.
			A. bipunctata				
26.5.63 .	Rothamsted	♂ (4)	12·0±1·3	4·3±0·5	7·7±0·9	0·9±0·09	.
	Spindle tree	♀ (12)	15·0±0·6	4·9±0·2	10·1±0·5	1·1±0·08	.
12.6.63 .	Broad beans	♂ (19)	9·9±0·3	3·6±0·1	6·3±0·2	0·7±0·07	.
		♀ (21)	15·6±0·5	5·4±0·2	10·2±0·3	0·8±0·07	.
27.5.64 .	Nettle plants	♂ (17)	10·1±0·3	3·9±0·1	6·2±0·2	0·7±0·07	11·6±1·2
		♀ (22)	14·8±0·6	5·3±0·2	9·5±0·4	1·1±0·09	25·1±2·6
22.6.64 .	,,	♂ (10)	10·9±0·5	3·9±0·2	7·0±0·3	0·4±0·03	15·4±2·7
		♀ (14)	16·8±0·6	5·8±0·2	11·0±0·4	0·8±0·06	28·8±1·3
11.5.65 .	Spindle tree	♂ (5)	10·3±1·0	3·8±0·5	6·5±0·6	0·8±0·2	14·4 .
		♀ (12)	14·3±0·8	5·0±0·3	9·3±0·5	1·1±0·2	24·2±2·6
2.6.65 .	,,	♂ (7)	10·6±0·6	3·8±0·2	6·8±0·4	0·4±0·09	9·0±1·0
		♀ (8)	14·9±1·2	5·0±0·4	9·9±0·8	0·6±0·1	16·7±1·3
19.6.65 .	Broad beans	♂ (9)	10·3±0·3	3·7±0·1	6·6±0·2	0·4±0·03	8·1±0·8
		♀ (10)	15·6±0·6	5·2±0·2	10·4±0·4	0·5±0·05	10·1±1·4
9.7.65 .	,,	♂ (6)	10·9±0·4	3·8±0·2	7·1±0·2	0·4±0·06	14·4±1·9
		♀ (8)	19·0±1·1	6·1±0·4	12·9±0·7	0·7±0·07	33·3±5·4
			P. quatuordecimpunctata				
10.6.63 .	Broad beans	♂ (19)	6·8±0·2	2·8±0·09	4·0±0·1	0·7±0·04	.
		♀ (18)	10·7±0·3	4·0±0·1	6·7±0·2	0·8±0·03	.
12.5.64 .	Nettle plants	♂ (9)	6·4±0·2	2·3±0·09	4·1±0·1	0·2±0·07	16·8±5·7
		♀ (11)	8·9±0·3	3·1±0·1	5·8±0·2	0·4±0·05	26·0±5·8
23.5.64 .	,,	♂ (8)	7·0±0·2	2·8±0·09	4·2±0·1	0·4±0·05	8·5±0·2
		♀ (12)	10·5±0·2	4·0±0·09	6·5±0·2	0·6±0·06	20·2±2·2
8.8.64 .	Insectary cages	♂ (8)	6·8±0·2	3·9±0·2	2·9±0·1	1·6±0·1	45·7±4·3
		♀ (6)	9·0±0·3	5·0±0·2	4·0±0·3	2·0±0·2	27·2±5·1

(September–November); from December to the end of February the rate slowed and in March and April it increased (fig. 2). These changes in rate were probably associated with changes in temperature, and, indeed, there is a close positive correlation between the rate of fat consumption and temperature (the regression coefficient was 0·0020 ± 0·0004 mg. fat per day per °C. ($P = 0·02$)); however, the rate at which fat was consumed was not dependent on changes in temperature alone, for fat was also consumed as the insects aged. A direct dependence of the rate of fat consumption on temperature could only be shown by keeping the insects at various constant temperatures and analysing samples of them at intervals; however, the results shown in figure 2 do indicate that the fast rate of fat consumption in the autumn was associated with the warm weather, the slower rate of the winter with cold and the faster rate in the spring with the onset of warmer weather. No information on the changes in fat content of *C. undecimpunctata* could be obtained because the sample was too small.

Overwintering *Coccinella* and *Adalia* were kept in glass vials with small pieces of cork at 1 to −3° C. (R.H. 55–70 per cent.) and at −2 to −10° C. (R.H. 75–90 per cent.) for 3–6 months. Analyses of samples showed that negligible amounts of fat but considerable amounts of glycogen were consumed at these temperatures; very few *Coccinella* died but about 50 per cent. of *Adalia* did so. After about six months at these temperatures, the proportion of glycogen decreased in *Coccinella* from 0·54 to 0·07 per cent. of the dry weight and in *Adalia* from 0·70 to 0·14 per cent. of the dry weight. By contrast, the fat contents of the samples were almost identical.

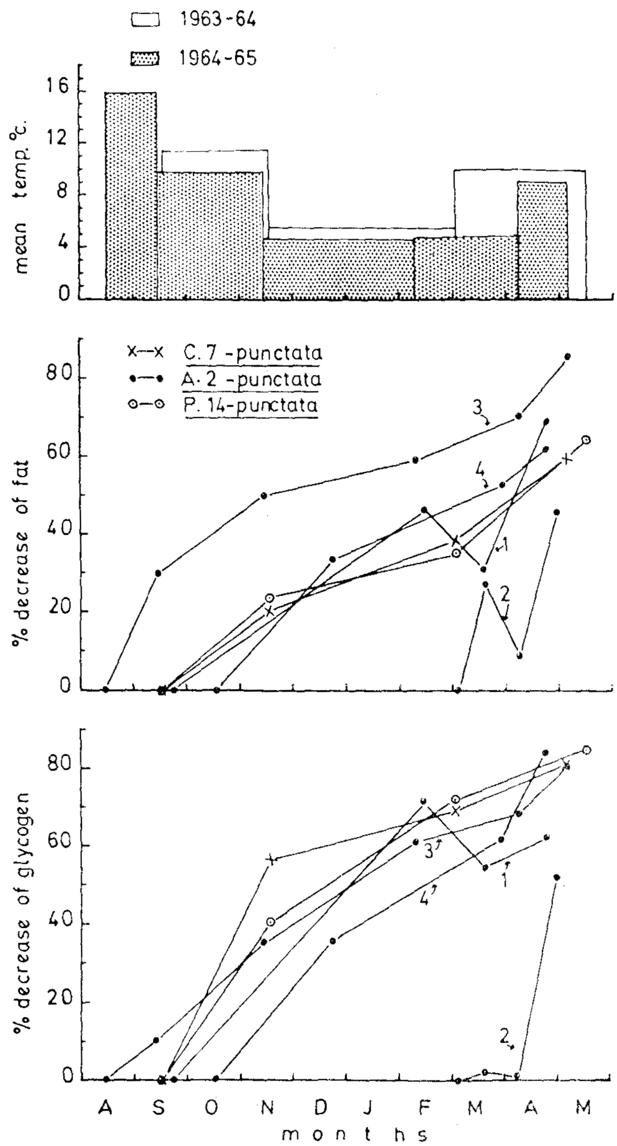

FIG. 2.—Decreases in fat and glycogen contents of hibernating adult Coccinellids, as percentages of the original amounts of these reserves and mean temperatures of the periods between samplings at the artificial hibernacula. *Adalia bipunctata:* (1, 3) in artificial hibernacula (1963–64, 1964–65); (2, 4) naturally hibernating (March, 1964, 1964–65).

Ushatinskaya (1955) showed that overwintering *Eurygaster integriceps* Putnam consumed carbohydrates, not fat, at low temperatures. Chino (1958) showed that the glycogen content of diapausing eggs of *Bombyx mori* L., kept at low temperature, is converted into sorbitol and glycerol. Dormant *Adalia* kept at room temperature contained some sorbitol and glycerol, detected qualitatively by paper chromatography by the method of Chino. Others kept at 0° C. for about a month contained traces of sorbitol, in amounts similar to those found earlier, but no glycerol. These experiments suggest that, in the cold (near 0° C.), fat is not consumed by *Adalia* and that glycogen is probably used directly as a source of energy.

In 1964–65, the rate at which fat was consumed by *Adalia* in the artificial hibernacula could be compared with that of insects found hibernating naturally. The average initial fat content of the insects in the artificial hibernacula was 2·7 mg. and of those found in the field, 2·1 mg. The insects in the artificial hibernacula consumed fat, but not glycogen, much faster than those hibernating naturally (fig. 2); the final fat contents of the two groups were 0·4 mg. and 0·8 mg. respectively.

During 1963–64, the rates at which insects of all three species in the artificial hibernacula used fat were very similar, except for a sample of female *Adalia* taken on 18th March, 1964, which contained an anomalously large amount of fat and glycogen although their live and dry weights were typical; the males of this sample were not anomalous as regards weight, fat and glycogen (Table I).

Just before emerging from hibernation (May, 1965), *Adalia* contained relatively less fat (mean, 14 per cent. of dry weight) than did *Coccinella* (23 per cent.) and *Propylea* (19 per cent.) (May, 1964). After feeding on aphids, female *Adalia* accumulated some fat but lost it again when they started to lay eggs; by contrast, the fat contents of *Coccinella* and *Propylea* decreased after feeding and egg laying without having shown any increase before the start of laying (Tables I and III).

Female *Propylea* collected from the field soon after emergence from hibernation and caged with aphids to feed on, laid eggs during June and July in 1964 and 1965;

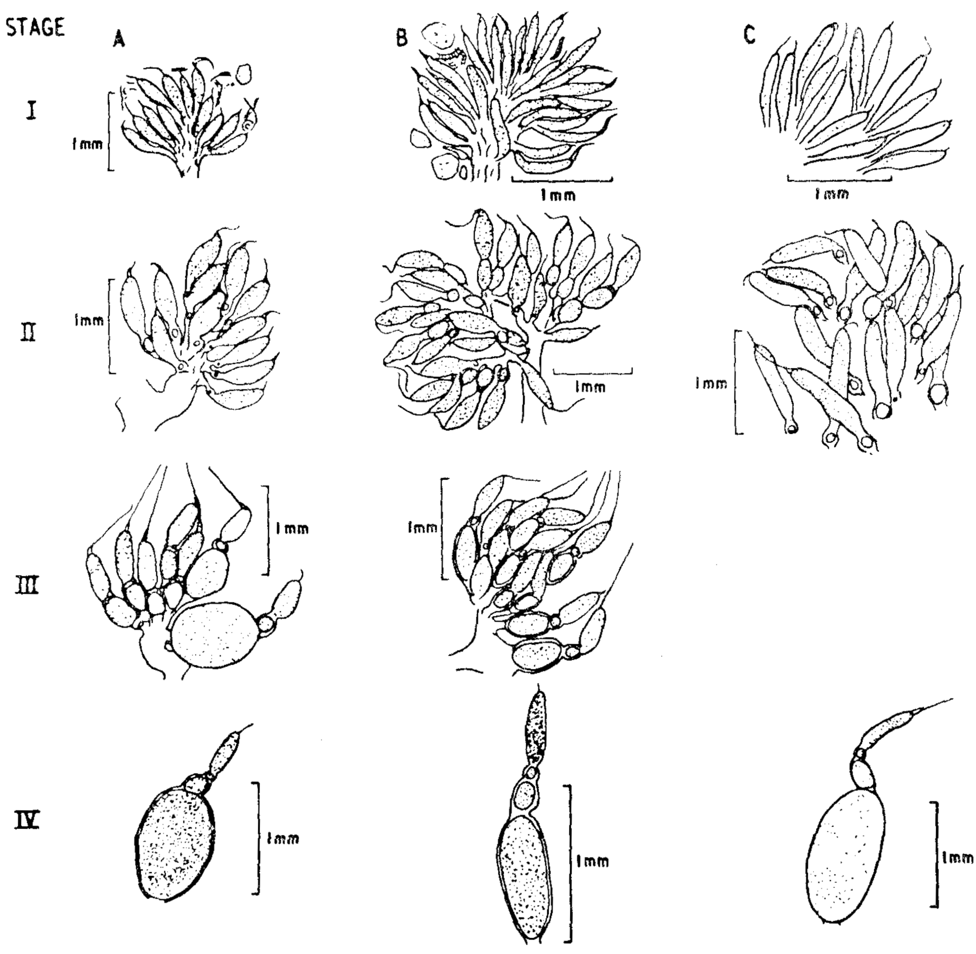

FIG. 3.—Stages of development of ovarioles of *Propylea quatuordecimpunctata* (A), *Adalia bipunctata* (B) and *Coccinella septempunctata* (C).

they stopped laying eggs at the end of July, re-accumulated fat, resorbed their ovaries and re-entered hibernation (Table III). Males also accumulated fat after mating had stopped. By contrast, female *Adalia* collected from the field at the same time, and treated in the same way, laid eggs after feeding on aphids and then died during July and August. No information of this kind could be obtained for *Coccinella.* These observations suggest that *Propylea* lives for more than one year and that *Adalia* lives for only one year. *Propylea* collected in mid-May, 1964, from nettles, where they were feeding on aphids, had immature ovaries and contained little fat, whereas those in the artificial hibernacula at the same time, also with immature ovaries but unfed, contained a much greater quantity and proportion of fat. The sample from the field contained more glycogen than did the caged insects, and it seems that the insects from the field had used up much of their fat and converted some of it into glycogen while searching for new habitats where they could feed (Tables I and III).

All three species contained much smaller initial amounts of glycogen than of fat, the mean glycogen content ranging initially from 0·4 to 1·2 per cent. of the dry weight. At the start of hibernation female *Coccinella* contained much more glycogen, and female *Adalia* significantly more glycogen, than did the males; males and females of *Propylea*, however, contained almost equal amounts of glycogen initially (Table I); later the differences were negligible.

At the end of hibernation, the insects contained 11 to 35 per cent. of the amounts of glycogen they contained initially.

There was no obvious correlation ($P > 0{\cdot}05$) between temperature and the rate of decrease of glycogen, as there was for fat and temperature, but, in general, glycogen contents decreased faster during the autumn, more slowly during the winter and faster again in the spring. After the adults emerged from hibernation and fed on aphids, the glycogen contents significantly increased, especially in females, which were then laying eggs (Tables I and III). Newly laid eggs of *Adalia* each contained 0·006 mg. fat and 0·2 μg. glycogen.

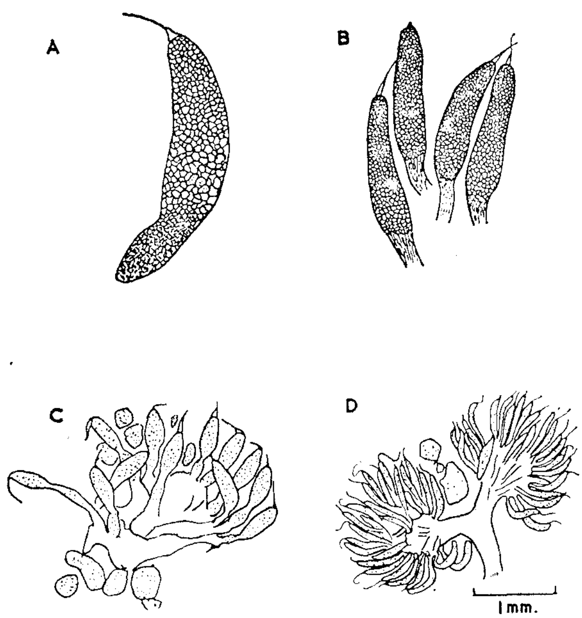

Fig. 4.—Immature ovarioles of hibernating *Adalia bipunctata* (A) and *Coccinella septempunctata* (B); resorbing ovarioles of *Propylea quatuordecimpunctata* (C); immature ovaries of hibernating *Coccinella undecimpunctata* (D).

Mating

Mating occurred occasionally (especially in *Coccinella*) before the insects hibernated, but never during hibernation. In the spring, soon after emergence from hibernation, the insects of all three species mated after having fed on aphids. Hodek & Čersakov (1958) observed that some *Semiadalia undecimnotata* (Schneider) mated before hibernating but that most mating occurred after hibernation and about two weeks before migrating to feeding sites. Hagen (1962) reported that in America *Hippodamia convergens* (Guérin) mated most often in the first warm days in February just before dispersing from the hibernation quarters.

The insects in the artificial hibernacula were not given food in the spring, and therefore did not mate, but others found in the field at the same time were mating and, on dissection, were found to have fed.

Number of ovarioles

The number of ovarioles varied with the species and even varied within the ovaries of an individual. The largest, *Coccinella*, had 40–59 (mean, 50·0) ovarioles, the smaller, *Adalia*, had 20–29 (mean, 23·6) and the smallest, *Propylea*, had 10–16 (mean, (12·0) ovarioles (Table IV).

TABLE IV.—*The number and the length (mm.) of the ovarioles of some Coccinellidae*

Species	*C. septem-punctata*	*C. undecim-punctata*	*A. bipunctata*	*P. quatuor-decimpunctata*
Number of ovarioles				
Range	40–59	25–27	20–29	10–16
Mean ± s.e.	50·0±1·1	26·3±0·3	23·6±0·1	12·0±0·1
n	12	4	184	48
Length of ovarioles				
	Undeveloped ovarioles			
Range	0·61–0·92	0·46–0·69	0·31–1·00	0·23–0·62
Mean ± s.e.	0·75±0·04	0·51±0·02	0·58±0·01	0·47±0·02
n	9	4	148	18
	Developed ovarioles (egg-laying stage)			
Range	1·64–2·55	.	1·09–2·55	0·91–2·18
Mean ± s.e.	2·18	.	1·74±0·03	1·68±0·06
n	1	.	46	10

Changes in the gonads

The Coccinellids entered hibernation with undifferentiated ovarioles, which remained unchanged until the early spring. The gonads were embedded in a large fat body richly supplied with tracheae, and the guts were empty (figs. 3, 4, stage I). In late April and early May, the ovaries of *Adalia* developed one egg in each ovariole (stage II) just before emerging from hibernation, but the ovaries of *Coccinella* and *Propylea* reached this stage only after the insects had emerged from hibernation and fed on aphids. When the insects were about to lay eggs there were typically two fully developed eggs in each ovariole (stage III). In late spring and summer, when egg laying was at its peak, the ovarioles characteristically contained three developing eggs (stage IV). Most *Propylea* with ovaries in stage IV resorbed their eggs in late July and hibernated again (fig. 4); this was associated with the re-accumulation of metabolic reserves. In contrast, *Adalia* died during July and August after ceasing to lay eggs.

Ovarioles shortened slightly during the first two months of hibernation and later lengthened slightly; they were longest during summer (fig. 5). Mature ovarioles, on the average, were three times longer than the immature ovarioles in stage I (Table IV).

It was difficult to distinguish dormant from active testes, but the diameter of testes of *Adalia* was least during the winter months and increased in the spring (fig. 6). Conversely, the length of the vesiculae seminalis increased during the winter and decreased in the spring.

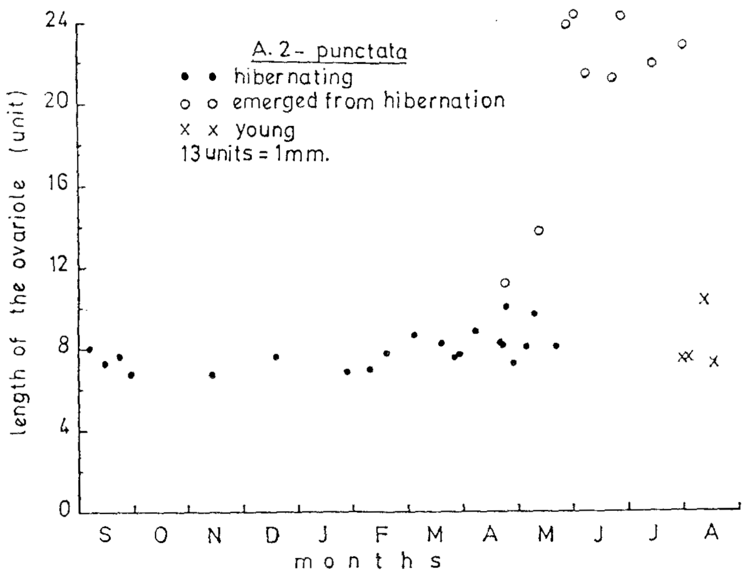

FIG. 5.—Changes in the length of the ovariole of *Adalia bipunctata*.

DISCUSSION

The Coccinellids entered hibernation with large fat bodies and contained considerable amounts of fat and some glycogen; on the average they contained 54 per cent. water; their guts were empty of food.

During hibernation in the artificial hibernacula, all three species lost water, but *Coccinella* and *Propylea* lost relatively more than did *Adalia*, which decreased significantly more in dry weight than did the others. *Adalia* presumably oxidised fats faster and lost comparatively little of the water so produced. Hagen (1962) reported that the water content of hibernating *Hippodamia convergens* remains remarkably constant and that the water balance is maintained by drinking. Hodek & Čerkasov (1963) suggested that the increase in water content of *Semiadalia undecimnotata*, newly arrived in hibernacula, could perhaps be produced by the oxidation of metabolic reserves or by drinking water. The insects in my artificial hibernacula were not able to drink, and the increase in water relative to dry matter in *Adalia* must presumably reflect the production of metabolic water.

Adalia emerged from hibernation with very little fat and glycogen but with comparatively more water. *Coccinella* and *Propylea*, which have larger reserves, would be able to search longer for aphid food in new habitats after emergence from hibernation.

Many insects use fat as a main source of energy during hibernation (Fast, 1964). The main fuel of the Coccinellids was also fat, the amount of glycogen being trivial in comparison; but at very low temperatures glycogen, not fat, was consumed. I have calculated by the methods of Weis-Fogh (1952) and Hocking (1953) that 99 per cent. of the total energy produced by consuming fat and glycogen together was provided by the oxidation of fat; the average metabolic rates of the hibernating Coccinellids were 5·0 (*Coccinella*), 6·5 (*Adalia*) and 5·6 (*Propylea*) Kcal./Kg./day. In *S. undecimnotata*, 64 per cent. of the initial fat is consumed during hibernation (Hodek & Čersakov, 1963), and this, I have calculated, provides 97 per cent. of the total energy produced during hibernation at a rate of 8·3 Kcal./Kg./day. Weis-Fogh (1952) calculated that the metabolic rate of the locust *Schistocerca gregaria* Forskål during flight was about 75 Kcal./Kg./h, and Cockbain (1961) estimated that *A. fabae* Scopoli during flight had a metabolic rate of 59 Kcal./Kg./h. I have calculated that, during hibernation, the Coccinellids had a mean metabolic rate of only 0·24 Kcal./Kg./h.

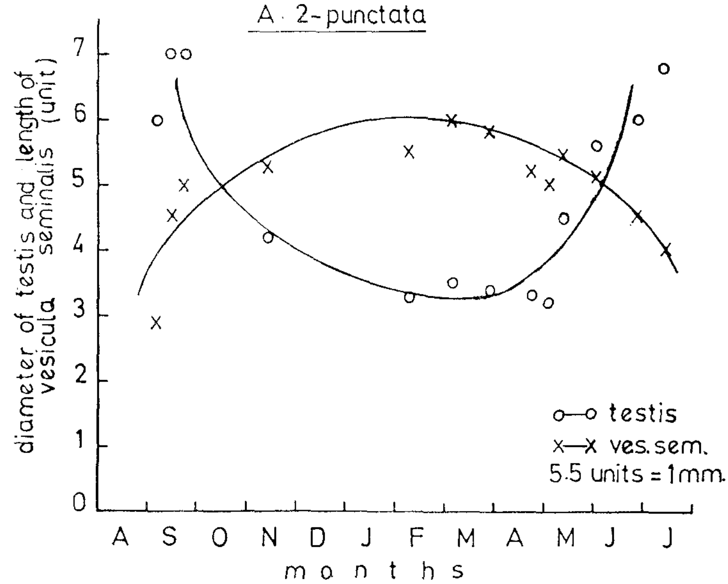

FIG. 6.—Changes in the diameter of testis and length of vesicula seminalis of *Adalia bipunctata*.

SUMMARY

When adults of *Coccinella septempunctata* L., *Adalia bipunctata* (L.) and *Propylea quatuordecimpunctata* (L.) entered hibernation during August and September in southern England, they contained 54 per cent. water; fat and glycogen were respectively 43 and 0·8 per cent. of the dry weight. Testes were mature but ovaries immature; the fat bodies were large, but the guts were empty. Mortality of all species (greatest in *Adalia*) was greatest at the start of hibernation; it decreased during the winter and increased again in the spring. During the hibernation period of about eight months, all species lost water, but *Adalia* lost a smaller proportion of water and consumed more fat and glycogen than did the others and had a higher metabolic rate. During hibernation, 67 per cent. of the initial fat was consumed, and glycogen decreased by 80 per cent. of the original quantity present. Most reserves were used up during the autumn when the weather was warm, less was used during winter and more again in the spring. After the adults had emerged from hibernation and fed on aphids, the fat contents decreased during egg laying. In late summer, *Propylea* stopped mating and laying eggs, resorbed their ovaries, re-accumulated fat and glycogen and hibernated again; *Adalia* died when egg laying finished.

The ovaries remained dormant during hibernation. At the end of hibernation and before feeding (late April), oogenesis began in *Adalia*, but the insects had to feed before the ovaries could mature. In *Coccinella* and *Propylea*, oogenesis occurred after the adults had emerged from hibernation and fed. Four stages of development of ovarioles were recognised.

I thank Dr. C. J. Banks for supervising this work, Mr. J. Forsyth for allowing me to collect hibernating *Adalia* from his house in Surrey, and the Syrian Government for a postgraduate scholarship.

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(Manuscript received 1st April, 1966)