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DORMANCY IN THE MOTH *EUROIS OCCULTA* L.
(*LEPIDOPTERA, NOCTUIDAE*)

A great number of insects overcome adverse environmental conditions in a special state of dormancy — in diapause. The term diapause is generally used to denote a kind of high intensity dormancy characterized by profound physiological changes, complete arrest of morphological processes, a marked fall in the metabolic rate, and by an obligatory cold-induced reactivation period initiating its termination. A distinction is usually made between obligatory and facultative diapause. The species influenced by the facultative diapause give two or more generations a year, and the induction of the diapause is controlled by environmental factors. The obligatory diapause is regarded characteristic of the univoltine species for whom it appears an essential stage in the individual development and is not subject to environmental influences (Lees, 1955; Beck, 1962).

During the last few decades some material has been published concerning the influence of environmental changes on the dormancy of various univoltine species of insects originally considered to be cases of the obligatory diapause. So Mansingh and Smallman (1966) state that the pupal diapause of the univoltine *Hyalophora cecropia* is controlled by the action of the photoperiod. According to the data presented by Gayspitz (Гейспиц, 1953), the univoltine moths *Leucoma salicis* L., *Euproctis chrysorrhoea* L. and *E. similis* L. develop without diapausing at an 18—20 hour photoperiod. Gayspitz also points out that the length of the day at which caterpillars of those species are reared, predetermines the instar in which caterpillars diapause. The same phenomenon could be observed in experiments on the univoltine moths *Dendrolimus pini* L. and *D. sibiricus* Tschetw. (Гейспиц, 1965). All instars of those species are susceptible to photoperiod influences; even repeated diapausing of one and the same caterpillar is not excluded. The decisive role in inducing diapause in species of this kind is played by the interaction of temperature and photoperiod. The caterpillars of both *D. pini* as well as *D. sibiricus* reactivate easily under conditions of long-day photoperiod without obligatory chilling. All that leads Gayspitz (Гейспиц, 1965) to the assumption that the univoltine species characterized by low intensity diapause must have some special synchronizing mechanisms to avoid untimely diapausing and enable individuals to make full use of favourable developmental conditions.

The above-mentioned cases of dormancy in the univoltine species of insects manifest a kind of dormancy different from and much more labile than the obligatory diapause. In recent classifications of insect dormancies

(Müller, 1970; Mansingh, 1971), the terms quiescence and oligopause are used to embrace labile cases of dormancy. Quiescence is defined as a kind of dormancy induced directly by some environmental factor to which the individual reacts within its natural tolerance limits without developing any specific adjustment mechanisms, whereas in oligopause the insects must have developed some physiological adjustments to survive adverse conditions. Mansingh (1971) considers that the species which enter oligopause must be moderately cold-hardy, but their dormant state must be of low intensity as it is shown by possible molting in winter and easy reactivation without cold treatment under favourable conditions.

Insects with labile dormancy have not been studied thoroughly yet. According to Mansingh, no insect whose dormancy period might be classified as oligopause has been described, although he thinks that *D. pini* might have served as an example of that kind (Mansingh, 1971). Studies on insects with labile dormancy are of essential importance for further perfection of dormancy classification and for further study in the evolutional development of dormancy.

The moth *Eurois occulta* L. who meets the winter in its caterpillar stage is one of the univoltine species of insects whose development and dormancy are easily influenced by environmental factors. The sensitivity of *E. occulta* to light exposure first attracted the attention of Danilevsky (Данилевский, 1961) who noted that at 23 °C the development of *E. occulta* was promoted by a longer photoperiod, but he did not conduct any studies on the relationship between photoperiod and dormancy. As shown by the data presented by Merivee (1972), *E. occulta* belongs to the species of obligatory diapause as its tissues can withstand freezing, i. e. it is a species of freezing-tolerance. According to Merivee the critical point for caterpillars of *E. occulta* (when 50 per cent of the population perishes) is reached after a 16-hour freezing at $-12°$. Hotko (Хотько, 1968) observes that caterpillars of *E. occulta* sometimes pupate under laboratory conditions already in September, although in nature this stage takes place as late as in May or June of the following year. This indicates the lability of the dormant state and shows that it can be easily terminated.

The aim of the present paper is to study the influence of the photoperiod on the development and the dormant state of *E. occulta* and to ascertain the peculiarities of its dormancy. For that purpose the development of caterpillars of *E. occulta* was continuously followed by measuring their head capsules; the respiration rates of both developing as well as diapausing individuals were determined, and the supercooling abilities of dormant caterpillars estimated. The data obtained will serve as a basis for an attempt to determine the type of dormancy in caterpillars of *E. occulta*.

Material and methods

E. occulta is a kind of moth whose caterpillars overwinter in mouldering leaves. The female moths of the *E. occulta* Tartu population were caught in the light trap. The moths were fed on 5 per cent sugar solution until eggs were laid. The eggs were incubated at room temperature. The newly-hatched caterpillars were placed into one-litre glass jars, 30 individuals in each jar, and reared at temperatures 17° and 21°. At both temperatures the caterpillars were exposed to photoperiods of 10, 12, 13, 14, 15, 16 and 18 hours. The caterpillars were reared on dandelion and thistle leaves. Food plants were changed every day. To estimate the rate of development, the head capsules of the caterpillars were measured under binoculars every other day. The development of the caterpillars was followed within a period of 100 days (from July to October).

The rate of respiration (in cubic millimetres per 1 gram of body weight in an hour) was determined manometrically with the help of the Warburg's apparatus at 20°. As we were interested not so much in absolute values of the respiration rate for all the instars as in the difference between the metabolic rates of the developing and the diapausing individuals, measurements of the respiration rate were started with the fourth instar in which the developmental differences are marked. The respiration rate for the developing caterpillars was determined in the sample of caterpillars reared at 21° and an 18-hour photoperiod, the optimal regime in our experiment. The respiration rate for the caterpillars in dormancy was measured immediately before storing them into their winter quarters. The average respiration rates for various instars given in Figure 2 are mean values of at least 6 measurements. After the hundredth day of the experiment the caterpillars showing retarded development were placed in jars filled with mouldering leaves and moss and dug into earth for the winter. In November, after 30 days in earth, the supercooling points of the caterpillars were determined thermo-electrically using a copper-constantan thermocouple repeatedly described in various papers (Горышин, 1966; Кожанчиков, 1961). By determining the supercooling points for different instars, the series measured contained 10—15 individuals. Table 3 presents the mean supercooling points for different instars with mean error.

Results and discussion

Marked differences could be observed in the developmental rates of the caterpillars of *E. occulta* at different temperatures and under different photoperiods. Up to the fourth instar the caterpillars developed at the same rate, irrespective of the length of the photoperiod, and showing only a little shorter instar duration at 21° (6 days on the average) than at 17° (8 days on the average). In the fourth instar a part of the population continued developing at the same rate, but the others slowed down in their development; they were entering the period of dormancy. All the caterpillars reared under photoperiods of a 10—14-hour duration, became dormant both at 21° and 17°. At the photoperiods lasting longer than

Table 1

The development of caterpillars of *E. occulta* under differing photoperiods at 17 °C

The duration of photoperiod in hours	Developing individuals, %	Average number of developmental days before pupation	Individuals in dormancy, %	Instar of dormancing individuals, %			
				V	VI	VII	VIII
10	—	—	100	50	50	—	—
12	—	—	100	40	60	—	—
13	—	—	100	43	57	—	—
14	—	—	100	—	93	7	—
15	3.0	90 (88 ... 92)	97	—	—	87	10
16	30	82 (75 ... 90)	70	—	—	60	10
18	40	74 (65 ... 90)	60	—	—	53	7

14 hours, a number of individuals continued developing, the number of developing caterpillars increasing proportionately to the days lengthening (Tabs 1 and 2). The developing caterpillars passed seven instars (Fig. 1). The duration of the developmental period before pupation
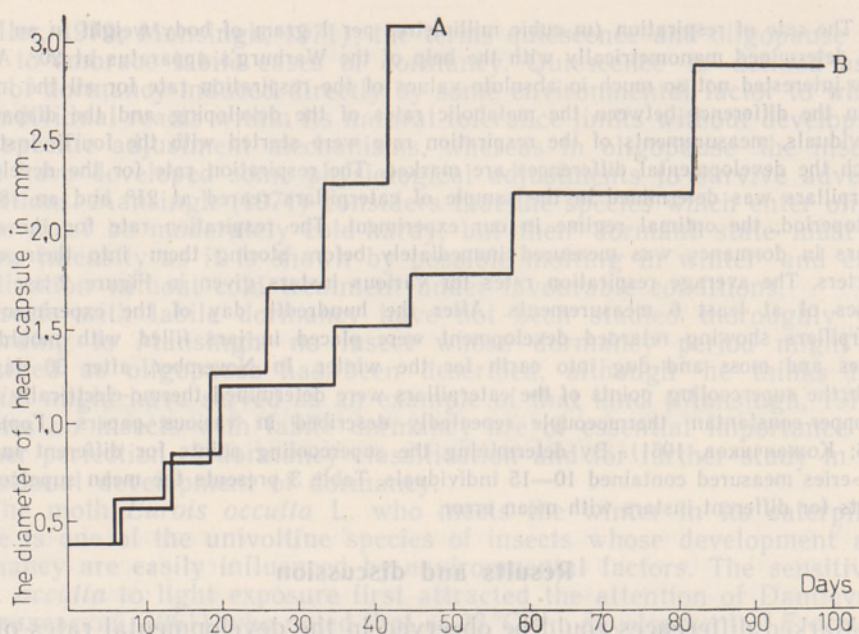
Fig. 1. Changes in the diameter of the head capsules in developing (*A*) and dormant (*B*) caterpillars of *E. occulta* at 21 °C and 18 hour photoperiod.

depended on the length of the photoperiod. The developmental period was the shorter the higher the temperature and the longer the day (Tabs 1 and 2). The pupal period was independent of the length of the photoperiod and lasted 12 days on the average, Tables 1 and 2 carry

Table 2

The development of caterpillars of *E. occulta* under differing photoperiods at 21 °C

The duration of photoperiod in hours	Developing individuals, %	Average number of developmental days before pupation	Individuals in dormancy, %	Instar of dormancing individuals, %			
				V	VI	VII	VIII
10	—	—	100	—	100	—	—
12	—	—	100	—	100	—	—
13	—	—	100	—	93	7	—
14	—	—	100	—	40	60	—
15	7	85 (74...90)	93	—	30	43	20
16	30	74 (63...92)	70	—	—	60	10
18	50	53 (52...61)	50	—	—	30	20

only the number of developmental days before pupation. The data given in Tables 1 and 2 concerning the developing individuals include all the caterpillars that pupated within the hundred days of the experiment. It is natural to consider that all the individuals whose development before

pupation lasted longer than 65 days had a very short period of dormancy, since after the fourth instar their instar durations lengthened, and at 17° some additional molting could be observed. However, in comparison with the individuals in diapause, they showed higher development potentials and could be regarded as developing individuals. The respiration rate in the developing individuals was at its highest in the fourth instar with 1,100 mm³ g/hr, then gradually diminishing to 430 mm³ g/hr in the seventh instar (Fig. 2).

Fig. 2. The respiration rates for developing (*A*) and dormant (*B*) caterpillars of *E. occulta* in cubic millimetres per a gram of body weight in an hour at 20 °C.

In the state of dormancy caterpillars do not cease feeding and moving. Their development is not completely arrested, it has only slowed down, to some extent. The development gets retarded, beginning with the fourth instar under all regimes, and the inhibition is the stronger, the shorter the day and the lower the temperature (Tabs 1 and 2). So under the 10-hour regime at 17° only 50 per cent of the dormant caterpillars reached the sixth instar within the 100-day period of development, whereas at 21° under the same light regime all the individuals developed into sixth instar caterpillars. The longer the day, the higher the intensity of development during dormancy. During their dormant state most individuals enter one more instar (Fig. 1) and in some cases even two more instars. The development into instars of higher degrees is compensated by a decrease in the Dyar's coefficient from 1.6 during the molt to the second instar to 1.2 during the molt to the eighth instar. Under longer photoperiods the caterpillars in the dormant state reached either the seventh or the eighth instar during their 100-day development (Tabs 1 and 2). The respiration rate of caterpillars in the dormant state remained considerably high (Fig. 2) covering in the seventh instar even as much as 69 per cent of the respiration rate of the developing caterpillar of the same instar. Both molting in the dormant state and the considerably high respiration rate are indicative of labile dormancy. As the larval diapause is physiologically characterized by hormonal inhibition of molting and by the absence of ecdysone, the growth and development hormone as well as the activation hormone (brain hormone) (Williams, 1952; Новак, 1972), then growth and development during dormancy indicate the presence of both these hormones in the hemolymph of *E. occulta* caterpillars. A question arises whether the above-mentioned continuous development during diapause is hazardous for the species in dormancy and whether all the instars are equal in withstanding winter frost. When one compares the supercooling points of different instars (Tab. 3), one can see no noteworthy differences there. The supercooling point is relatively low in caterpillars of the fifth instar, but its absolute value of −7.49° is rather high and cannot guarantee good survival in cold winters. As the tissues of these species are freezing-tolerant, natural selection has not resulted in the appearance of the supercooling ability in them, for there is no need for
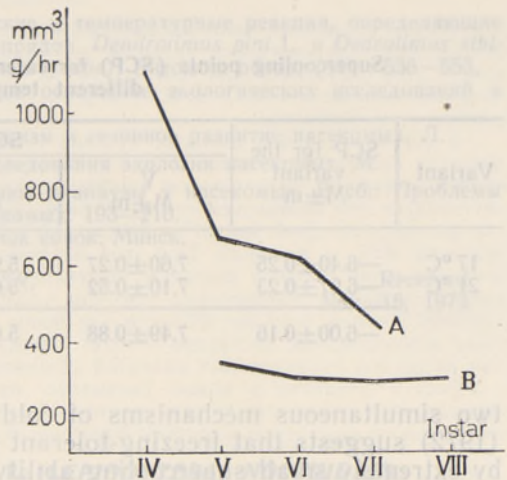
Table 3

Supercooling points (SCP) for caterpillars of *E. occulta* reared at different temperatures

Variant	SCP for the variant $M \pm m$	SCP for various instars			
		V $M \pm m$	VI $M \pm m$	VII $M \pm m$	VIII $M \pm m$
17 °C	—6.40±0.25	7.60±0.27	5.90±0.36	6.63±0.50	5.50±0.20
21 °C	—6.07±0.23	7.10±0.52	5.61±0.33	6.40±0.25	5.10±0.35
	—6.00±0.16	7.49±0.88	5.68±0.86	6.40±0.17	5.25±0.49

two simultaneous mechanisms of cold adjustment in a species. Merivee (1972) suggests that freezing-tolerant species are as a rule characterised by extremely small supercooling ability, usually around —5° or —6°. Our data confirm the suggestion.

The results of the experiment suggest that the caterpillars of *E. occulta* enter a considerably labile dormancy that can easily be terminated under conditions of a longer day and a higher temperature. Growth and development in diapause are not completely arrested, but only retarded to some extent. It means only some slight shifts and no thorough rearrangements in the hormonal balance of the caterpillar. In order to survive low temperatures the species has developed the mechanism of moderate freezing-tolerance. Judging by the description given, the term of diapause in its classical interpretation proves inadequate for the type of dormancy found in the caterpillar stage of *E. occulta*. According to the principles developed by Mansingh (1971), it can be classified as a case of oligopause, which permits certain shifts in the physiological mechanisms adjusting the caterpillar development to certain environmental conditions and leading to a moderate cold-hardiness. Under favourable conditions for development, the state of dormancy is easily terminated. This particular kind of dormancy makes it possible for the caterpillars of *E. occulta* to synchronize their development with natural conditions and make full use of warm autumn days. On the other hand, the period of winter frosts appears rather dangerous for the species as its cold adjustment is not well developed.

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ÖÖLASE *EUROIS OCCULTA*. L. (*LEPIDOPTERA, NOCTUIDAE*) PUHKESEISUNDIST

Resümee

E. occulta L. on röövikuna talvituv öölaseliik, kelle puhkeseisundiks on siiani peetud obligatoorset diapausi.

Tema röövikute kasvatamisel kahes temperatuuris (17° ja 21 °C) ning kasutades erinevaid fotoperioode (10, 12, 13, 14, 15, 16 ja 18 tundi), ilmnes, et nende kasv ja areng sõltuvad temperatuurist ja fotoperioodi pikkusest. Arenemine toimus kiiremini 21° juures. Erinevate fotoperioodide korral ilmnesid erinevused arenemise kiiruses alates IV kasvujärgust, mil osal röövikutest areng tunduvalt aeglustus ning nad jäid puhkeseisundisse. Kui fotoperioodi pikkus ületas 14 tundi, jätkas osa röövikuist kasvamist. Pidevalt arenevad röövikud läbisid seitse kasvujärku. 21° juures jätkas 15-tunnise fotoperioodi korral arenemist 7, 16-tunnise puhul 30 ja 18-tunnise puhul 50% röövikuist. 17° juures arenes samades valgusrežiimides pidevalt vastavalt 3, 30 ja 20% neist.

Puhkeseisundis röövikud jätkasid toitumist, liikumist ja kestumist; nende arenemine vaid aeglustus. Röövikutel esinesid lisakestumised, mis kompenseeriti Dyari koefitsiendi vähenemisega. 100 vaatluspäeva jooksul jõudsid 21° juures 18-tunnises fotoperioodis peetud 50%-st puhkeseisundis olevast isendist 20% VIII, 30% VII kasvujärku. Samas temperatuuris, kuid 10 tunni pikkuse fotoperioodi korral jõudsid kõik isendid ainult VI kasvujärku. Puhkeseisundis röövikute hingamise intensiivsus püsis suhteliselt kõrge, moodustades 50 kuni 69% samas kasvujärgus, kuid mittepuhkeseisundis olevate röövikute hingamise intensiivsusest. Puhkeseisundis röövikute allajahtumisvõime oli küllaltki väike, vaid −6,00°.

Puhkeseisundis esinevad kasvu- ja arenemisnähtused viitavad selle seisundi suhtelisele labiilsusele ning osutavad, et siin on tegemist teistlaadse puhkeseisundiga, kui seda on obligatoorne diapaus. Lähtudes Mansinghi poolt antud puhkeseisundite klassifikatsioonist, võime sedastada, et *E. occulta* puhkeseisund sarnaneb eelkõige oligopausile.

Анне ЛУЙК

О СОСТОЯНИИ ПОКОЯ СОВКИ *EUROIS OCCULTA*. L. (*LEPIDOPTERA, NOCTUIDEA*)

Резюме

E. occulta является видом, зимующим в стадии гусеницы. Состоянием покоя названного вида считалась облигаторная диапауза. При 17 и 21 °С и различных фотопериодах (10, 12, 13, 14, 15, 16 и 18 *ч*) проявлялась зависимость роста и развития от температуры и продолжительности освещения. Скорость развития гусениц при температуре 21° превышала таковую при 17°. При различных фотопериодах разница в скорости развития проявлялась с четвертого возраста. У части гусениц скорость развития замедлялась — они перешли в состояние покоя. Часть гусениц продолжала развиваться, но только

в условиях свыше 14-часового фотопериода. Так, при температуре 21° и 15-часовом фотопериоде продолжалось развитие у 7%, при 16-часовом — у 30% и при 18-часовом — у 50% гусениц. При температуре 17° и тех же фотопериодах развитие шло беспрерывно соответственно у 3, 30 и 40% гусениц. Беспрерывно развивающиеся гусеницы прошли семь возрастов.

В состоянии покоя развитие гусениц было заторможено лишь частично. Они продолжали питаться и линяли. В их развитии возникли дополнительные линьки, которые компенсировались уменьшением коэффициента Дайара. В покое гусеницы развивались интенсивнее при наивысшей температуре и самом длинном фотопериоде. Так, в течение ста подопытных дней при 21° и 18-часовом освещении 30% гусениц достигло седьмого возраста, 20% — восьмого. При этой же температуре и 10-часовом фотопериоде особи достигли лишь шестого возраста. Интенсивность дыхания гусениц в покое поддерживалась также на сравнительно высоком уровне, составляя 50—69% от интенсивности дыхания гусениц того же возраста вне покоя. Точка переохлаждения гусениц в покое была незначительна, составляя — 6,00°. Между точками переохлаждения гусениц разных возрастов существенных различий не отмечено.

Рост и развитие в покое указывают на его лабильность и иной тип покоя, чем облигаторная диапауза. Исходя из принципов классификации типов покоя Мансинга, состояние покоя гусениц *E. occulta* ближе всего к олигопаузе.

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