POINT OF VIEW

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Diapause development, diapause termination and the end of diapause

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Diapause development, diapause completion, diapause termination, diapause end, (re)activation, horotelic processes, tachytelic processes, quiescence, dormancy

Abstract. A workshop is an occasion to raise also "nonproductive" questions as stimuli for discussion between specialists from different fields: (1) What do we know about the processes leading to the end of diapause, and how can we discriminate this diapause end? (2) Is the diapause "normally" completed also when the "natural" diapause development is "substituted" by (re)activation?

It seems premature to search for criteria to directly monitor diapause end. We have to rely on the events of post-diapause development which can be recorded only after exposure to permissive environmental conditions. It should be defined clearly, in a study, whether the end of diapause is identified with the resumption of covert developmental potential or with the resumption of overt development. The crucial change to developmental potential should be recognized although it is not directly measurable.

The (re)activated adults can differ from adults that completed diapause development by decreased fecundity and/or persistence of photoperiodic response.

INTRODUCTION

One Nobelist said that science can make progress only when problems can really be grasped, when there is a methodical prerequisite for the research. This is a truthful remark and thus one cannot be much surprised that, in the studies of diapause, such nonproductive topics, as processes underlying diapause development, the moment of diapause end or the difference between the slow diapause development and the "hastened" activation, have been pushed aside.

However, our workshop might be a good occasion to raise such questions as provocative stimuli for discussion between ecologists, physiologists, biochemists and cryobiologists, as their approaches to diapause inherently differ. In short, these questions are:

(1) What do we know about the processes leading to the end of diapause, and can we discriminate this diapause end? (Section 1.)

(2) Is the diapause "normally" completed also when the "natural" diapause development is "substituted", or accelerated by activation, e.g., photoperiodic activation (Section 3) or morphological development produced by various stimulation (Section 2).

TERMINOLOGY

Although terminological remarks can be found in the compendia (Tauber et al., 1986; Danks, 1987) some are given here, particularly because the explanation of some terms is not uniform, and some terms are new. Terms **diapause** and **quiescence** are used in the usual way, **dormancy** as a general term for both types of arrest. Dormancy may be **aestivation** or **hibernation**. Andrewartha's term **diapause development** (physiogenesis) is used for the processes leading gradually to the end of diapause, to its completion.

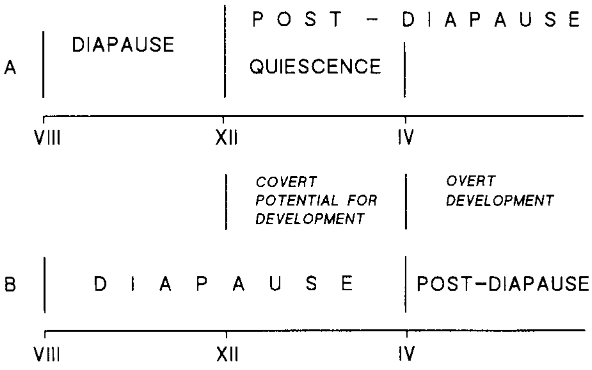

Fig. 1. Two approaches to diapause end, shown for hibernation diapause in cold temperate climate (e.g., populations from central Europe of the heteropteran *Pyrrhocoris apterus*; for clarity, the borders between individual phases are schematically indicated by lines, although there is a great variation in their duration; A and B show the contrasting approaches, the description of physiological states is given in italics).

For these processes also the term **horotelic** is used (borrowed from palaeontology [Simpson, 1944, 1953], it means "evolving at the standard rate"; Henderson et al., 1953; Hodek, 1981, 1983). Diapause may also be completed by **(re)activation**, by **tachytelic** processes ("evolving at a rate faster than the standard rate"). These neutral terms avoid the often criticized contradiction between "diapause" and "development" (e.g., Harvey, 1962; Sheldon & Macleod, 1974; Hilbert et al., 1985; Wipking, 1995). They emphasize the notion of dynamic completion by the Greek word "telos" meaning "fulfilment" and distinguish between the two interlocking, but not identical pathways leading to the end of diapause. In accordance with Danks (1987, p. 11), the term **"termination"** is avoided here, because it has been used in at least two ways – either identified with the whole process of diapause completion or only with its non-defined last phase. Thus, for some authors, "termination" is close to the **"end"** of diapause. The term **"diapause completion"** is used here in the sense of Hodek (1983, Hodek & Hodková, 1988) as a general term for any pathway (diapause development, activation) leading from diapause onset (or fixation) to diapause end. This usage differs from that of Danks (1987, Table 2), where it means end of diapause or resumption of activity. As it is discussed in detail further, the **diapause end** has been used at least in two meanings, our preferred (1) onset of covert potentiality of development (even if it is not realised) (Fig. 1A) or (2) overt resumption of development (Fig. 1B).

DISCUSSION

1. Diapause development and its end

Since the crucial change in diapause concept by the Andrewartha's (1952) classical review, diapause is viewed as a dynamic event. After the onset of diapause (or after a period of diapause "fixation", or intensification (Hodek, 1971a; Tauber et al., 1986), specific physiological processes progress which gradually complete the diapause stage. Various alternative pathways (under various environmental conditions) may lead to the end of diapause which is a prerequisite for the resumption of further morphogenetic development. For these physiological processes (Andrewartha's "physiogenesis") Andrewartha's term "diapause development" has mostly been used although some authors dislike it because of its contradictory nature (development of developmental arrest) and prefer other terms, e.g., "diapause regulating process" (Hilbert et al., 1985), or "diapause ending processes" (Schneiderman & Horwitz, 1958; Wipking, 1995). (See Danks, 1987, pp. 10–11 and the terminological chapter above.) In spite of these terminological differences the concept of diapause as a dynamic event has generally been accepted.

There is a great wealth of data showing important physiological differences between diapausing and developing (reproducing) insects, such as metabolic rate, or activity of enzymes (Harvey, 1962; Jungreis, 1978; Denlinger, 1985). Even more information has been accumulated on neurohormonal regulation (particularly by cerebral neurosecretory cells and endocrine glands) of the chain of events **after** diapause is completed, when the development is resumed (Denlinger, 1985, for review). These changes are often situated to a non-defined, final period of diapause, to "diapause termination".

However, there is little evidence what really happens **during** the diapause completion, indicated by gradual decrease of diapause intensity, although the dynamic nature of diapause development has been repeatedly proved. The old concept of diapause physiogenesis as gradual acetylcholine accumulation in the brain, observed during the months of "chilling" in *Hyalophora cecropia* pupae (Van der Kloot, 1960), appears abandoned and not many other findings have replaced it. Only rare histological studies of cerebral neurosecretory cells bring some evidence of histological changes **during** diapause development, e.g., Highnam (1958) in pupae of *Mimas tiliae*. Other studies reported, however, high levels of stainable material in neurosecretory cells during diapause and its release only **after** temperature increase, i.e., **after** diapause completion (two *Pieris* spp., for references on these and other species, see Denlinger, 1985).

When we do not know much about what happens during diapause we can hardly ascertain when diapause is completed. While outward signs can inform us that diapause was terminated **some time ago** we still miss some reliable criterion which would mark the decisive qualitative change to the potential for development. (Some possibilities will be discussed in Section 1.5).

Two concepts of diapause end (Sections 1.1.1 and 1.1.2) have arisen from this methodical problem. The researcher's choice between these concepts is affected by his preferred definition of diapause, climatic region or type of diapause. This essay does not aim to try to decide which of these two concepts is more adequate. It seems useful to stress here the difference between them as it has never been addressed specifically. Many authors seem unaware of this dilemma when they use the term "end of diapause" quite arbitrarily without any attempt at definition.

1.1. Two concepts of diapause end

1.1.1. Diapause end indicated by a covert developmental potential (Fig. 1A)

Clear evidence has been accumulated that the hibernation diapause in cold temperate climate is completed as early as around winter solstice, long before outdoor temperatures increase above the lower threshold for development. Examples can be found in various orders of insects. Our model is the adult diapause of the heteropteran *Pyrrhocoris apterus* (Hodek, 1971a). The end of diapause is indicated by a mere potential for development which can be realised only after an adequate increase in temperature. Under low field temperatures in winter, however, the resumption of development is directly inhibited. According to classic definitions, the insects remain then in post-diapause thermal quiescence. In photoperiodically responsive insects, the end of diapause is evidenced by the loss (irreversible or reversible) of photoperiodic response.

1.1.2. Diapause end identified with onset of development (Fig. 1B)

The endocrinologists view the diapause as inactivity of neuroendocrine system that regulates the morphogenetic development (or reproductive activity). By adding the appropriate hormone (or its mimic) development can often be resumed. In this view, the end of hibernation diapause can be recorded as late as in spring, and the mere potential for development, achieved around the solstice, is disregarded – as an event which cannot be **directly** measured.

One of the early reports on this concept is by Mansingh (1971), but also the authors of recent editions of textbooks or reviews adhere to this approach. In two quotations, the end of hibernation diapause is related to the increase of temperature, i.e., identified with the end of post-diapause thermal quiescence (Gillot, 1995). "For most insects diapause termination is not under photoperiodic control but occurs, under natural conditions, when suitable temperatures for development return in spring." (p. 644) "Diapause (of *Leptinotarsa decemlineata*) is terminated not by changing day length but by the increasing temperature of the soil." (p. 549)

In a review, the end of diapause is related to feeding (Bell, 1994): "... nutritional factors can often be important in the termination of diapause. In many bruchid species ... oogenesis is stimulated by adult females feeding on the pollen of the host plant ..."

1.2. Tropical/aestivation diapause

As can be expected, in most studies of tropical or aestivation diapause, the onset of development or absence of overt symptoms of diapause are used as criteria for diapause end. After diapause end, the environmental conditions are suitable for development (or at least its first phases) and thus no post-diapause quiescence can be observed. (Humidity will be discussed in Section 1.4). Thus, e.g., in a very detailed analysis of adult diapause in a tropical endomychid beetle *Stenotarsus rotundus*, the authors offer several symptoms of diapause termination. The earliest, increase in metabolic rate, precedes the other two (formation of oocytes and mating) by about two months. The authors therefore conclude: "designation of a time of diapause termination is greatly influenced by what criterion is adopted" (Tanaka et al., 1987). This is right, in general. However, in optics, suggested in Section 1.1.1, all three criteria are phenomena of post-diapause development. The end of diapause most probably occurred already sometime before the increase in metabolic rate.

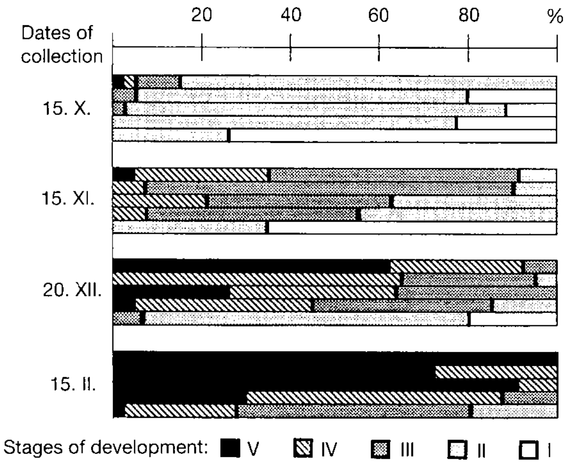

Fig. 2. Development of ovaries in the olive psyllid, *Euphyllura phillyreae*, as affected by host-plants and habitats, in northern Greece (Prophetou-Athanasiadou, 1993). Reaching stage III was the criterion for diapause end. Thus in late December diapause was mostly completed, with the exception of the population on olive trees (last line) where the end was about 2 months delayed.

1.3. Morphological and biochemical criteria of diapause end

Sometimes also in warm temperate regions, where the temperature is high enough after the end of hibernation diapause, no post-diapause quiescence is recorded. The authors observe

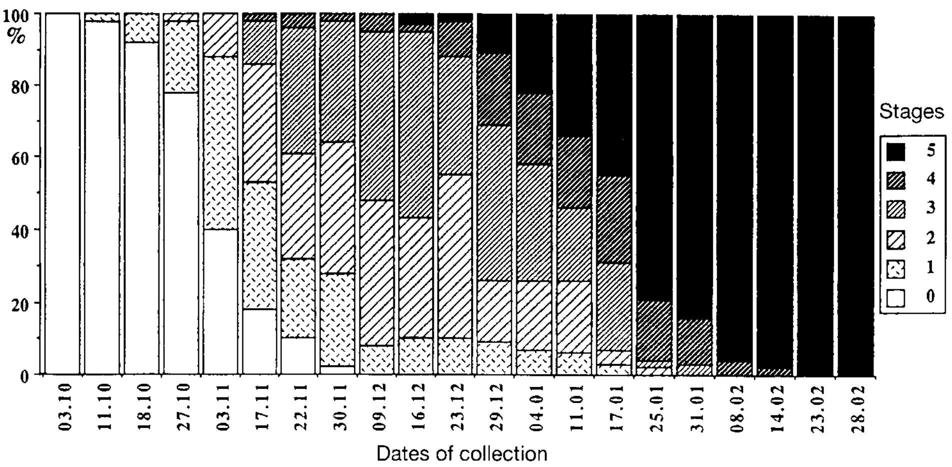

Fig. 3. Progress in the maturation of oocytes in winter females of *Cacopsylla pyri*, collected in an orchard in southern France. Reaching stage 2 indicates the end of diapause (Lyoussoufi et al., 1994). Thus diapause was completed in almost all females in mid January.

that the end of diapause more or less coincides with the onset of development, so they use morphological criteria for the end of diapause. Two recent papers on adult diapause of psyllids use a stage of maturation of oocytes as a morphological marker, in the olive psyllid *Euphyllura phillyreae* in northern Greece (Prophetou-Athanasiadou, 1993) and the pear psylla *Cacopsylla pyri* in southern France (Lyoussoufi et al., 1994). When outdoor-sampled females are dissected, in about 5–85% of the olive psyllids, the maturation of ovaries indicates an end of diapause around the winter solstice while in the pear psylla, this proportion amounts to 90% (Fig. 2 and 3). Similarly, the end of diapause has been evidenced by a visible criterion when the pharate first instar larvae of the gypsy moth, *Lymantria dispar japonica*, ingest yolk cells and become swollen (Suzuki et al., 1993).

Some recent histological and biochemical studies achieved a deep insight into diapause-dependent changes. Ultrastructural changes of the glia and other neuronal elements interacting with neurosecretory cells (Hartfelder et al., 1994) were described as diapause-dependent changes; however here the contrasting states, diapause vs. active, were studied, rather than the processes leading to the end of diapause. The study of the leaf beetle *Gastrophysa atrocyanea* had the latter aim; by systematic study of the period around the emergence, the authors were able to confirm the presence of the diapause glukoprotein still within the first 24 h **after** the emergence from the soil – while after this limit the diapause protein was absent (Ichimoro et al., 1990). It would probably be right to conclude that the specific glukoprotein is related rather to the absence of development than to diapause; diapause evidently ended before the emergence from the soil, when the "diapause" protein was still present. Thus neither the presence nor the absence of the "diapause" protein seems to be a good criterion of diapause end.

In two other insects diapausing in the soil, in the Colorado potato beetle, *Leptinotarsa decemlineata*, and a bumble-bee, *Bombus terrestris*, the reactivation of corpora allata occurs as late as **after** the emergence of overwintered females from the soil (Lefevere et al., 1989; Larrère et al., 1993). The resumption of activity of CA appears therefore to be a **consequence** and not the cause of diapause end.

1.4. Water as prerequisite for development

The complexity of the decision about the moment of diapause end increases when not temperature, but water or moisture are a prerequisite for the resumption of development. Often water is considered as essential for diapause completion. Beck (1968, p. 157) came across the problem "what criterion is used to mark the end of diapause state" when analysing the requirement for water prior to pupation in the European corn borer, *Ostrinia nubilalis*. "In *O. nubilalis* the neuroendocrine system was not activated until after the water requirement had been met (Beck, 1967)". He concludes: when "the activation of the neuroendocrine system and the secretion of prothoracicotropic hormone" is taken as "the first postdiapause physiological event" then "the lack of body water prevents the completion of diapause development, and the insect's need for water imbibition is not a postdiapause requirement" (Beck, 1968). However, it could be argued that when the water is needed for the first postdiapause event, this need **is** a postdiapause requirement.

Need for moisture or water in aestivation dormancy might be considered similar to the need for temperature values above a developmental threshold in the postdiapause thermal quiescence in hibernation dormancy.

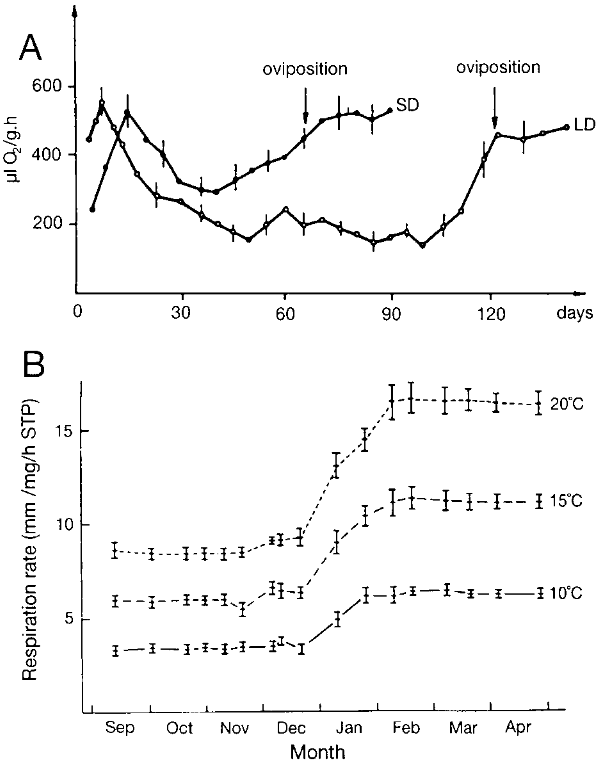

Fig. 4. Oxygen consumption in dormant adults of two coleopterans. Aestivating *Catops nigricans* was maintained at 10°C, 16L:8D (Engler, 1982), hibernating *Ips acuminatus* was maintained at 3°C (Gehrken, 1985).

1.5. Metabolic rate

Diapause is notoriously defined as a condition of extremely low metabolic rate. It might be assumed that its end is expressed by a steep and more or less immediate increase in oxygen consumption. This seems to be the case in the bark beetle, *Ips acuminatus*. Oxygen consumption increased rather steeply after winter solstice although the adults were maintained at 3°C in the dark (Gehrken, 1985) (Fig. 4B). A similar steep increase in metabolic rate was observed in a catopid beetle, *Catops nigricans*, about one month before oviposition (Engler, 1982) (Fig. 4A).

In other cases, however, the increase in metabolic rate occurred only under conditions enabling post-diapause morphogenesis, such as a temperature above certain threshold, feeding, moisture etc. In a classical paper, dealing with cyclopid copepod larvae (4th copepodite instar), Watson & Smallman (1971) found that in non-feeding post-diapausing copepodites the average oxygen consumption is still the same as in diapausing individuals (< 0.01 µl/h), while in fed individuals it is identical with developing copepodites (Table 1). Also in two heteropterans, *P. apterus* and *Aelia acuminata*, the steep increase in metabolic rate appears related rather to the starting morphogenesis than to the end of diapause as such (Hodek & Hodková, 1981).

TABLE 1. Effect of feeding on the metabolic rate of cyclopid larvae (Watson & Smallman, 1971).

Copepodit stage	n	O_2 consumption µl per individual per h		µl per mg dry wt. per h (average)
		range	average	
developing	18	0.03–0.14	0.06	12
in arrest				
refractory stage	12	—	< 0.01	< 2
competent phase (unfed)	9	—	< 0.01	< 2
competent phase (fed)	21	0.02–0.09	0.06	12

In our terms: refractory = diapause, competent = post-diapause quiescence.

1.6. Indirect criteria

In most ecological experiments, the changes in target organs are usually used as criterion for whether diapause was completed and thus the potentiality for development (in the sense described in Section 1.1.1) achieved. Often quite distant events are recorded, such as pupation, adult ecdysis or oviposition onset (severely but unfairly criticized by Jungreis [1978]). The time which elapsed between the transfer to laboratory conditions for incubation and, e.g., the oviposition onset (pre-oviposition period) can be used as a quantitative parameter (Hodek & Hodková; Fig. 5). Also earlier events may be followed such as egg vitellinisation by dissection, or some morphological markers on larvae or pupae by observation, e.g., appearance of adult "antennal discs" on pupae (Fraenkel & Hsiao, 1968; Denlinger & Wingard, 1978).

Usually, it is hoped that the phenomena recorded in the laboratory after transfer give reliable evidence of the original physiological state of the insects in the moment of sampling, in conditions that were different. In the case of overwintering dormancy, the sampled insects usually live at low temperatures, either in the field, or in experimental "chilling" conditions, while the incubation temperature is substantially higher – and arbitrarily chosen by the experimenter. The interpretation of results is ambiguous: has the recorded phenomenon been produced by events before sampling or by our manipulation? The recorded effect depends on the incubation temperature, and on the value of temperature increase. Sometimes the difference in temperature may be very great, around 20 to 30°C. Suspicions were expressed that such transfers to a highly contrasting temperature can be (at least partly) responsible for diapause completion (Hodek, 1978, 1983; Zaslavski, 1978, 1988; Danks, 1987, Section 14), which has usually been ascribed to the preceding exposure to low temperatures.

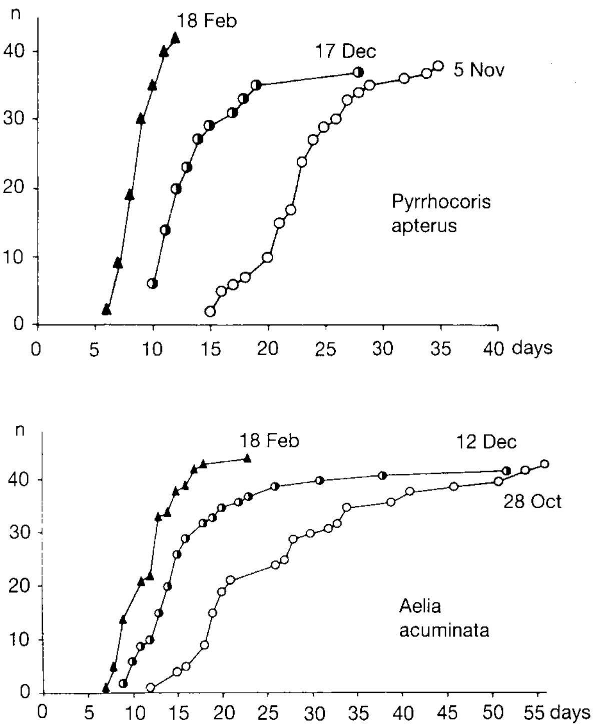

Fig. 5. End of adult diapause indicated by onset of oviposition in two heteropterans, *Pyrrhocoris apterus* and *Aelia acuminata*. Samples of September 10 were then kept in the laboratory under const 15°C and incubated at 25°C. Vertical axis – number of females which begun egg laying (Hodek & Hodková, 1981).

1.7. Has the diapause development an end?

Due to intra-population variation in diapause intensity, diapause development and post-diapause development often occur simultaneously in **different individuals** of the population, e.g., in *Pyrrhocoris apterus* (Hodek, 1971a) or *Psila rosae* (Collier et al., 1994). Thus the end of diapause within a population sample may extend over several months. The first individuals of *P. apterus* end diapause in mid-October; last insects complete diapause in January or even later (Hodek, 1971a).

In some insects, and in certain climatic conditions, the final phases of diapause and the early period of "post-diapause" development may merge with one another in **one individual**, as was reported from mild winter of England in winter eggs of the mite *Panonychus ulmi* (Cranham, 1972). In *Leptinotarsa decemlineata*, the thermal responses slowly change from those typical of diapause to those that characterize growth and development and thus also here the period between diapause and post-diapause development is not clearly demarcated (Tauber et al., 1994).

In fact, we might have a suspicion that diapause "never ends", in the sense of the end of horotelic processes of diapause development. It is quite probable that at least a short phase of activation (i.e., tachytelic processes) is included under natural conditions, particularly in spring in overwintering dormancy (see Hodek, 1983).

2. Transient reproduction after incomplete diapause development

Completion of diapause development is often combined with the loss of photoperiodic response (PHR). The loss can be reversible in insects showing recurrent PHR (Hodek, 1971b; Pener & Broza, 1971; Hodek & Hodková, 1992 for review).

However many post-diapause insects behave according to the "classic" scheme: they lose the PHR irreversibly and can thus develop, (i.e., in case of adult diapause they can reproduce) until death, in spite of diapause promoting photoperiod.

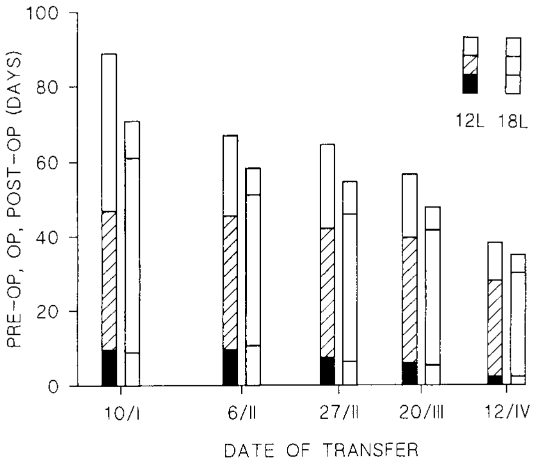

Fig. 6. Mean duration of pre-oviposition, oviposition and post-oviposition periods in *Pyrrhocoris apterus* females collected outdoors and incubated at 25°C, 12L:12D or 18L:6D (Hodek, 1974). (Low parts of the columns – pre-oviposition period, middle part – oviposition period, upper part – post-oviposition period.) While the pre-oviposition period is the same in both day-lengths, the duration of the other two periods differ, particularly in January.

This scheme is followed by the heteropteran *Pyrrhocoris apterus*: the adults sampled in the field after dormancy in May oviposit continuously in spite of the stationary short-day regimen (Hodek, 1968 et seq.). However, in winter (and in a very small proportion of the population also in early spring) long-lasting experiments reveal that the started oviposition activity is transient. In the samples from January and February all females oviposit at diapause promoting photoperiod, but they show a very long post-oviposition period: the maximum values are higher than 100 days (Fig. 6). Our assumption that such females responded to photoperiod appeared well founded. We transferred to long-day regimen those females which still lived after 8 weeks without laying eggs and most of them laid further egg batches (Table 2). The stimulation by the great increase in temperature and light intensity (and perhaps also other factors), apparently provoked oviposition in the females in which diapause intensity was already low. Such results were achieved repeatedly (Hodek, 1974, 1988) and indicate the limits for the general validity of photoperiodic responsiveness as a criterion of diapause.

TABLE 2. Transient oviposition in *Pyrrhocoris apterus* after winter transfer to short-day regimen (12L:12D, 25°C) (after Hodek, 1974).

Sampling		Ovipositing females %	Females which stopped oviposition at 12:12 and after 8 weeks without oviposition were transferred to 18:6			
			females		egg batches	
date	n		transferred n	resumed oviposition n	at 12:12 n	at 18:6 n
1 Jan	28	100	8	4	4.5 (3–6)	2.7 (2–4)
27 Jan	27	100	7	6	4.7 (4–6)	2.2 (1–5)
24 Feb	29	100	9	5	6.4 (5–9)	1.0 (1)

Although all females laid several egg batches at short-day regimen, some lived long (max. > 100 days) after the last batch. They were kept for 8 weeks and the still living females were then transferred to long-day regimen. Most laid further egg batches (after 1–4 week delay).

The above results may indicate that in *P. apterus* diapause development is not completed at the time when the absence of PHR is evidenced by the onset of oviposition at diapause promoting photoperiod. The horotelic processes go on apparently in a certain proportion of population much longer, probably until spring when activation by environmental factors (i.e., tachytelic processes) ends the diapause definitively. It is thus possible that our generally accepted conclusion on the usual end of hibernation diapause around winter solstice needs modification – it may not concern the total population in some insect species.

3. The "quality" of photoperiodic activation

Since as early as 1933 (Sabrosky et al., 1933) it is well known that adult diapause can often be activated by diapause averting photoperiod, although this type of diapause completion mostly does not end hibernation diapause under natural conditions. Photoperiodic activation is considered by some authors to be a kind of accelerated diapause development. We have tried to discriminate between these alternative two types of diapause completion by using the terms horotelic and tachytelic processes (see Section 1) because there is some evidence of their different nature. Two pieces of evidence will be mentioned.

3.1. Higher fecundity at short days

In the coccinellid *Ceratomegilla* (= *Semiadalia*) *undecimnotata* reared under short-day regimen, almost 90% of females oviposited in spite of the diapause promoting photoperiod of 12L:12D. Their pre-oviposition period was much longer (av. 60.3, med. 61, range 5–121 days) than under diapause-averting photoperiod of 18L:6D (av. 7.7, med. 7.5, range 4–14 days) (Hodek & Iperti, 1983). However, the fecundity of females kept at diapause-promoting short days was almost double (av. 824 eggs/female) of those kept at diapause-averting photoperiod (av. 455 eggs/female). This result appears rather surprising. It might be speculated that the very fast photoperiodic activation was less suitable for the neuroendocrine processes regulating oviposition than was the diapause-like delay under diapause promoting photoperiod. It does not seem plausible to relate the recorded difference to longer overall feeding because also the oviposition rate (number of eggs per female per week) was higher in short-day females.

3.2. No loss of PHR by photoperiodic activation

It has been observed in *P. apterus* (Hodek, 1968 et seq.) and other species diapausing in adult stage that the reproducing adults which have never undergone diapause development constantly keep the PHR. It concerns not only the adults reared under diapause-averting photoperiod but also those activated from diapause by such a photoperiod. Thus, the alternation of reproduction and reproductive arrest can be achieved repeatedly by changes in photoperiod. Certainly the physiological state of a "conditionally" ovipositing female is different from a female which underwent the "normal" diapause development and reproduces until death under any photoperiod. Thus it might be postulated that by the photoperiodic activation, diapause was not really completed, i.e., brought to its end.

CONCLUSION

In spite of a great amount of detailed studies on many insect species, our knowledge on horotelic processes underlying diapause development and tachytelic processes of (re)activation has remained still rather incomplete. It appears that the regulatory mechanisms are so diversified also within one type of diapause and one insect order (e.g., lepidopteran pupal diapause) that we even wonder whether they can be situated uniformly into the brain (for data, see Denlinger, 1985). In such a situation – when we are still obliged to tackle diapause mostly as a black box, studying the inputs and outputs – it is premature to search for criteria to **directly** monitor diapause end.

We have to rely on the events of post-diapause development which can be recorded only after exposure to permissive environmental conditions, i.e., after a shorter or longer delay **after** the end of diapause. We should be aware, however, what we are recording, and then make appropriate interpretations, e.g., about conditions which are prerequisite for the completion of diapause development. Also, it would be advisable to define clearly, in a study, whether the end of diapause is identified with the resumption of covert developmental potential or with the resumption of overt development. Although it is not so very important which terms we use for the phases of dormancy, it is emphasized that the existence of the crucial change to developmental **potential** should be recognized even if it is not directly measurable.

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