Controversial aspects of diapause development

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Abstract. Although some parts of diapause development have been clarified up by endocrinologists, knowledge of the underlying processes remains insufficient. The survey of ecophysiological aspects of diapause development has thus to be limited to inputs and outputs from the blackbox. The terms diapause development, diapause intensity, post-diapause quiescence, horotelic processes of diapause, and tachytelic processes of diapause (reactivation) are defined. Andrewartha's term diapause development has been accepted because it shows diapause as a dynamic event.

In about the last 20 years, some views on diapause development have been updated, while others have fossilised. The assumption that chilling is a general prerequisite for completion of diapause development in **all** insects still survives in part of the scientific community, in spite of much contradictory evidence and often due to inadequate interpretation of experiments (examples given in figures and tables). On the contrary, it has been generally recognised that in temperate climates overwintering diapause is usually already completed in early/mid winter and the dormancy is then temperature quiescence. The conception of multiple pathways of diapause completion postulates that diapause can be completed either by the normal (slow) progress of diapause development (horotelic processes), or by a faster activation (tachytelic processes). There are important differences between the mechanisms regulating activation and the horotelic processes. Thus, e.g., the photoperiodic response is lost during horotelic completion, while after photoperiodic activation it persists. In addition to photoperiodic activation other kinds of activation are being studied, particularly activation by high temperature.

Some conclusions can be made from modern studies on diapause development. In every individual, several (at least two) possible pathways exist that are evidently interlinked and mutually complementary. Thus the time of diapause passed at any condition has to be considered, as well as the exposure to very low temperatures. In temperature studies the experimental range ought to be adequately wide and less affected by a priori assumptions. Stimulation by temperature increase or improvement in food or other conditions has to be considered.

The success of diapause completion should be measured by at least four parameters: (1) incidence (%) of developmental steps; (2) duration of delay; (3) synchronization; (4) vigour of post-diapause insects (shown by long-term survival or fecundity). The last two parameters have usually been neglected.

INTRODUCTION

Diapause vs. quiescence. Fifty years ago, our thinking about diapause was changed in a major way: We began to view diapause as a dynamic phenomenon (a process that has to be completed), thanks to the classical review of Andrewartha (1952), where the concept of diapause development was introduced and explained as physiogenesis (physiological developmental processes), in contrast to the "normal" morphological development, morphogenesis. The half-century distance should be a good occasion to reflect how much Andrewartha's paradigm has been assimilated or perhaps developed by extensive studies. Instead of repeating the information already published in a short history of ecophysiological diapause studies (Hodek, 1999), the focus here will be on several problematic aspects of diapause development. Also I avoid quoting definitions of diapause because they may be easily found in compendia and review articles (Denlinger, 1985; Tauber et al., 1986; Danks, 1987; Hodek, 1996). However, two aspects should be stressed that have often been a source of misunderstanding.

(1) During diapause, morphogenesis is arrested, but growth, mobility or feeding often are not discontinued. One recent example that diapause is not a stand-still of growth was recorded during the larval diapause of a drosophilid fly, *Chymomyza costata* (Kostal et al., 2000): both the central nervous system and prothoracic wing discs increased in size during diapause. In diapause larvae of the corn-stalk borer, *Sesamia nonagrioides*, nonstationary supernumerary molts were reported (Gadenne et al., 1997). Low levels of juvenile hormone allow the previtellogenic growth of ovaries in diapause females of the carabid beetle *Pterostichus angustatus* (Holters, 1981). Vitellogenesis, however, is blocked until diapause completion.

(2) Another important characteristic of diapause, mentioned in all definitions, is its indirect dependence on environmental cues: while quiescence is caused by direct inhibition of development by conditions below or above developmental thresholds, diapause is a particular adaptive developmental arrest that is induced by so called "token stimuli". These environmental cues act as signals, but they do not directly prevent the morphogenesis. Understanding this difference between diapause and quiescence is essential for discussion of the controversial period of post-diapause, when development is directly prevented by the absence of some essential requirements.

POST - DIAPAUSE

DIAPAUSE		Danks 1987
	QUIESCENCE	Hodek 1983
		Tauber et al. 1986

Aug   Dec   Apr

COVERT POTENTIAL FOR DEVELOPMENT   OVERT DEVELOPMENT

DIAPAUSE   POST-DIAPAUSE

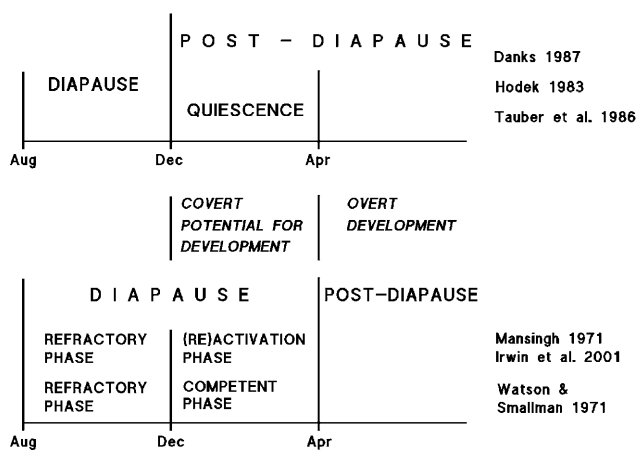| REFRACTORY PHASE | (RE)ACTIVATION PHASE | Mansingh 1971 Irwin et al. 2001 |
| REFRACTORY PHASE | COMPETENT PHASE | Watson & Smallman 1971 |

Aug   Dec   Apr

Fig. 1. Two conceptions of diapause and post-diapause shown for winter diapause in cold temperate climate.

Diapause development. There is plenty of evidence from ecophysiological experiments that the intensity of diapause gradually decreases through the period between diapause onset and diapause end. This process of decrease in diapause intensity, that was called diapause development and defined as physiogenesis by Andrewartha (1952), results finally in diapause completion. However, we still do not know what is the essence of the processes of diapause development.

The cascade of events/processes between these two points has been identified only partly. By physiological studies on neuroendocrine organs earlier outputs can be recorded, i.e. events that are situated some steps upstream of the changes in target organs. Already in the 1950s and 1960s, detailed studies on pupal diapause in *Hyalophora cecropia* and *Manduca sexta* (see, e.g., Wilson & Larsen, 1974, also for references to earlier studies) gave solid evidence that in the course of diapause development the brain resumes competence to stimulate by its hormones downstream organs (first endocrine glands). But the nature of the resumption of competence has remained an enigma. On the other hand, the resulting effect at the level of endocrine glands is relatively well understood (Denlinger, 1985; Hodkova, 1999). In several instances the progress of diapause development was shown by changes in responsiveness to exogenously added hormones. Thus, e.g., higher doses of juvenile hormone were needed for ovarian maturation in *Leptinotarsa decemlineata* at the beginning of diapause than in later stages of diapause development (Schooneveld et al., 1977). The increase in metabolic rate has often been reported as an indication of diapause completion. The steep increase in daily increment of respiration rate from 0.0054 to 0.1379 μl CO_2/24 h (measured at 25°C) strongly suggests completion of diapause approximately after 95 d in the eggs of *Lymantria dispar* kept at 5°C and 16L : 8D (Gray et al., 1995). However, usually the possibility has not been excluded that this increase is a symptom of starting morphogenesis, rather than of late diapause-development processes. In diapause adults of *Ips acuminatus*, kept at low tempera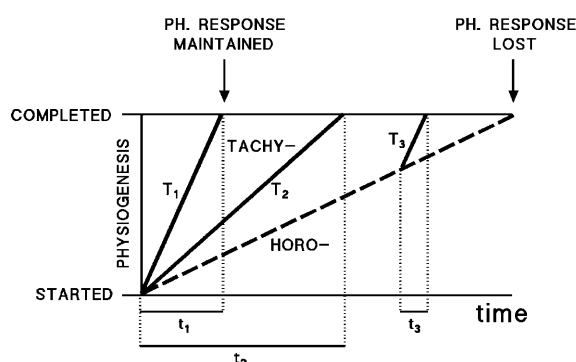ture of 10°C and in darkness, a significant increase in oxygen consumption in mid-overwintering could indicate the completion of diapause (Gehrken, 1985); although also in this instance 10°C appears to be above the developmental threshold. As Footitt and Cohn (2001) rightly warned it is essential to avoid confusing diapause-completing processes with post-diapause events. Recently, interesting biochemical changes were recorded in the pupal diapause of the flesh fly, *Sarcophaga crassipalpis* (Rinehart et al., 2001). The protein ultraspiracle (the dimerization partner of the ecdyson receptor) is not detectable in days 20–40 of diapause while it reappears in late diapause in day 50.

In spite of the great progress in physiological and biochemical studies our knowledge of the concrete nature of diapause development remains very limited. Thus I will review the studies recording the effect of environmental factors as inputs to a black box and the evidence of morphogenesis as outputs from it.

Post-diapause. Before starting the review, what is understood under the period of diapause has to be made clear. There exist two concepts of diapause (Fig. 1). According to the concept used in this review, diapause is over when the p o t e n t i a l for development (morphogenesis) is resumed. This potential cannot be realized if the environmental conditions are not favourable for morphogenesis: in such a state, defined as quiescence (Lees, 1955), morphogenesis is d i r e c t l y inhibited by low ambient temperature, dryness, absence of essential food, etc. For the contrasting approach, the whole time of inactivity of endocrine glands is diapause, which also includes the period when morphogenesis is inhibited directly (Fig. 1, below). Although this controversy may seem only terminological, it can produce important misinterpretation of findings and wrong decisions in pest management. Gillott (1995, p. 549) maintains that diapause of the Colorado potato beetle is terminated as late as by the increase in soil temperature. He thus contradicts the conclusions of long-term studies by de Wilde's school.

Some authors realised that the long diapause they were studying is not homogeneous and called the 2nd part the "activation phase" (Mansingh, 1971) or more adequately the "competent phase" (Watson & Smallman, 1971); the first part is the refractory phase in both papers (Fig. 1). To prevent misunderstanding, the reader of a given paper should definitely be informed which of the above two concepts of diapause has been used.

The term diapause development has not been accepted by all authors because of semantic controversy. Critics find the construction illogical and, formally, they are right: it speaks, in fact, about development of an arrest of development. Some examples of terms that were proposed to replace diapause development are listed by Danks (1987, in Table 2). However, most recent authors (but see "diapause ending processes" in Wipking, 1995) do not seem to be irritated by the semantic problems and are using the term, because of its great advantage - it stresses the dynamic aspect of diapause. This is why it will also be used here.

PH. RESPONSE
MAINTAINED

PH. RESPONSE
LOST

COMPLETED

PHYSIOGENESIS

TACHY–

T_1

T_2

T_3

HORO–

STARTED

t_1

t_3

t_2

time

Tachytelic processes (activation) can be more (T_1) or less (T_2) intensive and diapause completion is thus achieved in shorter (t_1) or longer (t_2) time. If the horotelic processes (diapause development) are more advanced the completion is attained faster (t_3 cf. t_1) by tachytelic processes of the same intensity (T_3).

Fig. 2. Interrelation between horotelic and tachytelic processes of diapause completion (from Hodek, 1983).

HOROTELIC / TACHYTELIC PROCESSES OF DIAPAUSE DEVELOPMENT

The accumulated experimental evidence has gradually made clear that the resumption of morphogenesis can be achieved by at least two types of processes of diapause development (Fig. 2). By Andrewartha's (1952) diapause development, diapause is completed in a rather slow way - in the order of months. Abundant experiments with photoperiodic activation have shown that the completion of diapause can be strongly accelerated - so that morphogenesis is resumed within only weeks. However, the resumption may be achieved also by high temperatures (as is discussed on this page, below).

Photoperiodic activation (tachytely). The first, pioneer findings on photoperiodic activation in mosquitoes by Baker date from 1935. In the 1960s and later, numerous studies of photoperiodic activation followed (for examples see Tauber et al., 1986; Danks, 1987, Tables 21 & 22). The wealth of information continued to grow, but the later studies did not modify the concepts given there. The experimental evidence on diapause development and activation has been interpreted in various ways. Danilevsky (1961, p. 14) rejected the term diapause development because he felt that the term development was inappropriate for the resumption of a previous condition, and proposed the term cold reactivation instead. He maintained that in a majority of species diapause is neutral to light conditions (Danilevsky, 1961, p.18) - and, in fact he was right, as far as termination of winter diapause in n a t u r a l conditions is concerned. Later he accepted the term photoperiodic activation, and analysed this mechanism in *Carpocapsa* (*Laspeyresia*) *pomonella* (Danilevsky & Sheldeshova, 1968). Both Vinogradova and Zaslavsky also used the term reactivation instead of diapause development (see below).

While the term photoperiodic (re)activation is adequate for the described mechanism and has since been generally used, the term cold reactivation has gradually been abandoned in papers published in English, evidently due to the

TABLE 1. Species in which diapause is completed in mid-winter (or analogous time for summer or tropical diapause).

Egg diapause	
Lepidocyrtus lignorum	Leinaas & Bleken, 1983
Chortoicetes terminifera	Hunter & Gregg, 1984
Caledia captiva	Groeters, 1994
Aulocara elliotti	Fisher et al. 1996; Fisher, 1997
Tortrix viridana	Du Merle, 1999
*Deois flavopicta**	Pires et al., 2000
Larval diapause	
Choristoneura fumiferana	Regniere, 1990
Curculio elephas	Menu, 1993
Allomyrina dichotoma	Yamanaka & Fujiyama, 1994
Sesamia nonagrioides	Lopez et al., 1995
Kytorhinus sharpianus	Ishihara & Shimada, 1996
Strophingia ericae	Miles et al., 1998
Pupal diapause	
Adult diapause	
Asellus aquaticus (Crustacea)	Tadini-Vitagliano et al., 1982
Culex tarsalis	Reisen et al., 1995
Tetranychus kanzawai	Mochizuki & Takafuji, 1996
Cacopsylla pyricola	Horton et al., 1998
Aulacophora nigripennis	Watanabe & Tanaka, 1998

*dry/cool season dormancy in a tropical insect (Di: IV-VII, post-Di quiescence:VII-X)

repeated findings that in the course of overwintering diapause the endogenous inhibition s p o n t a n e o u s l y disappears as early as in mid-winter (Table 1). This discrepancy led the Russian authors to use a more adequate term - cold sensibilisation (Zaslavsky, 1988).

Horotely vs. tachytely. In spite of using different terms Zaslavsky (1988) and Hodek (1981, p. 323, 1983) shared very similar views on the processes during diapause. They both stressed that the "slow" and "fast" diapause processes are principally different, but interlocked, and are mutually complementary or additive (Fig. 2). The processes progressing at usually lower rate are named horotelic (= evolving at standard rate - Simpson, 1944, 1953; Henderson et al., 1953), while the accelerated processes are tachytelic (= evolving at a rate faster than the standard rate) (Hodek, 1983). Zaslavsky (1988) used the terms spontaneous vs. inductive processes.

The effects of horotelic and tachytelic completion of diapause differ in an important way. While *Pyrrhocoris apterus* adults remain sensitive to photoperiod and discontinue egg laying at short days early after the photoperiodic activation (Fig. 3A), the horotelic completion of diapause results in a loss of photoperiodic response, i.e. egg laying is maintained at short days (Fig. 3B) (Hodkova & Hodek, 1989).

High temperature tachytely. The tachytelic completion of diapause may be achieved in some species or populations simply by high temperature, without photoperiodic activation. The earliest finding on termination of

A

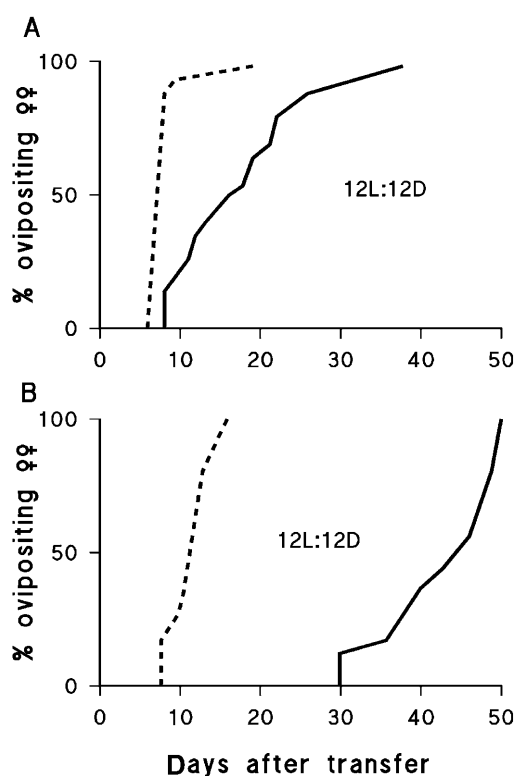**B**

Days after transfer

Fig. 3. Photoperiodic response after tachytelic completion of diapause at 26°C and 18L : 6D (A) and horotelic completion of diapause at 15°C and 12L : 12D (B). Dotted line indicates cummulative onset of oviposition; full line indicates cummulative cessation of oviposition (from Hodkova & Hodek, 1989).
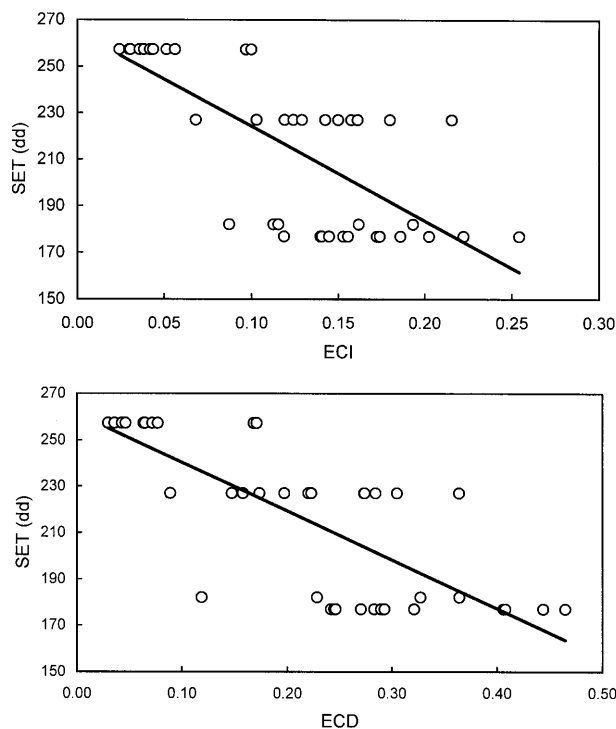

Fig. 4. Experimental treatments of diapausing eggs of *Teleogryllus commodus* (from Masaki et al., 1979).

diapause by high temperatures was probably that on eggs of a cricket, *Teleogryllus commodus*, by Browning (1952 a, b), Hogan (1960) and Masaki (1960). Later, Masaki et al. (1979) analysed this phenomenon in detail (Fig. 4).

TABLE 2. Species in which cool temperatures **are** a prerequisite for diapause development or shorten it (only rarely checked at an adequately wide range of temperatures; also it cannot be excluded that a temperature increase at transfer to incubation conditions participated in the effect of exposure to cool temperatures).

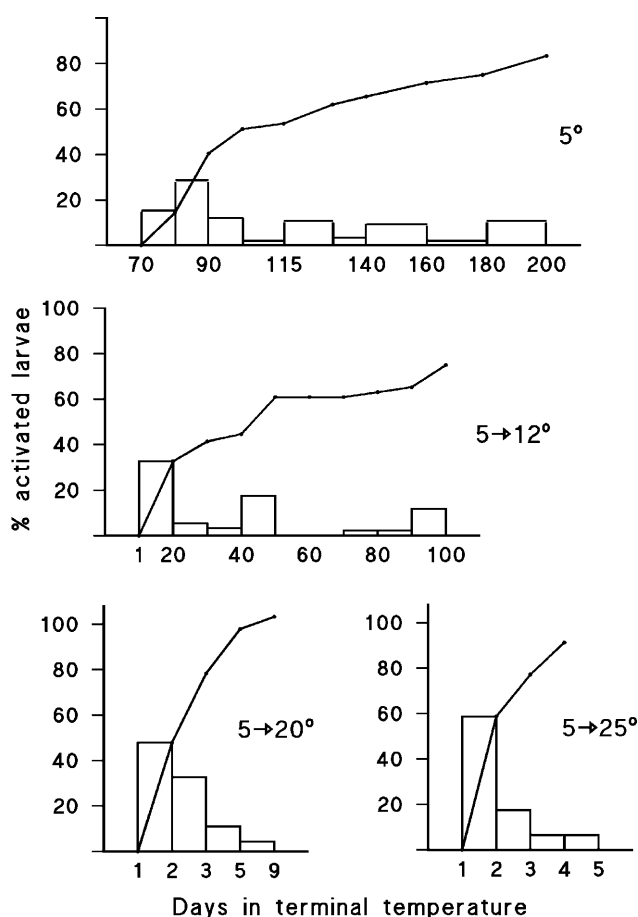| Egg diapause		
Eurytoma plotnikovi	4 or 18°	Tzanakakis et al., 1992
Locusta migratoria	15° better than 5° vs 20 or 25°	Tanaka, 1994
Rhopalosiphum padi	-5° vs 3°	Lushai et al., 1996
Aulocara elliotti	0–18° (opt. 7–8°) vs 30°	Fisher, 1997
Tortrix viridana	only 8°	Du Merle, 1999
Larval diapause		
Kytorhinus sharpianus	5–10°	Ishihara & Shimada, 1995 (but questioned by I & S, 1996)
Trichogramma minutum	15 + 2° vs 15°	Laing & Corrigan, 1995
Monochamus alternatus	10° vs 25°	Togashi, 1995
Psacothea hilaris	10° vs 25°	Shintani & Ishikawa, 1997a, b
Colpoclypeus florus	0, 4, 10°	Milonas & Savopoulu, 2000
Lagria hirta	perfect range 5–30°	Zhou & Topp, 2000
Pupal diapause		
Psila rosae	0, 5, 7°	Collier et al., 1994
Coloradia pandora	only 5°	Gerson et al., 1999
Adult diapause		
Argopistes biplagiatus	5 or 10°; 15° too high	Inoue, 1994
Dybowskyia reticulata	10° vs 25°	Nakamura & Numata, 1997
Thrips setosus	only 5°; 18° too high	Nakao, 1998
Gerris gracilicornis	7° vs 20°	Harada & Taniguchi, 2001

Fig. 5. Experimental treatments of diapause larvae of *Calliphora vicina* (from Vinogradova, 1991).

They concluded that (1) the eggs require high temperatures for a rapid termination of "the late stage" of diapause; and (2) low temperatures are not a requisite for the completion of diapause, although they are favourable for "the early stage" of diapause. An alternative interpretation might suppose that the upper figure shows the horotelic diapause development, in the middle figure a period of 60 days of horotelic diapause development at 20°C is followed by tachytelic activation at 30°C, and, in the lower figure, the increase in temperature by 10° to 20°C, again after the 60 days of horotelic diapause development at 10°C, represents the needed activation. It seems that in both cases tachytelic processes are started by the same 10° increase. This study is an example showing how the horo- and tachytelic processes are additive.

The discrimination between horotelic (spontaneous) and tachytelic (inductive) processes of diapause development is easy when characteristic cases are considered. Typical diapause-averting photoperiods produce distinct tachytelic processes. Similarly, a high temperature (or an important temperature increase) results in explicit tachytely, as may be indicated by the above results on *T. commodus* (Masaki et al., 1979). Less distinct levels of cues, such as photoperiods near the critical threshold or intermediate temperatures, produce complex responses, and often a mixture of responses is recorded. The mixed

response to the critical photoperiod follows from its definition. The response achieved in diapause larvae of *Calliphora vicina* exposed to 12°C is an example for the effect of intermediate temperature (Vinogradova & Bogdanova, 1984; Vinogradova, 1991, pp. 84–90) (Fig. 5). At the age of 40 days, diapause larvae from the region of Tomsk were transferred from the temperature of 5°C to higher temperatures of 12 or 20 or 25°C under the diapause-promoting photoperiod, or were kept at 5°C as control. Pupariation of the larvae indicated termination of diapause. About 80% of control larvae completed their diapause development within 200 days, clearly due to horotelic processes. Developmental threshold in *C. vicina* is below 5°C; thus the larvae could pupariate also at this low temperature. When the activating temperatures were 20 or 25°C the interval to pupariation was much shortened to 9 and 5 days, respectively. At these two high temperatures, tachytelic processes evidently completed diapause. However, in the case of transfer from 5 to 12 °C, when the pupariation delay was 100 days, the multimodal distribution of pupariation indicates that probably less than 40% of larvae responded in the tachytelic way. The last mode of 70–100 days fits fully into the range of the horotelic diapause development.

Horotely in the field. For the adult winter diapause of spring breeders most authors have accepted that diapause is completed in the field (by horotely) after 4 to 5 months after induction, and changes then into quiescence, during which morphogenesis is hindered just by low ambient temperatures (Table 1). According to this generally accepted view, and in contrast to laboratory experiments on photoperiodic activation of winter diapause, and also in contrast to estivation diapause, there is usually no cue or stimulus terminating diapause, although the course of diapause development may be modified by some factors, such as temperature more or less close to the optimum for horotelic processes.

Is diapause measured by timer(s)? The duration of diapause is programmed genetically, but also by the conditions in the course of diapause induction (Danks, 1987; Kalushkov et al., 2001). The duration of diapause development (and survival) may be different under different temperatures; however, there is a certain minimum duration of this period, called "refractory" by Watson & Smallman (1971). In the staphylinid *Oxytelus rugosus*, diapause development lasts 4 to 5 months and is completed without chilling (Topp, 1984, 1994). Topp speaks about a "specific time interval" needed and calls this feature "intrinsic" diapause. This concept resembles the rather old views expressed by Precht (1963, 1964) and Tischler (1963) in their papers on diapause of the lygaeid bug *Ischnodemus sabuleti*. They supposed that the duration of diapause is governed by a biological clock, "biologische Langzeituhren". In fact, we still cannot exclude the possibility that a timer measures the diapause, at least until we find some biochemical or molecular biological processes representing diapause development. Kai et al. (1995, 1999) reported that an enzyme served as interval

Cotesia glomerata −larval diap.

(sample 11 Dec)
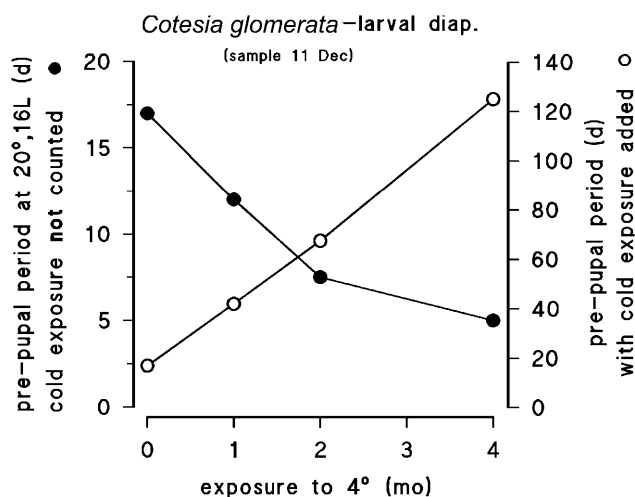

Haematobia irritans −pupal diap.

Fig. 6. The effect of cold exposure at 4°C (compared to the exposure at constant 20°C) on larval diapause in *Cotesia glomerata* with and without the "chilling" period (data from Ishii et al., 2000).
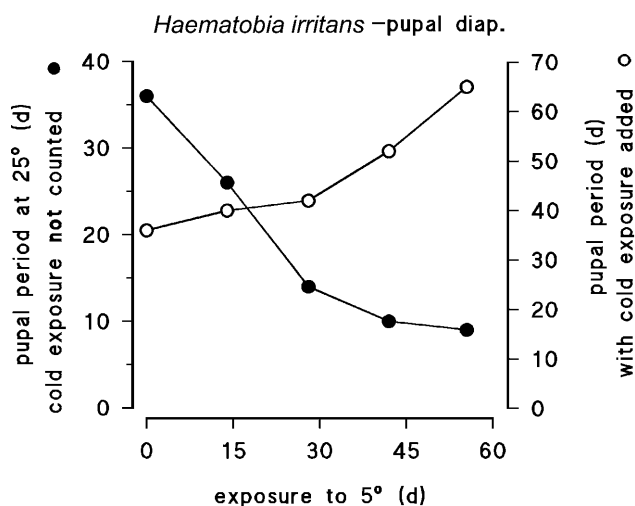
Fig. 7. The effect of cold exposure at 5°C (compared to the exposure at constant 25°C) on pupal diapause (pharate adult) in *Haematobia irritans* with and without the "chilling" period (data from Lysyk, 1999).

timer, measuring "chilling" during egg diapause in *Bombyx mori*.

Blake (1959) reported evidence of a circannual rhythm for larval diapause in a British population of the varied carpet beetle *Anthrenus verbasci*. Recently, Nisimura & Numata (2001) described a circannual phase response curve for the circannual pupation rhythm in a Japanese population of *A. verbasci*. The authors propose that a decrease in the photophase acts as an "autumn signal" causing a phase advance in subjective summer and a phase delay in subjective winter. Endogenous rhythm, alternating diapause and reproduction, was recorded in the ants *Formica aquilonia* and *F. polyctena* (Kipyatkov & Shenderova, 1990). While the chronobiological achievements in the field of circadian clocks are impressive, the problem of measuring the passing of time during diapause development has been neglected.

ROLE OF TEMPERATURE IN DIAPAUSE DEVELOPMENT

The function of temperature in diapause development has been a source of controversy and misunderstanding since the term and concept were coined by Andrewartha (1952). However, he cannot be blamed for later oversimplification and wrong generalisation of his paradigm. The pages dealing with the influence of temperature on diapause development (Andrewartha, 1952, pp. 56–59) demonstrate that the author was extremely cautious in explaining his concept. He wrote, e.g., : "For h e a l t h y completion of diapause the larvae (of *Cydia pomonella*) require to be held for several months at low temperatures." or "The association of low temperature with the disappearance of diapause is widespread but n o t q u i t e g e n e r a l " and he gives the range 5–13°C as an example of low temperatures. In spite of such clear limitations given by Andrewartha (1952) and a precise explanation soon afterwards by Lees (1955) many researchers concentrated their investigations on the sim-

plified assessment of whether the resumption of morphogenesis was possible without "chilling" (often even a control experiment was omitted) while the q u a l i t y of diapause development was neglected. Although the topic was clarified later in several compendia and review articles (Tauber & Tauber, 1976; Hodek, 1983; Denlinger, 1985; Tauber et al., 1986; Danks, 1987; Hodek & Hodkova, 1988), studies with such simplified aims are still being published and the overgeneralisation survives that "chilling" is a prerequisite for diapause development in a l l insects. It seems to be true in some cases (Table 2), while high temperatures enable completion of winter diapause in many other insects (Table 3); for earlier examples see also Hodek & Hodkova (1988).

In spite of the previous explanations by several authors, it has to be stressed again that ranges of temperatures effective for morphogenesis and for diapause development may overlap to different degrees. Thus using only one cool temperature is not an adequate approach to study the effects of temperature on diapause development. Rare was the use of a broad range of temperatures, as in the detailed studies on eggs of *Austroicetes cruciata* (Andrewartha, 1952), eggs of *Atrachya menetriesi* (Ando, 1983) and larvae of *Lagria hirta* (Zhou & Topp, 2000). The thermal optima are different for different processes; thus the optimum temperature is different for the incidence of diapause completion, rate/duration of diapause development or fitness of post-diapause individuals (which can be measured as longevity or reproductive ability). Lees (1955, p. 53) preferred duration over proportion as an "index of the completion of diapause development" and he did not mention fitness. His opinion probably affected many experiments. It appears, however, that all criteria yield important information for rating the value of temperature for diapause development. All these three parameters were monitored during diapause development in adults of the heteropteran *Pyrrhocoris apterus* (Hodek,

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TABLE 3. Species in which cool temperatures **are not** a prerequisite for completion of diapause development under diapause promoting photoperiod; winter diapause; papers listed in Hodek & Hodkova, 1988, which include 33 additional species, are not repeated here).

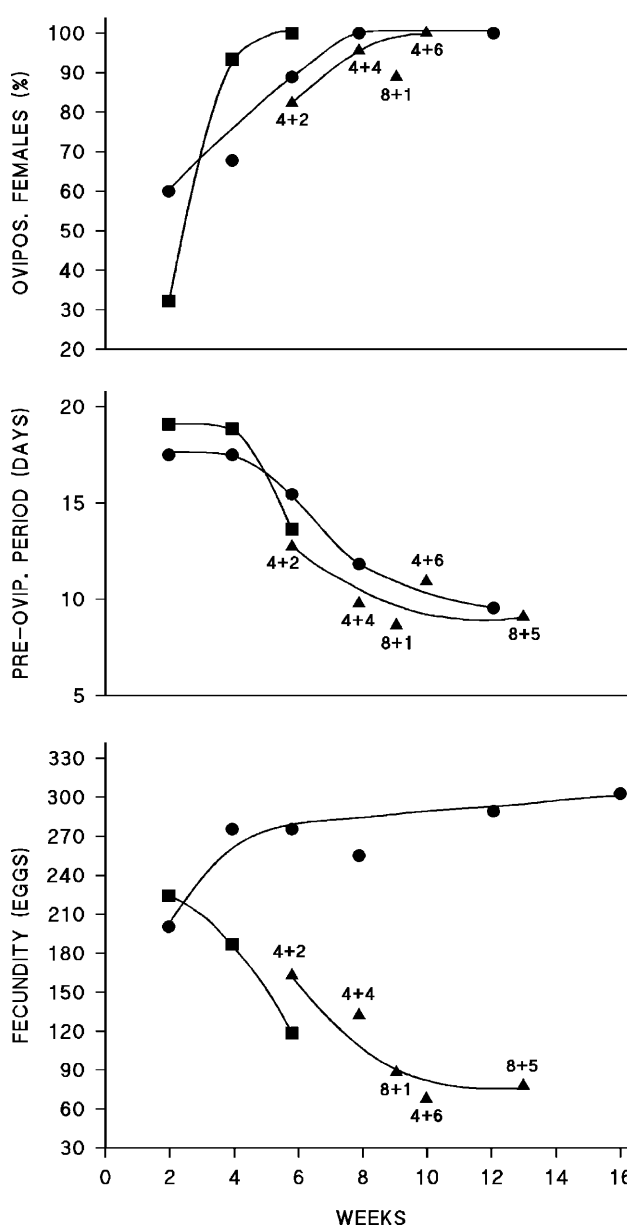| Egg diapause	
Teleogryllus commodus	Masaki et al., 1979
Chortoicetes terminifera	Hunter & Gregg, 1984
Diabrotica barberi (15 or 18° better than 0 or 3°)	Fisher et al., 1994
Caledia captiva	Groeters, 1994
Larval diapause	
Aphelinus varipes	Yu, 1992
Curculio elephas	Menu, 1993
Zygaena trifolii (50%)	Wipking, 1995
Choristoneura fumiferana	Han & Bauce, 1996
Argas reflexus (Di not sure)	Dautel & Knulle, 1998
Sesamia nonagrioides	Fantinou et al., 1998
Chlorops oryzae	Takeda & Nagata, 1998
Epilachna admirabilis	Takeuchi et al., 1999
Coleophora alticollela	Butterfield et al., 1999
Diprion similis	Melcher & Townsend, 1999
Pupal diapause	
Haematobia irritans	Lysyk, 1992, 1999
Agrius convolvuli	Shimoda & Kiuchi, 1997
Pieris melete*	Xue et al., 1997
Delia antiqua	Nomura & Ishikawa, 2000
Adult diapause	
Phytoseiid mites (4 spp.)	Veerman, 1992
Plautia stali*	Kotaki, 1998
Podisus maculiventris (partim)	Chloridis et al., 1997
Musca autumnalis	Krafsur & Moon, 1997
Bombus terrestris (queens)	Beekman et al., 1998

*low latitudes

Fig. 8. The effect of outdoor conditions (●) and laboratory exposure at 5 (■) or 16+5°C (▲) on reproductive parameters in *Pyrrhocoris apterus* females (recorded after transfer to 25°C and 12L : 12D; from Hodek, 1978).

1978, Fig. 8) and it was shown that temperatures suitable by some criteria were inadequate for allowing high post-diapause fecundity. In larvae of *Sesamia nonagrioides* the prepupal delay was slightly shortened by 16-day exposure to 5 °C, but mortality increased to 75% in comparison with only 8% at 25°C (Fantinou et al., 1998).

"Chilling" is part of diapause development. When the duration of diapause is used as a criterion, quite often the results on the effects of temperature on diapause development are misinterpreted because the duration of storage at low temperatures is not counted as part of diapause development. When this period is added, no or only a very smal shortening of diapause development can be recorded. Earlier examples (the tortricid *Choristoneura viridis* - Schmidt, 1977 and the tenthredinid *Pikonema alaskensis* - Bartelt et al., 1981) were noted by Hodek & Hodkova (1988, pp. 154, 156). A similar misinterpretation is found in a study on larval diapause of the braconid parasitoid, *Cotesia glomerata* (Ishii et al., 2000). The pre-

pupal period had not, in fact, "decreased with elongation of 4° exposure"; on the contrary, the duration of the prepupal period increases, when the time spent at 4°C is added (Fig. 6). The time spent at 4°C cannot be disregarded, because the authors report that in this insect "the diapause development can be completed at a temperature of e.g. 4°C".

In the pharate adult of the horn fly, *Haematobia irritans* (Fig. 7), a treatment by 5°C elicits diapause development only slightly less rapidly than exposure to 25°C (Lysyk, 1992, 1999). *H. irritans* has thus been added to a small group of insects in which diapause development can be completed equally well at both cool and high temperatures. Similarly, the egg diapause of *Chrysolina aurichalcea* lasts slightly longer when a part of diapause

development is spent at 3°C then when control eggs are kept continuously at 15°C (Fujiyama & Noda, 1996). (For earlier examples of double temperature optima see Hodek & Hodkova, 1988.)

Temperature exposure vs. increase. Another source of controversy is the inevitable large increase in experimental temperature when animals are exposed to low temperatures and then incubated at high temperatures, most often 25°C. If the low temperature is 5° or 10°C, the subsequent increase is abrupt, by 15° or 20°. Such an increase might represent a strong activating stimulus for the tachytely. It is difficult to distinguish the effect of the temperature during exposure from the effect of the increase (Hodek, 1978; Danks, 1987). In the sense of his concept of "steplike reactivation", Zaslavski (1988) denied the effect of cold exposure itself as he considered it to provide only a contrast to the subsequent incubation temperature. In his last paper, he assumed that the processes at low and high temperatures are integrated in such a way that the cumulative effect of low and then high temperatures is higher than the effect of warm conditions alone (Zaslavski, 1995, p. 411).

Role of cool temperatures. Many species require cool temperatures for successful completion of diapause development (Table 2). But even when diapause can be completed relatively quickly and at high incidence without chilling, cool temperatures lead to synchronous resumption of post-diapause morphogenesis and help to maintain the v i a b i l i t y of post-diapause insects. The condition of post-diapause adults is indicated by their reproduction and longevity (Fig. 8). It is perhaps the most serious drawback of studies on diapause development that the condition of post-diapause insects, stressed by Andrewartha (1952) by his words: "h e a l t h y completion of diapause", has been greatly neglected.

CONCLUSIONS

Every individual can follow several (at least two) possible developmental pathways that are evidently inter-linked and mutually complementary. Thus the time of diapause passed at any condition, including exposure to very low temperatures, has to be considered. Some authors were able to record two thermal optima for diapause development. In temperature studies the experimental range ought to be adequately wide and less affected then in the past by a priori assumptions. Stimulation by temperature increase or improvement in food or other conditions has to be considered.

The success of diapause completion can be estimated by at least four parameters; none of them can be dismissed. (1) The easily visible consequence of diapause completion, such as incidence of developmental steps, often is the only parameter measured. (2) The rate of diapause development, i.e., the delay or duration is frequently recorded. (3) The effect on synchronization of life-history events has been much less often considered. (4) In spite of its importance, the vigour of post-diapause insects (indicated by long-term survival or fecundity) has usually been neglected.

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