

## Review Article

# Adult Diapause in Coleoptera

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Recent studies dealing with adult (reproductive) diapause in the Coleoptera are reviewed, as a kind of supplement to the classic compendia. In the first two sections, the general characteristics of adult diapause are described and principal terms explained. Original articles dealing with 19 species from nine coleopteran families (Coccinellidae, Chrysomelidae, Bruchidae, Curculionidae, Carabidae, Silphidae, Scolytidae, Scarabaeidae, and Endomychidae) are reviewed. Finally attempts are made at generalisations from the papers reviewed, and hypotheses on diapause evolution are inferred. A polyphenic character of diapause is a prominent feature in *C. septempunctata* and *L. decemlineata*, but has been found also in other Coleoptera and in insects generally and often generates voltinism heterogeneity within populations.

## 1. Introduction

Adult diapause is the most common form of diapause in Coleoptera. It occurs in about 90% of beetle species [1], belonging mostly to the families of Coccinellidae, Chrysomelidae, and Curculionidae, and partly also Carabidae (the so-called carabid “autumn breeders” diapause as larvae). Another insect order with a high incidence of species entering diapause in the adult stage, is the Heteroptera with about 70% species. The lowest incidence of adult diapause is among species in the orders Lepidoptera and Hymenoptera (about 5% each).

## 2. General Remarks on Adult/Reproductive Diapause

To save space in discussions of individual species and avoid repetition, we describe the common characteristics here. (For more details see [1, 2].)

Diapause is an adaptive arrestment of development that helps synchronize active stages with suitable environmental conditions and so increase survival potential during unfavourable periods of the year. Insects that diapause as adults, the larvae and the young adults, develop when the food resources are present. For the stressful period without food (often lasting many months) adults prepare in time

by accumulating reserves (lipids, glycogen, proteins) and substances needed for resistance to future hazardous changes of environmental conditions. To begin early enough before the start of the dangerous period, diapause is induced by signals heralding the arrival of the unfavourable season; usually the cue is photoperiodic. Short (decreasing) day length serves as a signal of approaching winter and induces winter diapause (hibernation). In contrast, long-day photoperiods announce summer and induce estivation/summer diapause. Temperature and other environmental conditions act during the sensitive stage in concert with photoperiod in diapause induction or aversion (= prevention).

Such regulation is typical for facultative diapause that can, but need not, be entered in each generation. Quite often, however, the genetically fixed propensity is so strong that diapause, may be obligatory, is entered under any environmental conditions. Usually a population is not genetically homogeneous: both tendencies may be mixed, as we will see below, for example, in *Coccinella septempunctata* or *Leptinotarsa decemlineata*.

To terminate diapause, the insect has to go through diapause development, that is, horotelic processes of physiogenesis that often proceed best at temperatures in the range of 5–10°C, but cold is not always a prerequisite for the resumption of development [3]. In many cases, diapause may be terminated by tachytelic processes of termination that is

due to some environmental stimuli, such as a temperature increase or rainfall in case of summer diapause.

For quite a long period diapause research was focused only on hibernation/winter diapause, as the traditional view equated diapause with resistance to freezing. Estivation/summer diapause was long neglected, although it is rather common [4]. Quite often the terms hibernation versus estivation do not respond well to timing of seasons in the field: winter diapause may begin as early as in midsummer, as we will see below in several ladybird species.

Also, while hibernation lasts until spring, its diapause phase in temperate insect populations dwindles into postdiapause quiescence around the winter solstice. In this phase the morphological development of insects is arrested only directly by low temperature (or absence of food), and in spring (or by transfer to suitable laboratory conditions) morphological development is resumed.

The most conspicuous feature of adult diapause (often termed reproductive diapause) is the suppression of reproductive functions: maturing of ovaries and male accessory glands, and mostly also mating activity. Endocrinological regulatory pathways in adult diapause begin in the neurosecretory cells of brain whose axons terminate in corpora cardiaca. The pathway continues in another endocrinological organ, the corpora allata, where juvenile hormone is produced that regulates the activity of reproductive organs. In adults destined for diapause, food consumed is not used for maturation of gonads but for accumulating reserves. Thus the ovaries consist of threadlike ovarioles, so hidden in the much-enlarged fat body that they are sometimes difficult to find in dissection.

The above general traits were revealed in several coleopteran species that were studied in detail for many decades and published in series of papers, such as the studies on *Leptinotarsa decemlineata* and *Coccinella septempunctata*. The classic papers are not reviewed here as they are reviewed in the above-mentioned compendia [1, 2]. Here we focus on more recent findings, mostly those published in the last two decades. It may be warned that the basic paradigm of diapause, built in the previous century, had not yet been broken.

### 3. Coccinellidae

**3.1. *Coccinella septempunctata* L.** Among ladybirds, adult diapause has evidently been most studied in the originally Palaearctic species *Coccinella septempunctata*, the seven spot, that has in two recent decades invaded the Nearctic region and attracted attention of researchers there (e.g., [5]). Both in Europe and USA *C. septempunctata* has been found heterogeneous as to the induction of diapause (see Section 1).

In Bohemia (50°N, Western Czech Republic), the population in the autumn consists of two fractions. Although in some years aggregations of both sexes of dormant *C. septempunctata* may be found in their hibernation quarters in grass tussocks from early August onwards, one can also find actively feeding coccinellids on vegetation with aphids (often on different weeds, such as *Carduus* spp. and *Daucaceae*) for the whole of September and into

early October [6]. The physiological condition of these two fractions was determined by dissection immediately after sampling and after rearing. Whereas the alimentary canal in the dormant beetles was empty of food and there were no traces of vitellinization in the ovaries, the digestive tract was full of food in more than half of the active adults sampled and 13–20% of females possessed vitellinized oocytes or even eggs. The difference between the dormant and active beetles became striking when they were reared for three weeks under long days, at 19–22.5°C with plentiful aphid food; the ovarioles of about 85–90% of dormant females remained without any vitellinization, while about 90% of the females collected on plants possessed vitellinized oocytes after rearing [6].

Dissections in mid-July of females collected outdoors a fortnight after adult emergence indicated a strong tendency to univoltinism: 84–93% of the females, entered diapause. The offspring of overwintered adults (F 1) also displayed a high incidence of diapause despite rearing under long-day conditions of 16L:8D or 18L:6D with a surplus of suitable prey. When such experiments were repeated in five years the incidence of diapause in F 1 fluctuated between 60 and 90%. A gradual decrease in diapause incidence across generations suggests selection against a propensity for obligatory diapause under long days [6].

A dominant effect of photoperiod and its modification by temperature was documented in samples from the selected lines. Under long days diapause was prevented in most females and 87–96% females reproduced in spite of low temperatures (18 or 18.5°C, resp.). Under short days of 12L:12D or 8L:16D, diapause incidence was high (85–94%) at low temperature (about 18°C), but low at high temperature: at temperatures alternating between 24–25°C (night) and 27–28°C (day) only 10% entered diapause.

In central Europe and the Paris region (France), the progress of diapause development in *C. septempunctata* was monitored by transfers of adults from the field to the laboratory at 25°C. Diapause was completed in December–January, whereupon it was replaced by postdiapause quiescence that lasted until spring when, under the influence of temperature increasing above around 12°C, the adults dispersed from hibernation sites to localities with aphids, where they fed and reproduced [6].

Whereas field observations indicate a univoltine cycle in central Greece, a tendency to multivoltinism was documented in *C. septempunctata* in this region, when four subsequent generations were reared in modified outdoor conditions [7]. The conditions were improved by shading of the rearing cages from direct insolation and continually providing surplus of suitable aphid prey.

**3.2. *Ceratomegilla undecimnotata* (Schneider).** Similar to *H. convergens*, the relative role of food and photoperiod in diapause regulation in *C. undecimnotata* is not yet clear enough, although the share of food/prey appears important.

The earlier studies on this Palaearctic species were undertaken in France and Czech Republic [6]. Detailed laboratory and field studies in central Greece [8] widened our knowledge of diapause in this species. The authors dissected

the females of *C. undecimnotata* that were sampled from the field in mid-June. About 40–50% of nonreproductive females were recorded in the plain, while most females (70–100% in different years) were at the same time immature in aggregations on mountain summits, where they remained until spring. This should indicate a univoltine cycle. When, however, the beetles were provided with a surplus of aphids outdoors (under shading, but natural photoperiod), five subsequent generations were produced. With about 30% of immature females in the first three generations, such diapause incidence was not far from the field records from the plain. These data indicate that *C. undecimnotata* populations from central Greece are heterogeneous as regards the induction of diapause. These findings are similar to *C. septempunctata* and *H. convergens*.

Samples from mountain tops were regularly transferred to laboratory (25°C, long day 16L:8D, prey surplus). Females were activated under these conditions by tachytelic processes and laid eggs after a gradually shortened pre-oviposition period (92 d in July, 63 d in August, 20 d in September). This decrease in diapause intensity demonstrated the progress of diapause development by horotelic processes in the field.

All these results, similar to the French and Czech findings [6], indicate that *C. undecimnotata* is a long-day insect (long day is diapause preventing and not diapause inducing as assumed in the recent paper [8]). (The generic name *Hippodamia* used in [8] is not correct.)

**3.3. *Hippodamia convergens* Guerin.** In this common Nearctic aphidophagous ladybird, several possibilities of diapause induction were proposed by Hagen [9] for the plains of Northern California—and not much has been added later to his hypothesis. Originally, before the installation of irrigation systems, most individuals had an (obligatory ?) univoltine cycle (with a complex migration to mountains where enormous quantities of beetles aggregate for overwintering and are collected for biocontrol purposes). Later the Californian ladybird populations changed to multivoltine cycle, due to the high abundance of introduced aphids and are induced to diapause by photoperiod and temperature. However, diapause can still be nutritionally induced in a part of the population [9, 10]. In the upper coastal plain of South Carolina, diapause in *H. convergens* is terminated in December/January after the transfer to temperatures >15.5°C, despite short days 12L:12D [11].

We need to know much more about the combined action of food and other factors in this species. Such studies have evidently begun with the analyses of the role of nutritional factors (nonaphid protein rich alternative food) in the arid conditions. In the Great Plains region in the central USA *H. convergens* is normally bivoltine, with obligate winter hibernation and facultative summer estivation which creates the possibility for additional generations when conditions permit. Various cases of nutritional regulation of reproductive diapause were analysed in females of *H. convergens* in these populations [12, 13]. The importance of drinking sap on sunflower in the summer months in West Kansas was examined. Sunflower petioles and pollen as well as

lepidopteran eggs were provided to the beetles collected in early June. While these females did not oviposit in the absence of protein food, feeding on eggs of *Ephestia kuehniella* followed by pollen enabled 66% of the females to lay viable eggs at a low rate of 6.6 eggs/day. The females, transferred on 14 August to essential aphid food (*Schizaphis graminum*), laid six times more eggs.

These experiments stressed the adaptive role of the life cycle in *H. convergens* in that it enables survival during arid summer conditions when there is a shortage of the essential food, aphids. In the absence of protein-rich food, the 1st generation can enter diapause. Another tactic could be to wait in a state of lowered metabolism (but less lowered than in diapause) for the reappearance of essential aphid food, relying meanwhile on alternate foods. Then a switch to intensive egg laying can be quick, as was shown by a short oviposition delay of only 4 or 6–9 days on essential prey [12, 13].

**3.4. *Harmonia axyridis* (Pallas).** After the very early Russian studies from Asia (see [6]) only two Japanese papers were published, dealing with diapause of this coccinellid from east Asia—before its invasion to America and Europe. In Japan this bivoltine long-day insect hibernates in diapause [14, 15] and uses the polyol myo-inositol to increase its cold-hardiness [15].

After its arrival in Europe this invasive species was studied in South-Eastern France, Northern Italy, and Belgium and has become the most studied coccinellid. Facultative diapause of the multivoltine strain is induced by short-day photoperiod 12L:12D at 23°C and lasted 1–3 months; eggs of *Ephestia kuehniella* were used as a suitable alternative food [16–19].

## 4. Chrysomelidae

**4.1. *Leptinotarsa decemlineata* (Say).** It was probably the first insect model for the detailed experimental study of adult diapause. Thanks to the intensive research by the team of Professor Jan de Wilde, Wageningen, The Netherlands, particularly the physiological/endocrinological aspects of diapause have been intensively investigated since the late 1950's [20]. These studies are reviewed in the important compendia [1, 2] and in the introduction of a paper by de Wilde's followers [21]. Research on the prolonged diapause in *L. decemlineata* and its dependence of soil types was focused by the team of Professor Raisa Ushatinskaya, Moscow, Russia [22].

The main facts on diapause regulation from the classic Dutch studies will be given here to make the reading of more recent studies below more easy. Diapause is induced by short-day photoperiod: 10L:14D at 25°C have been used in Wageningen and 16L:8D was the long-day photoperiod. Both larvae and adults are sensitive to induction [23]. 20–30% of beetles enter diapause under any photoperiod; thus a propensity to obligatory univoltinism is indicated, similar to the case of *C. septempunctata*, discussed above. Diapause development in *L. decemlineata* progressed well under any

of three temperatures, 4, 12, and also 25°C, that is, it does not need period of low temperatures for its completion (similar to quite a number of other insect species [3]). At 4°C mortality was high (15% after 3 mo, 50–70% after 6–7 mo), while it was <10% at 12 and 25°C. Diapause development was faster at 25 than 12°C, and 50% of females spontaneously emerged from soil after 14 and 21 wk, respectively. Sensitivity to photoperiod is retained during diapause development at least to February: at this sensitive period, diapause can be terminated by only three long days. The females lose photoperiodic response for at least 5 wk after the completion of diapause development, but the responsiveness is restored 3 wk after diapause in a part of the population (recurrent photoperiodic response, discussed in Section 12). However, photoperiodic sensitivity is never lost completely, even after the completion of diapause it affects the rate of vitellogenesis and ovarian maturation.

Because of the importance of the Colorado potato beetle as pest, the primary insect defoliator of solanaceous crops in North America and Eurasia [24], research continues on different aspects. Flight incidence and duration in relation to mating was recorded by flight mills [25]. Mating has a pronounced effect on flight activity decreasing it in females, evidently because migration and reproduction interfere with each other, and increasing it in males—they may thus mate with females from different localities.

Oviposition and burrowing behavior (as contrasting characteristics of nondiapause versus diapause, resp.) were compared in 1st generation females along a 5° latitudinal gradient, in six populations from North Dakota and Minnesota, USA, and Manitoba, Canada. Four locations were sampled in the Red River Valley region (between 49°49'N and 47°00'N) and two in east central Minnesota (45°20'N and 44°44'N). Different incidence of oviposition was recorded under long days in the RRV region (0–1%) and in ECM samples (9–15%). The authors conclude that *L. decemlineata* has the capability of becoming adapted to local environmental drivers, while retaining intrapopulation variability [26].

Some Colorado potato beetles enter prolonged (>1 yr) dormancy, an event quite common in adults dormant in the soil, such as some curculionids discussed below. This phenomenon was studied earlier in Russian populations and those from Western United States, where a very high incidence (22%) was recorded. M. J. Tauber and C. A. Tauber [24] studied its frequency in the Upstate New York in a 10-yr field study and recorded an average 2.04 (0–72)% in 12,607 beetles. They explain this relatively low incidence in North Eastern United States by the late arrival of *L. decemlineata* after the introduction of cultivated solanaceous crops. In Western United States, in contrast, the Colorado potato beetle commonly occurs on wild solanaceous host plants in drought-prone habitats.

Both the effect of age of potato foliage and temperature are important in the prediapause beetles [27]. The adults consumed older foliage at a faster rate, particularly at the higher temperature of 17°C (compared with 11.5°C) and consumed 45% higher weight of leaves. It is assumed that there is a fixed requirement of accumulated reserves to

achieve prediapause satiation. If the food is less rich in needed substances, larger amounts have to be consumed.

In populations from Central Europe 70–80% of reproducing females develop under >15 h day length, while under <14 h day length all beetles enter diapause [28]. In experiments the photoperiod of 12L:12D was used as short day, and 18L:6D as long day. The index of food conversion was 5.4 under long days, but 7.2 and 11.9 under short days (at 20 and 25°C, resp.). Pupae were smaller under long days due to a greater loss of biomass during the prepupal stage that was almost twice as long as under short days.

The functional state of flight muscles was assessed by staining with commercially available (Sigma-Aldrich) tetrazolium salts; the color develops due to reduction of a colourless salt by mitochondrial enzymes [29].

The research on diapause of *L. decemlineata* continues also in the recent molecular biology age. In a study of gene expression patterns during the first 20 postemergence days in beetles programmed for diapause (at 8L:16D, 24°C), that is, in prediapause phase, oxygen consumption was measured in this period. The respiration rate increased from 0.4 mL/g/h on day 1 to 1.1 mL/g/h on day 4, and after a plateau between days 4 and 7 the oxygen consumption decreased to 0.08 mL/g/h on day 15. The CO<sub>2</sub> production followed the same curve, with an additional conspicuous peak on day 7. Among the clones of genes isolated, elevated levels of expression of the glycine-rich transcripts (that function in structural support of insect cuticle) persisted for four days longer in diapause-programmed beetles, compared with nondiapause adults. The differentially regulated genes were downregulated between days 13 and 20, that is, at the end of prediapause when the metabolic rate was already much decreased [30].

The series of papers by Yocum and coauthors has continued by a recent one [31]. Prediapause and diapause phases of development are well marked by expression of genes in laboratory reared adults. However, it is much less clear in field collected adults, evidently due to the polyphenic character of diapause, mentioned earlier. The authors conclude that this property contributes to the status of *L. decemlineata* as a “superpest” of potatoes [31]. This characteristic is similar to that in *C. septempunctata*, where also the plastic character of adult diapause is obviously associated with the “success” of the species [32].

**4.2. *Colaphellus bowringi* Baly.** A complex analysis of diapause regulation was conducted by Professor Xue and coauthors in a series of recent papers. The cabbage beetle, *C. bowringi*, is a pest of cruciferous vegetables in mountain areas of Jiangxi Province, China. There are four generations per year, one in spring and three in autumn. The beetle estivates and hibernates as adult in the soil. A life-cycle polymorphism was reported by Xue and Zhang 20 yrs earlier (for an English summary of that paper published in Chinese, see [33]). Although the adults enter diapause at the same time, they differ much in diapause duration (several months–two yrs) and thus they expressed heterogeneous voltinism. Without regard to diapause induction and duration, the post-diapause beetles emerge from soil either between late

February and early April, or between mid-August and early October.

*C. bowringi* is a short-day species (i.e., long days induce diapause), but the photoperiodic response is strongly affected by temperature. High temperatures enhance the diapause-averting effects of short days and suppress the diapause-inducing effects of long days. Diapause incidence is 100% at  $<20^{\circ}\text{C}$  at any photoperiod. Photoperiod plays a relatively small role in diapause induction; short days can prevent diapause only at temperatures above  $20^{\circ}\text{C}$ . The mechanisms ruling the complex seasonal life-cycle in *C. bowringi* are well explained by experimental results [33]. It is probably the first documented case of summer diapause induction by low temperature instead of high temperature. Diapause is entered by early-emerging individuals in April. The authors suggest that the photoperiodic and temperature controls of diapause induction have a different genetic basis.

Experiments on the effect of thermoperiods on diapause induction in *C. bowringi* showed again the importance of temperature, particularly during the photophase [34].

Other detailed experiments documented an important effect of host plants on diapause incidence in *C. bowringi* [35]. The highest incidence of diapause was caused by feeding on radish (*Raphanus sativus*) and the dark green variety of Chinese cabbage: the lowest incidence was obtained by feeding on the yellow-green variety of Chinese cabbage with thin leaves. Most adults entered diapause on mature and aged leaves. Diapause incidence was affected by host plants only within a certain range of photoperiods and temperatures; it was best manifested at  $25^{\circ}\text{C}$  and 13L:11D. Regardless of host plants, all adults entered diapause at  $20^{\circ}\text{C}$  or at 16L:8D, as indicated in the earlier papers.

There is no negative tradeoff between diapause duration and several parameters of performance in adults after diapause: the body weight, longevity, and fecundity of beetles with the longer diapause duration of 21 mo were higher than those with the shorter duration of 5, 11, and 17 mo [36].

Crossing a high diapause strain with a laboratory selected nondiapause strain showed that diapause capability is inherited in an incomplete dominant manner; maternal inheritance of diapause induction is stronger than paternal inheritance [37].

4.3. *Zygogramma bicolorata* Pallister. This chrysomelid was successfully introduced to Jammu and Kashmir, India for biological control of carrot weed, *Parthenium hysterophorus* L. Adults enter diapause from August to December with a peak in late November. They burrow into soil and are dormant about 1–3 cm bellow the surface. The incidence of burrowing adults increases with soil moisture and is higher in silty soil (47%) than in sandy soil (24%). Diapause is facultative as nondiapausing adults breed in winter under laboratory conditions. The beetles become active in March and, after having defoliated their host plants in an area, they disperse and need not be introduced to other areas. By treating the newly emerged beetles with human insulin (5 : g) the incidence of diapause was lowered and the fecundity increased [38].

In a population from Jabalpur, India, 64% of beetles entered diapause at  $26^{\circ}\text{C}$  and photoperiod was not important. Storage of females at  $10^{\circ}\text{C}$  for 6 mo did not lower their fecundity [39].

4.4. *Plagioderia versicolora* Laicharting. This is a species with facultative diapause that feeds on several species of willows. Experimental populations from the region of the river Ishikari ( $43^{\circ}\text{N}$ , Hokkaido, Japan) had both univoltine and bivoltine life-cycles and were most abundant on *Salix sachalinensis* Fr.Smids.

All females entered diapause at 10L:14D, but a rather high incidence also was recorded at 16L:8D (68% with a range of 40–100%) [40]. These are evidently results from rearing beetles on leaves of mixed quality, as only 10% diapause was reported in the 1st generation reared on 2–22 July on young leaves [41]. Diapause induced under short days of 10L:14D at  $22^{\circ}\text{C}$  was terminated by long days of 16L:8D at  $22^{\circ}\text{C}$  [42].

Later the effect of photoperiod and temperature (16L:8D and  $20^{\circ}\text{C}$  in the laboratory) was experimentally isolated from the effect of seasonally changing quality of host-plant leaves [41]. While the abiotic laboratory conditions were kept constant, the leaves of *S. sachalinensis* were collected in the field and thus gradually more mature leaves were provided. The reproductive parameters declined in the 2nd and 3rd generations, in comparison with the 1st generation. Diapause incidence increased from 10 to 60%, the pre-oviposition period increased from about 9 to 16%, and the fecundity during the first 10 days of the egg laying period decreased from about 50 to 18 eggs per female. The authors thus documented the effect of host plant age and suggested that the combination of both day length and host-plant conditions cuing diapause is adaptive [41].

4.5. *Galerucella californiensis* L. It was introduced to the United States for the biological control of purple loosestrife (*Lythrum salicaria* L.). The adults undergo a facultative reproductive diapause (the paper's abstract mentions obligatory diapause by mistake) during summer, autumn, and winter. Diapause can be averted by long days of 16L:8D and induced by 8L:16D. Adults are responsive to diapause-inducing photoperiods. The authors failed to isolate the cultures efficiently from insolation with white tissue tents as the natural photoperiod produced a seasonal effect; in early summer the ovaries matured better [43].

4.6. *Crioceris* sp. This undescribed chrysomelid species was studied in the Western Cape Province, South Africa ( $34^{\circ}35'\text{S}$ ) as a promising biocontrol agent of bridal creeper (*Asparagus asparagoides* (L.) W. Wight) with the intention to introduce it to Australia.

The majority of fully developed adults remain inside cocoons in soil for various periods of summer diapause. Field observations suggest that rainfall might be the cue for termination of diapause or dormancy. The effect of wetting was demonstrated in the laboratory. Only 29% ( $n = 135$ ) adults emerged from dry cocoons at  $20^{\circ}\text{C}$  within 76 days.

This proportion was substantially increased by wetting, and even more by repeated wetting.

No research addressed the mechanism of diapause regulation by physical and biotic environmental factors, although larvae were reared successfully to pupation in soil at 15 and 20°C [44].

## 5. Bruchidae

**5.1. *Callosobruchus subinnotatus* (PIC).** It is a major pest of stored bambara groundnut, *Vigna subterranea* (L.) Verd-court in sub-Saharan West Africa. Adult polymorphism was described in this bruchid, similar to that of some other species of the family, particularly *C. maculatus* (Fabricius), that was the model insect for a series of classic ecological studies by Professor Syunro Utida from Kyoto University, Japan, in the years 1954–1981. The terms for the two polyphenic forms, used in the earlier *C. maculatus* studies, were also used here although they do not seem very adequate: “active” and normal adults. While the normal adults have a high fecundity, low longevity, and lower tendency to dispersal, the “active” phase shows opposite qualities. Dissections reveal immature ovaries and male gonads, so we might consider this suspension of reproduction an adult diapause or at least a diapause-like phenomenon. Although high population density was suggested in several Utida’s articles to be the factor responsible for the development of “active” form, no attempts have been made to address this influence in *C. subinnotatus* [45].

Another congeneric bruchid, *Callosobruchus rhodesianus* (Pic), suffering from strong competition by *C. maculatus* on cowpea, *Vigna unguiculata* (Walp.) in Togo, Africa, reproductive diapause was recorded [46] in a part of population.

**5.2. *Bruchidius dorsalis* Fahraeus.** This multivoltine seed-eater occurs in Central and Southern Japan. Females oviposit on seedpods of the Japanese honey locust, *Gleditsia japonica*. Newly matured seeds are available from August to autumn, but the females may use also dry, hardened seeds; thus host seeds can be utilized almost the whole year.

In contrast to most insect species, in warmer regions *B. dorsalis* enters diapause in different developmental stages: final larval instars and adults. Even nondiapausing early instars may overwinter [47]. In Sagami-hara (35°34′N) 3 to 4 generations develop per year. Some autumnal adults produce the new generation before winter, while another part of the population overwinters before spring reproduction. Diapause is induced by short days and the first five days after adult emergence are sensitive to diapause-inducing factors.. Diapause incidence was higher and the critical photophase longer in cooler regions [48, 49].

## 6. Curculionidae

**6.1. *Curculio nucum* (L.).** This specialist of hazelnut trees has an obligate 2-yr cycle in France (45°46′N, 420 m a.s.l.) with one larval diapause in winter, pupation and ecdysis of adults (in soil) the next summer, and in the 2nd winter adult

diapause. In spring the overwintered adults emerge from the soil in April and appear on trees from May to early July [50]. Early emergence from the soil enables females to oviposit in nuts before they fully harden. As they cannot penetrate the mature nut, they must oviposit before July.

Females lose about 8.5% of their weight during overwintering, but their lipid content does not decrease. Thus the authors suppose that females use lipids accumulated during the larval stage for egg production and obtain other nutrients from adult feeding. Evolutionary forces triggering the obligate 2-yr cycle are discussed [50].

**6.2. *Exapion ulicis* (Forster).** This univoltine species consumes the seed of gorse, *Ulex europaeus*, that has peak fruiting in spring and was introduced to some countries for its biological control. Adults lay eggs in spring into young green pods where the larvae develop adults feed on leaves and flowers of gorse and then diapause in autumn and winter. In winter the beetles stay on branches and are able to resist cold. In Brittany, France, the species was studied together with *E. lemovicinum* (Hoffmann), a species that overwinters in the larval stage, to understand its cold-hardiness. *E. ulicis* adults are freezing intolerant, but exhibit a low supercooling point of –17°C. The regulation of diapause induction and termination was not studied [51].

## 7. Carabidae

**7.1. *Nebria salina* Fairmaire and Laboulbene.** This species is common in unproductive habitats, such as sand dunes and upland grasslands. This short-day insect is an autumn breeder that enters a summer diapause. Females require at least two months of exposure to short-day photoperiods of <12L:12D. Under long days of 18L:6D the ovaries do not mature. Still shorter days of 6L:18D stimulate better growth of ovaries. The males matured after two months irrespective of photoperiod.

In the field (Hamsterley, County Durham, UK) the main activity of *N. salina* was concentrated in September [52]. Thus, the life cycle of this species resembles the congeneric autumn breeder *Nebria brevicollis*, where diapause was studied in the 80’s by Hengeveld and Loreau (quoted in Telfer and Butterfield [52]).

**7.2. *Carabus yacoininus*.** When the authors transferred this spring breeder from the field to laboratory experimental photoperiods, the beetles showed a long-day photoperiodic response in autumn and early winter. In the course of winter the response was gradually lost, so that in late April the ovaries of females matured both in short and long days [53]. However, in summer the photoperiodic response resumed again. Thus *C. yacoininus* appears to be another case of recurrent photoperiodic response that was revealed for the first time in a pentatomid bug *Aelia acuminata* [54] and recorded later also in *L. decemlineata* and *C. septempunctata* (see above).

## 8. Silphidae

8.1. *Nicrophorus nepalensis*. This subtropical short-day breeding carrion beetle that occurs in Taiwan (24°45'N, 745 m a.s.l.) is active mainly in early spring (February–May) and also in autumn (October–November). Reproduction is best promoted at 20°C and a photoperiod of 12.5L:11.5D, but only in the presence of carrion, whereupon oviposition starts after 2 weeks. At a lower temperature of 15°C and 11L:13D, maturation is slower, so that the oviposition begins after about 9 weeks. In contrast, longer days (14L:10D) prevent oviposition at 25°C, but enable oviposition of 45–50% of females at 20°C. Summer diapause is an efficient adaptation as the development of offspring on carrion in summer would suffer from competition with more quickly developing dipteran larvae on quickly decomposing dead animals [55].

## 9. Scolytidae

9.1. *Ips typographus* L. The number of generations varies in different countries, similar to other insect species. Flight parameters were studied in young beetles from five populations: one in Denmark (56°51'N) and four in Sweden (between 57°40'N and 62°51'N). The flight propensity of beetles that emerged in the period 34–80 days was tested and those flying less than 100 s (“non-fliers”) were found by dissection to be in diapause with undeveloped ovaries and large fat reserves. The frequency of such beetles increased with increasing latitude from 35 to 70%. While “fliers” migrate to find a breeding site, diapausing “non-fliers” often overwinter on the ground beneath the brood tree [56].

In a Central European population, diapause was induced by <16L:8D at 20°C and the critical photoperiod (50% diapause incidence) was 14.7L:9.3D. Temperature of >23°C prevented diapause even at 12L:12D. Neither gonads nor flight muscles matured in diapausing adults. Overwintering adults, shown to be in diapause by their response to photoperiod, reproduced at the long-day photoperiod of 18L:6D but not at 12L:12D when transferred in October from the forest to laboratory 20°C [57].

## 10. Scarabaeidae

10.1. *Dasylepida ishigakiensis* Niijima and Kinoshita. This “white grub” is a serious pest of sugarcane on Okinawa Islands, Japan. It is the only scarabaeid beetle in which the regulation of adult diapause has been studied. Both larvae and adults of this subtropical beetle undergo diapause in a semivoltine (2-yr) life cycle. Adults emerge from pupae in the soil and stay there for about two months. This delayed emergence from the soil cannot be related to synchronization with food, because the adults have degenerated mouthparts and do not feed. The beetles begin to leave the soil in late autumn when cooler temperatures are favorable for mating. Sexual maturation in the laboratory is suppressed at temperatures of 25–30°C, but proceeds well at 15–20°C. Photoperiod does not seem to act in diapause regulation [58].

## 11. Endomychidae

11.1. *Stenotarsus subtilis* (=rotundus) Arrow. *S. subtilis* provides a case of tropical diapause that was studied in Panama [59, 60]. This beetle forms large aggregations for a long dormancy, comprising 6 months of the wet season and 4 months of the dry season. Breeding sites, food, and diapause-inducing factors all remain unknown. Experiments with beetles collected from aggregations revealed the role of environmental factors in diapause development. Although in Panama (9°N) the difference between the longest and shortest day is only 1 h, increasing day length from March onward stimulates weak development of corpora allata, primary oocytes, and flight muscles that had remained resorbed for about 6 months. Mating and dispersal coincide with the onset of rains in late April. Two-month exposures to contrasting humidities revealed that higher humidity also stimulates development of the aforementioned organs [59, 60].

## 12. Concluding Remarks

It is almost impossible to make general conclusions from the recent data given above on the diapause of beetles. There are at least two obstacles: (1) diapause is a seasonal adaptation (see the Introduction) and it apparently evolved independently in individual species under specific environmental selective pressures that ultimately result in a genetic basis. Diapause of individual species/populations is thus intrinsically diversified—and inherently resists generalization. (2) The conditions for reasonable comparisons are further aggravated by diverse research protocols that have been employed by individual researchers either arbitrarily or under various technical constraints. Even in the case of currently studied species (that often are economically important), such as some chrysomelids, curculionids, or coccinellids, research analyses have often remained incomplete. This is still even more true for fragmentary studies some of which are included here only to show the wide range of records.

In spite of these difficulties, we may try to deduce some general features (that may apply to other insect orders as well). No particular break of the classic paradigms was made in the recent papers. They rather were further corroborated and extended. The most general, and the most studied, is the signaling function of photoperiod, often modified by effects of temperature and food that announces seasonal transitions with astronomical precision. In particular populations, photoperiodic response is always adapted to geographic latitude, as has been shown above best in *L. decemlineata* populations originating from locations separated by about 5° latitude. In some common and widely studied species, such as the Nearctic coccinellid *H. convergens*, the evidence of the photoperiodic regulation has still remained rather scarce.

An effect of food quality implicated in several of the discussed species. The difference of old versus young leaves is well documented in *L. decemlineata* and *C. bowringi*; the effect of alternative food (e.g., pollen) versus essential aphid species has been studied in detail in *C. septempunctata* [6]

and *H. convergens* [12, 13]. In the ladybird *Ceratomegilla undecimnotata* (Schneider) the physiological age of host plant can even act through the aphid prey, as reported in the 70's see [61] (see also) [6].

The effect of population density has remained rather neglected in the beetles discussed here. The exceptions are early articles on the bruchid *C. maculatus*, where the effect was recorded long ago by Professor Utida, and the observations on *C. subinnotatus*.

As mentioned above, diapause adaptations are very plastic in response to selection. Similar to changes in photoperiod, beetles can adapt quite quickly to environmental changes associated with changes in food supply. Thus, for example, introduction of irrigation in arid areas led to the establishment of prey in two coccinellids, *H. convergens* in California and *Chilocorus bipustulatus* L. in Israel, and thereafter to changes in their life cycles [6].

It is worthwhile to speculate about a hierarchy of individual factors governing diapause regulation. The basic driver is usually photoperiodic response to the precise annual astronomical repetition of day length. We may assume that less rigid reactions to less predictable environmental changes in food availability and quality, and other factors such as temperature, humidity, and population density, can be superimposed. The archetypal nutritive factor is "prepared to enter the game" in the case of unpredictable events affecting prey abundance—and this is facilitated by phenotypic plasticity.

Polyphenic character of diapause is a very important feature in *C. septempunctata* and *L. decemlineata*, but it has been found also in other Coleoptera and in insects generally: populations are heterogeneous as to voltinism tendencies. For populations with mixed uni- and polyvoltine tendencies we might envisage a scenario which combines plasticity with resilience. One aspect of the life-cycle strategies is the "safety" ("insurance") factor of the univoltine trait which is permanently perpetuated in the gene pool and maintained (i.e., not selected out) despite the frequent momentary occurrence of conditions favourable for the production of an additional generation, since these transitory conditions are unreliable in the long run. However, polygenes facilitate population responses to changes in the environment. If there is a promising improvement they may "open the gate" for intermittent multivoltine development, that may be more or less appropriate to capitalize on transitory environmental improvement. The system remains resilient because the univoltine trait is maintained quite intensively. This scenario is adequate for *C. septempunctata* and perhaps also *L. decemlineata* living in temperate regions/climate. In different climatic areas, the regulation of voltinism can differ.

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