ANNUAL REVIEWS

Annual Review of Entomology

Diapause in Univoltine and Semivoltine Life Cycles

Hideharu Numata[1,*] and Yoshinori Shintani[2]

[1]Institute for the Future of Human Society, Kyoto University, Kyoto, Japan;
email: numata.hideharu.8r@kyoto-u.jp

[2]Laboratory of Entomology, Department of Environmental and Horticultural Sciences,
Minami Kyushu University, Miyakonojo, Japan; email: shintani@nankyudai.ac.jp

Annu. Rev. Entomol. 2023. 68:257–76

First published as a Review in Advance on
October 5, 2022

The *Annual Review of Entomology* is online at
ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-120220-101047

*Corresponding author

Keywords

bet-hedging, circannual rhythm, climate warming, phenotypic plasticity, prolonged diapause, seasonal adaptation

Abstract

Although it is generally more adaptive for insects to produce additional generations than to have longer life cycles, some insects produce one or fewer generations per year (univoltine or semivoltine life cycles, respectively). Some insects with the potential to produce multiple generations per year produce a univoltine life cycle in response to environmental conditions. Obligatory univoltine insects have a single long diapause or multiple diapauses in different seasons. Semivoltine insects have multiple diapauses in different years, a prolonged diapause for more than a year, or diapause controlled by a circannual rhythm. Diapause in these insects greatly varies among species both in the physiological mechanism and in the evolutionary background, and there is no general rule defining it. In this review, we survey the physiological control of univoltine and semivoltine insects' diapause and discuss the adaptive significance of the long life cycles. Although constraints such as slow development are sometimes responsible for these life cycles, the benefits of these life cycles can be explained by bet-hedging in many cases. We also discuss the effect of climate warming on these life cycles as a future area of research.

1. INTRODUCTION

Diapause: suspension or retardation of growth or reproduction that is not the direct result of prevailing adverse conditions

Diapause development: physiological processes gradually leading to the end of diapause

Obligatory diapause: diapause inevitably occurring in a genetically fixed developmental stage

Univoltine: one generation per year

Facultative diapause: diapause with plasticity in its induction

Prolonged diapause: diapause the period of which is extended for more than one year

Multivoltine: two or more generations per year

Semivoltine: fewer than one generation per year

Diapause is a state of arrested growth or reproduction that is not controlled by the direct action of environmental factors. In nature, diapause precedes the advent of adverse conditions and plays a predominant role in seasonal adaptations in insects. During diapause, morphogenetic and metabolic activities are usually low, but diapause development proceeds even at low temperatures (2, 16, 17, 71, 133). The induction and termination of diapause are usually controlled by photoperiod, temperature, and other environmental factors; however some insects show obligatory diapause, and diapause sometimes terminates spontaneously without any external stimuli (16, 17, 133).

Diapause can occur at any of the developmental stages and typically occurs at a species-specific stage and during a specific season. Egg (embryonic) and pupal diapause clearly show suspension of morphogenesis with no hatching and no adult emergence, respectively. Adult diapause is characterized by suppression of reproduction, even though diapause adults are sometimes behaviorally active (17, 71, 133). Furthermore, although some diapause larvae show complete suppression of morphogenesis, others undergo stationary ecdysis without growth (9). Larvae of a univoltine moth, *Eurois occulta*, increase their body weight more slowly and have a longer developmental period during shorter days but do not stop feeding (16). Moreover, elongation of the larval period due to photoperiodic conditions is often accompanied by an increase in body size, although only a few studies have determined both the larval duration and the increase in body size versus photoperiod (e.g., 78, 105, 157). In this review, we consider such elongation in addition to the traditional diapause because both elongation of the larval period with growth and larval diapause delay metamorphosis.

The annual number of generations is an important life-history trait because it affects population growth and varies with environmental conditions of the habitat (17, 133). It ranges from 1 in 30 years in a prodoxid moth (103) to 30 or more in a year in aphids (134) and varies even within a population of a species (e.g., 46, 147). Life cycles of insects without diapause generally do not show fixed voltinism because the temperature, with year-to-year differences, affects their developmental time (133). In insects with diapause, however, diapause plays a pivotal role in controlling the annual number of generations. Insects that have obligatory diapause usually also have univoltine life cycles. In contrast, in many insects that have facultative diapause, the annual number of generations is variable; such diapause may have evolved to produce additional generations when the environmental conditions are favorable (17, 133). Furthermore, some insects have life cycles of more than one year with prolonged diapause, showing yearly differences in the life cycle period (18).

Many pest insects that cause serious damage to agriculture or human health show multivoltine life cycles with a potential to increase their density rapidly and have also been the subjects of studies on seasonal adaptations. Most univoltine and semivoltine insects, in contrast, have obligatory diapause, and the control of their life cycles has been regarded as simple in comparison. However, the regulation of diapause intensity and developmental rate exists even in such insects, and we now know that univoltine and semivoltine life cycles have evolved to allow the insects to grow and reproduce in a limited season(s) (17, 133). From the viewpoint of diversity in insect life cycles, we review the control of diapause in univoltine and semivoltine insects and discuss the physiological mechanism and adaptive significance of long life cycles in these insects.

2. FACULTATIVE UNIVOLTINE LIFE CYCLES

2.1. Univoltine Life Cycles Without Diapause

Insects living in extremely cold regions seem to have univoltine life cycles. Examples of such insects include stoneflies growing in the short summer of subarctic regions in Alaska (121) and the Far East (136), although it is unclear whether they have diapause or not. It is possible to acquire cold hardiness without entering diapause (20), and, in fact, adults of the Himalayan midge *Diamesa kohshimai* are active even at –16°C (67). Some insects inhabiting arctic and subarctic regions, e.g., the moth *Gynaephora groenlandica* (70) and the beetle *Dendroides canadensis* (43), seem to lack the capability to enter diapause, and these insects have been believed to have life cycles without diapause (11). However, some arctic midges were shown to have an unknown diapause-like mechanism: Larvae that have matured before winter emerge as adults synchronously every year without further feeding after ponds thaw (19). Moreover, the Antarctic midge, *Belgica antarctica*, which has been thought to remain continuously active when temperatures are permissive, shows a programmed metabolic depression similar to an obligatory diapause (120). A simple question remains whether life cycles with a consistent seasonality are possible without diapause, given that temperature varies among years.

Phenotypic plasticity: capacity of a single genotype to show variable phenotypes in different environments

Long-day response: photoperiodic response in which insects grow and reproduce under long-day conditions

Latitudinal cline: a gradual change along latitudes in a phenotype of adjacent populations of the same species

Quantitative response to photoperiod: photoperiodic response occurring not in an all-or-nothing manner, but instead quantitatively according to the duration of the photophase

2.2. Univoltine Life Cycles with Facultative Diapause

Although insects with a facultative diapause potentially produce two or more generations per year, some of them show univoltine life cycles under natural conditions. In these species, the number of generations is restricted by low temperature or food conditions.

2.2.1. Univoltine life cycles with low-temperature forced diapause.

Insects that are multivoltine in warmer regions sometimes have univoltine life cycles in cooler regions. In most of these species, however, the plasticity in diapause induction has not been completely lost even in cooler regions, although they cannot produce two generations in those regions.

Local populations of a cool region in Russia (60°N) in two noctuid moths, *Viminia rumicis* and *Mamestra brassicae*, which are unlikely to produce a second generation in the field, have phenotypic plasticity: Approximately 70% of individuals avoid pupal diapause under an unnatural, extremely long photoperiod (16). The pierid butterfly *Pieris occidentalis* in subarctic regions of North America has one generation per year but has a facultative pupal diapause of which the induction is controlled by a long-day response. However, all individuals enter diapause under field conditions (109). In the nymphalid butterfly *Polygonia c-album*, there are univoltine and partially bivoltine populations, both with adult diapause. Even in a univoltine population, however, exposure to increasing photoperiods during the larval stage produced nondiapause adults (101). The bruchid beetle *Kytorhinus sharpianus* shows a geographic difference in the photoperiodic response for induction of larval diapause with a latitudinal cline in the critical daylength. Even a univoltine population in northern Japan has phenotypic plasticity in diapause induction, although the photoperiodic response curve is shallower than in multivoltine populations (51, 52). The phenotypic plasticity in these univoltine insects indicates that univoltine populations originate from multivoltine populations in warmer regions. In *P. c-album*, Nylin (101) suggested that the ability to show phenotypic plasticity has a selective value in exceptionally warm years.

The noctuid moth *Cymbalophora pudica* distributed along the Mediterranean coast, is mostly univoltine with summer prepupal diapause and autumn adult emergence. The entry times of diapause vary from spring to early summer. However, fast-growing larvae emerge as adults in spring, resulting in a bivoltine life cycle. The offspring of these adults also enter summer diapause later in the prepupal stage. The intensity of summer diapause is controlled by a quantitative response to photoperiod, particularly a change across or above 14 h that prevails in summer. Consequently, both univoltine and bivoltine fractions uniformly terminate diapause in early autumn (68).

2.2.2. Univoltine life cycles with food-mediated diapause.

Food conditions affect diapause induction and cause some potentially multivoltine insects to have univoltine life cycles (17, 133). In some insects, the offspring of the overwintering generation enter diapause in response to food

Hypermetamorphosis: variant of complete metamorphosis in which some larval instars are distinct from each other

Bet-hedging: a strategy that protects against unpredictably variable environments but results in lower mean fitness by producing different phenotypes in response to the environmental conditions

conditions, resulting in one generation per year. In some of these species, it is evident that food conditions modify the photoperiodic response and thereby affect the timing of diapause induction. The status of the host plant affects the induction of diapause, and the phenology of the host plants affects the life cycle of many phytophagous insects.

Although it has been reported that conditions of poor-quality or scarce food induce diapause, resulting in production of fewer generations per year (17, 133), there are also some examples in which superior food conditions produce univoltine life cycles. The pentatomid bug *Eurydema rugosum* shows a long-day response for induction of adult diapause. Adults do not enter diapause when reared on crucifer leaves in the nymphal stage, whereas they enter diapause when reared on seeds even under a long-day photoperiod (100). In the field, first-generation adults of *E. rugosum* emerged from mid-June, and most of them entered diapause on brown mustard plants that bloomed in early spring, with all of the plants dying by early summer. On cultivated crucifers that have green leaves all year round, however, most adults of the first generation reproduced, and those of the second generation, emerging in late summer, entered diapause (46). Food conditions favoring diapause in *E. rugosum* were not nutritionally inferior based on the performance of nymphs on these host plants. Thus, in *E. rugosum*, the developmental state of the host plants functions as a signal to determine the induction of diapause (46, 100).

A sufficient amount of food causes several potentially bivoltine insects to produce only one generation. Meloid beetles undergo hypermetamorphosis, with an immobile pseudopupal period at a late larval instar as the diapause stage. The pseudopupa has an unusual appearance, with its thick, highly sclerotized cuticle, aborted appendages, and closed mouth and anus. The blister beetle *Epicauta gorhami* has pseudopupal diapause at the fifth instar. This diapause is avoided at high temperatures, but at moderate temperatures, most larvae enter diapause, irrespective of photoperiod, when fed a sufficient amount of grasshopper eggs as food (111). However, when fed a small amount of food or deprived of food before full growth, larvae pupate directly from the fourth instar under a long-day photoperiod, producing an additional generation (113, 135) (**Figure 1**). The longhorn beetle *Monochamus alternatus alternatus* in Taiwan has a facultative larval diapause at the final instar, usually producing one generation per year. When pine bolts inoculated with larvae as hatchlings were abundant, the diapause incidence was higher, suggesting that food shortage has an inhibitory effect on diapause incidence. It was also shown experimentally that, when one bolt harbored two larvae, neither larva entered diapause. Therefore, food availability, together with larval interaction, is responsible for diapause induction, and the diapause-avoiding response is considered adaptive as a means of bet-hedging against unpredictable food conditions (137, 138).

In a polyphagous phytophagous tortricid, *Choristoneura rosaceana*, the incidence of larval diapause differs among host trees. Under both field and laboratory conditions, larvae feeding on chokecherry tend to avoid diapause, whereas those feeding on red maple or black ash tend to enter diapause. Experiments using artificial diets suggested that nutritional quality itself influences diapause induction (44). The whitefly *Trialeurodes lauri* always enters diapause at the fourth nymphal instar in nature and spends nine months in diapause, resulting in a univoltine life cycle. When fed fresh host leaves in the laboratory, however, this diapause is avoided, suggesting that close association with the phenology of the host plant results in the univoltine life cycle of *T. lauri* (26). The leaf beetle *Phratora vulgatissima* in Sweden is univoltine but sometimes produces a second generation in short-rotation coppice willow plantations where coppiced plants grow vigorously. Laboratory experiments indicated that host-plant quality affects the critical daylength for diapause induction. The use of host-plant quality as a diapause-inducing stimulus seems to be adaptive when food resources are unpredictable, such as when new host-plant tissue is produced after a disturbance (15).

In some insects, individuals in a cohort can produce different numbers of generations per year due to individual variation in the body size at a critical time of the season, which is affected by

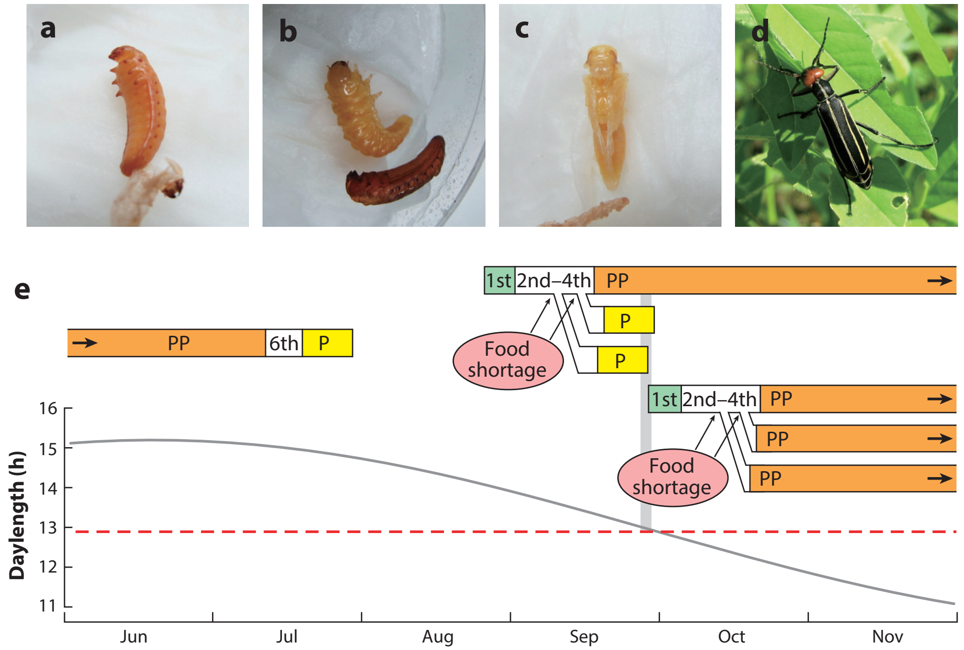

Figure 1

(*a–d*) Photographs of some developmental stages in the blister beetle, *Epicauta gorhami*. Note that the first-instar larva is active, slender, and highly sclerotized, and the shapes of the second to fourth instars (not shown) are similar to that of the sixth instar. (*a*) Pseudopupa. (*b*) Sixth-instar larva with a pseudopupa exuvia at the bottom. (*c*) Pupa. (*d*) Adult. (*e*) Schematic representation of the univoltine and bivoltine life cycles controlled by food quantity in *E. gorhami*, showing hypermetamorphosis (113, 135). P indicates pupae, and PP indicates pseudopupae. The red broken line indicates the estimated critical daylength for photoperiodic response at 25°C under food-deprived conditions. Although most larvae fed a sufficient amount of food enter pseudopupal diapause at the fifth instar, irrespective of photoperiod, those fed a small amount of food or deprived of food before full growth pupate directly from the fourth instar by responding to a long-day photoperiod. The earlier the food shortage is, the earlier the pupation or pseudopupation occurs. Those individuals that precociously metamorphosed to pupae in autumn become small adults, resulting in production of a second generation.

food conditions. Some odonatans in the Temperate Zone have flexible life cycles governed by regulation of nymphal development. These life cycles are classified into several types according to the nymphal response patterns. Regardless of the life cycle types, individuals of the same cohort emerge as adults in different years due to cohort splits based on the size or stage of the individuals at some time of the year (e.g., 13, 99). For example, the damselflies *Coenagrion hastulatum* (98), *Coenagrion puella*, *Ischnura elegans* (102), and *Calopteryx exul* (64) produce one or two generations per year, whereas two other damselflies, *Enallagma aspersum* (47) and *Lestes sponsa* (57), produce one generation per one or two years.

Cohort split: two or more cohorts produced according to whether the critical size or stage is reached before the critical time of the year

2.3. Univoltine Individuals in Principally Multivoltine Insects

In several insects with facultative diapause, conspecific individuals differ in their response to environmental conditions for diapause induction, and as a result, both univoltine and multivoltine life cycles often co-occur within a local population. Examples are found in the nymphalid butterfly *Aglais urticae* (147) and the bark beetle *Ips typographus* (106, 107), in which partial populations are insensitive to environmental cues and enter obligatory diapause. In *I. typographus*, the proportion of facultative and obligatory diapause phenotypes shows geographic variation in Europe. Several parasitoid wasps also show such variation in voltinism in a population, which may function as bet-hedging against unpredictable conditions (e.g., 22, 31).

Short-day response: photoperiodic response in which insects grow and reproduce under short-day conditions

3. OBLIGATORY UNIVOLTINE LIFE CYCLES

3.1. Univoltine Life Cycles with a Single Winter Diapause

Univoltine life cycles with winter diapause have been reported in many insects. These insects enter diapause regardless of the environmental conditions (obligatory diapause), and exposure to low temperatures is prerequisite for termination of the diapause. For example, embryonic diapause in univoltine strains of the domestic silkmoth, *Bombyx mori* (154), and the grasshopper *Austroicetes cruciate* (2); diapause at the pharate first instar in the spongy moth, *Lymantria dispar* (72, 77); and pupal diapause in the cecropia moth, *Hyalophora cecropia* (148), produce univoltine life cycles. Diapause in *L. dispar* lasts from mid-summer to the next spring, but its terminating factor is low temperature, and thus, it is regarded as a long winter diapause (79).

Effective temperature ranges for diapause development vary among species (3, 17, 71, 133). For obligatory embryonic diapause in the leaf beetle *Atrachya menestriesi*, the optimal range for diapause development is 4–10°C, and the diapause development is reversible; repeated exposures to temperatures of 7.5°C and 25°C decrease and increase the intensity of diapause, respectively (1). Contrary to the early view that low temperature is prerequisite for diapause termination, exposure to long days at higher temperatures has been shown to terminate diapause in many species, including univoltine *H. cecropia* (17, 76, 133). In most species whose diapause is controlled by photoperiod, however, the sensitivity to photoperiod is lost after exposure to low temperatures or even due to simple passage of time (17, 41, 132). In these species, diapause development is completed in winter, and postdiapause morphogenesis depends on temperature in a manner governed by the lower developmental threshold and required thermal summation. Low temperature not only terminates winter diapause, but also synchronizes postdiapause activities (41). In the univoltine gall midge *Pseudasphondylia rokuharensis*, synchronized adult emergence after termination of winter diapause in mature larvae, forced by low temperature, is critical because of its short adult longevity of only a few days (139).

In a few univoltine species, however, long spring days play an important role in diapause termination under natural conditions. The green lacewing *Chrysopa downesi* reproduces in spring and enters long diapause in the adult stage until the next spring. Adults retain sensitivity to photoperiod, and diapause is terminated by transfer from a short-day to a long-day photoperiod (131). A similar response was reported in the locust *Nomadacris succincta*, showing a univoltine life cycle with long adult diapause from summer to spring (128). In the univoltine weevil *Pissodes strobi*, with winter adult diapause, a long-day photoperiod increases both the proportion of ovipositing females and the number of eggs laid per female after low temperature treatment (142). In the univoltine cricket *Pteronemobius nitidus*, which overwinters in nymphal diapause at the penultimate instar, an increase in photoperiod accelerates nymphal development. This response reduces the seasonal variation in developmental stages caused by hatching times before overwintering and produces synchronous adult emergence in early summer (125–127).

In univoltine insects in which all individuals enter winter diapause at a specific developmental stage, environmental regulation of growth in another developmental stage plays an important role in their life cycles. Some univoltine insects with obligatory winter diapause show short-day responses that regulate their larval development (56, 78, 115). Such responses allow early developing individuals to become larger adults before winter. Southern populations of the univoltine cricket *Teleogryllus emma*, which overwinters in obligatory egg diapause, elongate the nymphal stage by responding to long days and become larger adults using thermal summation in warmer regions (78).

Recurrent photoperiodic response: photoperiodic response regained by postdiapause reproducing adults that have previously lost the sensitivity to photoperiod

3.2. Univoltine Life Cycles with a Single Summer Diapause

Some insects that grow and reproduce at lower temperatures show univoltine life cycles only with a summer diapause. In the rove beetle *Omalium rivulare* (140) and the leiodid beetle *Catops nigricaas* (141), adults enter obligatory summer diapause, which is terminated by short days at a low temperature. The geometrid moth *Inurois punctigera* shows a univoltine life cycle with pupal summer diapause. In habitats with severe midwinters, two sympatric groups reproduce allochronically in early and late winter, suggesting an incipient speciation process driven by midwinter disruption of the reproductive period (152). A small subtropical cockroach, *Margattea satsuman*, shows a univoltine life cycle with summer diapause at late nymphal instars, which is induced by long days and terminated by transfer to a shorter photoperiod (157).

3.3. Univoltine Life Cycles with Multiple Diapauses

Andrewartha (3) stated that no case is known in which diapause occurs in more than one stage in the same life cycle; however, in the years since, many species have been found to have multiple diapauses in an individual life. **Table 1** shows examples of univoltine insects that have multiple diapauses at different developmental stages in different seasons.

There are some univoltine species that appear to enter a single long diapause but have instead been shown to enter a series of multiple diapauses. The papilionid butterfly *Luehdorfia japonica* in Japan is a typical example. *Luehdorfia japonica* emerge as adults only in spring and remain as pupae until the next spring. Contrary to earlier views that this species has a single winter (32) or summer (45) diapause, Ishii & Hidaka (53, 54) found that there are two diapauses within an apparently single pupal diapause. The first is a summer diapause in an early developmental stage before adult morphogenesis and is terminated by short days at moderate temperatures (53). The second is a winter diapause in the pharate adult stage, in which adult morphogenesis has been completed, and is terminated by low temperatures (54). Therefore, *L. japonica* shows a univoltine life cycle with summer and winter diapauses as pupae. More species may appear to have a single long diapause that actually consists of a series of multiple diapauses.

Winter diapause is terminated by low temperatures, whereas summer diapause is terminated by short days in many insects, including species that show multiple diapauses (**Table 1**). In winter diapause, the onset of growth or reproduction is determined by increasing spring temperatures and, therefore, is synchronous irrespective of the time of diapause induction. In contrast, synchronous onset of growth after summer diapause is achieved by quantitative responses to photoperiod in some species, e.g., the crane fly *Tipula subnodicornis* (8) and the zygaenid moth *Elcysma westwoodii* (27).

3.4. Reproduction Over Multiple Years

As stated above, the sensitivity to photoperiod is lost with progress of diapause development in many insects. In several insects, however, postdiapause adults that have started oviposition in spring regain the sensitivity to photoperiod to allow them to re-enter diapause. The resumption of photoperiodism was first reported in the pentatomid bug *Aelia acuminata* (39) and called the recurrent photoperiodic response (40). In the univoltine carabid beetle *Carabus yaconinus*, some adults that have overwintered and reproduced in spring can survive to subsequent years,

Table 1 List of univoltine insects that have two or more diapauses at different developmental stages in different seasons

Species	Family	Diapause stage	Season	Induction	Termination	Reference(s)
Heteroptera						
Poecilocoris lewisi[a]	Scutelleridae	Fifth (final)-instar nymph	Winter	Short day	Low temperature	130; S.I. Tanaka, unpublished data
		Adult	Summer	Long day	Short day	130
Picromerus bidens	Pentatomidae	Egg	Winter	Obligatory	Low temperature	92
		Adult	Summer	Long day	Spontaneous	92
Coleoptera						
Leptocarabus kumagaii	Carabidae	Third (final)-instar larva	Winter	Short day	Spontaneous	117
		Adult	Summer	Obligatory	Short day	117
Hymenoptera						
Osmia cornuta and *Osmia lignaria*	Megachilidae	Prepupa	Summer	Obligatory	ND	108
		Adult	Winter	ND	ND	108
Eurytoma amygdali	Eurytomidae	Postfeeding larva (before defecation)	Summer	ND	Moderate temperature	143, 144
		Postfeeding larva (after defecation)	Winter	ND	Low temperature	143, 144
Lepidoptera						
Pryeria sinica	Zygaenidae	Egg	Winter	Obligatory	Low temperature	124
		Pupa	Summer	Obligatory	Short day	55
Elcysma westwoodii	Zygaenidae	First-instar larva	Winter	ND	ND	27
		Prepupa	Summer	Obligatory	Short day[b]	27
Luehdorfia japonica	Papilionidae	Pupa (before adult morphogenesis)	Summer	Obligatory	Short day	53
		Pupa (pharate adult)	Winter	Obligatory	Low temperature	54
Antheraea yamamai	Saturniidae	Pharate first-instar larva	Winter	Obligatory	Low temperature	145
		Pupa	Summer	Long day	Short day	62, 63
Dictyoploca japonica	Saturniidae	Egg (embryo)	Winter	ND	ND	145
		Pupa	Summer	Obligatory	Short day	93
Spilarctia imparilis	Arctiinae	Seventh–ninth-instar larva	Winter	Short day	ND	122
		Pupa	Summer	Short day	Long day	65
Syngrapha ottolenguii	Noctuidae	Second–third-instar larva	Winter	Short day	ND	153
		Adult	Summer	Long day	Spontaneous	153
Diptera						
Tipula subnodicornis	Tipulidae	Early instar larva	Winter	Short day	Low temperature	8
		Fourth (final)-instar larva	Summer	ND	Short day[b]	8

[a]This species is partially bivoltine.

[b]This termination is controlled by a quantitative response to photoperiod.

Abbreviation: ND, not determined.

and a recurrent photoperiodic response enables the adults to reproduce over multiple years (112, 116, 118). More insects that potentially have long life spans may show a recurrent photoperiodic response.

For many ant species in temperate and boreal regions, seasonal colony development is regulated by environmental temperature fluctuations, with both adult and larval diapause. Queens reproduce and overwinter several times during their prolonged brooding period. In some of these species, queens spontaneously cease and resume oviposition under constant conditions (59, 66), indicating that an endogenous rhythm controls the cycle of reproduction and diapause in queens and thus the seasonal development of the entire colony, although there is insufficient evidence to conclude that the rhythm is a circannual rhythm (see Section 4.4).

Circannual rhythm: an endogenous biological rhythm with a period of approximately one year

4. SEMIVOLTINE LIFE CYCLES

4.1. Semivoltine Life Cycles with a Single Diapause

The bark beetle *Dendroctonus rufipennis* in Canada has life cycles of one to three years. However, this species has only an obligatory diapause in the prepupal stage. If eggs are laid in a late season or in a cool year, larvae cannot reach the diapause stage before winter, overwinter without diapause, and enter diapause before the next winter. Under such conditions, this species shows a semivoltine life cycle with a single diapause (30).

4.2. Semivoltine Life Cycles with Multiple Diapauses

Some insects show semivoltine life cycles with diapause at two or more developmental stages. Some of them live in cool regions, and others have slow development rate living in warmer regions.

4.2.1. Insects in cool regions. In cool regions at higher latitudes or altitudes, some insects overwinter in diapause twice in the larval stage. In a northern part of Japan, the antlion *Hagenomyia micans* has a two-year life cycle, passing the first winter at the first or second instar and the second winter at the third (final) instar. However, some larvae take three years to mature, overwintering twice at the third instar (24). Larval development at the second instar is controlled by a long-day response, and a change from a short day to a long day is required for pupation (25). These long flexible life cycles seem to be an adaptation to the scarcity and unpredictability of food resources as ambush predators.

The cockroach *Periplaneta japonica* in northern Japan also shows a two-year life cycle, overwintering twice as diapause nymphs. Both the early diapause at younger instars and the late diapause at the final instar are controlled by a long-day response, with high temperature preventing diapause. Younger-instar nymphs enter early diapause under conditions of shorter daylengths and lower temperatures (110).

Burnet moths, *Zygaena* spp., in Europe show bivoltine, univoltine, or semivoltine life cycles with repeated diapause at various larval instars. For example, *Zygaena trifolii* in central Germany has one- to three-year life cycles. Larvae enter diapause irrespective of photoperiod, and diapause occurs at the third or any subsequent larval instar. Short days induce diapause at earlier instars, and larvae enter diapause at different instars even under the same conditions (150).

Ringlet butterflies, *Erebia* spp., in the European alpine zone comprise both univoltine and semivoltine species. The latter species enter obligatory diapause and overwinter twice as larvae, i.e., at the first or second instar and at the fourth (penultimate) instar. Long-term collection records of adult *Erebia* in Switzerland and Austria (1918–1990) showed that almost all of the 12 species with two-year life cycles flew as adults significantly more in odd than in even years. A field observation also supported this alternate-year flight activity. This activity pattern has been suggested to be a strategy to decrease mortality by parasitoid wasps, which probably cannot adapt to alternate-year activity (151).

Embryos of some katydids show diapause at two stages, i.e., initial diapause just after blastoderm formation and final diapause shortly before hatching. Ingrisch (48) examined the effect of temperature on embryonic development in 21 katydid species in Europe and found that there are three types of life cycles: a univoltine life cycle without initial diapause, a mixture of one- and two-year life cycles with facultative initial diapause, and a semivoltine life cycle of two or more years with a prolonged initial diapause. In northern and alpine regions of Japan, *Eobiana japonica* requires two or more years to complete its life cycle. Eggs remain in initial diapause for one to three years and in final diapause for one more year (35). The intensity of initial diapause varies, and repeated exposure to alternating low and high temperatures effectively terminates it (36).

4.2.2. Insects with slow development. Even in warm regions, insects with slow development show semivoltine life cycles. The cockroach *Symploce japonica* living in a forest in a subtropical island in Japan shows a two-year life cycle with three diapauses, i.e., winter diapause at midnymphal instars, summer diapause at later nymphal instars, and winter diapause in the adult stage, all of which are controlled by photoperiod (129). In the cricket *Gryllus argenteus* in a tropical arid highland in Malawi, both the number of nymphal instars and the duration of nymphal stages increase under short days. Based on the long-day response and the high lower threshold temperature for nymphal development of approximately 20°C, it is assumed that this cricket developed a three-year life cycle to adapt to the local climate, which has a long dry season lasting half the year (69).

Cicadas require an extremely long time to complete nymphal development, ranging from 2 to 17 years (114). Nymphs and adults feed exclusively on xylem fluid containing low concentrations of amino acids and only traces of carbohydrates. The low growth rate limited by this low nutritional condition and the cicadas' large body sizes result in long life cycles (60).

In particular, the life cycles of periodical cicadas, *Magicicada* spp., in North America have attracted the attention of researchers. Adults emerge synchronously within several days of every thirteenth or seventeenth year. It is unique to periodical cicadas that, in any one population of emerging adults, almost all are exactly the same age; in contrast, in nonperiodical cicadas, adults of various ages emerge together every year. Although the evolutionary background of this extreme synchrony and these cicadas' slow development has been intensively discussed, their physiological mechanisms are poorly understood (114, 149). Although it is unclear whether all overwintering nymphs are in diapause, a physiological mechanism must precisely regulate the nymphal duration. A field collection of nymphs in the 17-year periodical cicada *Magicicada septendecim*, over a 17-year period, showed that this species does not achieve synchronization by having uniform nymphal growth rates; instead, the cicada compensates for unequal growth rates (75). A physiological mechanism must count the years and precisely regulate the nymphal duration, and it seems probable that nymphs reaching the final instar earlier wait for slower ones to catch up before emerging as adults (114). In Karban et al.'s (61) study of a 17-year periodical cicada *Magicicada* sp., exposure of potted host trees with 15-year-old nymphs to cyclic changes in temperature and photoperiod, of which the period was half a year, resulted in both flowering of the host tree twice a year and earlier emergence of some cicada adults. Although Karban et al. concluded that the cicada keeps the nymphal development time stable by counting host seasonal cycles, it is also possible that nymphs directly respond to environmental cycles.

4.3. Prolonged Diapause

Some insects enter prolonged diapause and show semivoltine life cycles. The list of insects with prolonged diapause compiled by Danks (17) includes more than 145 species in 7 orders and examples of diapause in egg, larval, pupal, and adult stages. Prolonged diapause can evolve only when its benefit exceeds the costs of mortality, loss of metabolic resources, and loss of reproductive opportunity. The benefit has been explained by bet-hedging (85, 123). In most cases, only a fraction of individuals in a population remain in diapause for two or more years, showing polymorphism in adult emergence years within the same population.

Yukawa & Uechi (156) listed 14 gall midges that show such polymorphic adult emergence; six of them enter diapause at the first instar within the gall, whereas the other eight enter diapause at the third (final) instar on the ground after the gall drops or after they leave the gall. Sunose (123) explained that the prolonged diapause in the gall midge *Hasegawaia sasacola* serves to avoid mortality of the univoltine fraction of a population during a catastrophic shortage of food supply caused by mast-flowering of its host bamboo. Based on counts of catastrophic events during 18-year field surveys, Yukawa et al. (155) concluded that the prolonged diapause in another gall midge, *Illiciomyia yukawai*, provides an ecological advantage in surviving catastrophic events such as a serious shortage of host buds available for oviposition, a high percentage of parasitism, or an extremely low survival rate of host leaves.

Insects feeding on tree seeds often show prolonged diapause because seed production in many temperate trees varies among years. For example, postfeeding fourth (final)-instar larvae of the seed-feeding weevil *Curculio elephas*, which feeds on seeds of the European chestnut and acorns in France, enter an obligatory winter diapause for one to three years underground. This variability in life cycle duration has been regarded as an adaptation to yearly and unpredictable variability in masting of host plants (83). In heavier larvae and larvae egressing from the host fruit later, the proportion of prolonged diapause was higher. Because heavier larvae possess enough metabolic resources, and later larvae have a shorter time in which to consume such resources before winter, the proportion of prolonged diapause can be explained in relation to the loss of metabolic resources as the cost of diapause (84). Regarding variability of diapause duration, it is not easy to discriminate among a mixed evolutionarily stable strategy (ESS), a stable genetic polymorphism of pure strategies, and bet-hedging by a genetically single population. If long-cycle individuals compensate for this cost with better adult performance, then the compensation leads to a trade-off that could result in a mixed ESS or a genetic polymorphism. In *C. elephas*, however, adult performance was similar between individuals emerging after one and two years (83, 119). Therefore, the bet-hedging strategy is plausible because the cost associated with prolonged diapause cannot be completely compensated for by better adult performance (85, 119).

Similar life cycles were shown in three congeneric species feeding on oak seeds in Japan (74). In *Curculio sikkimensis*, diapause is terminated by low temperatures, as in many insects, but the large variation of this response produces one- to three-year life cycles (33). Repeated exposure to alternations of a low temperature of 5°C and a moderate temperature of 20°C accelerated diapause termination (34), as in the initial diapause of *E. japonica* (see Section 4.2.1). Moreover, the diapause intensity can be reversibly decreased by a low temperature and increased by a high temperature of 25°C (37, 38). Higaki & Toyama (38) suggested that this reversible change in diapause intensity prevents untimely completion of diapause before winter and assures a second overwintering.

Another seed-feeding weevil, *Exechesops leucopis*, also enters an obligatory winter diapause as postfeeding fourth (final)-instar larvae but does so within the seeds of host trees. The duration of diapause varies from one to four years, and adults emerging after one year are smaller than those emerging after two or more years. In contrast, adult body sizes were reduced by artificial elongation of diapause for an additional year. Therefore, the cost of diapause, i.e., loss of metabolic resources, restricts prolonged diapause in well-nourished larvae (82).

In the fruit fly *Rhagoletis cerasi*, adults after prolonged pupal diapause had lower lifetime fecundity than adults emerging within one year, and it is therefore likely that the prolonged diapause

Entrainment: coupling of a biological rhythm to an environmental cycle such that they have the same period and a stable phase relationship

Climate warming: long-term increase in temperatures; since the 1800s, human activities have been the main driver

evolved as a bet-hedging strategy (88, 90). Moreover, exposure to a low temperature terminates prolonged diapause, but if the exposure is continued, pupae return to diapause (89).

Prolonged initial diapause in embryos of katydids was pointed out as a strategy to overcome seasonally unpredictable adverse conditions, such as extreme drought, fire, depletion of food, and extraordinarily cool years (36, 49).

The longest diapause reported to date is 30 years in the prodoxid moth *Prodoxus y-inversus*, a specialist feeder on yucca and agave in desert areas of North America. Full-grown larvae enter diapause, the duration of which varies from 1 to 30 years. The life cycle of this species is closely synchronized with the development of inflorescences of the host plants, which vary in abundance depending on seasonal climatic conditions (103).

4.4. Regulation by Circannual Rhythm

The circannual rhythm regulates the seasonal life cycles of some organisms and has been reported mostly in hibernating mammals and migratory birds (29). In insects, Blake (7) first pointed out that an endogenous rhythm regulates the life cycle of the varied carpet beetle, *Anthrenus verbasci*. The pupation of *A. verbasci* showed a rhythmic pattern under both naturally fluctuating conditions and constant conditions in the laboratory. The larval ecdysis also showed a rhythmic pattern and occurred in restricted periods, and the period without ecdysis was regarded as larval diapause (7). It was later confirmed that the pupation in *A. verbasci* is controlled by a circannual rhythm: The rhythmic pupation shows the three major characteristics of biological rhythms, i.e., self-sustainability, temperature compensation in the period, and entrainment to an environmental cycle (96, 97). The life cycle of *A. verbasci* of one to a few years and the synchronous pupation in spring were explained by entrainment of the circannual rhythm to natural changes in photoperiod and the suppression of pupation by low temperatures in winter (86, 87, 97) (**Figure 2**).

The congeneric beetle *Anthrenus sarnicus* (4, 12) and the moth *Cossus insularis* (95) show similar pupation patterns to that of *A. verbasci* at constant temperatures in the laboratory. Because it takes a long time to show evidence of a circannual rhythm clearly, further research may show that many more insects with semivoltine life cycles possess this mechanism.

5. EFFECTS OF CLIMATE WARMING

Climate warming will prolong growing seasons; increase the effective cumulative temperature and developmental rate in most insects; and cause the loss of seasonal interaction between the predominant diapause-inducing factors, i.e., temperature and photoperiod (23, 28). In univoltine and semivoltine insects without diapause, climate warming may increase the number of generations per year. In univoltine insects with facultative diapause, it may also increase the number of generations per year because photoperiodic induction of diapause in such insects is mostly temperature dependent, and higher temperatures often hinder diapause induction.

The pentatomid bug *Dybowskyia reticulata* shows a temperature-dependent long-day response for the induction of adult diapause: Under a long-day photoperiod, adults enter diapause at 20°C or 25°C but not at 27.5°C or 30°C. In central Japan, the species showed a univoltine life cycle with long winter diapause in 1993, a relatively cool year, whereas a higher percentage of adults produced a second generation in warmer 1996 (94). In such insects, climate warming will definitely increase the proportion of bivoltine life cycles. Another insect species in which the number of generations has been increased by climate warming is the pyrrhocorid bug *Pyrrhocoris apterus*, which has facultative adult diapause. Although this species has typically been univoltine in the Czech Republic, climate warming will create conditions that facilitate the occurrence of a second generation in a year (42). Such increases in the number of generations per year by climate warming have been

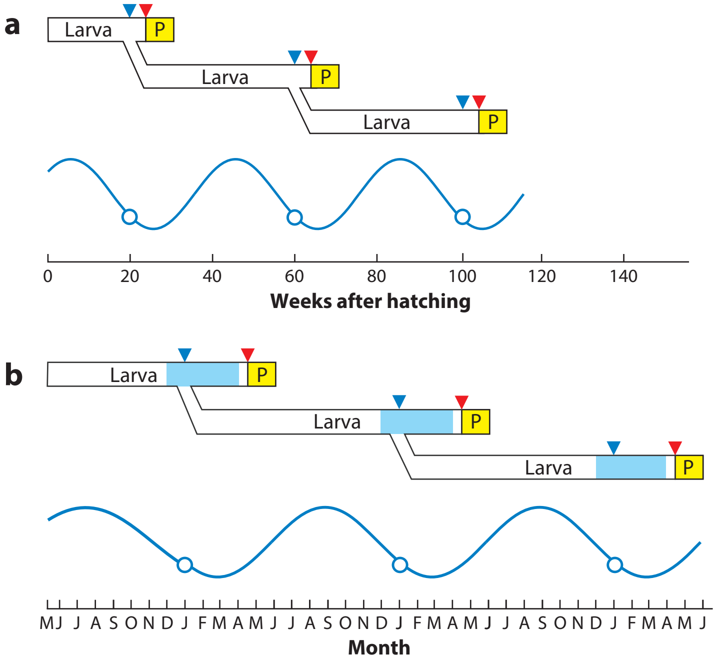

Figure 2

Schematic representation of the life cycle controlled by a circannual rhythm in the varied carpet beetle, *Anthrenus verbasci* (86, 87, 97). The blue sine curve indicates expected phase changes in the circannual rhythm. The blue circle and triangle indicate the opening of the gate for pupation. The red triangle indicates pupation. P indicates pupa, adult, and egg stages. The light-blue bar indicates suppression of pupation by low temperatures. (*a*) Under constant conditions of light–dark cycles with 12 h of light and 12 h of darkness at 20°C, the circannual rhythm oscillates with its endogenous period of approximately 40 weeks, and after opening of the gate for pupation, pupation occurs approximately 25, 65, and 105 weeks after hatching. (*b*) Under natural conditions, the circannual rhythm is entrained to the natural changes in photoperiod, and the period is exactly one year. After opening of the gate for pupation, low temperatures in winter suppress pupation, and pupation occurs in April every year.

reported or predicted to occur in other commonly univoltine insects with facultative diapause, e.g., the bark beetle *I. typographus* in northern Europe (58) and the leaf beetle *P. vulgatissima* (14) and the pine moth *Dendrolimus spectabilis* (10) in South Korea.

In addition to such plasticity in diapause induction, genetic shifts in life-history traits may also occur in response to climate warming. For example, in the cricket *Polionemobius mikado*, which has a wide latitudinal range with univoltine and bivoltine life cycles, a univoltine life cycle has been replaced with a bivoltine life cycle in the southernmost range of the univoltine life cycle over the past 40 years (81). In another cricket, *Dianemobius nigrofasciatus*, with similar life cycles, however, the boundary of univoltine and bivoltine life cycles has not changed over the same period (80).

In univoltine and semivoltine insects with obligatory diapause, however, the effects of temperature increase cannot be generalized because the mechanism(s) controlling their life cycles are different among the species: In some univoltine insects, the combination of longer summer and warmer winter may delay the onset of morphogenesis in spring due to insufficient winter chilling for diapause termination (5, 73). Furthermore, phenological asynchrony between the insects and seasonally limited resources is predicted to occur often due to heterogeneity in their responses to climate change, and consequently, population decline occurs (e.g., 6, 21, 146). In contrast, phenological advancement due to climate warming directly increases fitness in the cicada *Cryptotympana facialis* because advancement of hatching time into rainy seasons enhances the hatching success of postdiapause embryos (91).

Larvae of the moth *Thaumetopoea pityocampa* feed on pines and cedars in winter, pupate in spring, and emerge as adults in summer in the Mediterranean region. A fraction of pupae enter a prolonged diapause, producing life cycles from one to a few years. At both the lower and upper ends of the thermal range in winter, the incidence of prolonged diapause was higher than at intermediate temperatures (104). Salman et al. (104) suggested that climate warming will reduce and increase the incidence of prolonged diapause in this species in colder and warmer regions, respectively.

6. CONCLUSION

In general, it is more adaptive to produce additional generations than to have longer life cycles. Nevertheless, many insect species have evolved univoltine and semivoltine life cycles, as discussed above. Because both the ultimate and proximate factors for univoltine and semivoltine life cycles vary among species, it is not easy to summarize the whole overview of these life cycles. However, the ecological significance can be mostly categorized into two types. The first is adaptation to short periods suitable for growth and reproduction restricted by cooler climate, occurrence of dry seasons, or food availability. The second is bet-hedging for catastrophic events mostly produced by the life cycle of host plants. The physiological mechanisms producing long life cycles are various: a single long diapause for approximately one year, multiple diapauses at different developmental stages for different seasons or different years, prolonged diapause for more than a year, and a circannual rhythm. Because it is unequivocal that human influence has warmed the atmosphere, ocean, and land, and still continues to do so (50), how univoltine and semivoltine life cycles in insects are affected by climate warming is an important subject for future studies.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Elizabeth Nakajima for linguistic corrections.

LITERATURE CITED

1. Ando Y. 1983. Diapause and geographic variation in a leaf beetle. In *Diapause and Life Cycle Strategies in Insects*, ed. VK Brown, I Hodek, pp. 127–141. The Hague: Dr. W. Junk Publ.
2. Andrewartha HG. 1943. Diapause in the eggs of *Austroicetes cruciata*, Sauss. (Acrididae) with particular reference to the influence of temperature on the elimination of diapause. *Bull. Entomol. Res.* 34:1–17
3. Andrewartha HG. 1952. Diapause in relation to the ecology of insects. *Biol. Rev.* 27:50–107
4. Armes NJ. 1990. The biology of *Anthrenus sarnicus* Mroczkowski (Coleoptera: Dermestidae): I. Egg and larval development. *J. Stored Prod. Res.* 26:11–22
5. Bale JS, Hayward SAL. 2010. Insect overwintering in a changing climate. *J. Exp. Biol.* 213:980–94
6. Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.* 8:1–16
7. Blake GM. 1958. Diapause and the regulation of development in *Anthrenus verbasci* (L.) (Col., Dermestidae). *Bull. Entomol. Res.* 49:751–75
8. Butterfield J. 1976. Effect of photoperiod on a winter and on a summer diapause in two species of cranefly (Tiplidae). *J. Insect Physiol.* 22:1443–46

9. Chippendale GM, Yin C-M. 1973. Endocrine activity retained in diapause insect larvae. *Nature* 246:511–12
10. Choi WI, Park YK, Park YS, Ryoo MI, Lee HP. 2011. Changes in voltinism in a pine moth *Dendrolimus spectabilis* (Lepidoptera: Lasiocampidae) population: implications of climate change. *Appl. Entomol. Zool.* 46:319–25
11. Convey P. 2010. Life-history adaptations to polar and alpine environments. In *Low Temperature Biology of Insects*, ed. DL Denlinger, RE Lee, pp. 297–321. Cambridge, UK: Cambridge Univ. Press
12. Coombs CW, Woodroffe GE. 1983. The effect of temperature upon the longevity, fecundity and circannual development of *Anthrenus sarnicus* Mroczkowski (Coleoptera: Dermestidae). *J. Stored Prod. Res.* 19:111–15
13. Corbet PS. 2002. Stadia and growth ratios of Odonata: a review. *Int. J. Odonatol.* 5:45–73
14. Dalin P. 2011. Diapause induction and termination in a commonly univoltine leaf beetle (*Phratora vulgatissima*). *Insect Sci.* 18:443–50
15. Dalin P, Nylin S. 2012. Host-plant quality adaptively affects the diapause threshold: evidence from leaf beetles in willow plantations. *Ecol. Entomol.* 37:490–99
16. Danilevskii AS. 1961. *Photoperiodism and Seasonal Development of Insects*. Leningrad, USSR: Leningrad State Univ. (in Russian)
17. Danks HV. 1987. *Insect Dormancy: An Ecological Perspective*. Ottawa: Biol. Surv. Can.
18. Danks HV. 1992. Long life cycles in insects. *Can. Entomol.* 124:167–87
19. Danks HV, Oliver DR. 1972. Seasonal emergence of some high arctic Chironomidae (Diptera). *Can. Entomol.* 104:661–86
20. Denlinger DL. 1991. Relationship between cold hardiness and diapause. In *Insects at Low Temperature*, ed. RE Lee, DL Denlinger, pp. 174–98. New York: Chapman & Hall
21. Dewar RC, Watt AD. 1992. Predicted changes in the synchrony of larval emergence and budburst under climatic warming. *Oecologia* 89:557–59
22. Evans EW. 2021. Partial bivoltinism in a gregarious endoparasitoid: larval diapause as influenced by season and sharing a host. *Entomol. Exp. Appl.* 169:145–53
23. Forrest JR. 2016. Complex responses of insect phenology to climate change. *Curr. Opin. Insect Sci.* 17:49–54
24. Furunishi S, Masaki S. 1982. Seasonal life cycle in two species of ant-lion (Neuropteran: Myrmeleontidae). *Jpn. J. Ecol.* 32:7–13
25. Furunishi S, Masaki S. 1983. Photoperiodic control of development in the ant-lion *Hagenomyia micans* (Neuropteran: Myrmeleontidae). *Entomol. Gen.* 9:51–62
26. Gerling D, Guershon M, Erel E, Inbar M. 2011. Diapause and its regulation in the whitefly *Trialeurodes lauri*. *Bull. Entomol. Res.* 101:741–47
27. Gomi T, Takeda M. 1992. A quantitative photoperiodic response terminates summer diapause in the tailed zygaenid moth, *Elcysma westwoodii*. *J. Insect Physiol.* 38:665–70
28. Grevstad FS, Coop LB. 2015. The consequences of photoperiodism for organisms in new climates. *Ecol. Appl.* 25:1506–17
29. Gwinner E. 1986. *Circannual Rhythms*. Berlin: Springer
30. Hansen EM, Bentz BJ, Turner DL. 2001. Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). *Can. Entomol.* 133:805–17
31. He XZ, Wang Q, Walker JT, Rogers DJ, Lo PL. 2010. A sophisticated life history strategy in a parasitoid wasp: producing univoltine and multivoltine phenotypes in a local population. *Biol. Control* 54:276–84
32. Hidaka T, Ishizuka Y, Sakagami Y. 1971. Control of pupal diapause and adult differentiation in a univoltine papilionid butterfly, *Luehdorfia japonica*. *J. Insect Physiol.* 17:197–203
33. Higaki M. 2005. Effect of temperature on the termination of prolonged larval diapause in the chestnut weevil *Curculio sikkimensis* (Coleoptera: Curculionidae). *J. Insect Physiol.* 51:1352–58
34. Higaki M. 2006. Repeated cycles of chilling and warming effectively terminate prolonged larval diapause in the chestnut weevil *Curculio sikkimensis*. *J. Insect Physiol.* 52:514–19
35. Higaki M, Ando Y. 1999. Seasonal and altitudinal adaptations in three katydid species: ecological significance of initial diapause. *Entomol. Sci.* 2:1–11

36. Higaki M, Ando Y. 2000. Effect of temperature on the termination of prolonged initial diapause in *Eobiana japonica* (Bolivar) (Orthoptera: Tettigoniidae). *Entomol. Sci.* 3:219–26
37. Higaki M, Ihara F, Toyama M, Mishiro K. 2010. Thermal response and reversibility of prolonged larval diapause in the chestnut weevil, *Curculio sikkimensis*. *J. Insect Physiol.* 56:616–21
38. Higaki M, Toyama M. 2012. Evidence for reversible change in intensity of prolonged diapause in the chestnut weevil, *Curculio sikkimensis*. *J. Insect Physiol.* 58:56–60
39. Hodek I. 1971. Sensitivity to photoperiod in *Aelia acuminata* (L.) after adult diapause. *Oecologia* 6:152–55
40. Hodek I. 1979. Intermittent character of adult diapause in *Aelia acuminata* (Heteroptera). *J. Insect Physiol.* 25:867–71
41. Hodek I, Hodková M. 1988. Multiple role of temperature during insect diapause: a review. *Entomol. Exp. Appl.* 49:153–65
42. Honek A, Martinkova Z, Pekár S. 2020. How climate change affects the occurrence of a second generation in the univoltine *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *Ecol. Entomol.* 45:1172–79
43. Horwath KL, Duman JG. 1983. Photoperiodic and thermal regulation of antifreeze protein levels in the beetle *Dendroides canadensis*. *J. Insect Physiol.* 29:907–17
44. Hunter MD, McNeil JN. 1997. Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. *Ecology* 78:977–86
45. Ichikawa M, Nishiitsutsuji-Uwo J, Yashika K. 1956. Studies on the insect metamorphosis VI. Effect of low temperature on the morphogenesis of *Luehdorfia*-pupae. *Mem. Coll. Sci. Univ. Kyoto B* 23:19–26
46. Ikeda-Kikue K, Numata H. 2001. Timing of diapause induction in the cabbage bug *Eurydema rugosum* (Heteroptera: Pentatomidae) on different host plants. *Acta Soc. Zool. Bohem.* 65:197–205
47. Ingram BR, Jenner CE. 1976. Life histories of *Enallagma hageni* (Walsh) and *E. aspersum* (Hagen) (Zygoptera: Coenagrionidae). *Odonatologica* 5:331–45
48. Ingrisch S. 1986. The plurennial life cycles of the European Tettigoniidae (Insecta: Orthoptera). 1. The effect of temperature on embryonic development and hatching. *Oecologia* 70:606–16
49. Ingrisch S. 1986. The plurennial life cycles of the European Tettigoniidae (Insecta: Orthoptera). 3. The effect of drought and the variable duration of the initial diapause. *Oecologia* 70:624–30
50. IPCC (Intergov. Panel Clim. Change). 2021. *Climate change 2021: the physical science basis*. Rep., IPCC, Geneva. **https://www.ipcc.ch/report/sixth-assessment-report-working-group-i/**
51. Ishihara M. 1999. Adaptive phenotypic plasticity and its difference between univoltine and multivoltine populations in a bruchid beetle, *Kytorhinus sharpianus*. *Evolution* 53:1979–86
52. Ishihara M, Shimada M. 1999. Geographical variation in photoperiodic response for diapause induction between univoltine and multivoltine populations of *Kytorhinus sharpianus* (Coleoptera: Bruchidae). *Environ. Entomol.* 28:195–200
53. Ishii M, Hidaka T. 1982. Characteristics of pupal diapause in the univoltine papilionid, *Luehdorfia japonica* (Lepidoptera: Papilionidae). *Kontyû* 50:610–20
54. Ishii M, Hidaka T. 1983. The second pupal diapause in the univoltine papilionid, *Luehdorfia japonica* (Lepidoptera: Papilionidae) and its terminating factor. *Appl. Entomol. Zool.* 18:456–63
55. Ishii M, Johki Y, Hidaka T. 1983. Studies on summer diapause in zygaenid moths (Lepidoptera, Zygaenidae): I. Factors affecting the pupal diapause in *Pryeria sinica*. *Kontyû* 51:122–27
56. Johansson F, Rowe L. 1999. Life history and behavioral responses to time constraints in a damselfly. *Ecology* 80:1242–52
57. Johansson F, Stoks R, Rowe L, De Block M. 2001. Life history plasticity in a damselfly: effects of combined time and biotic constraints. *Ecology* 82:1857–69
58. Jönsson AM, Appelberg G, Harding S, Bärring L. 2009. Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, *Ips typographus*. *Glob. Change Biol.* 15:486–99
59. Kamitani S, Asakura K, Nakamura K. 2015. Effects of environmental factors on life cycle regulation in *Lasius japonicus* Santschi (Formicidae). *Sociobiology* 62:467–73
60. Karban R. 1986. Prolonged development in cicadas. In *The Evolution of Insect Life Cycles*, ed. F Taylor, R Karban, pp. 222–35. Berlin: Springer
61. Karban R, Black CA, Weinbaum SA. 2000. How 17-year cicadas keep track of time. *Ecol. Lett.* 3:253–56
62. Kato Y, Sakate S. 1981. Studies on summer diapause in pupae of *Antheraea yamamai* (Lepidoptera: Saturniidae): III. Influence of photoperiod in the larval stage. *Appl. Entomol. Zool.* 16:499–500

63. Kato Y, Yamauchi M, Katsu Y, Sakate S. 1979. Studies on summer diapause in pupae of *Antheraea yamamai* (Lepidoptera: Saturniidae): I. Shortening of the "pupal" duration under certain environmental conditions. *Appl. Entomol. Zool.* 14:389–96
64. Khelifa R. 2017. Partial bivoltinism and emergence patterns in the North African endemic damselfly *Calopteryx exul*: conservation implications. *Afr. J. Ecol.* 55:145–51
65. Kimura T, Takano H, Masaki S. 1982. Photoperiodic programming of summer diapause after hibernation in *Spilarctia imparilis* Butler (Lepidoptera: Arctiidae). *Appl. Entomol. Zool.* 17:218–26
66. Kipyatkov VE. 2001. Seasonal life cycles and the forms of dormancy in ants (Hymenoptera: Formicoidea). *Acta Soc. Zool. Bohem.* 65:211–38
67. Kohshima S. 1984. A novel cold-tolerant insect found in a Himalayan glacier. *Nature* 310:225–27
68. Košťál V, Hodek I. 1997. Photoperiodism and control of summer diapause in the Mediterranean tiger moth *Cymbalophora pudica*. *J. Insect Physiol.* 43:767–77
69. Kosumi T, Takeda M. 2017. Three-year lifecycle, large body, and very high threshold temperature in the cricket *Gryllus argenteus* for special adaptation to desiccation cycle in Malawi. *Sci. Nat.* 104:70
70. Kukal O, Duman JG, Serianni AS. 1989. Cold-induced mitochondrial degradation and cryoprotectant synthesis in freeze-tolerant arctic caterpillars. *J. Comp. Physiol. B* 158:661–71
71. Lees AD. 1955. *The Physiology of Diapause in Arthropods*. Cambridge, UK: Cambridge Univ. Press
72. Leonard DE. 1968. Diapause in the gypsy moth. *J. Econ. Entomol.* 61:596–98
73. Ma CS, Ma G, Pincebourde S. 2021. Survive a warming climate: insect responses to extreme high temperatures. *Annu. Rev. Entomol.* 66:163–84
74. Maeto K, Ozaki K. 2003. Prolonged diapause of specialist seed-feeders makes predator satiation unstable in masting of *Quercus crispula*. *Oecologia* 137:392–98
75. Maier CT. 1996. Connecticut is awaiting the return of the periodical cicada. *Front. Plant Sci.* 48:4–6
76. Mansingh A, Smallman BN. 1966. Photoperiod control of an "obligatory" pupal diapause. *Can. Entomol.* 98:613–16
77. Masaki S. 1956. The effect of temperature on the termination of diapause in the egg of *Lymantria dispar* Linné (Lepidoptera: Lymantriidae). *Jpn. J. Appl. Zool.* 21:148–57
78. Masaki S. 1967. Geographic variation and climatic adaptation in a field cricket (Orthoptera: Gryllidae). *Evolution* 21:725–41
79. Masaki S. 1980. Summer diapause. *Annu. Rev. Entomol.* 25:1–25
80. Matsuda N, Fujita S, Tanaka K, Watari Y, Shintani Y, et al. 2019. Robustness of latitudinal life-cycle variations in a cricket *Dianemobius nigrofasciatus* (Orthoptera: Trigonidiidae) in Japan against climate warming over the last five decades. *Appl. Entomol. Zool.* 54:349–57
81. Matsuda N, Tanaka K, Watari Y, Shintani Y, Goto SG, et al. 2018. Northward expansion of the bivoltine life cycle of the cricket over the last four decades. *Glob. Change Biol.* 24:5622–28
82. Matsuo Y. 2006. Cost of prolonged diapause and its relationship to body size in a seed predator. *Funct. Ecol.* 20:300–6
83. Menu F, Debouzie D. 1993. Coin-flipping plasticity and prolonged diapause in insects: example of the chestnut weevil *Curculio elephas* (Coleoptera: Curculionidae). *Oecologia* 93:367–73
84. Menu F, Desouhant E. 2002. Bet-hedging for variability in life cycle duration: Bigger and later-emerging chestnut weevils have increased probability of a prolonged diapause. *Oecologia* 132:167–74
85. Menu F, Roebuck J-P, Viala M. 2000. Bet-hedging diapause strategies in stochastic environments. *Am. Nat.* 155:724–34
86. Miyazaki Y, Nisimura T, Numata H. 2006. Phase responses in the circannual rhythm of the varied carpet beetle, *Anthrenus verbasci*, under naturally changing day length. *Zool. Sci.* 23:1031–37
87. Miyazaki Y, Nisimura T, Numata H. 2009. Circannual pupation rhythm in the varied carpet beetle *Anthrenus verbasci* under different nutrient conditions. *Entomol. Sci.* 12:370–75
88. Moraiti CA, Nakas CT, Papadopoulos NT. 2012. Prolonged pupal dormancy is associated with significant fitness cost for adults of *Rhagoletis cerasi* (Diptera: Tephritidae). *J. Insect Physiol.* 58:1128–35
89. Moraiti CA, Nakas CT, Papadopoulos NT. 2014. Diapause termination of *Rhagoletis cerasi* pupae is regulated by local adaptation and phenotypic plasticity: escape in time through bet-hedging strategies. *J. Evol. Biol.* 27:43–54

90. Moraiti CA, Papadopoulos NT. 2017. Obligate annual and successive facultative diapause establish a bet-hedging strategy of *Rhagoletis cerasi* (Diptera: Tephritidae) in seasonally unpredictable environments. *Physiol. Entomol.* 42:225–31
91. Moriyama M, Numata H. 2011. A cicada that ensures its fitness during climate warming by synchronizing its hatching time with the rainy season. *Zool. Sci.* 28:875–81
92. Musolin DL, Saulich AH. 2000. Summer dormancy ensures univoltinism in the predatory bug *Picromerus bidens*. *Entomol. Exp. Appl.* 95:259–67
93. Nagase A, Masaki S. 1991. Thermal and photoperiodic responses in aestivating pupae of *Dictyoploca japonica* (Lepidoptera: Saturniidae). *Appl. Entomol. Zool.* 26:387–96
94. Nakamura K, Numata H. 1998. Alternative life cycles controlled by temperature and photoperiod in the oligophagous bug, *Dybowskyia reticulata*. *Physiol. Entomol.* 23:69–74
95. Nakanishi T, Kaneda T, Nakamuta K. 2017. Effects of temperature on the development and circannual control of pupation in the carpenter moth, *Cossus insularis* (Lepidoptera: Cossidae), reared on an artificial diet. *Appl. Entomol. Zool.* 52:29–35
96. Nisimura T, Numata H. 2001. Endogenous timing mechanism controlling the circannual pupation rhythm of the varied carpet beetle *Anthrenus verbasci*. *J. Comp. Physiol. A* 187:433–40
97. Nisimura T, Numata H. 2003. Circannual control of the life cycle in the varied carpet beetle *Anthrenus verbasci*. *Funct. Ecol.* 17:489–95
98. Norling U. 1984. The life cycle and larval photoperiodic responses of *Coenagrion hastulatum* (Charpentier) in two climatically different areas (Zygoptera: Coenagrionidae). *Odonatologica* 13:429–49
99. Norling U. 2021. Growth, winter preparations and timing of emergence in temperate zone Odonata: control by a succession of larval response patterns. *Int. J. Odonatol.* 24:1–36
100. Numata H, Yamamoto K. 1990. Feeding on seeds induces diapause in the cabbage bug, *Eurydema rugosa*. *Entomol. Exp. Appl.* 57:281–84
101. Nylin S. 1989. Effects of changing photoperiods in the life cycle regulation of the comma butterfly, *Polygonia c-album* (Nymphalidae). *Ecol. Entomol.* 14:209–18
102. Parr MJ. 1970. The life histories of *Ischnura elegans* (van der Linden) and *Coenagrion puella* (L.) (Odonata) in south Lancashire. *Proc. R. Entomol. Soc. Lond. A* 45:172–81
103. Powell JA. 2001. Longest insect dormancy: Yucca moth larvae (Lepidoptera: Prodoxidae) metamorphose after 20, 25, and 30 years in diapause. *Ann. Entomol. Soc. Am.* 94:677–80
104. Salman MHR, Bonsignore CP, El Fels AEA, Giomi F, Hodar JA, et al. 2019. Winter temperature predicts prolonged diapause in pine processionary moth species across their geographic range. *PeerJ* 7:e6530
105. Salman TS, Vesala L, Hoikkala A. 2012. Photoperiodic regulation of life-history traits before and after eclosion: egg-to-adult development time, juvenile body mass and reproductive diapause in *Drosophila montana*. *J. Insect Physiol.* 58:1541–47
106. Schebeck M, Dobart N, Ragland GJ, Schopf A, Stauffer C. 2021. Facultative and obligate diapause phenotypes in populations of the European spruce bark beetle *Ips typographus*. *J. Pest Sci.* 95:889–99
107. Schebeck M, Hansen EM, Schopf A, Ragland GJ, Stauffer C, Bentz BJ. 2017. Diapause and overwintering of two spruce bark beetle species. *Physiol. Entomol.* 42:200–10
108. Sgolastra F, Kemp WP, Maini S, Bosch J. 2012. Duration of prepupal summer dormancy regulates synchronization of adult diapause with winter temperatures in bees of the genus *Osmia*. *J. Insect Physiol.* 58:924–33
109. Shapiro AM. 1975. Photoperiodic control of development and phenotype in a subarctic population of *Pieris occidentalis* (Lepidoptera: Pieridae). *Can. Entomol.* 107:775–79
110. Shindo J, Masaki S. 1995. Photoperiodic control of larval development in the semivoltine cockroach *Periplaneta japonica* (Blattidae: Dictyoptera). *Ecol. Res.* 10:1–12
111. Shintani Y, Hirose Y, Terao M. 2011. Effects of temperature, photoperiod and soil humidity on induction of pseudopupal diapause in the bean blister beetle *Epicauta gorhami*. *Physiol. Entomol.* 36:14–20
112. Shintani Y, Numata H. 2010. Adaptive significance of the recurrent photoperiodic response in a spring-breeding carabid beetle, *Carabus yaconinus*. *Entomol. Sci.* 13:367–74
113. Shintani Y, Terao M, Tanaka S. 2017. Adaptive significance of precocious pupation in the bean blister beetle, *Epicauta gorhami* (Coleoptera: Meloidae), a hypermetamorphic insect. *J. Insect Physiol.* 99:107–12

114. Simon C, Cooley JR, Karban R, Sota T. 2022. Advances in the evolution and ecology of 13- and 17-year periodical cicadas. *Annu. Rev. Entomol.* 67:457–82
115. Sokolova IV. 2007. Univoltine seasonal cycle and obligate diapause in the noctuid moth *Charanyca trigrammica* Hufn. (Lepidoptera, Noctuidae). *Entomol. Rev.* 87:793–98
116. Sota T. 1986. Effects of temperature and photoperiod on larval development and gonad maturation of a carabid beetle, *Carabus yaconinus* (Coleoptera: Carabidae). *Appl. Entomol. Zool.* 21:89–94
117. Sota T. 1987. Effects of temperature and photoperiod on the larval hibernation and adult aestivation of *Leptocarabus kumagaii* (Coleoptera: Carabidae). *Appl. Entomol. Zool.* 22:617–23
118. Sota T. 1987. Mortality pattern and age structure in two carabid populations with different seasonal life cycles. *Popul. Ecol.* 29:237–54
119. Soula B, Menu F. 2003. Variability in diapause duration in the chestnut weevil: mixed ESS, genetic polymorphism or bet-hedging? *Oikos* 100:574–80
120. Spacht DE, Gantz JD, Lee RE, Denlinger DL. 2020. Onset of seasonal metabolic depression in the Antarctic midge *Belgica antarctica* appears to be independent of environmental cues. *Physiol. Entomol.* 45:16–21
121. Stewart KW, Hassage RL, Holder SJ, Oswood MW. 1990. Life cycles of six stonefly species (Plecoptera) in subarctic and arctic Alaska streams. *Ann. Entomol. Soc. Am.* 83:207–14
122. Sugiki T, Masaki S. 1972. Photoperiodic control of larval and pupal development in *Spilarctia imparilis* Butler (Lepidoptera: Arctiidae). *Kontyû* 40:269–78
123. Sunose T. 1978. Studies on extended diapause in *Hasegawaia sasacola* Monzen (Diptera, Cecidomyiidae) and its parasites. *Kontyû* 46:400–15
124. Tamura M. 1981. Influence of temperature on the termination of diapause in the egg of *Pryeria sinica* Moore (Lepidotera: Zygaenidae). *Zoen-zasshi* 44:220–24 (in Japanese)
125. Tanaka S. 1978. Effects of changing photoperiod on nymphal development in *Pteronemobius nitidus* Boliver (Orthoptera, Gryllidae). *Kontyû* 46:135–51
126. Tanaka S. 1979. Multiple photoperiodic control of the seasonal life cycle in *Pteronemobius nitidus* Bolivar (Orthoptera: Gryllidae). *Kontyû* 47:465–75
127. Tanaka S. 1983. Seasonal control of nymphal diapause in the spring ground cricket, *Pteronemobius nitidus* (Orthoptera: Gryllidae). In *Diapause and Life Cycle Strategies in Insects*, ed. VK Brown, I Hodek, pp. 35–53. The Hague: Dr. W. Junk Publ.
128. Tanaka S, Sadoyama Y. 1997. Photoperiodic termination of diapause in field-collected adults of the Bombay locust, *Nomadacris succincta* (Orthoptera: Acrididae) in southern Japan. *Bull. Entomol. Res.* 87:533–39
129. Tanaka S, Zhu DH. 2003. Presence of three diapauses in a subtropical cockroach: control mechanisms and adaptive significance. *Physiol. Entomol.* 28:323–30
130. Tanaka SI, Imai C, Numata H. 2002. Ecological significance of adult summer diapause after nymphal winter diapause in *Poecilocoris lewisi* (Distant) (Heteroptera: Scutelleridae). *Appl. Entomol. Zool.* 37:469–75
131. Tauber MJ, Tauber CA. 1976. Developmental requirements of the univoltine species *Chrysopa downesi*: photoperiodic stimuli and sensitive stages. *J. Insect Physiol.* 22:331–35
132. Tauber MJ, Tauber CA. 1976. Insect seasonality: diapause maintenance, termination, and postdiapause development. *Annu. Rev. Entomol.* 21:81–107
133. Tauber MJ, Tauber CA, Masaki S. 1986. *Seasonal Adaptations of Insects*. Oxford, UK: Oxford Univ. Press
134. Tedders WL. 1978. *Important biological and morphological characteristics of the foliar-feeding aphids of pecan*. Tech. Bull. 1579, US Dep. Agric., Washington, DC
135. Terao M, Hirose Y, Shintani Y. 2015. Food-availability dependent premature metamorphosis in the bean blister beetle *Epicauta gorhami* (Coleoptera: Meloidae), a hypermetamorphic insect that feeds on grasshopper eggs in the larval stage. *Entomol. Sci.* 18:85–93
136. Teslenko VA. 2014. The life cycle and production of three common stonefly species (Insecta, Plecoptera) in the Kedrovaya River (the south of Primorskii Territory). *Entomol. Rev.* 94:1191–201
137. Togashi K. 2014. Effects of larval food shortage on diapause induction and adult traits in Taiwanese *Monochamus alternatus alternatus*. *Entomol. Exp. Appl.* 151:34–42
138. Togashi K. 2017. Effects of crowding on larval diapause and adult body size in *Monochamus alternatus alternatus* (Coleoptera: Cerambycidae). *Can. Entomol.* 149:159–73

139. Tokuda M, Yukawa J, Gôukon K. 2007. Life history traits of *Pseudasphondylia rokuharensis* (Diptera: Cecidomyiidae) affecting emergence of adults and synchronization with host plant phenology. *Environ. Entomol.* 36:518–23
140. Topp W. 1986. Imaginal aestivation in the rove beetle species *Omalium rivulare* (Coleoptera: Staphylinidae). *Entomol. Gen.* 12:51–55
141. Topp W. 1990. Selection for an optimal monovoltine life cycle in an unpredictable environment. Studies on the beetle *Catops nigricans* Spence (Col., Catopidae). *Oecologia* 84:134–41
142. Trudel R, Lavallee R, Bauce ER, Guertin C. 2002. The effect of cold temperature exposure and long-day photoperiod on the termination of the reproductive diapause of newly emerged female *Pissodes strobi* (Coleoptera: Curculionidae). *Agric. For. Entomol.* 4:301–8
143. Tzanakakis ME, Karakassis EJ, Tsaklidis G, Karabina ECh, Argalavini ICh, Arabatzis IG. 1991. Diapause termination in the almond seed wasp, *Eurytoma amygdali* Enderlein (Hym., Eurytomidae), in northern Greece and under certain photoperiods and temperatures. *J. Appl. Entomol.* 111:86–98
144. Tzanakakis ME, Veerman A. 1994. Effect of temperature on the termination of diapause in the univoltine almond seed wasp *Eurytoma amygdali*. *Entomol. Exp. Appl.* 70:27–39
145. Umeya Y. 1946. Embryonic hibernation and diapause in insects from the viewpoint of the hibernating-eggs of the silkworm. *Bull. Seric. Exp. Stat.* 12:393–480 (in Japanese)
146. Visser ME, Holleman LJ. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. B* 268:289–94
147. Wiklund C, Lehmann P, Friberg M. 2019. Diapause decision in the small tortoiseshell butterfly, *Aglais urticae*. *Entomol. Exp. Appl.* 167:433–41
148. Williams CM. 1946. Physiology of insect diapause: the role of the brain in the production and termination of pupal dormancy in the giant silkworm, *Platysamia cecropia*. *Biol. Bull.* 90:234–43
149. Williams KS, Simon C. 1995. The ecology, behavior, and evolution of periodical cicadas. *Annu. Rev. Entomol.* 45:269–95
150. Wipking W. 1988. Repeated larval diapause and diapause-free development in geographic strains of the burnet moth *Zygaena trifolii* Esp. (Insecta, Lepidoptera). *Oecologia* 77:557–64
151. Wipking W, Mengelkoch C. 1994. Control of alternate-year flight activities in high-alpine Ringlet butterflies (*Erebia*, Satyridae) and Burnet moths (*Zygaena*, Zygaenidae) from temperate environments. In *Insect Life-Cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control*, ed. HV Danks, pp. 313–47. Dordrecht, Neth.: Kluwer Acad. Publ.
152. Yamamoto S, Sota T. 2009. Incipient allochronic speciation by climatic disruption of the reproductive period. *Proc. R. Soc. B* 276:2711–19
153. Yamamura S, Ikarashi M, Sasaki M. 2008. Dual photoperiodic regulation to enable univoltine life cycle in alpine silver-Y moth, *Syngrapha ottolenguii* (Noctuidae: Plusiinae) without obligatory diapause. *Appl. Entomol. Zool.* 43:105–12
154. Yamashita O, Yaginuma T. 1991. Silkworm eggs at low temperatures: implication for sericulture. In *Insects at Low Temperatures*, ed. RE Lee, DL Denlinger, pp. 424–45. New York: Chapman & Hall
155. Yukawa J, Nakagawa K, Saigou T, Awa T, Fukuda T, Higashi M. 2013. Adult behavior of an ambrosia gall midge *Illiciomyia yukawai* (Diptera: Cecidomyiidae) and synchronization between its emergence and host plant phenology. *Entomol. Sci.* 16:400–12
156. Yukawa J, Uechi N. 2021. Life history traits. In *Biology of Gall Midges: Evolution, Ecology, and Biological Control*, ed. J Yukawa, M Tokuda, pp. 119–49. Berlin: Springer
157. Zhu DH, Tanaka S. 2004. Summer diapause and nymphal growth in a subtropical cockroach: response to changing photoperiod. *Physiol. Entomol.* 29:78–83