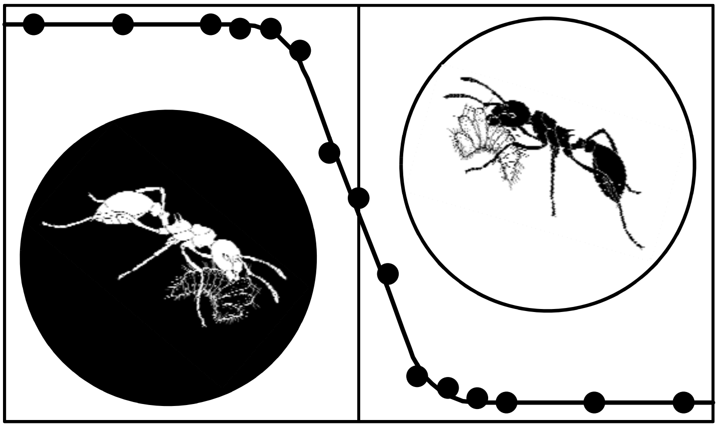
IVth European Workshop of Invertebrate Ecophysiology

St. Petersburg, Russia, 9 – 15 September 2001

ABSTRACTS

Edited by Vladilen E. Kipyatkov



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Dedicated to the memory of
Prof. Alexander S. Danilevsky
(1911 – 1969)

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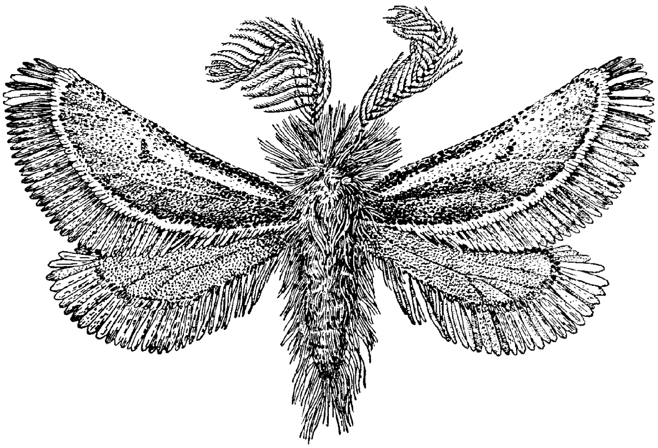
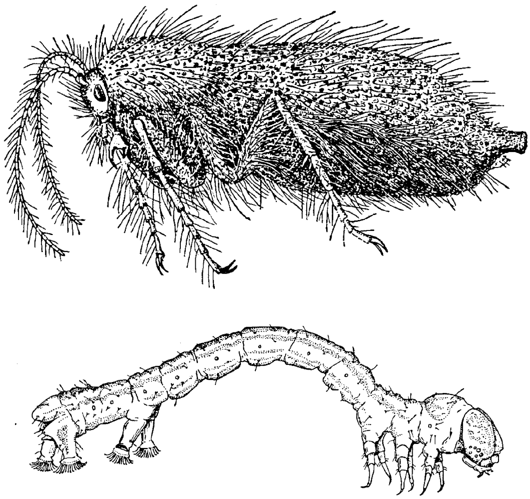
Alexander Danilevsky
(self-portrait, 1942)

This workshop is dedicated to the memory of the late Prof. Alexander S. Danilevsky (1911–1969), the former head of the Department of Entomology, Leningrad (St. Petersburg) State University, on occasion of his 90th anniversary and of the 40th year since the appearance of his famous book *Photoperiodism and Seasonal Development of Insects* first printed in Russian in 1961.

Professor
Alexander S. Danilevsky
(1911 – 1969)





A male (on the previous page), *a female and a caterpillar of* Cheimoptena pennigera *Danil. (Lepidoptera, Geometridae), a remarkable moth species described by A. S. Danilevsky from the deserts of South Kazakstan and Turkmenia. Imagoes have so unusual appearance and morphology that the species could only be placed in Geometridae after its larvae have been found. The seasonal life cycle of this species is similar to typical early-spring cycles of other moths characterized by a prolonged pupal diapause which continues throughout all summer, autumn and winter. Imagoes eclose and are active in January–February when mean daily temperatures are about 0°C in Turkmenia and -8...-9 in Kazakstan. The moths, however, fly only at day time, their activity being entirely dependent on the intensive solar radiation. The eggs laid by females in that time have no diapause and do not develop due to low temperatures until early spring (Entomol. Obozr., 1969, vol.48, issue 1, pp. 176–191).*

Professor Alexander S. Danilevsky and ecological physiology of invertebrates in St. Petersburg University

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Development of ecophysiological investigations of insects and other terrestrial arthropods in Russia is inseparably connected with the name of Alexander Sergeevich Danilevsky, and this IV European Workshop of Invertebrate Ecophysiology, dedicated to his memory on occasion of his 90th anniversary and of 40 years since the publication of his book "Photoperiodism and Seasonal Development of Insects", is held at St. Petersburg State University, where the main body of scientific and teaching activity of A. S. Danilevsky took place. Just here the scientific school of the University entomologists came into being. It is worthy known now as Danilevsky's school which develops creatively those fields of entomology that were of special interest for Danilevsky (ecological physiology and systematics).

Foreign entomologists are quite well aware of the main results of original ecological studies on insect photoperiodism and diapause, summarized in the above mentioned monograph by Danilevsky, inasmuch as after its publication by Leningrad University Press in 1961 it was translated and published in England (1965) and Japan (1966). Until now it is acknowledged as a classic textbook on seasonal photoperiodism of insects, retaining the high rate of citation. Unfortunately, the life of this distinguished personality and scientist, who stimulated the development of entomological research, highly important in terms of general biology, and educated many talented entomologists in Russia and some other countries of the former USSR is much worse known abroad.

A. S. Danilevsky was born on 4th March 1911 in the Ukraine (nearby the town of Mirgorod, Poltava prov.) in the family of descendants of the great Russian poet, A. S. Pushkin, and of the classic in Russian literature, N. V. Gogol' (in maternal line). He was also close relative of well known historical novelist G. P. Danilevsky (in paternal line). His grand-mother, Maria A. Bykova, was a grand-daughter of A. S. Pushkin, while his grand-father, Nikolai V. Bykov, was a nephew of N. V. Gogol'. His mother, Sophia N. Danilevskaya (the teacher by profession), was a great-granddaughter of A. S. Pushkin, and his father, Sergei D. Danilevsky (the agronomist by profession), was a grand-nephew of the novelist G. P. Danilevsky. Thus, Alexander Danilevsky was a great-great-grandson of A. S. Pushkin.

The young Sasha has spent his school years in Poltava, the environs of which (together with Agricultural Station and the City Museum) were the places, where he joined entomological and phenological study. After graduating from the school in Leningrad, he entered the Institute of Applied Zoology and Phytopathology, combining the education there (1930–1933) with specialization in lepidopterology under supervision of Prof. N. J. Kuznetsov, the known expert in insect systematics and physiology from Zoological Institute of the Academy of Science.

Sasha Danilevsky with his mother, Sofia Nikolaevna, and sister Irina. Poltava, 1926.

Successful research work, which began afterwards at the Institute of Plant Protection on food specialization of insects (this was the subject of his first publication in "Entomologicheskoye Obozreniye", 1935), was broken off by an exile to Kazakhstan in 1934 (in the course of mass political repressions after the murder of Sergei Kirov, a leader of Leningrad communists).

A. S. Danilevsky in the 50's.

But already in 1936 Danilevsky came back to Leningrad and entered the University as an aspirant at the Department of Entomology. Here he fulfils the study on ecology of silkworm *Philosamia cynthia* and its acclimatization (under supervision of Prof. B. N. Schwanvich). This work allowed him to acknowledge the great ecological significance of insect diapause in their adaptations to seasonal changes. And here he met the undergraduate student, Galina Shel'deshova, who became his wife, and all his life's and work's companion. However, the War (1941–1945) destroyed all the working and the family's plans: Galina went to Poltava, where on June 22nd she gave birth to the son, Sergei, and where they spent the whole period of German occupation, while Alexander Danilevsky joined the Soviet Army and served there firstly as a sanitary infantryman, but then in military hospitals as laboratory assistant, and at last as a specialist at the epidemiological laboratory of Leningrad front (in the position of lieutenant and then captain). Serving in the laboratory, Danilevsky succeeded in completing the dissertation for the Candidate of Biological Science, and in its defending within blockaded Leningrad at the 1st Medical Institute (April 5th, 1943).

In November 1945, being demobilized from the Army, Danilevsky returned to the Leningrad University, where he actively joined educating and scientific work at the Department of Entomology, firstly as an assistant, but from December 1946 as a docent. Just during this hard after-war time he initiated the study on the role of day-length in the control of insect diapause.

The first experiments of this type were carried out by Danilevsky together with Kira F. Geyspits and Ekaterina I. Glinyanaya at the Department and at the newly restored Laboratory of Entomology at the Biological Research Institute situated in the City suburb near Staryi (Old) Peterhof. The results were published in

1948–1949 in "Doklady Akademii Nauk". Similar experiments were carried out soon at the University field station ("The Forest on the Vorskla River") in Belgorod province, where Danilevsky has worked temporarily as a director. Usage of more southern insects (from Belgorod, and afterwards from Sukhumi) allowed to learn regularities of geographical variability in the photoperiodic responses of insects.

Catching mosquitoes larvae in Staryi Peterhof.

His pupil, Nikolai I. Goryshin, who has also made a great lot of things for modernization and automatization of laboratory equipment, participated in the first and all further steps of the experimental study of insect photoperiodism and diapause jointly with Danilevsky.

The great contribution to the knowledge of insect photoperiodism and diapause was made by Danilevsky by his monograph, "Photoperiodism and seasonal development of insects" (1961), in which he gave the profound analysis on significance, regularities, mechanisms and genetics of photoperiodic control of seasonal development in insects, and really ensured the creation of a novel ecological conception, describing mechanisms to control phenology and annual cycles of arthropods. The work on this book was completed when Danilevsky became the Head of the Department (1958), and its preparation for publication would not be possible without great help of his wife, Galina Shel'deshova, and his colleagues at the Department. The monograph, which was awarded the First University Prize, became a real springboard for the intensification of the study of different ecological and physiological aspects of seasonal photoperiodism in insects, mites and ticks, conducted by the whole group of younger scientists: Inessa A. Kuznetsova, Elena B. Vinogradova, Valentin N. Belozerov, Vera A. Maslennikova, Viktor P. Tyshchenko, Galina F. Tyshchenko, Tatiana V. Kind, Vladilen E. Kipyatkov, Aida Kh. Saulich, Tatiana A. Volkovich. Some aspirants from Armenia, Azerbaijan, China, Poland and Egypt took part in this research. Main results of this study were published in the collection of papers "Photoperiodic Adaptations in Insects and Acari" prepared by Danilevsky (as Editor) for the XIII International Congress of Entomology (Moscow, 1968).

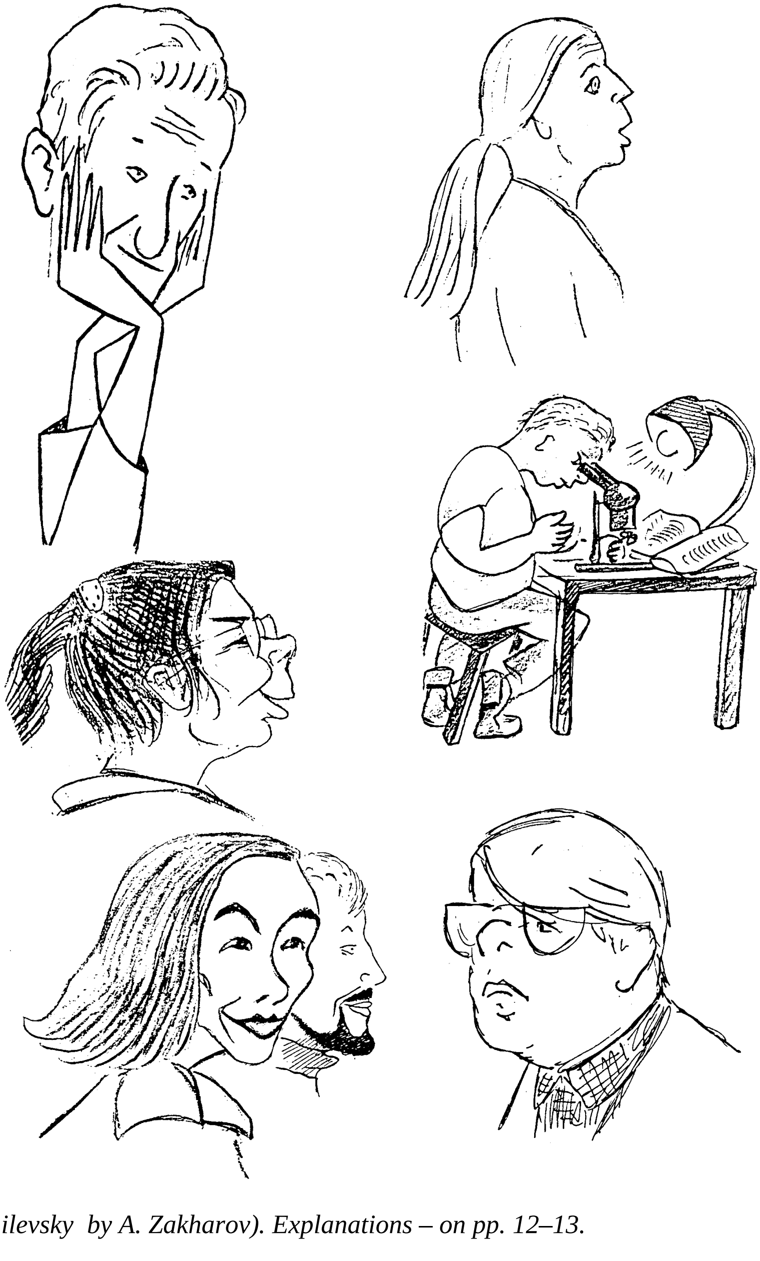
That time Alexander Danilevsky was elected as a Dean of Biological Faculty and had a great excess of administrative job. This was the cause of his unexpected premature Death after a heart attack which occurred on June 27th, 1969, when he planned already to finish his hard duties and to return to scientific work, beginning it with the business trip to Armenia. On the day of the Death he visited the Laboratory and famous Peterhof fountains along with known American insect physiologist G. Fraenkel.

The Department of Entomology after his Death was headed by his pupil, Viktor P. Tyshchenko, whose purposeful study on physiology of insect photoperiodism, the creation of two-oscillatory model of photoperiodic reaction, an analysis of evolution of these reactions and of diversity in token signals controlling diapause and active development in insects, ensured great progress for ecological physiology of invertebrates. His book entitled "Physiology of Insect Photoperiodism" (1977) represents the outstanding contribution to the subject, though some interpretations (particularly on principles in reception and treatment of photoperiodic information) were criticized by our colleagues from Zoological Institute, Russian Academy of Sciences (RAS), especially by Viktor A. Zaslavski (1984). It was a great loss when Prof. V. P. Tyshchenko died on May 24th 1986 after a hard illness.

Delivering a lecture.

The research in ecological direction has long been headed by Dr. N. I. Goryshin (the former Head of Laboratory), and is continued now by his two pupils, A. Kh. Saulich and T. A. Volkovich who study the seasonal control in bugs, lacewings and moths, by V. E. Kipyatkov leading the intensive study of seasonal adaptations of ants and other social insects, and also by V. N. Belozerov continuing his experimental study on seasonal photoperiodism of parasitic ixodid ticks (commencing also the study on reparative regeneration and endocrinology of ticks).

Professor Alexander S. Danilevsky *(in the upper left corner)* **with his pupils and followers in St. Petersburg University.** *Friendly jests by A. A. Stekolnikov.*



(A. S. Danilevsky by A. Zakharov). Explanations – on pp. 12–13.

Professor Alexander S. Danilevsky with his pupils and followers in St. Petersburg University. *Friendly jests by A. A. Stekolnikov. Explanations for the drawings on pp. 10–11.*

On page 10 (from left to right and from top to bottom):

Alexander Sergeevich Danilevsky (1911–1969) – in the upper left corner. A friendly jest by A. Zakharov.

Kira Fedorovna Geyspits (1917–1998) – the author of one of the first papers on insect photoperiodism carried out in Leningrad (St. Petersburg) University jointly with A. S. Danilevsky and published in 1948. She has done a lot of remarkable studies, including the inheritance of photoperiodic responses, the role of spectral composition of light and of the light receptors in the photoperiodic responses, the maternal influence on diapause and photoperiodic responses, the role of endogenous rhythms in photoperiodic control of development, etc.

Nikolai Ivanovich Goryshin – has long been a head of the Laboratory of Entomology in the Biological Research Institute, Leningrad (St. Petersburg) University. According to plans and design drawings by N. I. Goryshin the unique laboratory equipment, including precise photothermostats, was constructed in this laboratory which has in many respects determined the success of the researches on insect photoperiodism conducted under the supervision of A. S. Danilevsky. Goryshin is the author of a book *Technical Equipment for Ecological Research in Entomology* (1966). His own research was mainly on the relations between photoperiodic and temperature controls of the development and diapause.

Vladimir Ivanovich Kuznetsov – an expert in taxonomy and morphology of Lepidoptera, head of the Department of Lepidoptera in Zoological Institute, Russian Academy of Sciences, St. Petersburg, the co-author of A. S. Danilevsky (jointly published monograph on Tortricidae: Fauna of the USSR, 1968, vol. 5, issue 1), the author of about 200 papers devoted to systematics of Lepidoptera. In 2001 he has published a monograph *The New Approaches to the System of Lepidoptera of the World Fauna* (jointly with A. A. Stekolnikov).

Valentin Nikolaevich Belozerov – an expert in the field of photoperiodic control of seasonal life cycles in parasitic ticks of the family Ixodidae. He has first studied photoperiodic responses, including those connected with behavioural traits, in some species of *Ixodes* and other genera. Recently he took a great interest in experimental morphology and now is studying the regeneration of Haller's organ in Ixodidae.

Inessa Alekseevna Kuznetsova – an expert in the field of ecological physiology of insects, active participant of A. S. Danilevsky's ecological research group. She is the author of several works on the photoperiodic regulation of insect seasonal life cycles and on the physiology of insect fat body.

On page 11 (from left to right and from top to bottom):

Viktor Petrovich Tyshchenko (1937–1986) – has been a head of the Department of Entomology, Leningrad (St. Petersburg) University after A. S. Danilevsky from 1968 until his premature Death in 1986. He has worked in the fields of insect physiology, ecological physiology and arachnology. The author of books *A Key of Spiders of the European Part of the USSR*, *Physiology of Photoperiodism in Insects* (1976) and *The Fundamentals of Insect Physiology* (two volumes – 1976 & 1977). V. P. Tyshchenko developed the "two-oscillator model of the photoperiodic responses" and has been working on its experimental confirmation. In his last years was especially interested in the studies of quantitative photoperiodic responses.

Galina Fedorovna Tyshchenko (1938–1998) – has carried out a series of remarkable studies on the physiology of photoperiodic responses, including the research of the "skeleton photoperiods" effects realised jointly with his husband V. P. Tyshchenko.

Tatiana Vladimirovna Kind – an expert in the field of insect endocrinology and hormonal control of diapause, has carried out a series of remarkable works on hormonal regulation of larval and pupal diapause using cytological methods.

Anatolii Aleksandrovich Stekolnikov – a head of the Department of Entomology, St. Petersburg University since 1986. He was among the first specialists who used functional morphology of male and female genitalia in order to reconstruct the phylogeny of Lepidoptera. His monograph *The New Approaches to the System of Lepidoptera of the World Fauna* written jointly with V. I. Kuznetsov has been published in 2001.

Vera Aleksandrovna Maslennikova – was one of the first persons who studied photoperiodic responses in parasitic insects (parasitoids) in relation to photoperiodic and hormonal regulation of development of their hosts.

Sergei Ivanovich Chernysh – a head of the Laboratory of Entomology in the Biological Research Institute, St. Petersburg University, an expert in the field of insect immune defence. He has discovered an unknown part of insect immune system – cytotoxic hemocytes which are functionally similar to cytotoxic lymphocytes (natural killers) of vertebrates.

Vladilen Evgenievich Kipyatkov – professor at the Department of Entomology, St. Petersburg University. His main research field is the ecophysiology and seasonality in ants, including the effects of varying temperature and day-length on their development and behaviour. He has made a major contribution to the understanding of social responses and regulatory mechanisms evolved by ants for living in a seasonal environment. V. E. Kipyatkov is a President of Russian Language Section of the International Union for the Study of Social Insects (IUSSI) and also of Social Insect Section of the Russian Entomological Society.

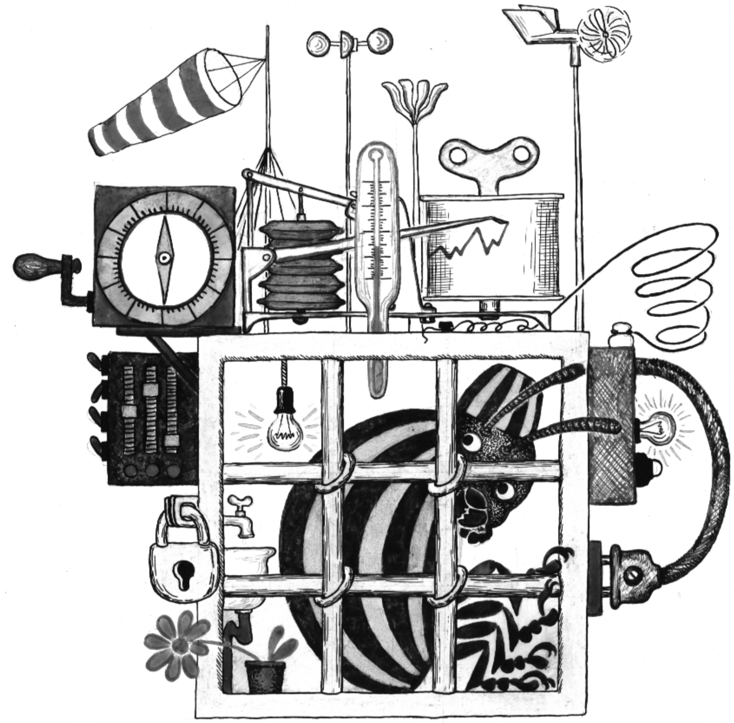
The important recent contribution to insect ecology is the book by A. Kh. Saulich "Seasonal development of insects and possibilities of their expansion" (1999). The scientific work of entomologists from St. Petersburg University is carried out in close contact with many institutes, both abroad (France, United States, Sweden, England, Poland, South Africa), and at home, especially with those, where the former graduates of the University conduct their ecophysiological studies. These are, for instance, E. B. Vinogradova, Sergei Ja. Reznik and N. P. Vagina at the Zoological Institute, RAS, Alexander N. Knyazev at the Institute of Evolutionary Physiology and Biochemistry, RAS, Vladimir N. Burov at the Institute of Plant Protection and many others.

The research in physiological direction is now developed by the present Head of Laboratory, Dr. Sergei I. Chernysh, and his group (T. V. Kind, A. P. Nesin, N. P. Simonenko, N. A. Gordya), who focussed their research on a set of problems from a non-specific resistance of diapausing insects to very important problem concerning mechanisms of humoral and cellular forms of insect immunity, and interrelations of immune and endocrine systems in insects. Some new research on insect pheromones is began by Vladimir D. Ivanov.

It is already more than a half-century since the beginning of experiments on insect photoperiodism initiated by A. S. Danilevsky, and they are seen now as a strong seedling, which develops now into a big international tree of ecophysiology of invertebrates, the small (though vivid and vital) branch of which is represented by Danilevsky's scientific school, highly recognized all over the world.

Prof. Alexander Danilevsky. *A friendly jest by A. A. Stekolnikov.*

Invited Lectures



Drawing by N. Yu. Kluge

The interaction of water, ice nucleators and desiccation in invertebrate cold survival

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It has long been assumed that survival, especially in freeze intolerant organisms, largely depends on the ability of the individual to supercool below the melting point temperature of its fluids. Thus freezing may be avoided until much lower temperatures are reached, which are invariably lethal. On the other hand, freeze tolerant forms supercool only slightly and survive the partial freezing of their (extracellular) fluids at high sub-zero temperatures before much lower lethal temperatures are reached. Increasingly, evidence in recent years has highlighted the role of water contained within a freeze intolerant organism in determining the sub-zero temperatures which can be survived by particular taxa. The quantity of contained water and its dissolved solutes, often in the form of polyhydric alcohols and sugars for the promotion of supercooling or cryoprotection, and its location and form (free or bound) are important characteristics for the cold survival of an organism. Ice nucleation in such supercooled solutions is promoted by a range of particles and substances of biological or physical origin, whereas antinucleation processes include antifreeze proteins and other mechanisms to reduce the possibility of ice nuclei being formed. Thus, a physical balance exists in the supercooled aqueous solutions of biological systems, although the supercooled state is often described as highly unstable. Reduction in water content through desiccation leads to an increase in cold hardiness for many species: the resultant smaller volume of liquid, increased solute concentration, and increase in the proportion of bound water relative to the total water content may be responsible.

Four case studies are discussed to examine the interaction of water, ice nucleators and desiccation in the survival of invertebrates and the viability of plant material:

- larvae of the freeze tolerant fly *Heleomyza borealis* in Arctic habitats;
- the freeze intolerant Antarctic springtail *Cryptopygus antarcticus*;
- the springtail *Onychiurus arcticus* in the High Arctic;
- cryopreservation of meristems of black currant (*Ribes ciliatum*).

Three of these case studies demonstrate a range of responses by different invertebrates to sub-zero temperatures, whilst the fourth is an example of the application of knowledge of natural systems to cryopreservation techniques.

At one end of the spectrum of cold response is the freeze tolerant larva of *Heleomyza borealis* in Arctic habitats, which can survive short exposures at

-60°C, its water content (2.2 $g.g^{-1}$ dry weight) and level of supercooling (c. -7°C) remaining almost constant over a wide thermal range (Worland, et al., 2000). The unfreezable or osmotically inactive water component is also stable at c.20% of the total body water content. Larvae lose little moisture to their surroundings in the soil microhabitat even during winter as their body fluids are in vapour pressure equilibrium with ice in their surroundings. The long term overwinter survival of populations of this species may be regulated more by the duration rather than the severity of cold exposure in its Arctic habitats.

Occupying a middle position in the spectrum of response is the freeze intolerant maritime Antarctic springtail *Cryptopygus antarcticus* which is dependent for its survival on the elimination, masking/sequestration of potential ice nucleators to avoid lethal freezing within the body. The dynamic nature of its bimodal supercooling point (SCP) profile (mean SCPs of c.-9 and -24°C) reflects a high degree of individual variation in the population. The numbers of active ice nucleators at the SCP temperature are greater in the upper group than in the lower one (Block & Worland, 2001). The mechanism underlying the survival of this species is based almost solely on the reduction of ice nucleation potential during extended periods of sub-zero temperatures. This is aided by a low level production of antifreeze compounds and considerable variation in body water content via environmental cues (Block & Harrisson, 1995). In the field, water contents range from 57 to 61% of fresh weight and individuals can survive losses of up to 20% of their body water. The population exhibits a significant annual cycle in body water content at Signy Island with minima in July [mid-winter] (1.2 $g.g^{-1}$ dry weight) and maxima in September [early spring] (2.0 $g.g^{-1}$ dry weight). Such partial desiccation increases its ability to supercool and thereby avoid freezing.

At the other end of response spectrum is the freeze intolerant collembolan *Onychiurus arcticus* which, under Arctic conditions, can survive up to 40% loss of its body water with concomitant depression of its SCP from c.-7 to -17°C to a point where only osmotically inactive water (16% of total body water) remains (Worland, et al., 1998). Trehalose appears to play an important role in this dehydrated state by the maintenance of cell integrity via membrane fluidity, etc. Driven to extremes, this species is unlikely to freeze in nature due to the loss of all its freezable water.

Finally, desiccation is now known to be a major pre-requisite to the successful cryopreservation of many biological materials using liquid nitrogen protocols, especially in the alginate encapsulation – dehydration technique. Recent studies (Dumet, et al., 2000) on the black currant (*Ribes ciliatum*) using Differential Scanning Calorimetry have demonstrated that reduction of meristem water content from c.2.2 to 0.1 $g.g^{-1}$ dry weight results in no detectable crystallisation (ice formation) and glass transitions being observed between -71 and -81°C, when cooling at 10°C min^{-1} from 10 to -150°C. Although this is a much slower rate of cooling than plunging into liquid nitrogen (c.160°C min^{-1}), it is indicative that high survival rates of meristems are achieved after the sample water content is reduced to a level where there is little or no freezable water present.

These examples highlight the different roles of which are played by water in three invertebrates. They exhibit increasing dependence on the elimination of freezable water from their systems to achieve cold survival. Although there are several similar features between the four systems, there appears to be no universal mechanism by which they cope with sub-zero temperatures and the ever present possibility of tissue freezing. Their survival strategies differ markedly. Water, ice nucleators and the desiccation process are the main components of each of their survival strategies, and these interact differently according to their particular environmental and physiological conditions. It may be concluded, however, that the activity of water itself is fundamental to all their responses to freezing temperatures.

References

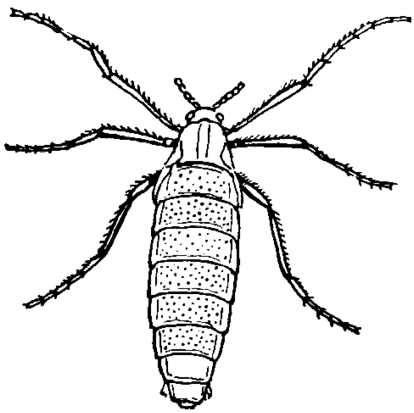
Block, W. & Harrisson, P.M. 1995: Collembolan water relations and environmental change in the maritime Antarctic. *Global Change Biology* 1: 347–359.

Block, W. & Worland, M. R. 2001: Experimental studies of ice nucleation in an Antarctic springtail (Collembola, Isotomidae). *Cryobiology* (in press).

Dumet, D., Block, W., Worland, M. R., Reed, B. M. & Benson, E. E. 2000: Profiling cryopreservation protocols for *Ribes ciliatum* using Differential Scanning Calorimetry. *CryoLetters* 21: 367–378.

Worland, M.R., Grubor-Lajsic, G. & Montiel, M.O. 1998: Partial desiccation induced by sub-zero temperatures as a component of the survival strategy of the Arctic collembolan Onychiurus arcticus (Tullberg). *Journal of Insect Physiology* 44: 211–219.

Worland, M. R., Block, W. & Grubor-Lajsic, G. 2000: Survival of *Heleomyza borealis* (Diptera, Heleomyzidae) larvae down to -60°C. *Physiological Entomology* 25: 1–5.



Studying intra-specific variability within cabbage root fly populations to produce pest forecasts

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The cabbage root fly (*Delia radicum*) is of considerable economic importance in northern Europe and North America, as its larvae destroy the roots of cruciferous crops not treated with insecticides. As with all insects, climatic conditions determine the rate of development of this fly. Thus the numbers of generations completed annually by the cabbage root fly varies between locations.

Spring emergence

Each year in the UK, cabbage root fly populations can develop through two full (first and second) generations and one partial (third) generation. Flies of the first, second and third generations are active during May, July and September respectively, although the precise timing obviously depends on weather conditions. Usually, only two generations of the fly are completed in the cooler northern regions of the country.

In 1976, we discovered a population of cabbage root flies in north-west England that emerged from overwintering pupae extremely late in the following spring. A small survey carried out in England and Wales during 1978–80 revealed that *late emergence* was not restricted to this one site. A subsequent survey, done by members of the IOBC working group on ‘Integrated control in field vegetable crops’, showed that patterns of fly emergence in the spring throughout northern Europe were as variable as those recorded in the UK. Since then other research groups have reported that *late-emerging* populations of this fly occur also in North America.

Diapause completion – ‘early-emerging’ and ‘late-emerging’ biotypes

Pupae of the cabbage root fly overwinter in the soil in diapause. Pupae enter diapause when the final larval instars are subjected to short photoperiods and/or temperatures below 15°C. At Wellesbourne, eggs that are laid on field crops after about 31 July each year give rise to diapause pupae. Such pupae are unresponsive to high autumn temperatures and must experience a period of cold during which diapause development is completed, before post-diapause development can proceed in the spring. Experiments using cooling incubators showed that low temperature was the major factor regulating diapause development of the cabbage root fly and that diapausing pupae had to be subjected to temperatures from 0–6°C for 22 weeks for all individuals in the population to complete diapause development. The lower the temperature between 0° and 10°C, the more effective it was in terminating diapause. There was also considerable intra-specific variation in the rate of diapause completion. In some pupae, diapause was complete after only 12 weeks exposure to cold, whilst others required the full 22 weeks.

Once diapause development was complete, pupae required a further 14 days at 20°C for most of the flies to emerge. The developmental threshold for post-diapause development is close to 4.3°C. In the field, 90% of the pupal population have usually completed diapause by early March, and the subsequent population of flies emerges generally during a 10–20 day period in late April – early May.

Further studies showed that *late-emerging* cabbage root flies have an additional period of diapause development. Unlike *early-emerging* flies, that start post-diapause development as soon as the cold phase of diapause development is completed and temperatures rise above the developmental threshold of 4.3°C, *late-emerging* flies also require an additional period at temperatures above 7°C before they start post-diapause development. This finding was supported by studies on the rate of oxygen uptake by diapause and post-diapause pupae and by studies on the levels of endogenous ecdysteroids monitored at various stages of development.

Cabbage root fly populations in the UK are often mixtures of the two developmental biotypes. In one area of England (24 x 30 km), which we sampled intensively using a grid of 6 x 6 km squares, we identified a gradient of biotypes in which the percentage of *late-emerging* flies ranged from 3%–85%. We believe that these emergence characteristics are determined genetically. Crosses between *early-* and *late-emerging* flies indicated that *early/late emergence* is determined by a single gene and that the allele for *late emergence* is dominant and that for *early emergence*, recessive.

Induction of diapause

Not only do cabbage root flies exhibit variation in the duration of diapause, they also show variable responses to daylength and temperature during the induction of pupal diapause. Members of the IOBC Working Group collected cabbage root fly populations from several sites in northern Europe, at latitudes that varied between 46 and 61°N. The flies that emerged were reared at Wellesbourne at a constant temperature of 17°C under five different photoperiods. Diapause was induced in all pupae reared under conditions that involved a photoperiod of less than 14 hours light per day. With photoperiods of 16 and 19 hours, the proportion of pupae that entered diapause was related to the latitude from which the original insects were collected. Almost all pupae from the two most northern sites entered diapause, whereas very few from the southern sites did. In general, the critical photoperiods for diapause induction increased with the latitude of the collection site.

Pupal aestivation

When temperatures are high, cabbage root flies can be induced into pupal aestivation during the summer months and this may delay emergence of the subsequent population of flies. Laboratory experiments showed that this induction occurred during the early part of the pupal stage. Once again there was considerable intra-specific variability and the percentage of pupae that entered aestivation increased as the temperature was increased from 20° to 27°C. Following the induction of aestivation, there was no constant period of arrested development. Instead, the pupae started to develop into flies as soon as temperatures fell below 20°C.

Forecasting cabbage root fly generations

Treatments to control cabbage root fly vary considerably. Insecticidal treatments include some, such as seed treatments and post-planting drenches, which are applied prophylactically and others that are applied as granules or foliar sprays in response to changes in fly numbers. Apart from insecticidal control, methods of biological and behavioural control are also now being considered at HRI. The success of any control treatment depends on being able to predict accurately when the stage of the fly most vulnerable to that particular control treatment is active. This led us to develop temperature-based methods for forecasting the field activity of the cabbage root fly.

The forecasts are generated from a Monte Carlo simulation that involves using rates of insect development to predict the phenology of the fly. By using this simulation model, rather than a simple day-degree model, it is possible to:

Incorporate, for each developmental stage of the fly, relationships between the rate of development and temperature

- Incorporate both linear and non-linear relationships
- Use different threshold temperatures for each development stage of the insect
- Incorporate information on intra-specific variability within a developmental biotype (based on the coefficient of variation of the rate of insect development)
- Incorporate information on intra-specific variability between developmental biotypes (the proportion of insects in the population that are either *early*- or *late-emerging*).

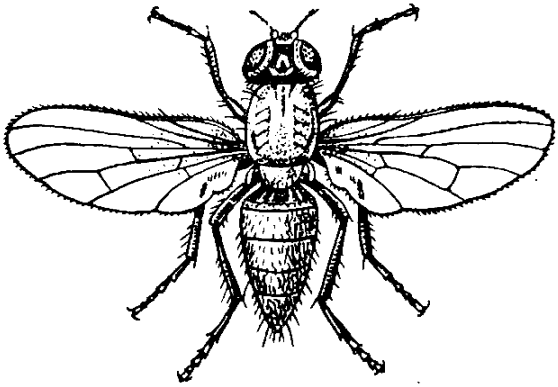
The method is feasible because it uses a fixed number of individuals from one generation to the next and simulates the timing of events rather than the population dynamics of the insects. It is also sufficiently flexible to allow insect resting phases (pupal diapause and aestivation) to occur at the appropriate instant for each individual, by using information on intra-specific variation in the insects' responses to the changes in temperature and daylength.

Forecast validation

The forecast has been validated using field monitoring data collected by sampling both adult cabbage root flies and cabbage root fly eggs. In general, the forecasts are accurate to about a week. Attempts have been made to obtain validation data from as many regions of the UK as possible.

Uses of the forecast

The cabbage root fly forecast is used by a number of commercial growers in the UK. It is available as part of a decision support software package, that can be used with the grower's own meteorological data. Alternatively, HRI supplies weekly fax or e-mail bulletins to growers about the activity of the fly within their growing region. Such forecasts are based on meteorological data collected from the national network of weather stations. Apart from being used to make short-term crop protection decisions, the cabbage root fly forecast has been used also to make longer-term predictions about how cabbage root fly phenology might be affected by global warming.



The range of insect dormancy responses

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Insect dormancy responses, in the broad sense of modifications of development, are reviewed. Most previous studies have considered detailed developmental responses to environmental conditions, especially photoperiod, or have defined the stage, seasonal placement or voltinism of particular species (for many sample references see Danks 1987, 1994). Here, I do not treat such specific details, but rather examine the range of responses from a general perspective. Such an examination suggests that the breadth of the responses available to insects and the extent to which they are coordinated have not always been fully appreciated. It shows how the responses integrate key environmental and developmental constraints, and generates conclusions that may be helpful for studying and understanding them.

The range of responses is extraordinarily wide for several reasons. First, there is a great diversity of environments, with different seasonal patterns and with different climatic stresses, habitats and natural enemies. Second, different taxa have different evolutionary histories, so that the basic structure of the life cycles of related taxa tends to be broadly similar. However, the life cycle of any given species has evolved in response to past rather than current conditions; this historical imprint leads to difficulties if interpretations are based too heavily on correlation with current environments. Third, adaptations must respond to both seasonal timing and resistance to adversity, so that adaptations that might be assumed to respond to resistance to winter cold or to summer drought, for example, in fact might respond instead to the timing of activity. Of course, such a balance is different in different species. Finally, not only development but also many other biological features of each species are coordinated in a successful life-cycle. Therefore, developmental and other traits are integrated.

Developmental options are introduced by examining the range of possible modifications of development, the diversity of components of each individual response, and different life-cycle durations. Other topics considered are the concepts of life-cycle pathways and of active and passive default responses, as well as some aspects of variation and trade-offs.

Modifications of development vary from a complete stoppage of development to greater or lesser changes in developmental rate. Responses can be all-or-nothing, such as the alternatives of diapause and non-diapause, but also can show gradations along a continuous scale. Both types of response occur in a single species. If the direction of a response changes as development proceeds, so that slower growth results first from short days but later from long days for example, the life cycle can be adjusted in complex ways. Larval development is commonly delayed by the addition of extra instars, and then larval size normally continues to increase at a relatively slow rate. The many possible dormancy states and the fact that developmental rates can be adjusted from very fast to very slow partly reflects the many potential uses of slower development, including protection against severe conditions, energy conservation, synchrony of the feeding stage with food, optimizing the timing of reproduction, and longer monitoring of potentially ambiguous environmental signals.

The diversity of developmental options is increased because life cycles as well as individual dormancy responses are made up from many successive, generally linked, components. For example, in many species diapause affects preceding or subsequent life-cycle traits.

The developmental responses of different species are coordinated so that their life cycles last for less than one year, exactly one year, or more than one year; some species have a range of durations. These differences in life-cycle duration and variability among and within species appear to be correlated chiefly with the level of resources and the degree of environmental stability.

A useful way to visualize life-cycle options is the concept of alternative pathways, which can be chosen by an individual in response to current environmental conditions that indicate the suitability of current and likely future habitats. This concept of life-cycle pathways emphasizes that a series of steps is required to complete development, allowing different alternative dormancy responses (such as slow development or fast development) to be included at various stages.

Another useful concept is the distinction between active and passive default responses. Many problems in understanding dormancy stem from a failure to appreciate that the default setting for development is different in different species. Species in which the default is active continue normal development unless there is a specific environmental change that cues a reduction in developmental rate or induces a diapause. Species with a passive default stop development at a given stage even when conditions stay the same. In such species, for example, diapause takes place whatever the conditions and ends only in response to a change from short to long photoperiods.

The types of variation, and the roles of both genetic programmes and external factors, provide further key information about dormancy responses. In particular, a stable habitat or different stable regional habitats can best be exploited by a fixed genotype or by local genetic adaptation. However, habitats that are variable or heterogenous on a small scale favour labile plastic responses that permit a given individual to adjust to the particular subhabitat it encounters. In some variable habitats environmental signals do not reliably indicate conditions in the future, preventing adequate plastic adjustments. Such environments favour “bet hedging”, whereby several fixed genetic morphs (polymorphism) or a very wide range of variation — that spread developmental types through time — provide insurance against unpredictable risks.

Most existing discussions of trade-offs emphasize relatively simple size-time relationships, but in fact there are many other potential trade-offs. This wide range of possibilities means that the likely resource trade-offs for a given species cannot be predicted in advance. Moreover, the fact that conditions can act simply as direct constraints to prevent or limit potential trade-offs has sometimes been overlooked. For example, there can be no trade-off involving time or size if resources are so limited that the growth allowed is close to the minimum feasible for survival.

Some general conclusions that help in understanding the range of dormancy responses emerge from this general examination:

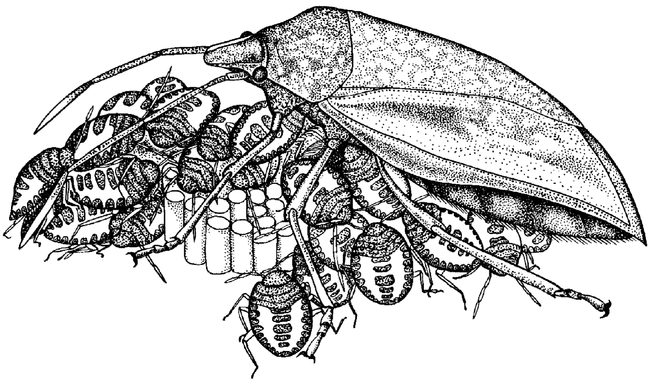
- The number of subcomponents and their ranges of expression are very wide, so that many options are available. The resulting complexities of response in turn reflect the enormous range of environments potentially inhabited by insects. The nature of the habitat, especially its predictability, determines the potential effectiveness of many of the developmental options.
- The developmental patterns and environmental responses of a given species reflect its evolutionary history in past environments. It may then be difficult to correlate observed responses with the conditions in current habitats.
- Adaptations that govern development can reflect the need to grow or reproduce while conditions are favourable or the need to survive while conditions are severe. The balance between these requirements varies among species, and their contributions to the structure of a given life cycle are not always obvious.
- Typical life-cycle pathways consist of very large numbers of simultaneous and successive components. Therefore, the components cannot be understood by studying them in isolation.
- Any single dormancy response can play one or more different roles in meeting developmental needs. For example, the rate of development can alter the timing of reproduction, mating strategies, the effects of competition, coincidence with suitable conditions, and so on.
- Default responses can be either active (development continues unless signalled otherwise) or passive (development stops unless signalled otherwise). The existence of these alternatives means that a broad approach is required to understand the action of environmental cues.
- Relatively minor effects that fine-tune dormancy responses can enhance survival. For example, food quality often modifies the incidence of photoperiodically induced diapause. However, it is difficult to identify and measure many of these minor effects.
- Resources in very short supply cannot be traded off. Such constraints mean that trade-offs are not inevitable.
- There are many potential linkages among life-cycle components, but any given element is not necessarily linked with any other element because specific coordination depends on how a particular life cycle is structured.

These general conclusions confirm that dormancy responses are remarkably diverse, complex and integrated. Studies of dormancy responses are likely to be more effective if they recognize this great potential range and complexity.

References

Danks H.V. 1987. Insect Dormancy: An Ecological Perspective. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, 439 pp.

Danks H.V. (ed.) 1994. Insect Life-Cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control. Kluwer Academic Publishers, Dordrecht. Series Entomologica 52, 378 pp.



Insect diapause: from a rich history to an exciting future

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Insertion of diapause into the life cycle requires mechanisms for monitoring environmental cues and then using this information to first halt and then reinitiate development at the appropriate time. The pioneering experiments on photoperiodism by Professor Danilevsky and his contemporaries laid the foundation for the rich and comprehensive view that we now have concerning the environmental regulation of diapause, the hormonal systems that direct the onset and termination of diapause, and the theoretical properties of the clock mechanisms involved in photoperiodism. The conspicuous void that persists in this field is understanding the molecular underpinnings of diapause, and it is this topic that serves as the focus of my discussion.

Though many genes are shut down during diapause, others are specifically expressed at this time. Classes of diapause-upregulated genes can be distinguished based on their expression patterns: Some are upregulated throughout diapause, and others are expressed only in early diapause, late diapause, or intermittently throughout diapause. The termination of diapause is accompanied by a rapid decline in expression of the diapause-upregulated genes and conversely, an elevation in expression of many genes that were downregulated during diapause.

Among the genes that are upregulated throughout diapause are genes that encode for two of the heat shock proteins, heat shock protein (Hsp) 23 and Hsp70. Both of these genes are upregulated at the very onset of diapause, expression persists throughout diapause and is then shut off within hours after diapause has been terminated. These proteins may be playing two distinct roles: providing a cryoprotective role and facilitating the shut-down of the cell cycle. Although the original observation of *hsp* upregulation during diapause was noted in the pupal diapause of the flesh fly, *Sarcophaga crassipalpis*, upregulation of *hsp70* appears to occur in several other species as well, including both species with larval and pupal diapauses.

Another category of diapause-upregulated genes are those that are expressed only in early diapause. Such genes could be of interest in bringing development to a halt or for removing developmental blocks that may enable diapause to be terminated. An unidentified gene in *S. crassipalpis* fits this expression profile, along with a cold-induced gene in *Bombyx mori* and a gut protein in *Lymantria dispar*.

Genes upregulated late in diapause have the potential to contribute to events surrounding the completion of diapause and the resumption of development. *Ultraspiracle* (*usp*) is one such gene in *S. crassipalpis*. This gene encodes a protein that forms a heterodimer with Ecdysone Receptor, and it thus serves a key role in the cell's response to ecdysteroids. Interestingly, the elevation in expression of *usp* in late diapause coincides with the pupa's increased responsiveness to ecdysteroids. This upregulation of *usp* perhaps represents a preparative step that enables the pupa to respond to the ecdysteroids released at the end of diapause.

Another category of diapause-upregulated genes are those that are expressed intermittently during diapause. Certain metabolic events during diapause are periodic. This is especially in diapausing flesh flies and pierids that display infradian cycles of oxygen consumption. Days of barely detectable oxygen consumption are interspersed with 1–2 day periods of elevated oxygen consumption. Thus far, we have found one gene with an expression pattern that reflects these cycles: a gene that encodes a 60S ribosomal protein PO, an AP3 endonuclease. This gene is strongly expressed only during the days of low oxygen consumption, whereas little expression can be noted during days of high oxygen consumption. Proteins of this type are multifunctional and appear to be essential for efficient protein translation, for DNA repair, and for protection against hypoxic stress. It is thus interesting that this gene is most highly expressed during the intervals of low oxygen consumption.

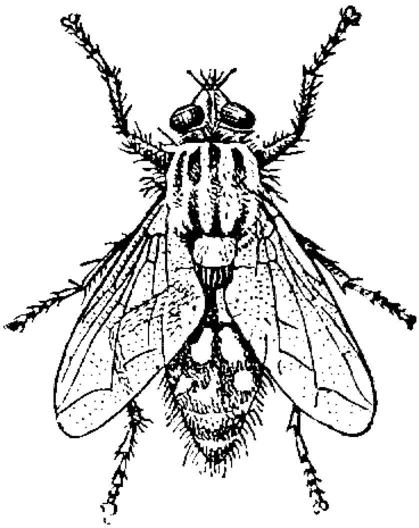
Diapause-downregulated genes are potentially of equal interest. Although many housekeeping genes may be in this category, the shutting down of certain genes has the potential to contribute to the regulation of diapause. One possible candidate in this category of genes is the cell cycle regulator, *proliferating cell nuclear antigen* (*pcna*). This gene is downregulated in flesh flies at the onset of diapause and expression remains undetectable until diapause is terminated. During diapause cells of the fly brain remain locked in a G_0/G_1 cell cycle arrest. Though the expression patterns of several cell cycle regulators remain unchanged during diapause, *pcna* is dramatically downregulated at this time, suggesting a possible role for this gene in shutting down the cell cycle during diapause. Another diapause-downregulated gene encodes Hsp90. This heat shock protein is upregulated when ecdysteroids are present and downregulated when they are absent. One possibility is that Hsp90 associates with the ecdysone receptor/ultraspiracle complex, and is essential for the proper functioning of this heterodimer. The concurrence of the absence of ecdysteroids during pupal diapause in the flesh fly and the downregulation of *hsp90* is consistent with the idea that the action of ecdysteroids and expression of *hsp90* are indeed linked.

At this point , we have only a few examples of genes involved in the diapause response. The photosensitive stage in which diapause is programmed, different phases of diapause, and the early events associated with diapause termination will all be critical stages to search for diapause-specific patterns of gene expression. With a few important regulatory genes already in hand, it is now possible to seek both upstream and downstream genes of interest. As more diapause-associated genes are identified, it will hopefully be feasible to construct a regulatory hierarchy for diapause.

Information from a wide range of species will be valuable for identifying common regulatory elements. Embryos, larvae, pupae, and adults all have the capacity for diapause, but do the same molecular events underlie diapause in all these stages? Tantalizing data on the heat shock proteins suggest that upregulation of these genes may be a common feature in dormancies as different as sporulation in bacteria, insect diapause, and mammalian hibernation. Are other patterns of gene expression shared in dormancies across taxa? The search to identify the major genes involved in the shutting down of development and to identify unifying themes in the regulation of diapause offer exciting challenges for the future.

Reference

Denlinger, D.L. 2002. Regulation of diapause. Annu. Rev. Entomol. (in press).



Variations in the brood rearing cycle between populations of the polygynous ant Myrmica rubra L. living at different latitudes

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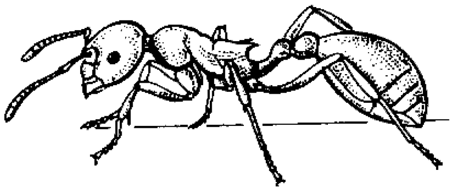
The brood rearing cycle that occurs in nearly all ant species is increasingly disrupted by a cool period (winter) at increasingly high latitudes. At high latitudes where brood rearing is restricted to seven or less months per year, ant species adapt by I) improving the thermal characteristics of their nests, ii) adapting metabolically so that "live faster" and respond more quickly to changing temperatures, and iii) take one or more years to complete a brood cycle. The common Holarctic ant genus *Myrmica* has largely evolved along the third path which necessitates brood hibernation. All *Myrmica* species in all environments, have split brood cycles - whereby some larvae from eggs laid in early summer, develop rapidly to become workers (rapid brood) while others develop more slowly, hibernate and become either workers or new queens in spring (diapause brood). Recently the St. Petersburg group have shown that in extreme environments the cycle may take three years.

In a complimentary study to that of the St. Petersburg team (see pp. 93, 102–103 and 113 in this book), we have shown that local populations adapt to increasingly high latitudes in all three ways outlined above. *Myrmica* ants of the same species from high latitudes have higher resting respiration rates and higher Q10's. Within the widespread polygynous *Myrmica rubra*, northern populations rear brood more quickly, and northern brood develops more quickly, compared to southern populations when reared under common-garden conditions. We hypothesised that individual queens are pre-disposed to producing different proportions of rapid and diapause brood. If so, we might expect queen from southern populations to invest more heavily in rapid brood and northern queens to produce more diapause brood even when reared under common laboratory conditions. Given that polygynous colonies generally produce far more eggs than the workers can rear and if the queens are quite variable in the amount of rapid brood they produce, a more complex scenario for polygynous colonies is that different types queens might achieve higher reproductive success according to the climate in any particular year. This would represent a trade-off between increased fitness at the colony level (which benefits all members in the long term) and decreased fitness for some individual queens in the short term. Here we report the results from a study of *M. rubra* queens which investigates variability in queens from different latitudes.

In this experiment we set replicated cultures of queens with workers from nests of *M. rubra* gathered from seven populations, to rear brood under common garden conditions. The geographic spread of the populations represented a considerable spread of latitude and longitude. Following the pattern established in earlier experiments, for growth of overwintered brood, queens from northern populations tended to lay eggs slightly earlier than southern ones, and workers reared them more quickly. There was no consistent pattern in the proportion of rapid brood produced although northern populations produced less. A difference in fat content, a measure of fitness, noted previously between northern and southern populations, was carried through into the next generation of workers derived from hibernated brood, even though they had all spent a year in identical laboratory conditions with abundant food. This indicates that the differences are probably inherited rather than acquired. This results are interpreted in terms of life-history adaptation to local climates and the ability of local populations to adapt to rapid climate change.



Diapause development in insects

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Introduction

It is fair to admit that we still do not know much about the processes underlying diapause development (DD) and limit our research to input to and output of a black-box. The region, considered as black-box by us, ecophysiologists, has been reduced to a certain extent by endocrinologists. Different humoral mechanisms were naturally described in diapause of larvae, pupae and adults. Moreover, diversity in humoral regulatory schemes were found even in diapause of one developmental stage (Denlinger, 1985).

Only very few findings have brought first indications on biochemical or genetic mechanisms that might be involved. To stimulate further progress in this direction, we shall try to survey what we know about DD from the point of view of ecophysiology, i.e. about the events before and after the black-box.

Some terminology cannot be avoided: essential terms as diapause completion, diapause end, post-diapause quiescence, horotelic processes of DD, tachytelic processes of DD = diapause (re)activation – have to be defined and discriminated.

Diapause – a dynamic state

In a pivotal moment of history of diapause studies, Andrewartha (1952), half century ago, introduced the notion of DD, i.e. of diapause as a dynamic state, changing dramatically in its course from diapause onset to end. Evidence of these changes, described most often as a decrease in diapause intensity, has already been brought for so many arthropod species that there are no more doubts about DD as a real event.

Some old views on DD have been modified, other conceptions are still kept by a part of the scientific community. In spite of many studies that disproved its general validity, the hypothesis of “chilling” as a prerequisite for completion of DD still survives. Mostly it is due to inadequate interpretation of experiments (examples will be given). On the contrary, the fact that in temperate climate diapause is usually completed already in early/mid winter has been generally adopted. The less frequent studies on aestivation diapause have still left unanswered the important questions about spontaneous vs. activated completion of aestivation and particularly the problem of the effect of humidity on DD vs. post-diapause development.

Horotelic/tachytelic processes of DD

Diapause can be completed by at least two types of processes. Apart from the spontaneous progress of DD (horotelic processes), a faster completion can be achieved by activation (tachytelic processes)(Hodek 1983). Although some researchers take the activation for only a faster DD that represents in principal the same mechanism, there is evidence of important differences. Thus the photoperiodic response is lost due to the completion of diapause by spontaneous DD, while after photoperiodic activation the photoperiodic response persists. Photoperiodic activation achieved due to stimulation by diapause averting photoperiods has most often been studied. However, also other kinds of activation, particularly the activation by high temperatures, have begun to be studied. When such an activation represents alternative to the spontaneous DD in the same insect population (sample), a good evidence is given for the multiple pathways of diapause completion (Danks 1987). Interesting models for studying the processes of DD are yielded by the cases where diapause completion is accelerated by injury, disease or parasitization.

Recurrent photoperiodic response

Although the irreversible loss of the photoperiodic response has generally been considered an indication of diapause completion in all insects, recurrent photoperiodic response (Hodek 1979) has been found since seventies in many cases of adult diapause. It was shown that the loss of photoperiodic response can be reversible: after several weeks of reproductive activity under diapause promoting photoperiods the insects resume photoperiodic response and discontinue reproduction. In insects living for two/several seasons this mechanism appears indispensable for the induction of the next diapause.

DD and cold hardiness

The relationship between DD and cold hardiness has not yet been studied in many species (Denlinger, 1991). In the heteropteran *Pyrrhocoris apterus*, diapause promoting daylengths induce diapause and also an increase in supercooling capacity – which is later further increased due to cold acclimation by low ambient temperatures. While the diapause condition is a prerequisite for the first phase of cold hardiness, the relation of diapause to later phases of cold hardiness is weak and gradually disappears. After diapause termination around the solstice, when the potential for development returns and the post-diapause morphogenetic development is inhibited only by adverse ambient conditions, cold hardiness is highest (Hodková & Hodek, 1994). This is made possible by the traits persisting from the diapause syndrom (de Wilde, 1970). “Overt benefits of diapause” can be retained by post-diapause insects (Tauber et al., 1986, p.58).

References

Andrewartha, H.G., 1952: Diapause in relation to the ecology of insects. Biol. Rev. 27: 50–107.

Danks, H.V., 1987: Insect Dormancy: An Ecological Perspective. Biological Survey of Canada, ,Ottawa, 439 pp.

Denlinger, D.L, 1985: Hormonal control of diapause. In: Kerkut, G.A., Gilbert, L.I. (Eds) Comprehensive Insect Physiology, Biochemistry and Pharmacology, Vol. 8. Pergamon Press, Oxford, pp.354–412.

Denlinger, D.L., 1991: Relationship between cold hardiness and diapause. In: Lee Jr., R.E. & Denlinger, D.L. (Eds), Insects at Low Temperature. Chapman & Hall, New York & London, pp. 95–127.

Hodek, I., 1979: Intermittent character of adult diapause in Aelia acuminata (Heteroptera). J. Insect Physiol. 25: 867–871.

Hodek, I., 1983: Role of environmental factors and endogenous mechanisms in the seasonality of reproduction in insects diapausing as adults. In: Brown, V.K. & Hodek, I. (Eds), Diapause and Life Cycle Strategies in Insects. Junk, The Hague, pp. 9–33.

Hodková, M., Hodek, I., 1994: Control of diapause and supercooling by the retrocerebral complex in Pyrrhocoris apterus. Entomol. Exp. Appl. 70: 237–245.

Tauber, M.J., Tauber, C.A., Masaki, S., 1986: Seasonal Adaptations of Insects. Oxford University Press, New York, 411 pp.

De Wilde, J., 1970: Hormones and insect diapause. Mem. Soc. Endocrinol. 1970: 487–514.

Regulation of brood nest temperature in honeybee colonies (Apis mellifera carnica)

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Honeybees (*Apis mellifera*) form colonies with several tens of thousand of individuals. Most colony members are sterile workers which are doing almost all the work that has to be done. Their great number allows that all tasks can be performed simultaneously, e.g. foraging, brood rearing, comb building, defence and thermoregulation. Reproduction is done by one fertile female (queen). Male honeybees (drones) are present only temporarily in the colony. In contrast to other social hymenopterans like wasps and bumblebees the whole honeybee colony survives cold seasons even in moderate climates.

Throughout the year, one challenge a honeybee colony faces is to regulate temperature to meet the requirement of the brood. Brood development is most efficient at about 35°C. If brood is reared at lower or higher temperatures, malformations of wings and mouthparts occur and mortality increases (Himmer 1927, 1932, Muzalewskij 1932, Weiß 1962, Eskov 1982). The time needed for development from egg laying to eclosion is usually 21 days for worker brood, but development is delayed if temperature sinks below 35°C (Soose 1954, Eskov 1982). Therefore great effort is made to achieve optimal nest climate.

The nest consists of several vertical combs which are built inside a cavity (e.g. a hollow tree). Cavities with apertures larger than 60 cm² are avoided and unnecessary nest openings are sealed with resin to minimise drafts (Seeley 1985). Further control of microclimate is achieved by workers behaviourally.

If the hive becomes too warm, water is collected from outside and is spread as a thin film on the combs (Lindauer 1954). Cooling is achieved by fanning and evaporation of water. Sometimes a part of the colony temporarily leaves the hive and clusters at the entrance.

If the hive becomes too cold, the bees crowd together into a cluster on the combs to prevent heat loss. Furthermore, heat is produced actively by the powerful flight muscles in the thorax (Esch et al. 1991, Heinrich & Esch 1994). However, this heat production is not associated with any visible movement of the bee or its wings and is thus difficult to observe.

Colonies which lack brood can tolerate nest temperature in a wide range, not falling below 18°C in the centre and 10°C in the periphery of a bee cluster. These two temperatures are critical minima for adult bees. If chilled below 18°C, they cannot generate the action potentials needed to activate their wing muscles and temperatures lower than 10°C immobilise honeybees (Seeley 1985).

In the past, temperatures of bees were measured with thermocouples that had to be implanted into the thorax. Esch (1960) showed that single worker bees which are engaged in brood incubation maintain thoracic temperatures above 35°C and repeatedly boost the temperature up to 40°C. These workers often sit motionless on the comb (Esch 1960, Schmaranzer et al. 1988). Furthermore, they visit empty cells in the neighbourhood of sealed brood cells (Kleinhenz et al. 2001).

Contactless infrared thermography allows to measure thorax surface temperatures of bees without any disturbance (Stabentheiner & Schmaranzer 1987). In our experiments we used this method to measure the temperatures of all bees in the brood area simultaneously.

We were interested to learn whether worker bees adjust their body temperature to the needs of the brood.

Material and Methods

Honeybees (*Apis mellifera carnica*) were kept in a 2-frame observation hive in the bee lab of the University of Würzburg. The hive contained a queenright colony with about 2000 workers and was kept indoors, however able to forage in the open. The glass covering the brood area was replaced by infrared-transparent plastic film that allowed thermographic measurements. Cooling was achieved by removing the walls of cells opposite to the side of observation and by attaching a hollow metal block (5 x 2.9 cm) to the middle wall in the centre of the brood area (9 x 9 cm). Workers were kept only on the intact observation side of the comb. Water of different temperatures (manipulation temperatures T_M = 15, 20 and 35°C) was then pumped through the metal block, thus manipulating the temperature of the brood and brood cells. Thermographic recordings (Radiance PM, $\lambda = 3.5 – 5.6$ µm; $\epsilon = 0.97$ (Stabentheiner & Schmaranzer 1987)) of the bees in the brood area were made during each manipulation, with each manipulation temperature (T_M) lasting 30 minutes. Still images were digitised every two minutes and recorded by a computer. Thorax surface temperatures (T_{Th}) of bees were calculated with camera-specific computer software (AmberTherm 1.28).

Results

The thermoregulative behaviour of worker bees were different in the manipulated brood area (14.5 cm²) compared to the surrounding non-manipulated brood area (58.5 cm²). The more the brood was cooled, the higher were the thoracic temperatures (T_{Th}) of the bees on the brood.

Manipulated brood area (14.5 cm²):

Mean T_{Th} of workers increased after begin of manipulation. At low manipulation temperature T_M, the percentage of bees with $T_{Th} > 35°C$ increased (data from 15 still images each):

$T_M = 35°C$ 40.6% (n = 183)
$T_M = 20°C$ 53.0% (n = 107)
$T_M = 15°C$ 66.2% (n = 139)

During manipulation the highest means of T_{Th} (1 image each) were:

$T_M = 35°C$ $T_{Th} = 35.3 \pm 2.3°C$ (n = 14)
$T_M = 20°C$ $T_{Th} = 37.3 \pm 3.5°C$ (n = 14)
$T_M = 15°C$ $T_{Th} = 39.3 \pm 3.1°C$ (n = 11)

Number of workers did not change significantly within each manipulation (t-Test, $p<0.05$).

Non-manipulated brood area (58.5 cm²):
Percentage of bees with $T_{Th} > 35°C$:

$T_M = 35°C$ 39.8% (n = 287)
$T_M = 20°C$ 44.1% (n = 320)
$T_M = 15°C$ 48.7% (n = 351)

During manipulation the highest means of T_{Th} were:

$T_M = 35°C$ $T_{Th} = 35.6 \pm 2.8°C$ (n = 50)
$T_M = 20°C$ $T_{Th} = 36.8 \pm 2.2°C$ (n = 41)
$T_M = 15°C$ $T_{Th} = 36.7 \pm 2.6°C$ (n = 49)

We conclude that honeybees are able to detect the need for local warming and to adjust their thermal response to the intensity of cooling. Interesting is, that no clustering on the cold manipulated brood nest occurred. However Seeley (1985) writes that clustering begins when the temperature in the nest drops below about 18°C. To test the role of clustering in brood nest thermoregulation the experiment has to be repeated with lower manipulation temperatures.

Literature

Esch H. (1960): Über die Körpertemperaturen und den Wärmehaushalt von *Apis mellifica*. Z. vergl. Physiol. 43: 305–335.

Esch H., Goller F., Heinrich B. (1991): How Do Bees Shiver? Naturwissenschaften 78: 325–328.

Eskov E.K. (1982): Pchelovodstvo 11: 28. (Summary in "Die Biene" Nr. 5/1983).

Heinrich B., Esch H. (1994): Thermoregulation in Bees. American Scientist 82: 164–170.

Himmer A. (1927): Ein Beitrag zur Kenntnis des Wärmehaushalts im Nestbau sozialer Hautflügler. Z. vergl. Physiol. 5: 375–389.

Himmer A. (1932): Die Temperaturverhältnisse bei den sozialen Hymenopteren. Biol. Rev. 7: 224–253.

Kleinhenz M., Bujok B., Fuchs S. & Tautz J. (2001): Body temperatures of worker bees (A. m. carnica) visiting comb cells. Apidologie (in press, 2001).

Lindauer M. (1954): Temperaturregulierung und Wasserhaushalt im Bienenstaat. Z. vergl. Physiol. 36: 391–432.

Muzalewskij B.M. (1933): Erfolge bei der Bebrütung der Bienen im Thermostatzimmer in U.S.S.R. Archiv für Bienenkunde 14(4): 146–152.

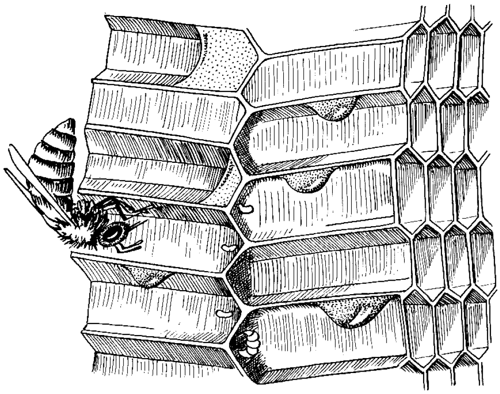
Schmaranzer S., Stabentheiner A., Heran H. (1988): Wissenschaftlicher Film: Thermografie bei Bienen. Mitt. Dtsch. Ges. Allg. Angew. Ent. 6: 136–139.

Seeley T. (1985): Honeybee Ecology, A Study of Adaptation in Social Life. Princeton University Press, Princeton.

Soose E. (1954): Einfluss der Temperatur auf die Ausgestaltung von Flügelindex und Panzerfarbe der Honigbiene (Apis mell.). Archiv für Bienenkunde 31(2): 49–65.

Stabentheiner A., Schmaranzer S. (1987): Thermographic Determination of Body Temperatures in Honey Bees and Hornets: Calibration and Applications. Thermology 2: 563–572.

Weiß K. (1962): Über die Lebensfähigkeit von offener und verdeckelter Brut ausserhalb des Bienenvolkes. Zeitschrift für Bienenforschung 6(4): 104–114.



Ecophysiological consequences of variability in diapause intensity

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Diapause intensity (DI) is a physiological trait that can be measured by the duration of diapause under certain conditions of environment. This trait is remarkably variable among different species of insects, ranging from only less than a few weeks to 10 years or more. DI is also highly variable within a species and even a population, although such variations are not always observable under the field conditions. Both genetic and phenotypic factors may be involved in DI variability.

The adaptive function of diapause depends on the proper timing of its initiation and termination, and the latter is primarily dependent on DI. Despite this ecophysiological importance in understanding diapause, DI (particularly its variability) has not been adequately explored. In this report, I will summarize data mainly obtained in our laboratory and comment on the ecophysiological significance of our findings. Author names (years) are given only for citations from other sources.

Genetic variation in DI

In the field, different populations of the same species may be dormant for different durations in accordance with the local seasonal conditions, but this does not necessarily reflect the genetic variation in DI. The genetic factors in controlling DI can be detected only in the laboratory. In the field cricket *Teleogryllus emma*, for example, the Shikoku (33°N) and Hokkaido (43°N) strains are different in DI as indicated by the mean(±sd) durations of the diapause egg stage of 209±28 and 112±14 days, respectively, at 20°C. Reciprocal crosses produced hybrid eggs with mean egg stages (165±23 and 165±27 days, respectively) intermediate between the parents. The duration of the egg stage does not segregate in F_2 so that a polygenic system seems to be involved in controlling DI.

Geographic clines of DI

In *Teleogryllus emma*, DI shows a geographic cline along the climatic gradient in the Japanese Islands, decreasing from south to north. This variation can be mostly explained by the regression of DI on the temperature conditions during overwintering (October to April). The clinal variation in DI is thus due to selection against untimely termination of diapause before winter. Such a risk is higher in the warmer south than in the cooler north, hence DI would be higher in the south than in the north.

In multivoltine species, however, reversed clinal variations in DI may occur along the same climatic gradient, presumably due to genetic correlations between the incidence and intensity of diapause. The tendency toward a lower incidence of diapause in a southern multivoltine life cycle might be associated with a lower DI.

Response to artificial selection of DI

If DI clines are results of natural selection, they might be reconstructed by artificial selection. Such an attempt has been continued in the last 20 years with the subtropical ground cricket *Dianemobius fascipes* originated from Ishigaki Island (24°N). Several lines derived from one group of adults have been selected for different durations of egg stage at 25°C, 12L12D. After 22 to 70 generations of selection (depending on the generation time), lines showing a graded series of DI have been obtained, the mean egg stage ranging from about 17 to 130 days at 25°C. This result strongly suggests the formation of DI clines by natural selection.

Phenotypical plasticity of DI

DI is a highly plastic trait and varies in response to seasonal cues. The noctuid moth *Mamestra brassicae* passes winter and summer in different types of diapause. DI is much higher for overwintering than for oversummering, being programmed by the daylength in the larval stage: winter diapause is induced in short days while summer diapause in long days. Further fine tuning of DI in each type is performed in response to the seasonal changes of daylength. DI is increased by the lengthening days before the summer solstice but decreased by the shortening days thereafter. Winter DI also varies with the larval photoperiodic conditions; shortening days tend to increase winter DI compared with stationary short days. Programming of DI in response to daylength and temperature before the diapause stage also occurs in the geometrid moth *Abraxas miranda* and the arctiid moth *Spilarctia imparilis*. In all these cases, the variations in DI result in a more synchronized termination of diapause than otherwise.

In many species, however, the diapause terminating process itself is under the incessant control of environment. In the saturniid moth *Dictyoploca japonica*, for example, summer diapause is terminated faster under short days and low temperatures than under long days and high temperatures. This response should be distinguished from the programming of DI. The two different mechanisms work together to ensure the timely completion of diapause.

DI variability expressed as polymodal eclosion

Eclosion from a diapausing population may extend over several seasons, resulting in a polymodal diapause termination. This eclosion pattern can serve as a bet-hedging strategy. Two different kinds of DI variability may underlie such polymodal eclosion. One is the coexistence of different genotypes with widely separated DI distributions within a population. The sawfly *Neodiprion sertifer* probably represents such a situation. Adults eclose from cocoons after passing 1, 2, 3 or more winters in the field and in widely separated periods of about 100, 260, 400, and 750 days after cocoon spinning under constant conditions (Sullivan & Wallace, 1967).

A unimodal genetic distribution of DI can also result in a similar polymodal termination of diapause over several years. The alpine katydid *Eobiana japonica* enters diapause at two different embryonic stages termed as initial and final diapause stages, respectively. The final diapause ends after overwintering once, but the initial diapause requires 1—3 winters to be completed. When constantly kept at 25°C, however, the cumulative percentage of eggs terminating initial diapause continuously increases until about 900 days of incubation. The unimodal distribution of DI is thus split into several groups because the cold requirement is fulfilled after one winter in some eggs with lower DI but not in others with higher DI.

This situation can be mimicked in a much shorter time span by exposing diapause insects to repeated cycles of short chilling and warming. In winter diapause pupae of *Mamestra brasicae*, 6 cycles of 5°C for 15 days and 26°C for 10 days resulted in 4 peaks of adult eclosion at 26°C after the 3rd, 4th, 5th and 6th periods of chilling, respectively.

Variability in DI expressed after overwintering

In many species of insects, winter diapause is inferred to be terminated before spring, because they start development when transferred to a high temperature in mid winter or earlier. The saturniid moth *Hyalophora cecropia* shows, however, a bimodal adult eclosion after overwintering: a small peak of eclosion occurs about one month ahead of the major one (Waldbauer & Sternburg, 1973), indicating variation in DI within the population.

In the peach fruit moth *Carposina sasakii* also, adults emerge from cocoons after winter in two peaks, the first one at the beginning of June and the second at the end of the same month. Larvae leave the infested fruits from August to December to construct diapause cocoons in the soil. The earlier the larvae spin cocoons and enter diapause, the later the adults would emerge in the following spring (Ishiguri, unpublished). Possibly, DI in the larvae is controlled by some factor in the larval stage.

Concluding remarks

DI is primarily determined (or programmed) in the process of either obligatory or facultative induction of diapause. It can be modified further by environmental factors in the early stage of diapause. The course of physiogenesis set by DI may include different phases with different responses to environmental factors (cf. Hodek, 1983; Danks, 1991). Thus, diapause is terminated through a highly complicated chain of reactions starting already in the process of its induction. We know almost nothing about this sequence of events.

“Copepods in the green” – comparing life histories and diapause of copepods and insects

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The copepods are considered the most abundant multicellular group on the earth, outnumbering even the insects, which include far more species, but fewer individuals. Copepods form the largest and most diversified class of crustaceans, and at present include over 14.000 species, 2.280 genera and 210 families. During their considerable evolutionary history, starting in the Lower Cretaceous, copepods have spread to all the continents and successfully colonised about all the available water and moisture habitats on the earth. They inhabit oceans and continental waters, semiterrestrial habitats or live in symbiotic or parasitic relationships with a whole array of other organisms. They are also well adapted and even specialised to very different salinity regimes, from marine and hypersaline waters to continental freshwater bodies, and to a wide range of temperature from the polar to the hot springs waters. As they constitute the highest biomass of any animal group in the oceans, they are commonly called “the insects of the sea”. The systematics of copepods has been subjected to numerous revisions during the last decade and before, but the great majority of all published papers on ecology, life histories and diapause are confined to the three orders Calanoida, Cyclopoida, and Harpacticoida, which mainly include the free-living forms.

An underlying assumption pervading much of the life history theory is that at least part of the variation observed within and among populations is genetically determined and represents local adaptations to specific environments. A great amount of phenotypical plasticity is nevertheless involved in the life history of copepods. The factors behind this – habitat distribution of all instars during development, predator activities, temperature and food history of the reproducing females – will commonly help explain length of cycles and reproductive patterns.

Long periods of food limitation in arctic and temperate waters, in which many copepods are distributed, forms a yearly and predictable repeated pattern. All indications suggest that the copepods are unable to survive these extended periods at normal activity levels. Overwintering in diapause is an appropriate strategy since it serves to minimise the rate of energy loss and allows the animals to sustain themselves on stored lipid reserves for several months. Lipid compounds accumulated during autumn are used during the subsequent spring reproductive period, when large amount of energy are invested in structures related to egg and offspring production. Reproduction is nearly always confined to the warm season. Timing of reproduction to coincide with favourable environmental conditions – food and temperature – is of decisive importance in the phenology of copepods, and is often dependent upon the synchronising effect of an intervening diapause phase. The rapid warming-up of the water masses following the strong insulation in spring at northern latitudes, synchronises thereafter the life cycle so that development, growth and reproduction are optimised with the environmental regime. Males and females occur simultaneously and nauplii are produced within the spring bloom of algae and bacteria.

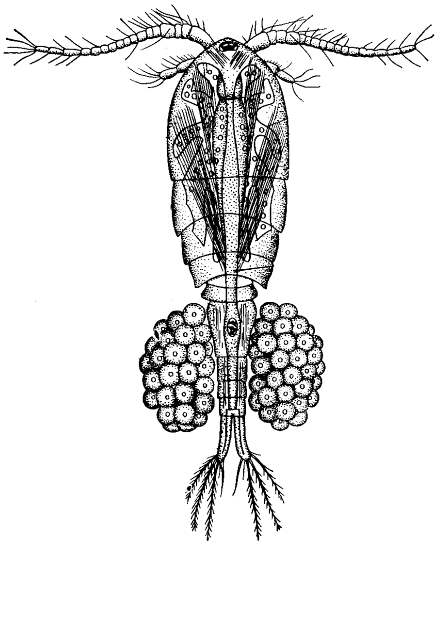
Diapause is an arrest of development and reproduction, synchronised with unfavourable parts of the season and protecting an organism against extremes of climatic conditions, predator activity or lack of food. Diapause in copepods is analogous to insect diapause. In the physiological sense it is a syndrome, comprising elements of morphogenesis, metabolism, ecological resistance and sometimes behaviour. An ecological meaningful analysis of diapause should therefore include several interacting, constantly changing variables, the altering reactions of the organisms to external stimuli, and the seasonally changing environmental cues. Duration of diapause is usually considered a good indicator of intensity of diapause, but the duration of diapause was not related to the intensity of diapause in a comprehensive study of diapausing cyclopoid populations and species.

Local populations of cyclopoid copepods are often composed of different cohorts, overwintering in the benthos under anaerobic conditions or in the plankton close to the sediment surface, ensuring the population a greater amount of buffering against ecological catastrophes. For studying evolutionary factors influencing life histories of copepods, research has been initiated to compare population losses during dormancy in different habitats. Stored body lipid has a secondary effect by influencing buoyancy and vertical movements in the water masses and thus minimising the energy needed to overwinter in the plankton.

Prior to diapause initiation a trade-off was observed between ability to reproduce and ability to enter physiological arrest. This could also be due to a necessary seasonal tuning of the ovarian development. A distinct degradation in the digestive system of copepods is also associated with this phase. The low egg production obtained by feeding animals during and shortly after induction of diapause may indicate that stored lipid was not used for egg release during this period of the year. Probably only recently ingested food in the laboratory was used for immediate offspring production, while the considerable amounts of stored lipids, originating from food collected during autumn, were allocated for early oogenesis and metabolic maintenance during period of low food abundance during the subsequent spring, after a necessary intervening diapause phase.

Two contrasting types of resting stages are observed in copepods, embryonic or egg diapause (with direct or delayed development) and late instar diapause, generally confined to copepodid stages IV–V. In addition, some species have been found to possess early instar and some adult diapause. More conspicuously is the common observation that many species possess eggs which may show delayed hatching for up to several hundred years, producing a so-called “egg-bank” structure, comparable to “seed-bank” in plants. The existence of such a storage bank may have far-reaching evolutionary implications concerning future population composition, thus providing a mechanism to connect cohorts many generations apart. It allows also species specific stability in unstable environments.

Since the copepod group is abundant in all kinds of water ecosystems, selection have produced a wide variety of life histories. Many pelagic oceanic and inland water species have been extensively studied for many decades, and are therefore known in considerable detail. Since both insects and copepods are arthropods, scientists working on copepods have frequently profited by advances in insect ecology and physiology. Literature on insects therefore constitute a significant part of the references cited in all major papers on e.g. copepod life cycle and diapause. The aim of this paper is to present some recent advances in studies on copepod life histories and diapause, which could be of interest for entomologists as well.



Photoperiodism and seasonal adaptations in some phytophagous heteropterans

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There are many heteropterans that feed on plant seeds in the Kyoto-Osaka area (about 35°N), central Japan. Do they have similar photoperiodic responses and life cycles? In this paper, I show photoperiodic responses in nine of these species. All of them overwinter as diapause adults, and are classified in Pentatomidae except *Riptortus clavatus* belonging to Alydidae. However, their photoperiodic responses varied so much, and I discuss their adaptive significance.

1. Riptortus clavatus

This species feeds on seeds of legumes, and produces three generations a year. The induction of adult diapause was controlled by a long-day photoperiodic response. The critical daylength was about 13.5 h at 25°C, which corresponds to the length of late-August days including twilight at 35°N (Numata and Hidaka, 1982). This photoperiodic response well explains the emergence of diapause adults in September and October in the field.

2. Dolycoris baccarum

This is a polyphagous species that feeds on seeds of various plants, such as legumes, crucifers, gramineous grasses, and composites. Its life cycle and photoperiodic response were similar to those of *R. clavatus* (Nakamura and Numata, unpublished).

3. Plautia crossota stali

This species is also polyphagous, and feeds on seeds of various plants, such as the cherry, the mulberry and cypresses. The life cycle and the photoperiodic response were similar to those of *R. clavatus* and *D. baccarum* (Numata and Kobayashi, 1994).

4. Aelia fieberi

This species feeds on seeds of gramineous grasses. The induction of adult diapause was controlled by a long-day photoperiodic response. However, the critical daylength was about 14.5 h at 25°C, which is longer by 1 h than those of the above three species and corresponds to the length in late-July days including twilight at 35°N. With this response, adults of the second generation entered diapause in August, although temperature seemed to be sufficient for producing another generation. Although seeds of gramineous grasses existed in the field from spring to autumn, some of them were unsuitable for nymphal development as food. All the suitable food disappeared in August. Therefore *A. fieberi* has a longer critical daylength and enters diapause as early as August, showing a bivoltine life cycle (Nakamura and Numata, 1997).

5. Nezara viridula

This is a polyphagous species that feeds on seeds of various plants, such as legumes, gramineous grasses, and crucifers. It showed a long-day photoperiodic response for the induction of diapause, and the critical daylength was about 12.5 h at 25°C, which is shorter by 1 h than those of *R. clavatus*, *D. baccarum* and *P. c. stali* (Musolin and Numata, unpublished). In 1960s, this species was distributed in the southern part of Japan but not in Osaka, although it is now common in Osaka. The shorter critical daylength may reflect the subtropical origin of this species. However, it is still unclear whether *N. viridula* produces more than three generations a year and overwinters in Osaka, or migrates from southern overwintering sites every year.

6. Nezara antennata

This species is also polyphagous like *N. viridula*. Contrary to the above five species, adults of *N. antennata* entered diapause both under long-day and short-day photoperiods at 25°C. Only when adults were transferred from a long-day to a short-day photoperiod, they began to lay eggs. It is suggested that adults of the first generation develop under long-day photoperiods, enter summer diapause, and begin to lay eggs only after decreasing of daylength. Thus, the long-day-short-day response ensures a bivoltine life cycle (Numata, unpublished). Nymphs of this species are not tolerant to high temperatures as compared to *N. viridula*. Therefore, this summer diapause induced by a long-day photoperiod has a function to avoid unfruitful production of nymphs in the hottest season.

7. Graphosoma rubrolineatum

This species feeds on seeds of Umbelliferae. Some individuals showed a long-day photoperiodic response, and the critical daylength was about 14.5 h at 25°C. However, more than 50 % of adults entered diapause even under a long-day photoperiod. It is, therefore, suggested that some adults of the first generation that develop under long-day photoperiods produce the second generation whereas the others enter diapause and overwinter. Host plants of *G. rubrolineatum* produce seeds only in a limited period around early summer in Osaka, and the absence of suitable food is the primary factor determining the timing of diapause induction (Nakamura and Numata, 1999).

8. Dybowskyia reticulata

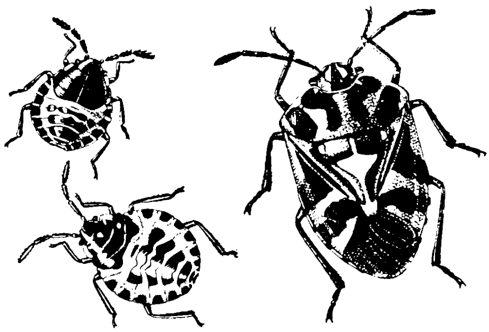
This species also feeds on seeds of Umbelliferae. Most adults entered diapause irrespective of the photoperiod at 20 and 25°C. At 27.5 and 30°C, however, adults raised under a long-day photoperiod prevented diapause. Even though the seeds of the host plants occur in a restricted period around early summer, *D. reticulata* may produce a second generation in warmer years. The response to temperature with a threshold between 25 and 27.5°C brings about a switch between the univoltine and bivoltine life cycles (Nakamura and Numata, 1998).

9. Eurydema rugosum

This species feeds on seeds and leaves of crucifers. When fed on seeds of the oilseed rape, most adults entered diapause irrespective of the photoperiod, although they showed a long-day photoperiodic response on leaves of the same plant at 25°C (Numata and Yamamoto, 1990). In the field, the brown mustard *Brassica juncea* bloomed in early spring and the whole plants died by early summer. When growing on this plant, adults of the first generation emerged in early summer, and most of them entered diapause. However, some cultivated crucifers kept green leaves all year round. On these plants, most adults of the first generation reproduced and those of the second generation emerging in late summer entered diapause. Therefore, *E. rugosum* shows either a univoltine or bivoltine life cycle, depending on the phenology of host plants (Ikeda-Kikue and Numata, 2001).

References

Ikeda-Kikue, K. and Numata, H. (2001) Acta Soc. Zool. Bohem. 65 (in press)
Nakamura, K. and Numata, H. (1997) Ann. Entomol. Soc. Am. 90: 625–630.
Nakamura, K. and Numata, H. (1998) Physiol. Entomol. 23: 69–74.
Nakamura, K. and Numata, H. (1999) Appl. Entomol. Zool. 34: 323–326.
Numata, H. and Hidaka, T. (1982) Appl. Entomol. Zool. 17: 530–538.
Numata, H. and Kobayashi, S. (1994) Experientia 50: 969–971.
Numata, H. and Yamamoto, K. (1990) Entomol. Exp. Appl. 57: 281–284.



Understanding insect life cycle regulation: the optimality approach

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How can we better “understand” insect life cycles, I. e. go beyond empirical and descriptive studies of one system after the other? To be able to do this we need a unifying theory on which to base explanations, generalisations and predictions. Since nature is a product of evolution, evolutionary theory can provide this theoretical base and we can use optimality reasoning. We can ask ourselves what the traits of an organism will be like if traits resulting in higher evolutionary fitness are typically those which will be observed. By way of illustration, I will briefly delineate some results from my research group, studying the evolution of seasonal plasticity with butterflies as model insects. In particular, I aim to show how optimality reasoning gives us the means to *interpret* and *explain*, to *generalise* and to *predict*.

1. Photoperiodic thresholds for diapause induction have been observed to show latitudinal variation among populations in relatively stationary insects (Danilevskii 1965). This can be easily *explained* in adaptive terms, and it is for this reason possible to *generalise* to other insects under similar circumstances and thus *predict* similar patterns. Latitudinal variation was indeed found in, e.g. *Polygonia c-album* (Nylin 1989) and *Pararge aegeria* (Nylin et al. 1995b).

2. Variation in photoperiodic thresholds within populations has seen comparatively little study. Ignorance of this type of variation may be one source of erratic forecasting and of difficulties with explanations using hindsight. It could be expected that often some proportion of the population should follow a life cycle with a smaller number of generations per year than the average. This is because in some very poor years only these individuals will succeed in giving rise to offspring reproducing the next year. This reasoning was used to *explain* such a pattern in *Pieris napi* (Wiklund et al. 1991), but to my knowledge, *predictive* studies are lacking.

3. Males often enter the reproductive population before females, a phenomenon known as *protandry*. When e.g. monitoring insects for pest management it is important to be aware of such temporal patterns. The pattern itself can be *explained* by sexual selection theory (Wiklund and Fagerström 1977), which can also be used to *predict* exceptions, as was done in a comparative study of two populations of *Pararge aegeria* (Nylin et al. 1993).

From protandry theory, males can also be *predicted* to be more prone to enter diapause than females under near-critical conditions, i.e. the sexes should differ in photoperiodic thresholds (Wiklund et al. 1992). This was indeed found in several species of butterfly, and was also used to *explain* the same pattern in another butterfly, which was not studied by us (Nylin et al. 1995a).

4. It was observed in crickets that development time was progressively shorter the shorter the daylengths used for rearing (Masaki 1978). This was given the adaptive *explanation* that it serves to ensure that all individuals reach the developmental stage suited for diapause in time for winter, because in autumn shorter daylengths signal later dates.

When similar reaction norms were observed in *P. aegeria*, we could *generalise* from crickets to butterflies to provide an adaptive explanation (Nylin et al. 1989). In this case, reaction norms with shorter development times in shorter daylengths were observed both in a range of long daylengths (inducing direct development) and in a range of short daylengths (inducing diapause). Thus, we *generalised* also between developmental pathways, reasoning that under direct development a shorter daylength instead means less time to produce another generation, and hence still a need for a shorter development time.

5. For a more critical test of the adaptive hypothesis, we performed a series of true experiments on this and related satyrine butterflies.

First, we compared reaction norms in *P. aegeria* from different latitudes, *predicting* steeper reaction norms relating development time to daylength in the north (where the seasonal amplitude in daylength variation is highest). This pattern was indeed found (Nylin et al. 1995b).

Second, we compared two closely related species of *Lasiommata* butterflies differing in the stage used for hibernation. In one species individuals spend the winter as half-grown larvae, so that late-instar larvae occurs before summer solstice when daylengths are increasing. In the other species, hibernation is in the pupal stage, so that late-instar larvae occur in the autumn when daylengths are decreasing. Hence short daylengths should signal the need to complete development rapidly in the latter species, but the reverse should be true in the former. This *prediction* held true, as demonstrated by reaction norms with opposite slopes (Nylin et al. 1996).

Next, we compared reaction norms before and after hibernation in two species that spend the winter in the larval stage, so that daylengths in the field are decreasing in early instars and increasing in late instars. G*eneralising* from the previous late-instar results in these and other species, we *predicted* opposite reaction norms to be displayed by the same larvae in early instars, and this was what we found (Gotthard et al. 1999).

Finally, we investigated how temperature interacts with photoperiod and the developmental stage of the larvae in one of these species. We reasoned that in autumn (pre-hibernation larvae) high temperatures "should" be used to speed up growth and development in short daylengths, because they signal a late date. The effect should not be equally strong at long daylengths that signal plenty of time left in the season. The opposite should be true in the spring (post-hibernation larvae). These interactions were exactly what we found; in fact, temperature had negligible effects on larval growth rates when daylengths suggested that there was ample time for completing development (Gotthard et al. 2000). Such results graphically illustrate the need for more plasticity and life cycle regulation studies based on optimality reasoning and life history analysis.

References

Danilevskii, A. S. 1965. Photoperiodism and seasonal development of insects. *(English edition) Oliver & Boyd, Edinburgh and London* .

Gotthard, K., S. Nylin, and C. Wiklund. 1999. Seasonal plasticity in two satyrine butterflies: state-dependent decision making in relation to daylength. *OIKOS* 84: 453–462.

Gotthard, K., S. Nylin, and C. Wiklund. 2000. Individual state controls temperature dependence in a butterfly (Lasiommata maera). *Proceedings of the Royal Society of London Series B-Biological Sciences* 267: 589–593.

Masaki, S. 1978. Seasonal and latitudinal adaptations in the life cycles of crickets. *In: H Dingle (Ed) Evolution of insect migration and diapause Pp 72–100 Springer-Verlag, Berlin-New York* .

Nylin, S. 1989. Effects of changing photoperiods in the life cycle regulation of the comma butterfly, Polygonia c-album (Nymphalidae). *Ecol Entomol* 14: 209–218.

Nylin, S., K. Gotthard, and C. Wiklund. 1996. Reaction norms for age and size at maturity in Lasiommata butterflies: predictions and tests. *Evolution* 50: 1351–1358.

Nylin, S., P. O. Wickman, and C. Wiklund. 1995a. An adaptive explanation for male-biased sex ratios in overwintering monarch butterflies. *Animal Behaviour* 49: 511–514.

Nylin, S., P. O. Wickman, and C. Wiklund. 1995b. Life-cycle regulation and life history plasticity in the speckled wood butterfly: are reaction norms predictable? *Biological Journal of the Linnean Society* 55: 143–157.

Nylin, S., P.-O. Wickman, and C. Wiklund. 1989. Seasonal plasticity in growth and development of the speckled wood butterfly, Pararge aegeria (Satyrinae). *Biol J Linn Soc* 38: 155–171.

Nylin, S., C. Wiklund, P. O. Wickman, and E. Garciabarros. 1993. Absence of trade-offs between sexual size dimorphism and early male emergence in a butterfly. *Ecology* 74: 1414–1427.

Wiklund, C., and T. Fagerström. 1977. Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia (Berl)* 31: 153–158.

Wiklund, C., S. Nylin, and J. Forsberg. 1991. Sex-related variation in growth rate as a result of selection for large size and protandry in a bivoltine butterfly (Pieris napi L.). *Oikos* 60: 241–250.

Wiklund, C., P.-O. Wickman, and S. Nylin. 1992. A sex difference in reaction norms for direct/diapause development: a result of selection for protandry. *Evolution* 46: 519–528.

Selection for larval development time in the blow fly Calliphora vicina alters the maternal critical daylength

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Larval diapause in the blow fly *Calliphora vicina* is characterised by greatly delayed pupariation. Adult female flies subjected to the long days of summer produce larval progeny that pupariate rapidly (i.e. they become nondiapause larvae) whereas those that experience short autumnal days give rise to larvae that delay pupariation (i.e. enter diapause) (Vinogradova and Zinovjeva, 1972; Saunders, 1987). Diapausing larvae acquire a degree of cold tolerance (Saunders and Haywood, 1998) and pass the winter in the soil, delaying pupariation until the spring. For a population of *C. vicina* from the Edinburgh area (55°N) the maternal critical daylength is about 14½ hours/24.

Using a diapause depleted laboratory strain of *C. vicina*, selection for larval development time (early or late pupariation) led to either the elimination of diapause or its full restoration within very few generations without altering the critical daylength. Selection for delayed pupariation (high diapause) under LD 16:8 (a 'long' day at 55°N), however, led to an apparent shift in the critical daylength from about 14½ to about 16½ hours/24 and a rise in diapause incidence under the longer photoperiods. Such selection appeared to produce a population of flies whose photoperiodic responses resembled a natural population from a much more northerly latitude. Experiments are now in progress to ascertain whether selection has altered phase relationships of the circadian 'clock' oscillators to the light cycle, or merely raised the incidence of diapause at each daylength.

References

Saunders, D.S. (1987) Maternal influence on the incidence and duration of larval diapause in *Calliphora vicina. Physiological Entomology* **12**, 331–338.

Saunders, D.S. and Haywood, S.A.L. (1998) Geographical and diapause-related cold tolerance in the blow fly, *Calliphora vicina. J. Insect Physiol.* **44**, 541–551.

Vinogradova, E.B. and Zinovjeva, K.B. (1972) Maternal induction of larval diapause in the blowfly, *Calliphora vicina. J. Insect Physiol.* **18**, 2401–2409.

Latitudinal and local geographic mosaics in host plant preferences as shaped by thermal units and voltinism

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In high latitude locations in North America with "constrained" seasonal thermal unit accumulations, such as central Alaska, there are barely sufficient degree days above the base developmental threshold for tiger swallowtail butterflies (*Papilio* species) to complete mating, egg & larval development in time to reach the diapausing pupal stage. Numerous adaptations of different life stages allow successes to be maximized under these limiting conditions at latitudes of 65 degrees North (Ayres and Scriber, 1994). Photoperiod-insensitive (obligate) diapause of pupae is a characteristic of these populations, and also perhaps of the entire *Papilio canadensis* species, even into the Great Lakes region between the USA and Canada. This trait is X-linked in *P. canadensis* (females are the heterozygous sex in butterflies).

Similarly, strong selection pressures (for rapid growth, smaller pupal sizes, bigger eggs and neonate larvae, shorter molt durations at low temperatures, and selection of the most nutritious host plant species for oviposition) due to severe thermal constraints may be operational in lower latitude "cold pockets". These areas have very few freeze-free days between the last Spring and first Fall freezes. For example, in northern Michigan (45–46 degrees North), these cold pockets are classified in the same plant hardiness zone (category #3; USDA Misc. Publ. #1475) as Fairbanks, Alaska. The average freeze-free period of summer growth is only 70 days (and in 10% of the years, it is only 40 days; Scriber, 1994). For the 50 years from 1930–1979, the average dates for the last spring freezes in these northern Michigan cold pockets were June 5^{th}–25^{th} (or as late as July 10^{th} in 10% of the years). Combined with the early Fall freezes in this same area (August 25^{th} on the average, but August 15^{th} in 10% of the years), insect growth is constrained and the climatic region even looks like Alaska and northern Canada, with stunted black spruce, larch, paper birch, balsam poplar, and aspen.

However, unlike the situation in Alaska, the immediate surrounding area (only 50–100 km outside) of the "cold pockets" is much warmer, averaging 90–125 freeze-free days with more than sufficient seasonal degree days to easily support the completion of the life stages of the univoltine *P. canadensis* swallowtail butterflies. As with the general continent-wide latitudinal bands pattern of cold areas and thermal constraints (and "intense" selection pressures) alternating with warmer bands with "relaxed" selection pressures (Scriber and Lederhouse, 1992), it was postulated that the cold pockets would operate the same way (locally and longitudinally as well as latitudinally; Scriber 1996). To assess this possibility, and the hypothesized adaptations of these populations, we conducted several studies of these Michigan cold pockets and surrounding areas during the last decade. The 1991–2000 period includes both the coldest and warmest years ever recorded.

The "voltinism-suitability hypothesis" postulates that insect herbivores with severe thermal constraints for completion of the generation will select the most nutritious host plant species for larval growth with local specialization by ovipositing females. In contrast, those insect populations with abundant seasonal "degree day" accumulations will not be as selective of the best hosts since they can complete development to the diapausing pupal stage on all host plant species. At these warmer locations local polyphagy is observed, which may be advantageous for other reasons (e.g. escaping generalized parasites and predators).

One obvious concern for this geographically-based host preference model is that host leaf quality does not remain constant throughout the season. In fact, different species of trees have leaves that are unique in their timing of bud-break. Normal fully-expanded and mature leaves have distinct water and nitrogen contents (which index nutritional "suitability" for larval growth of most leaf chewers; Scriber, 1984; Mattson and Scriber, 1987). Also rates of decline in nutritional quality (i.e. increase in leaf toughness and decline in nitrogen and water) are also unique for different tree species.

The interaction between the local abiotic thermal unit accumulations and biotic host preferences is mediated by a geographic mosaic of cold pockets and "phenological twisting" of relative host plant suitabilities. In Michigan, white ash (and other *Fraxinus* species) rapidly declines in quality after the leaves have fully expanded, which is most of the season (mid-May through abscission in September) in southern Michigan. However, because of delayed bud-break and slow leaf expansion relative to other host plant species such as cherry (*Prunus* species), basswood (*Tilia*), paper birch (*Betula*) and quaking aspen (*Populus tremuloides*) or balsam poplar (*P. balsamifera*), ash actually provides the highest quality leaves for larval growth in the cold pockets for most of the growing season (mid-June to late July). Outside of these coldest areas ash leaves have already rapidly declined in nitrogen and water (in early June), having actually become a much poorer host than cherries, some aspens, and birch for fast larval growth of *Papilio canadensis* in the north (as for *P. glaucus* to the south). This "phenological twist" of ash quality locally, inside the cold pockets, may explain the surprisingly strong oviposition preferences for ash leaves of *Papilio* females here as opposed to areas outside (Scriber 1996). Leaf samples across a 200 km northern longitudinal transect illustrate the higher quality of ash (*Fraxinus americana*) leaves in the cold pocket relative to those ash leaves from outside. There is a lack of such geographic twist in the patterns for cherry species, aspens, and birch.

In southern Michigan (latitude 41.5–42.5°N), the average degree day accumulations (1930–79) reflect enough thermal units for potential completion of two generations for the tiger swallowtail butterfly, *Papilio glaucus* in most years.

However, success of this second generation reaching the diapausing pupal stage depends very much upon the choice of host plant species. Poor hosts such as paper birch, spicebush, sassafras, choke cherry and white ash do not permit two generations to be completed. This is also an area south of the hybrid zone and here the tiger swallowtails almost entirely *P. glaucus*, which has a photoperiod-induced pupal diapause tendency. Some individuals seem to "assess" their developmental stage and diapause as a possible "bet-hedge" for surviving the oncoming winter. Others do not diapause, and when on poor hosts in the second generation, simply fail to reach the pupal stage before the leaf quality severely declines (or abscission occurs). Some actually freeze to death as 4th and 5th instars while trying to complete development of the second generations as late as mid-October (Scriber and Gage, 1995).

Recent trends in regional climate warming have been documented throughout the Great Lakes region and New England, with 1998 and 1999 as especially warm years as indicated by seasonal degree day accumulations. Weather data from transects across the northern Michigan cold pocket show considerable year-to-year variation in the growing season degree days. While the "cold pocket" is still evident in 1998 and 1999 transects, it was unlikely to have imposed a strong constraint on completion of larval development as it had clearly done in the cooler 1970's and early 1980's, as well as in 1992, 1993, and 1994. This regional climate warming allows us to evaluate the degree of "relaxation" of host preference (and other) selection gradients from the cold pocket outward.

Trait clines have been documented north and south of the butterfly hybrid zone in Michigan, central Wisconsin, New York State and Vermont since the early 1980's. Considerable northward introgression has been observed for detoxification of and oviposition preferences of tulip tree leaves, morphological wing traits, and PGD-100 and HK-100 allozymes. However, there has been little introgression of other *P. glaucus* traits (such as facultative diapause, dark morph females, and LDH-100 allozymes) across the hybrid zone. A strong selection pressure on some trait and close linkage of LDH-100 with that trait therefore seems likely at latitudes of the interspecific hybrid zone. However, we have not yet been able to thoroughly document intraspecific genetic changes in the cold pocket populations, if they have occurred recently.

One change that has occurred in the last 3–4 years southward, near the southern edge of the hybrid zone at the regions corresponding to the average degree-days accumulated seasonably of 2500–2700 F (1400–1500 C), is the increased frequency of "false second generations". These July flights are not true second generations derived from the first one that year (in late May or June), because there are insufficient degree-day accumulations for pupal, egg, and larval development to be possible. We have proposed that occurrences of these "false" second generations may basically be the result of interspecific hybridization and genetic introgression. Specifically we have shown that such second flights could result from staggered adult eclosion times from overwintering (diapausing) pupae. For example, the adults of *P. canadensis* emerge early (15–43 days; mean 28 d at

14 C degrees), with *P. glaucus* last to emerge (26–73 days; mean 56 d). The interspecific hybrids between these two species emerge at times intermediate to those of the parental types (29–52 d; mean 37 d), and these could be the "false second generation" flights we have observed in July after the first early summer peak. Electrophoresis of the New York/ Vermont population (Washington Co. NY/ Bennington Co. VT) suggests that the first adults are in fact very "canadensis-like", while the "false" second flight reflects significant genetic introgression from *P. glaucus*. Morphological traits (forewing lengths, diagnostic black wing bands in the hindwing anal cell, etc.) support this pattern for "false"a second generation flights in the NY/VT population and also throughout all of Massachusetts.

References

Ayres, M.P. and J.M. Scriber. 1994. Local adaptations to regional climates in *Papilio canadensis* (Lepidoptera:Papilionidae). *Ecological Monographs* 64: 465–482.

Mattson, W.J. and J.M. Scriber. 1987. Nutritional ecology of insect folivores of woody plants: water, nitrogen, fiber, and mineral considerations. In F. Slansky, Jr. and J.G. Rodriguez (eds.) *Nutritional Ecology of Insects, Mites, and Spiders*. John Wiley, NY. pp. 105–146.

Scriber, J.M. 1984a. Insect/Plant Interactions - Host plant suitability. In W. Bell and R. Carde (eds.) *The Chemical Ecology of Insects*. Chapman and Hall, London, pp. 159–202

Scriber, J.M. 1994. Climatic legacies and sex chromosomes: latitudinal patterns of voltinism, diapause size and host-plant selection in 2 species of swallowtail butterflies at their hybrid zone. In H.V. Danks (ed.) *Insect life-cycle polymorphism: theory, evolution and ecological consequences for seasonality and diapause control.* Kluwer Academic Publ., Dordrecht, Netherlands. pp. 133–171.

Scriber, J.M. 1996. A new cold pocket hypothesis to explain local host preference shifts in *Papilio canadensis*. 9th Intern. Symp. Insects & Host Plants. *Entomol. expt. & appl*. 80: 315–319.

Scriber, J.M. and R.C. Lederhouse. 1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbivores. In M.R. Hunter, T. Ohgushi and P.W. Price (eds.) *Effects of Resource Distribution on Animal-Plant Interactions*. Academic Press, NY. pp 429–466

Scriber, J.M. and S. Gage. 1995. Pollution and global climate change: Plant ecotones, butterfly hybrid zones, and biodiversity. In J.M. Scriber, Y. Tsubaki, and R.C. Lederhouse ((eds.*) Swallowtail Butterflies: Their Ecology and Evolutionary Biology.* Scientific Publishers, Inc., Gainesville, FL. pp. 319–344.

Ecophysiological and morphological variations in the Culex pipiens complex mosquitoes (Diptera, Culicidae)

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The *Culex pipiens* complex mosquitoes distributed almost over all world are of great fundamental, medical and veterinary importance. They are known as bloodsuckers actively attacking the humans, primarily in urban environment and as vectors of various agents (the lymphatis filariosis, Japan, St. Louis and West Nile encephalitises, Rift Valley fever and avian malaria). High ecophysiological plasticity and intricate taxonomic structure of this complex have long attracted attention of specialists. The *Culex pipiens* complex includes *C. p. pipiens* [*pipiens* s. str. (anautogenous) and *molestus* (autogenous) forms], *C. p. quinquefasciatus, C. p. pallens, C. p. australicus, C. torrentium* and *C. vagans*. The taxonomic status of some members is still open to discussion. This complex is unique because a relatively small morphological differentiation and great variation of the diagnostic features are coupled with the significant ecophysiological differences (autogeny, stenogamy or eurygamy, reproductive diapause).

The main morphological differentiating characters include the structure of the male genitalia, larval siphon and some others. In males of diagnostic value is the DV/D ratio (Rozeboom, 1951). This ratio is smaller (<2) in *C. p. pipiens*, being larger (>4) in *C. p. quinquefasciatus* and intermediate in *C. p. pallens*. However, its clinal variation in the population groups from southeast Asia and North America and also considerable typological variation diminish the diagnostic value of this genital feature. Among all larval structures the siphonal index was widely used to discriminate two worms in *C. p. pipiens*. Ecological, physiological and geographical variations are recorded in the siphonal index of *C. p. pipiens*. Our special ANOVA analysis (Vinogradova et al., 1996) showed that the mean siphonal index is strongly correlated with adult physiology (autogeny) and larval ecology (water body type). It may be used with certainty to differentiate between populations of two forms, being usually <4.4 in the *molestus* form and >4.8 in the *pipiens* form. The combinative (genetic) variation as consequence of the crosses between distinct forms and modificative variation due to the temperature of development were also recorded for the siphonal index of *C. p .pipiens*.

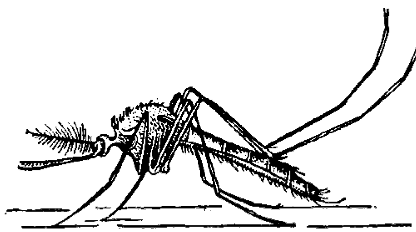
A crucially new step in the working out the morphological diagnostics of the *C. pipiens* complex members is connected with the use of discriminant analysis. Kruppa (1988) first estimated the degree of morphological divergence between members using the Malanobis distance and established for every of them the stages more suitable for diagnostics.

The members of the *C. pipiens* complex differ by next alternative ecophysiological features: 1. Autogeny (the production of the first egg rafts without a blood meal) or its absence. Only the *molestus* form is autogenous. 2. Stenogamy (the ability to mate in small cages) or eurygamy (the requirement for a larger space for mating). The *molestus* and *quinquefasciatus* members are stenogamous, whereas the remainder is eurygamous. 3. Reproductive diapause or inability to overwinter. Only the molestus and *quinquefasciatus* members are nondiapausing.

The distinct members of *C. pipiens* complex may be differentiated by the enzymic characters. The isozyme patterns were studied in the populations from USA, Egypt, Italy, Israel and the former USSR. In latter case both forms of *C. p. pipiens, C. vagans* and *C. torrentium* may be identified by their isozymic spectra of four polymorphic enzymes (GPI, PGM, IDH and ME).

Biotopic specialization of larvae are recorded in the *C. pipiens* complex, but it is not absolute and a few mixed populations occur in nature. *C. vagans, C. torrentium* and *p. australicus* prefer the more clean, meso- or oligotrophic waters, whereas *C. p. pipiens* and *C. p. quinquefasciatus* inhabit the wide spectrum of habitats including very polluted, polysaprobic waters. The *C. p. pipiens* larvae occur in eleven of 12 known types of larvae mosquito habitats. In moderate zone the permanent molestus populations may exist whole year round only in such specific ecological niche as flooded underground sites (basements, etc.) in cities.

In moderate zone three mechanisms providing the isolation between the *molestus* and *pipiens* forms in sympatric populations may be recorded: 1. The biotopic specialization of larvae 2. The diapause inheritance pattern in cross between the *pipiens* and *molestus* forms. It is inherited as a recessive character, therefore all F1 hybrids cannot diapause and must be eliminated during winter, only a small part of F2 hybrids (23%) enter diapause 3. The pattern of the precopulation behaviour (steno- or eurygamy) and also the different mating places.



What determines the strategy of cold hardiness ?

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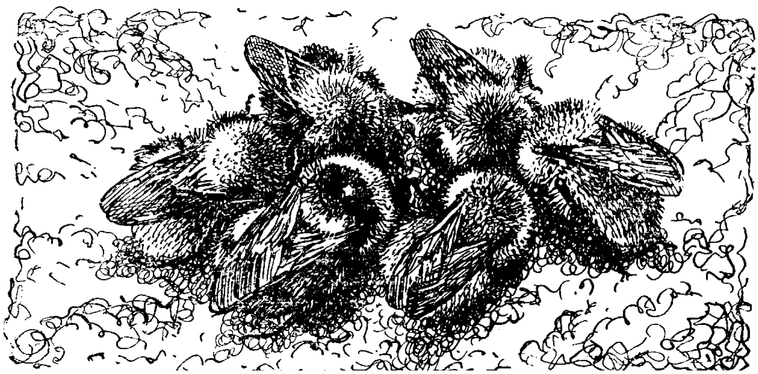
Cold-hardy insects survive low temperatures by freeze avoidance or by tolerance to freezing. Freeze avoiding organisms promote supercooling by removing all ice nucleating substances (food particles and proteins) from their body fluids. Many species enhance their supercooling capacity further by accumulation of polyols to multimolal concentrations and by producing antifreeze proteins. Freeze-tolerant organisms mask the activity of injurious ice nucleators by securing a protective extracellular freezing at a high subzero temperature. They may also reduce the amount of water frozen by polyol accumulation and hence become highly cold hardy.

Although these two strategies are in several respects fundamentally different, there are also similarities which allow certain species to switch between the strategies.

The strategy used is probably determined by a number of factors. Tolerance to freezing seems to be preferred by alpine organisms, which combine cold exposure at night and activity in the day time, and which have an intact enzymatic system and food particles in the intestine. Freezing tolerance is also promoted by large body size, which makes supercooling difficult. Also organisms exposed to extremely low temperatures are likely to be tolerant to freezing, because the polyols have a far greater cold-hardening potential in freeze-tolerant than in freeze-avoiding organisms. Since frozen fluids are in vapour pressure equilibrium with ice, also organisms with poor water conserving capacity are likely to develop freezing tolerance. The choice of strategy may also be influenced by the levels of metals in the body fluids. Since the increase of solute concentrations to toxic level is assumed to be an important cause of injury during freezing, the presence of one solute such as for example Na at high concentrations in the body fluids of a species should not favour the strategy of freezing tolerance. In spite of this expectation, several species with high extracellular Na concentrations (such as carabids) are tolerant to freezing, implying that these species possess special protective mechanisms to counteract toxic Na concentrations.

Also shortage of certain substances may influence the choice of cold hardiness strategy. Organisms exposed to toxic trace metals may produce large amounts of metallothioneins to protect themselves. Metallothioneins are notorious for their high content of cystein, which is also an important component of the antifreeze proteins of many insects. Since cystein levels are usually low, insects exposed to high levels of trace metals may have spent so much cystein for metal detoxification that they are unable to produce sufficient amounts of antifreeze proteins to stabilize supercooling. This may make the strategy of freezing tolerance favourable also in metal exposed insects.

In agreement with this, the strategy of supercooling is likely to be found in small organisms, in insects which may be inactive over so long periods that they can undergo cold hardening changes incompatible with activity, and in insects having a cuticle with low water permeability.



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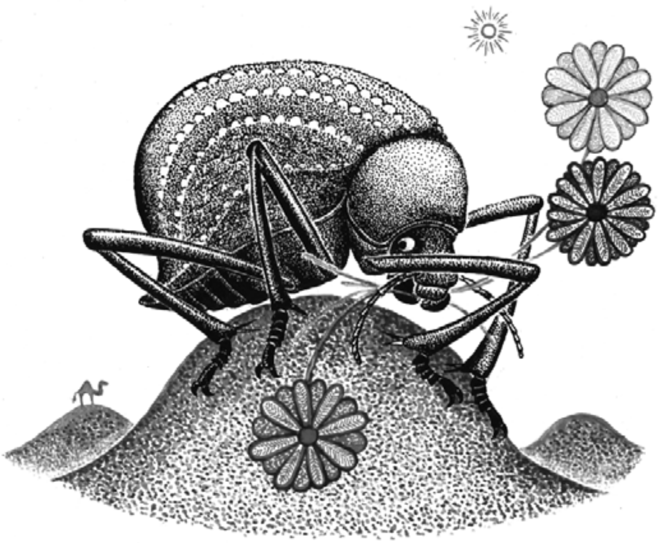

Drawing by N. Yu. Kluge

Study of terpenoids from excrements of larvae of Siberian moth Dendrolimus superans Butl. fed on different host plants

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The Siberian moth *Dendrolimus superans* Butl. is dangerous pest of coniferous forests in Siberia and Russian Far East. Periodic outbreaks are characteristic for this species and occur every 10–15 years causing total defoliation and, eventually, death of trees. The total area of coniferous forests, which have been destroyed by the Siberian moth since the beginning of the 20th century, was more than 13,000,000 hectares. Chemical changes in soil affected by huge amount of feces coming from the caterpillars feeding on coniferous needles seem to be among the main reasons of slow growth of young fir trees in damaged ecosystems. However, chemical composition of feces remains practically unknown. The present study begins a series of investigations on the transformations of chemical compounds of coniferous needles by Siberian moth caterpillars.

Pupae of Siberian moth were collected from natural population in the taiga forest composed of Siberian pine (*Pinus sibirica*), fir (*Abies sibirica*) and Siberian spruce (*Picea obovata*) and were used as a basis for laboratory rearing. All studies were conducted with the larvae of 5th instar from the laboratory population. Those larvae were reared on the fir shoots in a 17 h light: 7 h dark regime at 24±1°C and 60–70% RH. The larvae were reared on the respective host plant (Siberian pine, fir or spruce) for 3 days before feces collection. Then fresh feces and needles (1 g) were extracted with distillated hexane (4 ml) for 24 h. The volatile part of the hexane extracts of needles and excrements were studies by GC-MS using quadruple MS (Hewlett-Packard MSD 5971) coupled to a HP 5890/II GC fitted with an HP-5 (30 m **x** 0.25 mm I.D., film thickness 0.25 μm) fused silica column. The percentage composition of the essential oils was computed from GC peak areas without using correction factor.

It is well known that needles of Siberian pine, fir and Siberian spruce differ in content of terpenoids. In our experiments the extraction of fir needles resulted in amount of terpenoids which was 39 times as much as from pine and 8 times as much as from spruce. The larvae metabolize most of terpenoids of the needles; we have found that content of terpenoids in excrements ca. 3, 6 and 8 times less than in needles for spruce, fir and pine respectively.

In case of fir and spruce, content of most of terpenoids in experiments is decreased as compare to needles except for borneol. Increase of content of borneol seems to result from enzymatic hydrolysis of bornyl acetate, which is the main component of the needles extract. For the pine, there is decrease of content of all main components. In the case of spruce, low boiling terpenes disappeared almost completely. There are also certain changes in content of some oxygenated terpenoids. The role of detoxication enzymes in terpenoid metabolism is discussed.

Effects of population density on beet webworm Loxostege sticticalis L. (Lepidoptera: Pyraustidae): evidence of phase polymorphism

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The beet webworm *Loxostege sticticalis* L. is dangerous pest in Eurasia. The larvae feed on almost 100 species of plants. Periodic outbreaks occur every 10–15 years causing serious economic damage.

The moths are well-known to migrate over long distances. The marching behaviour of the larvae was repeatedly observed during outbreaks. The marching behaviour is major characteristic of gregarious phase of armyworms (e.g. *Spodoptera exempta*), which exhibits a density-dependent phase polymorphism.

Despite this, many aspects of biology and ecology of beet webworm remain unknown. This is particularly true for its population dynamics in the periods of low density. Before our studies there were no data about effects of density on population parameters of the beet webworm.

We have studied the effects of larval density on mortality, development, fecundity, weight, colouration and photoperiodic reaction.

Beet webworm larvae were placed into 0.5 L glass cages just after hatching at densities ranged from 1 to 100 individuals per cage. They were fed with fresh leaves of burdock (*Arctium lappa*). We monitored larval mortality, duration, colouration (in the end of 5^{th} final instar), pupal weight, fecundity of butterflies. Effect of density on the photoperiodic reaction was studied under 13, 14^{30}, 17^{30} hrs-light photoperiods and densities 1, 2, 10, 50, and 100 larvae per cage.

The mortality did not depend on density and stayed at low level even if density was highest. There was large density range (from 1 up to 20–50) when pupal weight and fecundity were not affected by density. Larval duration and sex ratio did not change significantly. We have found strong density-dependent change of larval colouration. The proportion of caterpillars with dark pigmentation increased with the growth of density. The densities above 5–10 larvae per cage caused the forming of black-coloured larvae. We have found that the isolation of crowded (100 per cage) larvae in beginning of 1–3th instars prevented dark pigmentation. However, the isolation in beginning of 4–5th instars caused forming of dark colouration only in ~40% of population. The experiments demonstrated essential decrease in percentage of diapausing pronymphs with the increase of larval density. We conclude that the density-dependent phase polymorphism is characteristic of the beet webworm.

Maternal experience in photoperiod can affect diapause response in Daphnia's offspring

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Seasonal adaptations of organisms present a special interest for understanding of microevolution. They combine results of environmental selection at genotype level with adjustment of annual cycle to fluctuated environmental factors at phenotype level. Maternal control is one of mechanism of such adjustment when diapause is a universal seasonal adaptation known in wide range of plants and animals to overcome unfavorable selection of environment. It was found recently that *Daphnia* could transform diapause response on food fluctuation in offspring via maternal control. Here we show at first for water invertebrates that *Daphnia* is able provide offspring with photoperiodic information on maternal environment via maternal control.

In experiments we used a single clone of *Daphnia pulicaria* which origins from Lake Constance (Central Europe) maintained in stable conditions (24 H light, 20°C) for years that should minimize previous maternal effect. Four other clones from the same lake were tested for diapause induction in control conditions. Population of this species in Lake Constance has no males and produces ephippia with amictic eggs.

We cultivated *D. pulicaria* at 20°C in flow-through vessels (8–12 individuals each). At the first step we grow females in four combinations of day length (16 and 10 hours) and food (*Scenedesmus acutus* with controlled carbon content in concentrations 1 and 0.2 mg C L^{-1}). At the second step offspring (third clutch after female maturation) of these four mother's lines were transferred into 12 combinations (3 replicates each) of photoperiod/food conditions in offspring environments with the same in mother environments. In reference lines offspring raised at the same conditions as their mothers. To avoid preliminary photoperiodic induction in embryos we transferred mothers without eggs into alternative day length but the same food conditions where females stood until neonates appeared.

As soon as offspring had produced the first juvenals we treated the tested animals by complex of factors to induce diapause that included: 24 hours stay in filtered through 0.2 mcm membrane lake water (food shock), than two days stay at 16°C temperature and 8 hour-day-length (thermal and photoperiod shocks). During last two days we added small amount of algae to prevent death of these animals caused by starvation. Than we returned tested animals back to the same conditions they were grown and observed their reproductive traits till the third clutch after the treatment.

We did not find a diapause response for animals raised at second step under rich food conditions even in short day length both in mother and offspring environments. All responses that could be recognize as maternal effects we found for offspring environment with poor food.

Statistic analyze (ANOVA-MANOVA) indicates that producing of diapausing eggs in offspring significantly depends at first on food conditions in which offspring grows (MSE = 6429; $F>42$, $p < 0.00001$). The next important for diapause induction factors were combinations of photoperiod and food conditions in which mother were raised and combinations of these three first variables (MSE=1536; $F>10$; $p< 0.003$).

Effect of mother experience in photoperiod on diapause induction in offspring is known in some insects and mites. Step-by step adjustment of animals in a chain of generations during shortening of day length is recognized as the mechanism that optimizes seasonal adaptation in insects to diapause induction. Our results mainly correspond with it.

Maternal control of photoperiod response offspring seems like can also be used in such seasonal adaptations in *Daphnia* that do not really exist in terrestrial communities. Planktonic *Daphnia* in stratified lakes in summer time produces intensive diurnal vertical migrations inspired by predator presence. During daytime they stay into cold, food-, and lightless conditions and move up to the surface for foraging after sunset. All these factors are known also as the main environmental cues inducing winter diapause in *Daphnia*. Embryos in brood chamber of females are recognized as the sensitive stage for photoperiod but they very rare switch to diapause since late June until fall.

We discovered that if mother was grown into long day and in rich/poor food it determines low diapause response in offspring even grown in short day. Such situation is possible for *Daphnia* with diurnal vertical migrations into hypolimnion.

It possibly means that female by migrating in daytime into hypolilnion are able artificially produce short day photoperiod for eggs they bear in brood chamber. This can work against induction of diapause in offspring in this time. This hypothesis if it is confirmed could add new view on the role of vertical migrations in *Daphnia*'s seasonal adaptations.

The genetic heterogeneity of gall midge, Aphidoletes aphidimiza, from some geographical population by fecundity, developmental rate and photoperiodic response

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The investigation of two gall midge *Aphidoletes aphidimiza* Rond. (Diptera, Cecidomyidae) populations from Volgograd and St. Petersburg showed their difference by inheritance factors which determine insects fecundity and developmental rate. By individual selection the strain with high gall midge fecundity was isolated from St. Petersburg population. The strain with shorter (on 0.5–2 days in different temperature) insects developmental rate have been isolated from Volgograd populations. Last strain kept their specificity after more then 20 mass-breeding generations without supporting selection. It was tasted by different practically important signs (longevity, fertility, viability, sex ratio, sensitivity to insecticides) and gave no difference or was better in comparison to population usually used in greenhouses. Selected strain gave good results in control of aphids in St. Petersburg region greenhouses especially at lover temperature in spring period.

But investigation of gall midge from another one (Murmansk) geographical population showed that by developmental rate insects have no significant difference from selected strain. So mentioned above and some other populations (from Vologda and Voronezh) of gall midge are tested by photoperiodic reaction, insects fecundity and developmental rate.

Both practical and scientific importance of the genetic polymorphism detection in beneficial insects will be discussed.

The genetic polymorphism of the codling moth (Laspeyresia pomonella) populations from Ararat valley by developmental rate and diapause determination

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We studied the possibility for genetic control of the pest populations growth by the regulation of generation numbers. The codling moth completely developed larvae from the next generation after overwintering have been collected in 3 biotopes of Ararat valley. The insects from one biotope were quite different from other two by the percentage of diapause. This fact together with extremely high number of diapausing insects on the whole at the rising daylight period of larvae development are wary difficult to express from diapause photoperiodic regulation point of view. To understand the mechanisms of these phenomenon the genetic heterogeneity of collected codling moth have been investigated and selection of the obligatory diapausing strains at the long (18 h) daylight were started.

Using the single-pair crosses the genetic heterogeneity of codling moth was founded by the possibility to diapause at long daylight and both developmental rate before and after diapause. Some F1 families from all investigated biotopes (breeding in a standard laboratory conditions on apples) was quite different by these signs. At the same time there is no correlation between fiddling larvae developmental rate and the time of postdiapause development. The significant difference by the developmental rate of diapausing and not diapausing larvae was founded only in a few families. The larvae from one biotope developed with significantly less rate than from another two, but without correlation with percentage of diapause. Insects from two biotopes showed significant difference by postdiapause developmental rate and the third one was intermediate. Selection of individuals diapausing at long daylight after 7 generations gave the possibility to isolate the codling moth strain with high proportion (90-100%) of such insects. This sign sowed the dominant inheritance, but in some generations the proportion of diapausing larvae unexpectedly drooped down. Subsequent investigations of this strain at breeding on different diets showed that these insects have the normal long-day photoperiodic reaction. We isolated the inheritance factors which determine not the obligatory diapause but the high sensitivity of codling moth to some substance produced by ripening apples. This substance (or substances) can induced the codling moth diapause so as short daylight. From this position all results which are described above become clear.

The results are discussed from the grate importance of genetic polymorphism in codling moth adaptation to variability of different ecological factors (including anthropogenic) point of view.

Photoperiodic control of nymphal diapause in the North American tick, Ixodes (Ixodes) scapularis Say (Acari: Ixodidae)

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The tick *Ixodes scapularis* as the main vector of Lyme borreliosis in United States, is well studied by American ixodologists both in epidemiological, and ecological aspects. Its life cycle in the northern parts of the distribution is completed only in 3–4 years, due to delays in development of engorged larvae, nymphs and adult females, which can overwinter in the state of developmental diapause, together with unfed ticks in the state of behavioural diapause (Yuval, Spielman, 1990; Lindsay et al., 1998). In this respect this tick is quite similar to European and Eurasian representatives of the same genus and subgenus – the forest tick, *I. (Ixodes) ricinus,* and the Taiga tick, *I. (I.) persulcatus.* Unfortunately, factors and mechanisms controlling commencement and cessation of diapause in *I. scapularis* are not studied until now, in contrast to its palaearctic relatives (Belozerov, 1982, 1998), though the knowledge of its peculiarities is necessary for better understanding the tick phenology and more reliable forecasting tick population dynamics.

We succeeded to conduct special experiments on the effect of photoperiod upon developmental diapause in nymphs of *I. scapularis* (Middle Atlantic population), received by the Martinovsky Institute from Parasite Biology Laboratory, USDA (Maryland). Unfed nymphs at the age of 2–7 weeks were placed into two alternative photoperiodic regimens - LD (long-day, 22L:02D) and SD (short-day, 12L:12D) at 20°C, and after 2 months they were fed on white mice (under LD conditions). Engorged nymphs from both photoperiodic regimens were divided into two groups, that were maintained afterwards in the same or alternative regimen (at 20°C) during 5 months (with registration of apolysis and ecdysis).

The obtained results demonstrated for the first time the distinct dependence of nymphal development (with or without diapause) in *I. scapularis* upon photoperiod, according to the norms of two-step photoperiodic response of SD-LD type. Non-diapause development of engorged nymphs was possible only in LD conditions, especially when they were maintained before feeding in SD conditions. This was observed in 100% of such nymphs (with their apolysis in 48–50, and with ecdysis in 71–76 days at 20°C after engorgement). Some nymphs (10–23%) from LD regimen developed with no delay also (being placed into LD regimen after engorgement). But all engorged nymphs placed into SD regimen, showed stable and long delay of development (with no signs of apolysis during 5 months). Thus, all studied representatives of ticks from *I. ricinus* species complex (both from Palaearctic, and Nearctic) are characterized by common mechanisms controlling seasonal development of nymphs by means of two-step SD-LD photoperiodic reaction.

On the tolerance of earthworm Eisenia nordenskioldi (Oligochaeta, Lumbricidae) for extremely low soil humidity in the Northeast of Asia

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The Earthworm *E. nordenskioldi* is a well-known example of a broadly valent species that has colonized tundra, forest and forest-steppe zones in Asia and partially East Europe. The 8-ploid race, distributed in the Northeast of Asia is tolerant both to freezing (Berman, Leirikh, 1985), and extremely low soil humidity (3–5%). Like some other animals, this species is capable of surviving drought in capsules. The Ecophysiology of earthworms in capsules has been investigated for *Aporrectodea caliginosa* (Semyonova, 1967; Bysova, 1977), but the water balance has remained practically unknown. Current research fills this gap.

E. nordenskioldi earthworms, collected at the end of July, were placed with soil in glass tubes closed by cotton-gauze plugs and kept in darkness at room temperature; each of the 50 tubes contained 6 specimens of similar live weight (±5 mg). With the soil drying, the animals stopped feeding, rolled themselves up into balls (by 2–3 specimens) and formed capsules made from the soil, fastened by slime and excrement. Once in 10 days (the experiment was run for 76 days) 12 animals were tested for water content, another 12 for glycogen, lipids, glucose, and polyols. We also studied soil humidity and temperature conditions in the natural habitats of the species and monitored interannular dynamics of earthworm numbers in these habitats.

It appears that, similarly to other earthworm species, *E. nordenskioldi* is tolerant for a short-term loss of water in the open air (up to 50% of the body weight), and at the decrease of soil humidity down to 15–18% forms capsules, in which the animals can stay for up to two months under a gradual fall of the surrounding soil humidity down to 5%. During the encapsulation, the animals weight decreased to 42%, but water content in their tissues remained practically stable. The loss in body weight corresponded to the decrease of dry substance amount by 1/5, and water by 2/3; the share of glycogen and lipids falls by 4 times. At the moment of encapsulation the rate of reserve substances consumption fell sharply, indicating the general slowing down of metabolic rates. Thus, the capsule dramatically reduced the earthworm's water loss, allowing for the maintenance of the body liquid homeostasis at the expense of metabolic water, produced during the utilization of reserve substances. As a whole, encapsulation was so effective, that the consequences of a long drought will not significantly affect the population structure during a more favorable subsequent year.

The described adaptations allow earthworms to sustain long periods of hard moisture deficiency and it make possible for them to colonize not only permanently mesophytic biotopes, traditional for them, but also periodically dry habitats, which makes a special contribution to the formation of the huge geographic range of this species.

Cold hardiness of earthworms (Oligochaeta, Lumbricidae) of Northern Eurasia

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It was traditionally thought that earthworms could not tolerate frost in soil. However, the ubiquitous distribution of *Eisenia nordenskioldi* in Siberia (including the Arctic islands) in permafrost-affected soils has put this view in doubt. Studies have shown that this species successfully overwinters in frozen state at temperatures down to -30°C and, thus, its distribution is not limited by wintering conditions (Berman, Leirikh, 1985).

Another widely distributed species, *Dendrobaena octaedra,* also penetrates into the zonal tundra. Earthworms of a local population near Magadan survive freezing; the temperature that is absolutely lethal for them is -16°C, while the coldest soil temperature in the earthworm's biotope does not go below -10°C. *D. octaedra* from the vicinity of Moscow were found to be freeze tolerant as well (a small sample was studied). For the whole range of *D. octaedra* in Eurasia and North America clear relation between the species distribution boundary and the wintering temperature of -12 ... -14°C can be traced on a map of minimum winter soil temperature at 3 cm depth (Berman et al., 2001).

According to our preliminary results among common species of earthworms in Moscow region, *Dendrodrilus rubidus* and *Aporrectodea rosea* do not withstand cooling below 0°C. In *E. fetida*, only about 14% of specimens survived after exposure to -1°C in frozen soil. However, *Lumbricus rubellus* and *L. castaneus* successfully sustained -1°C, and *A. longa* and *A. caliginosa* kept alive for four days at -3°C, but died at -5°C. Supercooling point for *A. longa* was defined as -1.0°C, for *A. caliginosa* -1.2°C, for *L. castaneus* -1.8°C, and for *L. rubellus* -2.9°C. By -1°C all earthworms that survived this temperature, remained unfrozen and kept insignificant mobility at a tactile irritation, despite the contact with ice crystals in frozen soil. Earthworm cocoons withstand much lower temperature. Thus, *E. nordenskioldi* cocoons endure temperatures below -35°C (Berman, Leirikh, 1985), *D. octaedra* -20°C, *A. caliginosa*, *Allolobophora chlorothica*, *D. rubidus tenuis*, *D. rubidus norvegicus* down to -8°C (Holmstrup, Westh, 1995). According to our data, *D. rubidus tenuis* cocoons can successfully overwinter at temperatures down to -35°C. Along with the high rates of onthogenetic development, that allows the species to survive under extreme conditions and to have cosmopolitan distribution despite the absence of cold hardiness under negative temperatures in earthworms.

Our results on cold hardiness of *E. nordenskioldi*, *D. octaedra* and *D. rubidus*, along with the published evidence on the biology of these species, allows us to estimate the role of cold hardiness in their geographic distribution and, in particular, the colonization of cold regions. To understand the limiting effect of minor cold hardiness in other investigated species, additional research is required.

Microhabitat distribution of the springtails (Collembola, Entognatha) in Kiev Polesye

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Horizontal structure of soil population is an important indicator of stability of the ecosystem. N. M. Chernova paid attention to the particular units of fine horizontal structure of collembolan population distributed as concentrically located circles around trunks of trees.

Dynamics of springtails' population in these microhabitats, located in following way: A – near trunks, B – under crown and C – between crowns was analyzed. Our investigations were conducted in the mixed pine-and-oak forest in Kiev Polesye during autumn-winter season. No such investigation had been carried out before in Ukrainian Polesye (the south border of southern Taiga).

The most characteristic displacement of springtails' population during autumn-winter season was observed near trunks and between crowns. The highest density of collembolan community (93 700 spec./m^2) near trunks in September decreased during autumn and winter. The other way, the lowest level of density (12 800 spec./m^2) between crowns increased since September to January. In February both reached one half of their autumn values. The character of the spatial microhabitat distribution of Collembola in different litter and soil layers was similar except in November after drastic fall of temperature. Such modifications of springtails' distribution probably indicate the displacement of the most active centres of destruction process.

The defined regularity in the distribution of single collembolan species was observed mainly in the cases of low density. Particularly, *Neanura muscorum* in September, November and January and *Schoettella ununguiculata* in November and February were found near trunks. *Folsomia manolachei* in November and February and *Proisotoma minima* during autumn and winter occurred under crown and between crowns. In addition, distribution of representatives of collembolan biomorphs showed the difference in soil conditions in crown-space position. Some biomorphic groups of springtails, for example, hemiedaphobionts and euedaphobionts were spread almost evenly in relation to the trunks and crowns. Specimens of atmobionts were found mainly near trunks or under crown but rarely between crowns. The dynamic changes of the quantity and of the distribution of springtails are considered as seasonal displacement of basic–species populations. Our investigation showed complicated changes in collembolan population from summer to autumn and winter. Characteristic features of the spatial distribution of single species and their dynamics combine *Shoettella ununguiculata, Friesea mirabilis , Sphaeridia sp. gr. pumilis, Sminthurinus niger,* species of the genus *Orchesella* into summer-autumn group of population; *Oligaphorura absoloni, Protaphorura spp., Mesaphorura spp., Isotomiella minor, Folsomia fimetaria, Pseudosinella alba, Megalothorax minimus* – into winter group. Under conditions of sufficient humidity the temperature restricts the level of density for springtails' population.

Chrysomelid beetles in the Subarctic: temperature thresholds, daily rhythm of activity and time budgets

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Three leaf beetle species (*Gonioctena pallidus*, *G. linnaeanus*, *Chrysomela collaris*) were studied in the Low Ob' region (Polar Urals) in 1998–2000, in the first half of July. All of them are common here in tundra and shrubbery sites on different *Salix* species. In laboratory experiments the lower temperature thresholds for growth of the last instar larvae were found to be 4.8°C for *G. pallidus*, 6.0°C for *Ch. collaris* and 9.8°C for *G. linnaeanus*.

Larval behaviour was examined in natural habitat of each species using daily observations. Twenty marked larvae were simultaneously under observation. A kind of activity for each larva (feeding, moving, molting and so on) and its position on a plant were registered at hourly intervals. The common place for *G. pallidus* larvae was shown to be the lower leaf surface; they come to upper surface or to tip shoot leaves only at 5–9 a.m., and at these hours you can see round you thousands of larvae undetectable before. In the day period when basking is possible 70% of larvae avoid sunlight, while 63% of *Ch. collaris* and 83% of *G. linnaeanus* larvae are placed then openly rising their body temperature by means of solar radiation. Dark colouration (in contrast with green *G. pallidus* larvae) helps their basking. The larvae of these two species pass to leaf underside or to inner part of willow bush mainly for "night" period, *Ch. collaris* larvae - also in the hottest hours of the day, and all species seek here a shelter against rain and wind.

Leaf beetle larvae feed when air temperatures exceed threshold ones, be it "day time" or "night time". The feeding intensity of *G. linnaeanus* larvae was the highest in periods when they could feed. They have however the shortest feeding time because of night temperature fall (14.9 hours in a day vs. 22.5 h in *G. pallidus* and 20.4 h in *Ch. collaris*) and it was calculated for 24-hours period that all species spent approximately 30% of their time in feeding. Feeding of *G. linnaeanus* is high and stable in the middle of the day while two other species demonstrate the high morning (7–10 a.m.) peak of feeding activity and somewhat lower evening (16–21 p.m.) peak. Only a small proportion of time (7–10%) is used for moving by these three species. So the large part of the day is free of feeding and moving but this "waste of time" is not connected with necessity of basking.

Time budget of north chrysomelid larvae doesn't depend on their threshold temperatures. Different temperature thresholds of chrysomelid species are however the possible reason of differences in day rhythm of their larval activity. Necessity of basking also is different according to temperature thresholds.

Rhythms of hatching of resting eggs and population cycle of Polyphemus (Crustacea, Branchiopoda)

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The life cycle of the populations of Branchiopoda consists of the alternating periods of active life and resting. Little is known about the resting period, which is usually the longest. The present study was conducted with the use of the resting eggs of *P. pediculus*, a model species of freshwater shallows. In laboratory experiments 10–1000 eggs were kept in Petri dishes in water, dried at 15–21, 2–6 and 0°C from one day to 3 years. In field experiments eggs were kept in a water body in hatcheries 200 in each at different depths for a year. Eggs retain viability after staying in water at summer temperatures and freezing for 3 years, and drying for 3–11 months. Resting eggs hatch only after staying in water at 2–6°C for not less than 4–5 months. This occurs in groups, bears a pulse, undulating character, which corresponds to the inborn individual rhythmicity of development of eggs. Mass emerging of the young occurs once per day in the well-illuminated water layers in non-dense clumps. The number of new-borns in daily groups and the intervals between the latter vary. The totality of daily groups form a seasonal wave of emerging of the young. It characterizes the length and the intensity of hatching in a certain environment. Seasonal rhythmicity has one wave per year. In natural waters emerging of the young occurs only in spring at 2–8°C. In laboratory daily and seasonal rhythmicity is retained, but it is more prolonged. Not more than 13% of eggs hatch during one wave. Emerging of young from a clump occurs during 2–3 years. The totality of waves characterize multi-years rhythmicity of emerging of the young from the clump. Intensity of hatching decreases with every wave. During the resting period eggs of *P. pediculus* undergo cryptobiosis, anabiosis and rebiosis, the latter being the only obligatory. Cryptobiosis and anabiosis may be one-season, or multi-season alternating. Their length, frequency of recurrence and the temperature regime influence the survival of eggs, the intensity and duration of their hatching. Rebiosis is regulated by a combined action of the inborn rhythmics of development of eggs, the temperature, the illumination, and the concentration of metabolites excreted by eggs. Temperature is the main exogenous factor. The conditions of development and emerging of the young are genetically determined, reflect the environment where the species evolved. They determine the time and frequency of appearance of the new population and, therefore the population cycle of the species. The latter is genetically determined, and stable under any dwelling conditions. *P. pediculus* is always monocyclic. Local populations are genetically heterogenous. During the resting period they are represented by eggs laid in different local populations in course of several years, and having the resting period of different length. During the period of active life the population consists of generations, which originated from resting eggs of different actual age.

Role of dopamine in adaptation of Drosophila adults to unfavourable conditions

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It has been shown in many studies (ours included) that when insects are exposed to unfavourable conditions, their contents of octopamine (OA) and dopamine (DA) increase steeply as soon as 15 min after the beginning of the exposure. It has been also repeatedly demonstrated that under normal conditions biogenic amines regulate energy metabolism of insects. On this basis, the increase of contents of biogenic amines in insects under stressful conditions is assumed to promote their adaptation. What is more, almost nothing is known about effects of the basic level of biogenic amines (their content under normal conditions) on adaptability. The present study is an attempt to clarify the situation.

We studied DA content and viability under normal and unfavourable temperature conditions (38°C, 60 min for DA analysis and 4 hours for viability test) in *D. virilis* and *D. melanogaster* wild type strains as well as in those with mutations of the genes involved in OA and DA metabolism. It has been established that: (1) In *Drosophila* wild type males DA content is considerably higher than that in females. The males survive heat stress much worse than females. (2) Viability of *D. melanogaster* individuals of strains with different OA contents (those devoid of the amine or with its considerably decreased content) after an exposure to heat stress does not differ from that of wild type flies. (3) Viability of flies of *D. virilis* and *D. melanogaster* strains with doubled DA content (as compared to wild type) is dramatically decreased. (4) Hybrid F1 males from reciprocal crosses of *D. virilis* strains with normal and doubled DA content (owing to a mutation on X chromosome) differ in surviving heat stress: F1 males with a doubled DA content are characterized by a considerably lower viability than those with a normal amine content.

Thus we have revealed a negative correlation between basic DA content and viability under stress, and an absence of such correlation for OA.

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The impact of artificial environmental manipulations on Antarctic soil faunal communities

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The extreme terrestrial environments of the maritime Antarctic are experiencing rapid changes in temperature and water availability while, additionally, being exposed to the spring “ozone hole”. As a great simplification of their temperate counterparts they, therefore, may provide sound models on which to base wider predictions and studies of biological response to climate change.

This paper describes results from two climate manipulation experiments. The first, carried out within the remote Two Step Massif on southern Alexander Island (c. 72°S), studied a simple ecosystem based on autotrophic microbes, with a fauna dominated by microinvertebrates (nematodes, tardigrades, rotifers). The second study examined a much more complex community near Palmer Station, Anvers Island (c. 65°S), with a flora consisting of mosses and flowering plants, and fauna of microarthropods (mites and springtails) and a wingless fly.

Studies at the two sites gave apparently contradictory results. On Alexander Island, local environmental manipulation led to large (up to 2–3 orders of magnitude) increases in soil nematode abundance within one year, with the changes maintained after 3–4 years. However, over a similar 3 year time period, soil microarthropod populations on Anvers Islands showed very little or no response of abundance to environmental manipulations. Although several species showed significant responses to one or more environmental variables, there was no consistent pattern across species. However, the significance of any effects directly attributable to climate manipulation appear to be dwarfed by the spatial clumping that is characteristic of these soil microarthropods.

Overall, these studies indicate that elements of the soil fauna may be buffered from some of the impacts of climate change, in line with the results of some Arctic studies. It is also clear that other soil communities may be much more sensitive, and respond rapidly to climate change.

Geographical variability of photoperiodic responses Pyrrhocoris apterus (Heteroptera, Pyrrhocoridae)

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The possibility of broad intra-areal distribution of insects is ensured by a certain number of physiological adaptations, which allow the insect species to correlate life cycles with zonal and geographical characteristics. The presence of the intraspecific heterogenety of insects is indicated by certain ecological parameters: ability to diapause, lability of responses controlling the diapause, voltinisme, characteristics of thermal sensitivity, parameters of a photoperiodic response (PhPR).

The present work provides data of studies on the geographical variability of Linden bug *Pyrrhocoris apterus (Heteroptera, Pyrrhocoridae).* The culture of the insect species is represented by nine geographical populations of Linden bug from different parts of the area - beginning with southern regions - Bishkek (42.5°N), Krasnodar (45°N) and up to the northern boundary of species distribution - Tyumen (57°N). The value of the norm of the response to light mode has been chosen as a character, well-expressing an interpopulational diversity. Kirghiz population distinguishes by a low value of the critical photoperiod (in the mode of 28°C), it makes 14 hours. The critical threshold for tyumen population comprises 17.5 hours per daylight. Remaining populations (Belgorod (50°N), Volgograd (48.8°N), Samara (53.2°N), Munich (48°N)) take an intermediate place; the value of their threshold length achieves 15 hours. The results obtained provide evidence of the modification of the photoperiodic threshold value approximately for 1.5 hours per each 5 degrees of the geographical latitude.

Along with the investigations mentioned above the estimation of the geographical forms heterogenety in accordance with promotion to the East was carried out. The studies concern the populations of Linden bug coming from the vast territory which covers the stripe from 12° of eastern longitude (Munich) to 89° of eastern longitude (Bishkek), this territory being diverse in climate continentality. Differences in the threshold daylength of the mentioned above insect species (and equally of the species living in neighbouring latitudes but being far from each other in terms of longitude) being relatively poorly expressed, a definite relationship between of PhPR parameters and the geographical latitude has not been revealed.

The population originating from the valley situated at the altitude of 800 m was investigated. Climatic parameters of highland regions are similar to those of northern zones; climate continentality increases with the parallel fall of temperature. The alpine form of *P. apterus* from Bishkek (42.5°N), which is the most southern sample among the investigated ones, has the lowest threshold of PhPR and demonstrates a pronounced tendency to the active development.

Respiratory water loss in the flightless dung beetle, Circellium bacchus (Fabricius)

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Circellium bacchus is a flightless telecoprid (ball-rolling) dung beetle, endemic to the Afrotropical region, where it is found in a few restricted populations in the eastern Cape of South Africa. Its apterous condition and large size (mass ranges from 6 to 12 g) are adaptations to a semi-arid habitat.

Telecoprid dung beetles detach a portion of dung from a dropping, roll it some distance away from the source and then bury it, or place it in a grass tussock. Ball-making, when the beetles are either immersed in the dung or exposed to the elements, may take several minutes, or hours. Ball-rolling is fairly rapid but may still require exposure to ambient humidities. When not actively foraging, most beetles spend periods underground. Females of some species may spend several months buried in a brood chamber tending their brood ball. *C. bacchus* lives for several years, which requires them to survive the dry season underground in a state of torpor. These behaviours are likely to reduce water stress in a xeric habitat. *C. bacchus* is assumed to be a poor competitor against other large, flying telecoprids, and is therefore confined to drier habitats. This beetle is active in the sun for long periods, walking between widely scattered dung pats, thus is under selection pressure to reduce water loss.

C. bacchus has eight spiracles on each side of the body. The metathoracic spiracle and six abdominal spiracles open into the subelytral cavity, which is sealed. The mesothoracic spiracle is the largest and most exposed, occurring ventrally in the membrane connecting the prothorax and mesothorax, behind the coxal cavities of the prothoracic legs. In this position it opens into the “waist” between the thorax and abdomen. The concealment of these spiracles may help to reduce respiratory water loss.

When at rest a cyclic form of respiration, known as discontinuous gas exchange, is used by *C. bacchus*, releasing a burst of carbon dioxide approximately once an hour when the spiracles open. Flow-through respirometry was used to measure water loss in this state. Respiratory water loss was found to primarily occur during the burst periods, when the spiracles open. A second experiment showed that water is lost mainly through the larger mesothoracic spiracles, during the burst periods, as compared to the metathoracic and abdominal spiracles which are situated under the elytra. These results indicate that respiration and water loss are closely linked in this beetle, which uses discontinuous gas exchange through a limited number of spiracles to reduce respiratory water loss while at rest.

Inter- and intraclonal variability of photoperiodic response in pea aphid Acyrthosiphon pisum (Homoptera, Aphididae)

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Aphid photoperiodism has been a subject of extensive study for nearly 80 years. However, the previous investigations were generally based on a detailed analysis of a single clone or on an analysis of several clones, but at few photoperiods (PHs). Furthermore, the investigations were mostly focused on determination of morphs, whereas the effect on fecundity and duration of reproduction was not studied at all at extremely short PHs. The present study is devoted to a detailed experimental study of photoperiodic effect on the reproduction of pea aphid from two locations near St. Petersburg. From a total of 21 clones collected on peas, we chose 7 clones, which were most different in the ratio of sexual morphs under short PHs at 20°C. The effect of constant PHs (from 0 h to 24 h) on: 1) sex and female morph determination of the offspring, 2) fecundity, 3) duration of reproduction, 4) dynamics of offspring morph appearance and fecundity during the reproductive period was studied in wingless viviparous females of the chosen clones. In addition, the variability of characters mentioned above was studied in wingless and winged viviparous females of 2 clones.

The ratio of sexual morphs (males and oviparae) varies between clones at the same PH. All clones demonstrate a threshold long-day photoperiodic response of female morph determination, producing viviparae at long PHs and predominantly oviparae at short PHs. The observed critical PH varies from 11 h to 12 h 30 min, but in two clones it corresponds to 16 h 40 min and 17 h 20 min. The male production depends distinctly upon the clone (maximal percentage – 32–66%). In addition, a unisexual clone of pea aphid, which produces no males but a great quantity of oviparae, was described.

The fecundity depends not only on PH, but also on the clone. The critical PHs of changes of fecundity and duration of reproduction are one hour longer, than those of female morph determination. The vivipara production, fecundity and duration of reproduction increase at extremely short PHs (0–4 h), similarly to what is observed at long PHs.

The dynamics of offspring morph appearance and fecundity during the reproductive period is generally similar in females of all studied clones. The most of offspring is produced during first 10-14 days of reproduction. The winged and wingless females of the same clone have some differences concerning the age of larviposition onset and duration of the reproductive pause.

The photoperiodic limits of ovipara and male production have different relative positions for the progeny of winged and wingless females. The range of PHs inducing active ovipara production in winged females is nearly twice as wide as that in wingless females. Winged females produce fewer males. They are more viable and reproduce longer, but have a lower total fecundity. The reproductive features of winged and wingless females are consistent with their different ecological roles.

Seasonal development of benthic crustaceans (Harpacticoida, Copepoda) and amphibian insects (Plecoptera) in a river in the Northern Urals

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For more than a decade since April to October the monitoring of seasonal and interannual dynamics of numbers and biomass of bottom organisms was performed. Their life cycles were studied on a station belonging to the Laboratory of Ecology of Aquatic Organisms (Institute of Biology) situated in the middle streams of the Shchuger river. A considerable part of results of monitoring certain invertebrate groups was published (Shubina,, 1986). V. N. Shubina passed to the authors the crustaceans and larvae of Plecoptera from zoobenthos samples which served the material for analysing the dynamics of quantitative development and species composition of these animals in the river. In order to determine the species composition of Plecoptera and to define the terms of their flying out, adult insects were caught in the grass and in the shoreline bushes with an entomological net scoop.

The Shchuger river is a large right tributary of the Middle Pechora. It springs from the south slope of the Northern Urals. The river is alpine all through its length. Seasonal changes in population structure and number of crustaceans and amphibian insects in the water body occurred in specific climate and weather conditions of the Northern Urals (severe long winters, short biological summer, low total temperatures of water and air). During the time of studies, the total of water degree-days during ice-free seasons (May–October) varied between 777.0 and 1553.5°C.

The fauna of harpacticoid copepods was represented in the river by nine species, of which most abundant were *Paracamptus schmeili*, *Maraenobiotus brucei brucei*, *Attheyella dentata*, *A. nordenskjöldi nordenskjöldi*, *Moraria duthiei* and *M. schmeili*. Reproduction in most species took place in the first half of vegetation season (with temperatures of 5.3–22.0°C). Only *A. nordenskjöldi nordenskjöldi* reproduced in June–September. The highest abundance (336.01 $\pm$ 258.44 ind./m^2) of Harpacticoida in the river was noted in August–October with water temperature of 11.5–17.9°C, owing to maturation of generations of all abundant species. In warmer years reproducing individuals appeared in the river earlier than in colder years.

Fauna of stoneflies in the river consisted of 24 species. The peak in the numbers of these insects was noted at the end of August during mass emergence of larvae from eggs. Maximal biomass of stoneflies was under the ice (in April), by domination of species *Arcynopteryx compacta, Diura nanseni, Capnia pygmaea, Taeniopteryx nebulosa*. The highest values of frequency, numbers and biomass of stoneflies in the benthos were registered in the most cold and full-watered year in the whole monitoring period. Extremely warm year was distinguished by extremely low number of stonefly larvae during the whole observation term. Monovoltine type of life cycle is established. Life cycle proceeded without winter growth stop in two abundant species - *A. compacta* and *D. nanseni.*

An experimental study of alternative life-history strategies in the Anisopteromalus calandrae species complex (Hymenoptera, Pteromalidae)

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We have recently found that *Anisopteromalus calandrae* (Howard), an effective parasite of various stored-product pests, actually harbours two reproductively isolated sibling species. These species differ in some morphological and karyological features, male sound signals as well as in many life-history characteristics and behavioural traits. We studied these parameters using two laboratory populations of *A. calandrae*, ICSP (Ascot, UK) and MSU (Moscow, Russia) having n = 7 and 5 respectively. Both strains were reared on *Sitophilus granarius* (L.) (Curculionidae).

Our experiments demonstrate that MSU females have larger body size and avoid ovipositing on host larvae, whereas ICSP ones are smaller and attack all accessible host stages, from fourth-instar larvae to pupae, without any distinct preference. Differences in egg size between the strains have obvious positive correlation with those in female body length of these wasps. MSU females have lower egg production and strongly female-biased sex ratio, whilst wasps of the other population have much higher fecundity and sex ratio close to 1:1. Preimaginal development is substantially quicker in the ICSP strain, though its eggs are always destroyed by conspecific females in the case of superparasitism. Oviposition in the MSU strain is usually preceded by incomplete host paralysis and followed by marking of infested grains, whereas ICSP wasps paralyse attacked hosts more completely and never display kernel-marking behaviour. Most of these biological characteristics are presumed to constitute alternative life-history strategies which are best interpreted in terms of r/K continuum. The MSU and ICSP strains are thus respectively considered as K and r strategists. However, adult longevity is much higher in the latter population, probably as a result of modification of the general r/K pattern due to the aggregated distribution of hosts.

Host-choice experiments which involved ICSP and MSU strains along with another three populations from the USA, I. e. Fresno (California) with n = 5 as well as Bamberg (South Carolina) and Savannah (Georgia) both having n = 7, show that these parasites have considerable preference for attacking different hosts. Specifically, wasps with n = 5 prefer to oviposit on *Lasioderma serricorne* (F.) (Anobiidae), whereas others prefer to attack *S. granarius*. Although both species can develop on alternative hosts, parasites with n = 7 are normally associated with Curculionidae and Bruchidae, the other species always being found on Anobiidae. Since many differences between these host groups, including the ability to subsist on restricted food resources, duration of preimaginal development and fecundity, can also be interpreted in terms of an r/K continuum, this relationship may represent adaptations of the different wasp species to certain life-history traits of their preferred hosts.

Trophic activity of soil fauna in winter

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Last decades actively develops an ecotoxicology of soil animals. The effects of many pollutants (heavy metals, pesticides, organic pollutants) are studied. The physiology of influence of these xenobiotics is widely investigated. Most of investigations are carried out on animals in physiologically active state (in field in summer, in laboratories at temperature optimum). But animals inhabiting the polluted areas are being damaged the whole time. Animals exposed of pollutants are more endangered under extremal conditions (while moulting, coming into and out of diapause, wintering). In ecotoxicological studies is a priori assumed that animals are not active in winter and thus not exposed by influence of pollutants.

For estimation of trophic activity of soil animals in winter an investigation in year 2000 was carried out in the surroundings of Borovsk town (about 100 km to the south from Moscow). Late autumn (before snow falling) in spruce forest 5 Barber pitfall traps and 40 bait-lamina-tests (with 16 holes each) by Torne (1990) method were set. Data were taken each 2 weeks with temperature and thickness of snow blanket measurements.

During all the season in the traps invertebrates are occurred, mostly spiders, staphylinid beetles and collembolans. In November at the temperature around 0°C and thickness of snow blanket of 3–4 cm the number of caught animals was about one-fifth of July one. The trophic activity (according to the bait-lamina-tests data) was 30.9% (in July – 59.5%). With reduction of temperature to –10... –12°C (at some days till –20... –25°C) and increase of blanket of snow to 35–55 cm in January–February decreased the catchability to 5–14 invertebrates per 5 traps per 2 weeks. Part of perforated holes in bait-lamina-test reduced to 1.4–3.0%. But the activity was not excluded even at the hard frosts. The direct coupling between inclement of weather and animal activity was observed. At the same time animals awaken mass from diapause if the environment conditions reaches the threshold optimal values.

It is possible that trophic activity of soil fauna in winter is caused by ecological but not physiological mechanisms. The definite part of organisms are not in diapause, active or not, but they are at direct dependence of environmental conditions. These animals are exposed to the negative influence of xenobiotics in winter too. This effect has to be taken into consideration in ecotoxicological studies of pollutants on soil animals.

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Hormones interrelationship in the control of Drosophila reproduction under unfavourable environmental conditions

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It is well-known that under normal environmental conditions ecdysteroids together with juvenile hormone (JH) control the reproductive function in insect females. It has been also established that metabolism of JH and 20-hydroxyecdysone (20HE) is in turn regulated by brain hormones, biogenic amines in particular. Recently it has been discovered that biogenic amines can play a regulating role not only in synthesis, but also in degradation of JH. Therefore, interrelation of the hormones regulating insect reproduction under normal conditions has been studied fairly well. However, there is practically no information on the hormones= relationship in the case of unfavourable conditions. Here we present the results of our study of stress exposure effects on the contents of octopamine (OA), 20HE and fertility in flies of *D. virilis* strains contrasting in the levels of JH metabolism, as well as on JH metabolism and fertility of *D. melanogaster* strains contrasting in OA and dopamine (DA) contents. We also discuss interaction of the hormones in the control of *Drosophila* reproduction under stress conditions.

We demonstrate that (I) under normal conditions individuals of a *D. virilis* strain with a high JH degradation level that decreases steeply under stress have considerably lower contents of OA and 20HE and higher fertility than flies of a mutant strain with a low JH degradation level that does not change under stress; (ii) heat stress causes an increase of OA and 20HE contents and a decrease in fertility in the former, while in the latter contents of both hormones and fertility do not change. We also show that (I) under normal conditions in octopamineless females of the strain $T\beta h^{nM18}$ *D. melanogaster* and females of the strain *Ste* with a doubled DA content JH degradation is different as compared with wild type flies: it is increased in young and mature $T\beta h^{nM18}$ females and decreased in young and increased in mature *Ste* flies; (ii) $T\beta h^{nM18}$ flies are sterile, and fertility of the strain *Ste* is considerably lower as compared with the wild type strain; (iii) under unfavourable conditions flies of mutant strains of *D. melanogaster* develop a stress reaction like wild type individuals: their levels of JH degradation and fertility decrease; however their stress reactivity (levels of reaction) of JH metabolism and fertility systems differs drastically from that in wild type strains.

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Low temperature promotes the regeneration of once histolysed flight muscles and flight behaviour in a water strider, Aquarius paludum

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Diapause adults of a water strider, *Aquarius paludum* have long-wings and move between water bodies and diapause sites on land probably by flights (Harada *et al.*, 2000). Aims of this study are first, to examine effects of exposure to low temperature on the condition of flight muscles and flight preference for diapause and reproductive adults, and second, to monitor flight muscle condition of diapause adults from October through winter to May (1998–2001) in Kochi (33°N), Japan.

Reproductive adults in late summer (all long winged) were collected from a pond in Kochi, and kept under 15.5L–8.5D, at 20°C which are promoting reproduction. First instars of the next generation were kept under the long- or short-days (12L–12D) , at 20°C. Half of adults under the long-days or short-days were chilled at 7°C for 48 h from the 40th day after emergence. Another half of adults were kept at 20°C. Flight propensity, supercooling point (SCP) and condition of flight muscles were examined after 1 week from the end of chilling. Chilling made SCP lower especially for diapause adults (-14.75±1.43°C [mean±SD]: chilling, short-days; -13.56± 1.30°C: non-chilling, short-days; -14.06±1.70°C: chilling, long-days; -13.50±1.66°C: non-chilling, long-days). Chilling promoted significantly higher flight propensity rather than no chilling only for diapause adults (Mean flight index: 43.9 after chilling, 19.6 after non-chilling). For reproductive and long-winged adults, 91.2% of 34 adults had well-developed flight muscles 1 week after the chilling, whereas it was only 32.4% of 49 adults not exposed to 7°C. When they which emerge in October or November were first exposed to the low temperature at the beginning of winter, flights of diapause adults seem to be promoted for the moving to adequate diapause sites on land. Part of second generation adults which emerge in late summer in Kochi enter diapause after reproduction and participate in overwinter and reproduce in spring together with the third generation (Harada, 1994). The second generation adults may once histolyse their flight muscles in the occasion of the reproduction in late summer (Harada & Kawamura, unpublished). The first exposure to the low temperature in early winter might make once histolysed flight muscles of them regenerated for flights to overwintering sites.

Overwintering adults were collected in fall, 2000 from a water way in Kochi and kept under natural conditions through the next spring. Some of them (12–18 adults) were sampled in October 20, December 10, December 25, February 15, March 15, May 17. , and proportion of adults having well developed flight muscles were 19, 25, 83, 17, 18 and 33%, respectively. The data suggest that flight muscles were well developed in fall, once histolysed during overwintering on land in mid winter and then regenerated in spring for flying back to water bodies. The nutritional resources derived from flight muscle histolysis might be used for another function effective for overwintering, eg. wax on the surface of bodies, as an hypothesis. This project was supported by grants from The Japanese Ministry of Education and Science and Culture (Grant No. 10740361: 1998–2000; Grant No. 11794001: 1999–2002).

Cold, heat and drought hardiness of a water strider, Aquarius paludum

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Resistances to severe conditions as low temperature in winter, high temperature in summer and drought on terrestrial are obligatory factors for survival in very large distribution as 2/3 area of Palaearctic area by a water strider, *Aquarius paludum*. Critical low temperature for survival was about –3°. Survival hours were examined at the –3° for diapause adults promoted by short-days of 12L–12D and reproductive adults by long-days of 16.5L–7.5D. Hours in survival by Sapporo (43°N) strain at –3° were 40.0 on average and much longer than those by Iriomote island strain (24°N: 10.5 hrs) and Kochi strain (33°N: 7.5 hrs) for reproductive adults kept under long-days. The long survival hours of 40 by the Sapporo reproductive adults were about twice value of 18 h shown by Sapporo adults in diapause. In Sapporo, reproductive adults seem to have many occasions when they suffer low temperature during night in spring and early fall. High resistance to low temperature shown by reproductive adults might be effective for surviving the low temperature on water bodies in spring and early fall.

Usually, diapause adults of *Aquarius paludum* overwinter on land during November to March. Recently, we found a very interesting population in Nangoku city (33°N) (Nangoku strain) which appears on water bodies even in mid winter. Adults of the population are almost monomorphic of short-wings, and not in diapause but in quiescence in winter, and they overwinter on water bodies when weather is relatively moderate, whereas they move on land near to the shore when it is cold (Harada & Sasaki, 2000). Diapause adults in the Nangoku strain could not be induced by short-days at all. However, short-days can cause longer survival hours of 41.0 on average shown by reproductive adults at -3° rather than those by reproductive adults kept under long-days (14.5 h). The high resistance to low temperatures by the winter reproductive adults under short-days are very advantageous because they seem sometimes suffer low temperature on the open water bodies in winter. Nangoku city is located near to the critical region between Temperate and Subtropical zones, the strategy that adults are not in diapause but reproductive even in winter might be advantageous for fitness in the future if the global warming will be going on.

Diapause adults collected in fall in Kochi survived for about 40 hrs on average in the dry-out condition with 70% of relative humidity. The survival hrs shown by diapause adults in fall before moving on land for overwintering were about twice of those by reproductive adults of overwintered and the first generation.

The reproductive adults of Naha (27°N) strain (*A. paludum amamiensis*) kept under long-days of 15.5L–8.5D showed slightly lower lethal high temperature (41.09) rather than that by Kochi strain (42.96). All the reproductive adults in Naha (Subtropical area) show long-wing morph in summer (Harada, 1998) and they might avoid high temperature by flights even if they don't have high resistance to high temperature. This project was supported by grants from The Japanese Ministry of Education and Science and Culture (Grant No. 10740361: 1998–2000; Grant No. 11794001: 1999–2002).

Changes in glycogen and lipid content during starvation, and its consequence for drought tolerance in the collembolan, Folsomia candida (Willem)

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The aim of this study was to investigate effects of starvation on the physiology behind drought tolerance in *Folsomia candida*. Bayley & Holmstrup (1999) showed that *F. candida* accumulates myoinositol and glucose to increase the haemolymph osmolality and consequently balance its water content during exposure to natural drought regimes. These solutes are expected to be synthesized from glycogen or lipid, and it is hypothesized that starvation will affect the amount of these storage products.

The glycogen content was determined with a new HPTLC densiometric method. So far the results show that glycogen account for only 0.6% of the dry weight in control animals. Since myoinositol and glucose constitute 8% of the animals´ dry weight after 5 days of exposure to 98,2% RH (Bayley & Holmstrup, 1999) glycogen cannot act as the only substrate for synthesis of these molecules. Testerink (1981) showed that in the collembolan *Orchesella cincta* the lipid content decreased from 15% of the dry weight to 10% within 7 days of starvation. An analysis in progress will reveal the fate of lipid reserves during starvation and drought in *F. candida*. Furthermore the content of sugars and polyols in animals exposed to starvation prior to drought will be determined by HPLC.

References

Bayley M. & Holmstrup M. 1999: Water vapor absorption in arthropods by accumulation of myoinositol and glucose. *Science* 285: 1909–1911.

Testerink G.J. 1981. Starvation in a field population of litter-inhabiting Collembola. Methods for determining food reserves in small arthropods. *Pedobiologia* 21: 427–433.

Composition of membrane lipids in relation to diapause and environment in Pyrrhocoris apterus (Heteroptera)

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In the conventional view, the winter adaptation of membrane phospholipids is induced by temperature decrease. Using an insect model, *Pyrrhocoris apterus*, we find that short days and low temperatures affect the phospholipid molecular species profile in a similar manner. Both the short-day photoperiod and low winter temperatures induced an increase in the proportion of molecular species with palmitic acid ($C_{16:0}$) esterified to *sn*-1 position of glycerol and a decrease in molecular species with C_{18} fatty acids. In contrast to most other organisms the unsaturation ratio does not increase with decreasing temperature. The effect of short-day photoperiod is mediated via the endocrine gland, the corpus allatum (CA). Extirpation of the CA from insects reared at long-day photoperiod has a similar effect as rearing the insects at short-day photoperiod. The effect of CA is related to the induction of diapause by short days. Non-diapause mutant insects reared at short-day photoperiod have the phospholipid profile similar to that in the wild type insects reared at long-day photoperiod. We propose that the winter remodelling of membranes is triggered by daylength shortening prior to temperature decrease. While the fatty acid composition of phospholipids is regulated by both temperature and photoperiod, the head group composition seems to be regulated only by temperature. Similar to most other organisms, the proportion of phosphatidylethanolamine increases and that of phosphatidylcholine decreases with decreasing ambient temperature.

Desiccation tolerance and water vapour absorption in soil-dwelling Collembola by accumulation of sugars and polyols

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Soil arthropods are usually considered as being transitional between aquatic and terrestrial forms in particular with respect to water balance. They have been written off as having no physiological adaptations to water stress because of the high permeability of their skin. Here we show on the contrary, that common representatives of this fauna have a water vapour absorption mechanism capable of meeting the entire water requirements of the organism during the same range of drought survived by plants. We suggest that this mechanism is probably common in soil arthropods and that their physiological adaptations to desiccation require re-evaluation. This statement is backed up by the startling fact that the desiccation tolerance of soil arthropods has not been investigated in the range of relative humidities dictated by the extraction of water by plants throughout the root zone. Rather, they have been investigated at much lower humidities where these animals survive from minutes to hours.

Physiological and biochemical responses to desiccation were studied in species of hygrophilic Collembola, *Folsomia candida*, *F. fimetaria* and *Protaphorura armata*. The temporal changes in water content, body fluid osmotic pressure, and accumulation of sugars and polyols during desiccation stress, equivalent to severe soil drought are reported. The species initially lost about 50% of their initial content of osmotically active water. Within seven days *F. candida* and *F. fimetaria* had re-established their preliminary water content by absorbing water vapour from the atmosphere. *P. armata* also significantly increased their water content over the following 10 days. The species were able to resume their hyperosmotic status relative to the desiccating environment they were placed in. Accumulation of sugars and polyols made an important contribution to this phenomenon.

Adult Diapause in Episyrphus balteatus (Diptera: Syrphidae)

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Episyrphus balteatus is one of the most important antagonists of cereal aphids in Germany. Unfortunately little is known about the overwintering status of this hoverfly, although it is assumed that early spring activity is related to mass development and aphid regulation capacities in summer. Only very few descriptions of hibernating individuals exist and successful overwintering is deduced from some records of flight activities in mild winter periods, early spring or late autumn. Regarding some studies about long distance migration in late summer to southern areas two hypotheses concerning the winter period exist:

1. *E. balteatus* is overwintering in substantial numbers in Northern Germany.
2. *E. balteatus* migrates to Mediterranean regions in late summer and immigrates during spring.

To confirm or reject the first hypothesis we study in detail the overwintering biology of this species in northern Germany by laboratory and field experiments. This poster presents results from physiological studies dealing with the diapause phase. We focussed on the determination of sensitive stages, diapause manifestation and the stimuli controlling induction and termination of diapause.

The results suggest that only females hibernate in a reproductive diapause, which is induced in larval stages (L_2 and L_3) by short-day photoperiods in late summer. In adults diapause is expressed in ceased ovary development and hypertrophy of fat body.

Thermal environment and developmental requirements of seed predators of Taraxacum officinale

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The ripening inflorescences of dandelion (*Taraxacum officinale* L.) are populated by several seed predator insect species of which dominant are *Ceutorrhynchus puncticollis* Boehman (Coleoptera, Curculionidae) and *Olibrus bicolor* (F.) (Coleoptera, Phalacridae). Since the growth and ripening of dandelion inflorescences is quick the time available for pre-pupal development of these species is short. We expected that both species adapted to short development by decreasing lower development threshold and/or sum of effective temperatures required to complete the egg and larval development. The temperature requirements for pupal development of both seed predator species were studied in the laboratory, at constant 20, 22, 25 and 28°C. The lower development thresholds were established at 6°C for *C. puncticollis* and 13 °C for *O. bicolor*. Assuming developmental rate isomorphy (Jarošík, Honìk and Dixon, this Workshop) these values were used as estimates of egg and larval developmental thresholds. The biological time available for egg and larval development was estimated by recording the development of dandelion inflorescences. Under natural conditions the pre-flowering, flowering and pre-dispersal phases lasted in the average 9.1, 2.7 an 9.6 d. The sum of effective temperatures available for *C. puncticollis* (193 day degrees) was apparently sufficient to complete the pre-pupal development while the time available for *O. bicolor* (48 day degrees) was not sufficient and the larvae probably visited several ripening inflorescences before pupation. Compared to related curculionid species biological time available for development of *C. puncticollis* is short. The rapid development of dandelion inflorescences thus exerts a pressure on increasing developmental rate of this seed predator. Supported by grant 521/99/1116 of GACR.

Food induced variation of thermal constants for larval development of Autographa gamma

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While the lower development threshold (LDT) of different development stages of a population of an insect species is often identical and subject to evolutionary constraints (Jarošík, Honìk and Dixon, this Workshop) the sum of effective temperatures (SET) is plastic, particularly in the growing larval stage. When feeding larvae of a species with food of different quality we would expect uniform LDT accompanied by variation of SET. This prediction we tested by investigating the effect of different diets on thermal requirements for development of larvae of a polyphagous species *Autographa gamma* (L.) (Lepidoptera: Noctuidae). The larvae were kept at 15.0, 22.3 and 26.7°C and fed by leaves of 13 dicotyledoneous herb and tree host plant species. As expected, the LDT varied between 9.1 and 10.6°C (average 9.8±0.5°C) and did not significantly differ between particular diets. By contrast, SET differed as much as 2.3 times (167 to 384 day degrees). The development length was proportionate to food quality and negatively correlated with the metabolic efficiency of food conversion. Due to autocorrelation of LDT and SET, both values were negatively correlated. However, the slope of correlation was small compared to the values expected for between-species trends resulting from adaptation to thermal environments (Trudgill, Squire and Honěk, in prep.). Supported by grant MZe M 01-01-03.

Aphids of the subantarctic archipelagos of Kerguelen and Crozet: how to succeed in colonization?

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Kerguelen (48°25'–50°S, 68°25'–70°35'E) and Crozet (45°75'–46°30'S, 50°15'–52°30'E) archipelagos are situated in the subantarctic area of the Southern Indian Ocean. Monthly mean temperatures fluctuate between 2.1°C (July) and 7.7°C (February) on Kerguelen and between 3.0°C and 7.9°C on Crozet. The total annual rainfall is 2400 mm on Crozet and varies from 3200 mm in the western part of Kerguelen to 750 mm in the eastern part. The wind is usually very strong on both islands. On these islands, terrestrial ecosystems are relatively simple and characterised by a poor biodiversity and a high rate of endemism. From the 19th century, seals and whales resources exploitation and scientific expeditions have increased human activity and landing and therefore favoured accidental and wilful introduction. 6 aphid species have been found on these islands. They have been probably introduced with their host plants. This paper aims to present the first elements of the dynamic and the genetic of aphid populations in order to understand why they succeed in colonization.

Two aphid species out of the six found on the two archipelagos were common in nature. *Myzus ascalonicus* was the most abundant species on both archipelagos. This species is known from Europe, India, Japan, Australia, New Zealand, North and South America. *M. ascalonicus* is polyphagous. It was particularly abundant on two subantarctic plants, *Acaena magellanica* (Rosaceae), the most abundant plant at low altitude (<200 m) and *Cotula plumosa* (Asteraceae) and on two introduced Asteraceae, *Taraxacum erythrospermum* at Crozet and *T. officinale* at Kerguelen. *M. ascalonicus* has been monitored by a permanent sampling program during 3 years. 90% of aphids were usually caught between February and May, *i.e.* when the mean daily temperature was above 4°C and number of frosty days below 10. Populations disappear between July and December. As this species is only parthenogenetic, active stages may survive during the winter.

Rhopalosiphum padi, presumably palearctic in origin, is now virtually world wide. *R. padi* is typically a cyclical parthenogenetic species with a single sexual generation (with fecundation and egg laying on a tree) alternating with several asexual generations breeding on grasses. Some clones may reproduce only parthenogenetically. Only one clone of *R. padi* has been found on both archipelagos. This clone was genetically similar to sexual clones from Europe but was unable to produce sexual morphs under inducing experimental conditions. On Kerguelen and Crozet, *R. padi* colonized many Poaceae, mainly the autochthonous grass, *Poa cookii*, and, in a lesser extent, the introduced *P. annua*. 90% of aphids were caught between March and May.

Further studies concerning factors of mortality, overwintering strategy, plant resources availability and genetic diversity should make it possible to specify the scenario of introduction of these species.

Latitudinal, caste and interspecific differences in the duration and temperature dependence of pupal development in three species of the ant genus Myrmica

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The duration and temperature dependence (measured as a coefficient of linear regression of developmental rates on temperature) of pupal development were studied in three species, *Myrmica rubra*, *M. ruginodis* and *M. scabrinodis*, from four geographically remote regions – Kiev (50°30' N), Yurievets, Vladimir prov. (56°15' N), Vyritsa near St. Petersburg (59°15' N) and Chupa, Karelia (66°15' N). A significant effect of geographic origin on the duration and temperature dependence of development of worker and male pupae was discovered in all three species studied. In *M. ruginodis* the pupal development in more northern populations was shorter at higher temperatures and longer at lower temperatures in comparison with more southern populations. This was connected with the increase of temperature threshold and of temperature dependence of development (higher slopes of regression lines of developmental rate on temperature), and with the respective decrease of the sum of effective temperatures with the advance to the North. The rate of pupal development in *M. ruginodis* and *M. scabrinodis* from northernmost region (Chupa) was significantly higher than in more southern populations over the whole temperature range from 16 to 24.5°C because of some decrease of temperature developmental threshold with the temperature dependence of development being as high as before. An entirely opposite situation was found in *M. rubra*. Temperature dependence of development in *M. rubra* worker pupae from two populations studied (Yurievets and Vyritsa) did not differ but in more northern of them the temperature threshold was a bit higher and the developmental rates were significantly lower at all temperatures. Male pupae of all three species had shorter developmental times in comparison with worker pupae at all temperatures studied. The queen pupae from Chupa developed more slowly that the worker and male pupae from the same population over the whole temperature range. The development of *M. scabrinodis* worker and male pupae was found to be less dependent on temperature and was longer in comparison with *M. rubra* and *M. ruginodis* pupae from sympatric populations of Vyritsa and Chupa. The temperature threshold of pupal development was lower in *M. scabrinodis* than in *M. ruginodis*. Populations of *M. rubra* and *M. ruginodis* in Yurievets had almost identical developmental thresholds and thermal lability of pupal development. The pupal development in more northern *M. ruginodis* population (Vyritsa) was more temperature dependent and had a higher threshold in comparison with a sympatric *M. rubra* population.

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The advantages of being cold: Natural winter microenvironments influence energy consumption and potential fecundity of goldenrod gall flies, Eurosta solidaginis (Diptera: Tephritidae)

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We studied the influence of two overwintering microenvironments on survival and potential fecundity of goldenrod gall flies, *Eurosta solidaginis* (Diptera, Tephritidae), to understand how insulation by snow affects a cold-hardy ectotherm. These freeze-tolerant larvae are found in nature overwintering above the snow on standing goldenrod stems (supranivean) or below the snow on broken stems (subnivean). When covered by snow, the subnivean larvae were well insulated and thus protected from the coldest temperatures of the winter, but, because they were warmer, they were also consuming more energy than their supranivean counterparts. The subnivean group, being closer to the ground, also experienced greater warming during sunny spring days and their galls were less prone to drying than those of their supranivean counterparts. By winter's end the subnivean larvae exhibited significantly lower rates of emergence (83.5% vs. 93.0%) and reduced potential fecundity (274 + 11 eggs/female vs. 336 + 17 eggs/female). These differences were likely due to higher metabolic rates in the insulated subnivean microenvironment which reduced the energy available for morphological development and egg production in the spring. We conclude that cooler winter microenvironments can have a strong positive effect on overwintering ectotherms, particularly those that rely on energy stores accumulated during the autumn to produce eggs in spring. The enhanced reproductive output of insects overwintering in a colder microenvironment may be a selective force promoting the evolution of increased cold-hardiness.

Geographical variation of photoperiodic response in a predatory bug, Orius sauteri, and the selection of non-diapause strain.

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Orius sauteri is known as an important predaceous natural enemy of agricultural pests such as thrips, spider mites, and aphids. Since short days induce reproductive diapause only in females but not in males in this species, only females (usually inseminated) are able to survive the winter. The critical photoperiod for diapause induction in the Sapporo population (43.0°N) was estimated to be L14:D10 to L14.5:D9.5 at 22°C, but geographical variations in the photoperiodic response were observed depending on the populations collected, namely, 1) a clinal change of critical photoperiod was observed, and 2) the southern populations tested showed more gentle slope in the photoperiodic response curve than northern ones. Some females of the Tsukuba population (36.0°N) laid fertile eggs even under such short daylength as L11:D13 or L12:D12 conditions. Non-diapause strain has been selected from these females breeding under L11:D13 condition. More than 80% of the females became to lay eggs under this condition after 5th generation. Another non-diapause strain has also been selected from the different species of *Orius* under the same condition. The advantages of the use of non-diapause strain as a biological control agent will be discussed.

Thermal constants in insects and mites: variation or constraints?

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The published information indicated a large intraspecific variation of lower temperature threshold for different development stages of many species. The differences may be either real or arise in consequence of biassed data on development length. We tried to decide this difficulty by a new method, testing the data for "rate isomorphy". An organism shows "rate isomorphy" when the proportion of total developmental time spent in a particular developmental stage does not change with temperature. In this case the lower temperature threshold is the same for all developmental stages. We tested the incidence of rate isomorphy in 7 species of mites and 342 species (some of them represented by several populations) from 11 insect orders, using data on development lengths from temperatures where the relationship between the rate of development and temperature is linear. Proportion of total developmental time spent in a particular stage was plotted against temperature and the existence of rate isomorphy inferred from a zero change in proportion. Rate isomorphy was detected in 243 (57 %) of 426 populations. In the rest of the cases rate isomorphy was violated by deviations in the proportion of time spent in a stage by an average of 0.2% at the mean of the range of temperatures of all the data sets (11°C). Consequently, in insect and mite species, all the developmental stages appear to have the same population-specific lower developmental threshold. There are indications that a common lower thermal threshold may constrain the development in groups of related species.
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A comparative study of drought tolerance in nine species of Collembola

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Soil living collembolans can be regarded as having a mode of life in between the aquatic and truly terrestrial with regard to their water balance and osmoregulation. For example, they have no special protection against desiccation such as impermeable cuticula. However, recently Bayley & Holmstrup (1999) demonstrated that the soil dwelling collembolan, *Folsomia candida*, was capable of actively regulating its osmotic pressure by the synthesis of sugars and polyols and thereby survive appreciable levels of drought stress, even below the permanent wilting point of plants. Investigations among other species of soil dwelling collembolans have shown similar results (Holmstrup *et al*, *in press*). All the species studied so far are euedaphic species living in an environment where relative humidities range between 96 and 100%, but epedaphic and hemiedaphic species of collembolans experience a much wider range of relative humidities. It is also known that some epedaphic collembolans have evolved cuticular structures with much lower transpiration rates than euedaphic collembolans. However, does the ability to active volume regulation using sugars and polyols exist over the range of cuticular transpiration rates present in hemiedaphic and epedaphic collembolans?

To elucidate this question we have investigated a broader range of species covering euedaphic to hemiedaphic and epedaphic species. We have investigated drought tolerance as the survival of 7-day acute exposure to a range of drought levels, the water permeability of the cuticle, changes in body fluid osmolality and the presence of different sugars and polyols. Nine species of Collembola were studied: *Protaphorura armata*, *Folsomia candida*, *Folsomia fimentaria*, *Hypogastrura assimilis*, *Heteromurus nitidus*, *Isotoma anglicana*, *Sinella curviseta*, *Pogonognathellus flavescens* and *Orchesella cincta*.

Large variation among species was seen in both cuticular permeability and drought survival, although no clear correlation between these two parameters appeared, except in one case. The epedaphic species, *O. cincta*, had both a low cuticular permeability and a high drought survival. These results suggests that collembolans are using, and sometimes combining, several strategies when faced with drought stress. These strategies consist of production of osmolytes, cuticular protection and probably also behavioural responses.

Learning in workers of the ant, Myrmica rubra, depends on the stage of a colony seasonal life cycle

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The learning in worker scouts was investigated during the acquisition of multi-choice maze task on the basis of two social motivation – brood transport or foraging. The superfast learning with a predominance of correct solutions (up to 98%) and habit optimization were observed under conditions of brood transport motivation or high level of food motivation. When a lower level of food motivation was used the number of movement in a cycle and it's duration increased, the number of correct solutions decreased and they became more variable due to prevailing of exploratory activity. The experiments carried out in autumn and winter allowed to discover the dependence of learning ability on a colony seasonal cycle. One series of experiments was carried out in September–October during rainy, dusky weather, under artificial light and temperature of 15–18°C. The colony's needs for food decreased at that time and, thus, the maze foraging habit has not formed: there was only 49% of correct solutions, and in the end of experiment the number of movements in a cycle diminished as a result of exploratory activity. In another series conducted in October–December under artificial light and temperature of 21–22°C, when the ants had enough food, maze habit became stable, there were 86% of correct solutions, but the exploratory activity caused a high number of movements in a cycle and the absence of optimization. In these two series the indices of maze foraging habit were worse on the whole than those in experiments carried out in summer. The foraging habit formation in same hungry colony was better in June than in September. We conclude that the maze habit formation in worker ants during foraging was worse in autumn and winter periods due to low food motivation, but the learning ability under brood transport motivation remained at the same level.

Influence of exogenous factors (light and temperature) on the daily rhythm of adult eclosion in Trichogramma embryophagum (Hymenoptera, Trichogrammatidae)

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It is well known that the adult eclosion in most of insects occurs only during the certain period of day often named as "gates". The egg parasitoid *Trichogramma embryophagum* also exhibits the distinct daily rhythm of emergence which could be synchronised with external photo- or thermoperiod. In the present work we attempted to elucidate if there is a period during the day when the eclosion is endogenously blocked and could not be induced by external stimuli. For this purpose the separate and combined influence of light and temperature on the adult emergence was studied in different time of 24-hour cycle.

Before the eclosion all individuals were reared under the same regimen (LD = 12:12, 20°C). However, just in the day when records of emergence were made the time of light-on was shifted on the earlier hours . Thus, the period of darkness (scotophase) was changed from 0 to 12 h in different treatments. In additional variants of the experiment insects experienced 2-hour high temperature pulse (30°C) just before or just after the onset of photophase. The fraction of specimens eclosed within 2 h after the beginning of the action of exogenous factor was used as a parameter of the response to this stimulus.

The obtained results showed that light-on or temperature step-up could induce eclosion in certain percentage of individuals at any time of 24-hour cycle. Moreover, the extent of response to stimuli was found to change during the day. Light-on induced more intensive eclosion than sharp rising of temperature, and the combination of these factors caused cumulative effect. The simultaneous action of light-on and temperature step-up exerted much more considerable influence than could be expected based on their separate impacts. On the contrary, high temperature pulse preceding the onset of photophase inhibited the response of individuals to light-on. This interaction was more pronounced in the first half of 12-h scotophase.

The data suggest that the adult eclosion daily pattern in *T. embryophagum* is based on the quantitative changes in thresholds to the external stimuli rather than on qualitative “opening and closing of the gates” . Furthermore, the result of combined influence of light and temperature seems to be a cumulative effect, rather than simple sum of their effects. These factors cooperate to regulate the eclosion daily rhythm apparently by modification of the sensitivity of organism to one another.

High level of the responsiveness to the exogenous stimuli seems to provide the plasticity of the eclosion rhythm and synchronisation of adult emergence with the local weather conditions. This feature may be considered as a one of the adaptations to unpredictable weather conditions in northern regions.

Some effects of low temperature on the adult eclosion rhythm in Culex pipiens pipiens f. molestus

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It is well known that the circadian rhythms of many insects are modified by direct influence of the temperature. However, the following question remains explored insufficiently, may the temperature change during the early development cause adaptive modifications of daily rhythms observed at the subsequent stages of ontogeny? The present work was aimed to investigate some effects of cooling applied to the different developmental stages on the adult eclosion rhythm in the mosquito *Culex pipiens pipiens f. molestus.*

The experiments were carried out in temperature-controlled chambers under the photoperiod LD=16:8. Control group was reared in constant 25°C temperature conditions all time, until the end of the eclosion. In some other experiments the individuals experienced short-term cooling (32 h under 15°C) during a larva stage or at the pupal stage, the rest of development occurred at 25°C. The onset and the end of cryophase coincided with light-off and light-on, correspondingly. Moreover, in a one of the groups the emergence was registered among the pupae reared constantly at 15°C.

In the control conditions the distinct eclosion rhythm was observed with the peak preceding light-off, emergence was suppressed at the end of the scotophase and at the beginning of photophase. No considerable differences in the eclosion daily pattern were recorded between the individuals that have experienced short-term cooling at the 2-d, 3-d or 4-th larval stage and those of the control group. However, in the experiment where the pupae were temporarily subjected to 15°C, the subsequent eclosion rhythm become less pronounced and the percentage of the adults emerged during the first half of photophase increased. In the individuals eclosed directly under the constant low temperature conditions the peak of the rhythm shifted in the beginning of the light period, in comparison with the control.

The results obtained signify that the adult eclosion rhythm in *C. pipiens pipiens f. molestus* can be modified both by constant direct influence of low temperature and by previous short-term cooling at the pupal stage, thereby the rate of emergence increases at the first half of photophase. Such temperature sensitivity seems to promote the mosquito emergence during the daytime hours which are the warmest. *C. pipiens pipiens f. molestus* mostly inhabits the urban underground biotopes, where the daily fluctuations of external factors are often negligible. In this connection, the observed response to cooling is supposedly non-adaptive and may be considered as an evidence of the some old biorhythmic features being conservatively fixed during the adaptation of this mosquito form to synanthropic conditions.

Life cycle and phenology of arctic tiger-moth Grammia olga (Lepidoptera, Arctiidae)

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Field studies of *Gr. olga* were carried out in the central mountain part of the Wrangel Island (Mamontovaya River valley). In this area this species is characterized by high density. Most of the larvae were collected in June and July 1993 and 1994. Living specimens were weighed, the larval instars were determined (total number 724). The growth and development of larvae was obtained in the laboratory.

The observation on *Gr. olga* indicate that it passed through seven larval instars. Larvae hibernates in all instars. The 4–7 instars were recorded in the first warm days of summer, the 1–3 instar larvae – few days later. All the 7-instar larvae pupated at the early of summer, but one specimen of 6-instar larvae (in laboratory) moulting in 7-th instar and ten day later pupated too. Pupation of *Gr. olga* larvae undoubtedly takes place under plant causions without cocoons. Imago emerges at the end of the June – middle July. In laboratory (at mean temperature of about 20°C) the pupae development lasts 10–14 days. Oviposition was recorded at the end of June, the larvae hatched 11 days later. In laboratory conditions their moulting began in ten days and in early August (when observation was ceased) most of them reached 2-instar with weigh of 5–7 mg.

The larvae 2–6 instars in nature more often feeds on *Salix polaris, S. glauca, Dryas punctata, Carex spp., Saxifraga oppositosolia, Oxytropis wrangelii, Oxyria digyna*. Larvae feeding on flowers were recorded in the period of blooming and changes of food plant according to mass flowering the different species – *Salix glauca, Oxytropis wrangelii, Dryas punctata*. The period of larvae moulting occurred after two-three weeks after hibernation (in the summer with middle weather conditions – at the second part of June). Some time later (first decade of July) larvae development stopped. They disappeared on soil surface. After that few larvae were recorded under plant causions. In the early and warm summer 1993 it was happened at the end of June, in very cold summer season (1994) they continue to feed until the end of July.

In laboratory conditions 15 larvae with different instars (2, 3, 5) moulting only once per season. All 5 specimens of 4 instars moulting twice per season and among other larvae only one 2-instar larvae moulting twice too. In 1993 all larvae in laboratory stopped feeding at the end of June and in 1994 – at 20 of July, nearly at the same time with disappearing larvae in nature.

The observation on *Gr. olga* permits to suppose, that the total life cycle for the majority of specimens from one cohort occupies about 5 year. In spite of the some flexibility in single specimens development, all flexibility of life cycle is restricted. The period of larval development occurred only in the one month in first part of summer. Observation in the summers with very different warm conditions show that this tiger-moth is sufficiently rigidly bound in a life cycle. Thus, *Gr. olga* has a prolonged life cycle that is typical of arctic invertebrates. According to phenology it is the most similar with *Gynaephora groenlandica* (Wocke) – the high arctic moth of the family Lymantriidae (Kukal, Kevan, 1987, Kukal, Dawson, 1989) in spite of *Gr. olga* seem to be able to use a wide range of host plants.

Ecophysiological adaptation by Myrmica ants to short summers

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All *Myrmica* species in all environments, have split brood cycles – whereby some larvae from eggs laid in early summer, develop rapidly to become workers (rapid brood) while others develop more slowly, overwinter and become either workers or new queens in spring (diapause brood). At high latitudes where brood rearing is restricted to five or less months per year, *Myrmica* species adapt by changing both physiology and behaviour.

We have shown that local *Myrmica* populations adapt to increasingly high latitudes in the following ways. (1) The photoperiodic control of diapause, although important in southern regions, loses its former role and is progressively replaced by a mixture of endogenous controls and induction by temperature cues in boreal and subarctic populations. (2) The length of colony's intrinsic seasonal cycle of brood-rearing and the number of rapid brood pupae produced vary according to the latitude of their site, decreasing in northward direction. (3) In extremely northern populations colonies do not rear rapid brood at all, but instead most overwintered larvae pupate during summer, and only a few may overwinter once more. (4) *Myrmica* populations from higher latitudes have higher Q10s and, thus, their metabolism is more intensive than that of southern populations at higher temperatures but less intensive at lower temperatures. Consequently, the individual metabolism in northern populations appears more temperature dependent allowing them "to live faster" and to respond more quickly to changing temperatures. (5) Northern populations of *M. rubra* rear brood more quickly, and northern brood develops more quickly, compared to southern populations when reared under common-garden conditions. (6) The development of eggs, larvae and pupae from northern *Myrmica* populations is more temperature dependent (higher slopes of regression lines of developmental rate on temperature), is characterised by higher temperature thresholds and proceeds faster at temperatures above 16–18°C in comparison with the development of the same brood stages from southern populations. (7) Owing to the changes in habitat preferences and the improvements of the thermal characteristics of the nests ants in more northern regions rear their brood even at higher average temperatures in comparison with their southern counterparts.

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Reaction norm in response to temperature may change to adapt brood development to boreal and subarctic climates in Myrmica ants

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It is generally supposed that arctic and subarctic poikilotherms should be better adapted to grow and develop at low temperatures compared to their temperate counterparts. Indeed, the threshold temperatures for respiration, activity, feeding, development and emergence have long been shown to be very low in many arthropod species of northern origin. Although ants have successfully penetrated as far to the North as the forest-tundra zone surprisingly few studies have been devoted to the thermal requirements of development in boreal and sub-arctic species and populations of ants.

We studied the effects of temperature on brood rearing in colonies of *Myrmica rubra, M. ruginodis* and *M. scabrinodis* collected at four latitudes: Kiev (50°30' N), Vladimir (56°15' N), St. Petersburg (59°15' N) and Chupa (66°15' N). The differences between colonies kept at low (14–18°C) and high (20–25°C) temperatures in the occurrence of repeated diapause among overwintered larvae and in the duration of the intrinsic seasonal cycles of oviposition and rapid (non-diapause) brood production appeared much more pronounced in ants from northern populations. It means that northern colonies produced eggs and pupae under lower temperatures evidently worse in comparison with colonies from southern regions. At the same time higher temperatures apparently had a stimulating effect on the colonies from northern populations preventing the diapause onset and thus extending the cycles of oviposition and brood-rearing. Besides that the development of eggs, larvae and pupae from northern populations was more temperature dependent (higher slopes of regression lines of developmental rate on temperature), had higher temperature thresholds and proceeded faster at temperatures above 16–18°C in comparison with the development of the same brood stages from southern populations.

We conclude from this that the reaction norm of *Myrmica* colonies in response to temperature changes according to the local climate in such a way that egg production, brood rearing, and the growth and development of individuals become more temperature dependent in more severe environments with colder and shorter summers. Consequently *Myrmica* colonies from northern populations need on the average higher temperatures in their nests for successful production of new adults as compared to southern ants. The data on nest microclimate show that northern colonies rear their brood even at higher average temperatures than southern ants owing to the adaptive changes in habitat preferences and the improvements of the thermal characteristics of the nests.

Thus, contrary to a lot of other arthropods, *Myrmica* ants adapt to boreal environment by relying upon relatively higher temperatures for more rapid development. In a sense northern *Myrmica* colonies are more thermophilic and more stenothermic in comparison with those living in the South. This peculiar feature is undoubtedly related to the fact that originally thermophilic ants manage to exist in boreal regions only owing to special construction of their nests destined to collect sunshine and to rise the temperature inside.

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Life cycle and development of the retrocerebral complex in the cricket, Gryllus argentinus, under laboratory conditions

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Life cycle and development of the retrocerebral complex in the cricket *Gryllus argentinus* were investigated under conditions of laboratory culture. The total duration of non-diapaused developmental cycle of *G. argentinus* (“from egg to egg”) under maintaining crickets in groups in laboratory conditions (26°C temperature, 49% humidity, 12h light – 12 h dark photoperiod, universal food diet, absence of predators) was 97–116 days.

Adult animals were found to pass through several periods of development during their life. Females have 4 such periods: precopulative, copulative, productive and postproductive ones. The precopulative period lasts, on the average, for 7 days (from molt till first copulation). The copulative period lasts for 2.5–3 months and is periodically interrupted by the productive period (egg-laying) that may amount to 30–70 days depending on the degree of spermatheca filling. Taking into account possible repeated copulations, alternation of these period may occur. The length of the postproductive period preceding animal’s death is about 2 days.

In males 3 periods of imago development may be distinguished: precopulative (ca. 4 days), copulative (ca. 30 days) and postproductive ones (ca. 2 days).

Under laboratory conditions females predominantly lay groups of eggs. The set size varies from 2 to 11 and, in some cases, to more than 11 eggs. The embryonic development lasts, on the average, for 15 days.

The total duration of larval development under laboratory conditions is about 80 days and the number of larval ages is nine.

All stages and periods of ontogeny, features of behavior (including acoustic, defense, territorial and sexual behavior) as well as the parameters of development in a group are comparable to those described for *Gryllus bimaculatus* and are preserved in full measure under conditions of a long-standing laboratory culture.

Microanatomy and topography of the retrocerebral complex in the cricket *G. argentinus* were also studied in 1st age larvae, deutonymphs and adult females. Several topographically significant parameters were selected to describe the localization of the retrocerebral complex and its elements in the head capsule and their linear dimensions were determined. On the basis of primary measurements the secondary parameters were calculated to estimate the asymmetry of arrangement of the organs of the retrocerebral complex.

Behavioural adaptations of the honeybee, Apis mellifera, to long overwintering

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Honeybee colonies Apis mellifera are widely distributed in the cold climate zones where overwintering period lasts for 5–7 months. Main strategy of social wasps and bumblebees is to grow reproductive females with reserves of fat. They are able to overwinter in diapause or stupor under the ground or tree rind, where they are inaccessible for the predators. Large honeybee colonies cannot use passive defence against the enemies. There are three possible reasons which cause the necessity to hold high temperature of winter cluster and high level of metabolism: (1) The necessity of defence against the enemies; (2) The impossibility to use cold and viscous honey; (3) The very high (in comparison with another overwintering insects) chill coma temperature (> 10°C).

Honeybee eats up to 500 mg of honey during winter, that is 5 times her own weight, at the same time other insects use only a part of their fat body (10–20% of the weight). Several honeybees behavioural adaptations give them the possibility to overwinter successfully: (1) ability to accumulate the large quantities of honey in the nest, (2) reproductive diapause in autumn-winter period, (3) ability to form winter cluster, and (4) preservation of the defensive capacity during winter.

There exist essential differences in the winter hardiness of different races of the honeybee. Dark European forest bees and especially their Middle-Russian population have the highest wintering ability. From the beekeepers point of view Middle-Russian bees are very aggressive and have large swarm ability. The attempts the use the gentle southern races with excellent honey productivity sometimes gave good results, as sometimes southern bees overwintered excellently. The physiological differences between races with large and low overwintering abilities are almost unknown, but there are several clear behavioural differences. Races with high wintering ability have: (1) early start of reproductive diapause, (2) weak reaction to the fall of nectar flow, (3) weak reaction to the winter and early spring short-term warmings.

The well-known facts of excellent wintering success of southern Caucasian bees in Northern regions give us the grounds to insist that these differences are not principal.

It is possible to explain the rapid spreading of the honeybees from the tropics into the regions with long winters by a number of quickly appeared behavioural adaptations which were fixed by rigid natural selection.

To our opinion the speed of appearance of behavioural adaptations is higher than that of physiological ones. The real absence of well-known physiological differences between races with different winter hardiness and the high and almost equal chill coma temperatures support this hypothesis. It stays unclear why honeybees could not reduce the chill coma temperature as this would give them a great advantage including the decreasing of winter cluster energy losses.

Low temperature storage of the predatory midge, Aphidoletes aphidimyza

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Aphidoletes aphidimyza is a polyvoltine species with larval facultative overwintering diapause. Larvae are predators and are commercially used to control aphids in greenhouses. Attempts to develop methodology for the cryopreservation of *A. aphidimyza* embryos have been unsuccessful so far and studies of low temperature storage have met with mixed results. Low synchrony of adult emergence in individuals which passed through the diapause development was recognized as a serious problem for the practical use of low temperature storage in this insect. The suitability for low temperature storage may considerably differ among different populations. The commercial populations are usually selected for the best parameters of population growth rather then for the best cold storability. Thus, we attempted to identify characteristic features of a population, which could serve as a source for genetic selection of a strain combining both good performance in greenhouses and good storability at low temperatures. The populations with inherently high intensity of diapause and high level of cold hardiness should be considered first (Kostal et al., in prep.). Further, we investigated into optimization of the low temperature storage protocol in order to improve survival rate and synchrony of adult emergence after long time storage (up to one year). When diapausing larvae are to be stored, the termination of their diapause appears to be a prerequisite for a good synchrony of adult emergence (10–90% of individuals emerge within ca 20 days). This may be achieved either by chilling (for a period of time which is population-specific) or by a brief exposure to the vapour of *n*-hexane. Further improvement of synchrony (to ca 10 days), was achieved by exposure to 30°C for 1 week just after the end of storage period. When non-diapausing larvae were stored, their mortality rates were higher, but the survivors emerged rapidly and highly synchronously (within 2–3 days) (Kostal and Havelka, 2001). Thus, repeated positive selection of individuals who are able to withstand long time storage at low temperature, while being in non-diapause state, emerges as a promising way to obtain a population with the best parameters of low temperature storability, including the synchrony of adult emergence after storage.

References

Košťál V., Havelka J., Šimek P. (in prep.). Low temperature storage and cold hardiness in two populations of the predatory midge *Aphidoletes aphidimyza*, differing in diapause intensity.

Košťál V., Havelka J. (2001). Low temperature storage and synchronization of adult emergence in the predatory midge *Aphidoletes aphidimyza*. *Cryobiology* 41, in press.

Cryoprotective role of polyols independent of the depression of SCP in diapausing adults of Pyrrhocoris apterus (Heteroptera: Insecta)

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In the Czech populations of the red firebug, *Pyrrhocoris apterus* (L., 1758), the individuals of prevailing brachypterous wing-form enter the reproductive diapause in response to environmental cues such as short photoperiod, low temperature and high population density, through their effects on the neurohumoral system. Overwintering adults of *P. apterus* do not tolerate freezing of their body fluids and rely on supercooling for winter survival. The temperature at which the body fluids start to crystallize (the supercooling point, SCP) sets the lower limit of survival but the capacity to survive low temperatures close to the SCP for extended periods of time (> 24 h) develops only gradually and thus, the maximum cold hardiness is attained with a certain delay after the SCP had reached its lower limit (Košťál & Šimek, 2000).

In this study it was shown that the diapausing cold acclimated adults of the bug *Pyrrhocoris apterus* accumulate four polyols, ribitol, sorbitol, mannitol and arabinitol, in sum concentrations of up to 100 mM. The accumulation starts only when the temperature drops below a threshold found between +5° and 0°C. The supercooling capacity (*SCP*) is not affected by polyol accumulation and remains constant at a median of -17°C. Cold hardiness, measured as survival time (*Lt50*) at -15°C, increases from ca 1 day to ca 1 week in parallel with polyol accumulation. There is a linear relationship with tight statistical correlation (r = 0.98) between the sum concentration of polyols in haemolymph and $Lt50_{-15}$. When the mixture of ribitol and sorbitol is injected into the haemolymph of the bugs acclimated to +5°C, so that the sum concentration of polyols increases from 2.5 to 83.1 mM in haemolymph, or from 0.07 to 6.61 μg/mg of fresh weight in the whole body, the *SCP* remains unchanged, but survival rate at -14°C/3 days increases approximately 3 fold in comparison to untreated controls. Such results were interpreted as an evidence for cryoprotective role of accumulated polyols independent of the depression of *SCP*.

Reference

Košťál V., Šimek P. (2000). Overwintering strategy in *Pyrrhocoris apterus* (Hetroptera): the relations between life-cycle, chill tolerance and physiological adjustments. *Journal of Insect Physiology* 46, 1321–1329.

Relating antifreeze proteins to the thermal hysteresis they create

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Many insects produce so-called antifreeze proteins (AFP) as a component of their cold hardening. AFPs displace the growth of ice in a solution to a temperature below the equilibrium freezing point of the crystal. The presentation will outline mathematically the mechanism by wich these proteins cause this phenomenon.

Life cycle of earthworms Eisenia nordenskioldi (Eis.) (Oligochaeta, Lumbricidae) in southern forest-steppe

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Eisenia nordenskioldi (Eis.) is a polyzonal, ecologically plastic species of Siberian origin. The study of its perennial life cycle was made in the oak forests in south-eastern part of European forest-steppe. Wild population was represented by four age groups: two juvenile groups (animals of two generations), animals with forming external sex characters (with tubercula pubertatis) and mature animals (with tubercula pubertatis and clitellum). Last group can be represented by different generation of animals. Mature lumbricidas can live more than two years and breed repeatedly. Their fertility varies from one up to six cocoons per animal per year.

The typical year cycle of worms consists of the following season periods: spring activity, suppressed vital activity, aestivation, autumn activity, hibernation. The hibernation ends in the middle of April. The worms become active with the temperature starting from +4 – +5°C, when litter and soil are saturated with moisture. At that time they feed on litter. Their breeding is most active, juvenile animals are growing; starting from the middle of May new generation is hatching from cocoons. The average body mass of mature animals is maximal – 968 mg.

With the beginning of drought worms are migrating to the upper layers of soil. According to the results of the laboratory experiment the body growth of juvenile animals decreases more than three times as a result of the consumption of soil organic. Starting from the beginning of July the soil is more dry (Ψ=2.03 MPa). The worms stop feeding, roll into balls but the animals still keep an ability to move. The growth stops. The body mass of mature animals drops to 715 mg.

Low soil moisture (Ψ=3.0 MPa) leads to aestivation. All worms are encapsulating. Rolling into balls decreases the body surface to provide more economical water and metabolic regime. The stiffness is possible. The average live body mass of mature animals is 414 mg. The water percentage drops to 80% comparing with 85% at spring and the beginning of summer. Death of animals is observed, mostly among young and old generations.

The autumn activity increases with the moisturizing of soil and drop of temperature. The water metabolism is restored. The body mass of all age groups increases. That period is marked with the second peak of breeding. During experiment (t = +7 – +5°C) the pre-hibernational growth of juvenile animals was registered.

At the beginning of November the population comes to the hibernation. The changes of the state of worms at that time were studied in the laboratory experiment with the temperature regime of "soft winter" (t = +5...-1.5°C). During four months the worms lost about 12% of body mass. The example of *E. nordenskioldi* shows that seasonal life cycle of earthworms depends on hydrothermal regime of soil. It was estimated that body mass of animals correlates with soil moisture. Development of worms starting from hatching to maturity takes three years but can vary according to weather fluctuations. The survival of that frost-resistant species at the southern border of the distribution range is limited by the conditions of summer draught.

The breathing patterns of bumblebee Bombus terrestris foragers at low temperatures (0°…10°C)

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There occur periods in the life of bumblebee foragers when they are exposed to low temperatures. In case of pollen deficit the foragers are active outside the nests in early mornings and late evenings, especially in low-temperature conditions in late spring. So far there are only scarce data available about the respiration pattern of foragers, and their respiration modes at low temperatures have not yet been studied either.

In the present work the cyclicity of gas exchange, the muscular ventilation and metabolic rates were recorded by means of an electrolytic respirometer and a flow-trough respirometer (CO_2 analyzer), both combined with an infra-red optical actographic device that allows to record the muscular contractions inside the insect body and correspondent body movements. The universal insect chamber was spacious enough to able the bee to walk inside it, and it was connected by a polyethylen tube to one of the two mentioned respirometer types. The insect chamber was placed into a selenium microrefrigerator with controlled temperatures. At times the insect was visually observed inside the insect chamber under a stereomicroscope.

At 10°C the shivering with frequency of 4–7 Hz was a sign of stress state lasting commonly 2–5 minutes. The abdominal vigorous telescoping movements (1–2 Hz) were externally well visible, and these were also regarded as stress symptoms lasting for 5–20 minutes at the beginning of measurements. After recovering from the handling and apparatus stress the foragers showed clear discontinuous gas exchange cycles, or DGCs, with a frequency of 5–8 cycles per hour. The appearance of clear DGCs was usually considered as a sign of immobility of the insect.

At 10°C the CO_2 bursts were ventilated by abdominal weak contractions. It was characteristic that the periods of DGCs alternated with periods of active or muscular ventilating made by externally almost unnoticeable abdominal contractions. We did not consider the immobility of bumblebees at 10°C to be a state of turpor. The bumblebee foragers were restrained and periodically motionless in a spacious insect chamber even at 22°C in daylight, after having been accustomed to these conditions.

At 5°C the clear DGCs persisted, but now the CO_2 bursts were not actively ventilated. At this temperature the DGCs sometimes also alternated with active ventilating movements (0,3–0,6 Hz) well seen on the recording lines of the electrolytic respirometer as well as on recordings of the infra-red optical device.

At 0°C the foragers showed typical gas exchange microcycles, while on the recording line there occurred irregular sharp peaks due to the abrupt air intakes into tracheae (0.1–0.2 Hz), and the opposite signals due to CO_2 microbursts. However, even at 0°C the cold-adapted foragers displayed periodically weak externally invisible abdominal contractions.

There did not exist any distinct cold stupor point in bumblebee foragers. The moving activity decreased gradually at lowering temperatures up to 3°C in the cold-adapted individuals. From our study we concluded that at low temperatures the foragers exploited energetically most economical mode of respiration – the cyclic gas exchange.

The investigation role of multicomponent cryoprotective system in the cold hardiness of Aporia crataegi L. inhabiting Central Yakutia

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Our researches of a phenomenon cold hardiness *Aporia crataegi L.* were based on the assumption of a key role cryoprotective substances in formation of this phenomenon. As a result of this research the method of ethanol extraction of cells worms an extract being multicomponent system was received. It consist from proline, glutamine acid, soluble component, presumable N-acetylglucosoamine.

In researches of seasonal dynamics of change of the quantitative contents separate components of extract and also contents of water in organism of worms during 1998–2000 was shown that the summary quantity of extract 's components in overwintering worms is maximum in the cold month: January, February, thus change quantitative contents of separate components has synchronous character that testifies about their interaction in structure ethanol soluble extract. *Aporia crataegi L.* does not fall into organisms subjecting to noticeable dehydratation during season of diapause (water content in January month averages 72.9%) but process dehydratation as well as for other hexapods, is accompanied by an intensification production of hydrophilic substances which is capable to retain bound water in the cells. One of biochemical mechanism protecting hexapods from an extraordinary dehydratation is use F aminoacids in the formation of cocoon.

It is known, that formation of a cocoon from a white-transparent film, which is congestion of white threads by depth 1 micron by a microscope is one preparatory stage to the winter season for the worms *Aporia crataegi L.* From the same building stuff will be derivated the strong thread with the help by which one the sheet jacks are attached to branches of a bush and do not fall down even at strong and choppy wind. As shown in a number of researches the cocoon plays the relevant role in protection of an organism against an excessive dehydratation in the season of low zero temperatures.

The investigated extract has cryoprotective activity in relation to peripheral blood lymphocytes of the man. From this point of view specially active use extract is at multistage freezing-straight thawing of lymphocytes at the presence of the cryoprotector the efficiency surpassed those glycerol (being on today by on the best cryoprotector) in more, than 3 times.

Thus, the investigated extract *Aporia crataegi L.* is possessing cryobiological activity, as have shown our researches, the function of an aminoacid component is not only the protection of cells from cold damage, but also preservation of the body hexapod from an excessive dehydratation on conditions of dry winter air.

Ecological-physiological peculiarities of acquisition and retention in memory of individual experience in the honeybee (Apis mellifera L.)

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The capability for associative learning and retention of acquired skills in memory is characteristic of all known insect species. This capability is the most complex in insects with the social mode of life. The data that we and other researchers have accumulated by the present time (Menzel, 1989; Kamyshev, 1998) indicate a close interrelation of congenital and acquired components in the process of formation of complex instinctive forms of the insect behaviour and, thereby, a plasticity of the behaviour that previously seemed stereotypic.

Realization of genetic information that determines capability for the honeybee associative learning is controlled by ecological factors. This is indicated by the data that we obtained on seasonal variability of the capability for learning. Thus, parameters characterizing the associative function (formation of conditional reflexes and their retention in memory) are elevated more than 1.5-fold in August–September compared with the first half of summer (June–July). Probably, this is due to the appearance of the autumn generation of honeybees that are able to retain in memory the characters of the location of the honeybee hive throughout the whole autumn-winter-spring period. A triggering mechanism of such phenomenon might be changes in proportions of the light and dark parts of the 24-hr period. A. V. Cherednikov (1967) was the first to show the role of the above ecological factor in the honeybee family life activity. Our study carried out in cooperation with M. S. Ragim-zade indicates importance of the temperature regime for performance of the associative function. Thus, migration of honeybee families of a certain race to inadequate climatic (temperature) conditions led to a disturbance of both the summer food-procuring and the conditional reflex activities, with an impairment of the balance of excitatory and inhibitory processes. Comparison of dynamics of formation of the memory trace in different insect species (honeybee, Drosophila) has allowed the conclusion to be made about a close association of the species ecology and concrete time parameters and qualitative and quantitative peculiarities characterizing the retention in memory of the acquired individual experience (Meller, Davis, 1996; Menzel, 1999).

The whole evidence obtained in recent-year studies indicates both a similarity of the main regularities of learning and memory, which have been revealed in insects and mammals at the behavioural level, and a universal character of the underlying physiological (organization of neuronal circuits) and molecular-biological mechanisms. Our studies have shown for the first time the role, similar with that in mammals, of the glutamatergic system in learning of the honeybee and a necessity of coactivation of ionotropic and metabotropic glutamate receptors for formation of the short-term and long-term memory traces. Further studies are to be performed to reveal an ecological component of processes occurring at the molecular-biochemical level.

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Geographic variation of the response to photoperiod in the ant, Myrmica ruginodis (Hymenoptera: Formicidae)

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Detailed studies of geographic differences in the significance of photoperiod for the seasonal cycle of *M. ruginodis* were undertaken by conducting two experiments in 1998 and 1999. In 1998 cultures of ants from 3 geographic points – Kiev, 50°N; Vladimir, 56°N; St. Petersburg, 60°N, – were kept at the optimal 12-hours daily thermoperiod (15/25°C) under the following categories of daylengths: long day, intermediate and short day (17.5, 16, 15 h, respectively, for ants from Kiev population and 22, 17.5, 16 h for those from Vladimir and SPb populations) and the time of larval diapause onset (i.e. the time when no more pupae appear in a culture) was determined. Control groups were kept under 12-h daylength. In 1999 ants from 2 localities – Belgorod, 50°N and Peterhof, 60°N, – were kept at the optimal temperature (22 ± 1°C) under long-day, intermediate, short-day and autumnal photoperiods (17, 16, 15, 14 h and 20, 18, 16, 15 h, respectively) to determine the time of diapause onset in queens (i.e. the time of oviposition ceasing). 13-h daylength was used as the control regime. Before the start of both experiments (mid-July) ants were kept under similar conditions (22-h daylength at the respective thermal regimes).

The time of the onset of larval diapause in ants from Vladimir and SPb did not differ significantly between the photoperiods or between the populations and was close to the natural timing of the event (early August). Ants from Kiev showed quantitative response to daylength, which resulted in faster inducing of larval diapause under shorter day conditions. Even under 16-h daylength (that characterises early August at 50°N) the dates of larval diapause onset were close to natural ones (late August). In the 1999 experiment all queens in cultures from the both populations entered diapause under daylengths 13 to 15 h in 2 to 9 weeks, in contrast to all other treatments (16 h and longer), where some queens were laying eggs until the end of the experiment (October, 12), while others entered diapause.

Thus, photoperiodic control of seasonal cycle in *M. ruginodis* exists in the southern areas (50°N), since diapause-inducing 15-h daylength is observed there in late August. In more northern areas (56°, 60°N) larval diapause is induced by intrinsic factors. In contrast, in queens of ants from 60°N and 50°N responses are similar: all the daylengths used form two ranges, one having diapause-retarding (16 h and longer) and another one – diapause-inducing effect (15 h and shorter). At higher latitudes in nature *M. ruginodis* queens enter diapause in late August, when the daylength there is about 16 h. Their non-adaptive response supports the idea of the southern origin of northern populations of the species. Therefore, at latitudes at least 56°N and higher photoperiodic control of seasonal cycle of the species is replaced by intracolonial and temperature controls.

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What determines the stage of ontogenesis at which the diapause occurs

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For invertebrates passing time in the state of diapause it is vital to shift as quickly as possible to utilization of the environmental resources when favourable conditions return. The delay in this deed threatens in that the ecological niche will be occupied by other organisms. The species capable of feeding and reproducing instantly after reactivation possess an ecological advantage in the struggle for existence over species which were in the resting state at one of the stages of embryogenesis and had to lose the time at the beginning of the favourable season for completion of their development. Why then the embryonal diapause is so common? (The embryonal diapause of mammals is not discussed here, since adaptation of the embryo positioned in the mother's womb to deterioration of the environmental conditions is secured rather due to reactions of the mother, but not of the embryo itself.).

The diapause is a regulated state of an organism and requires energy. A regulatory physiological system is a combination of bonds between cells differentiated into various directions . The bonds within an organism are actually interactions of the cells. Any interactions independently on their nature are essentially the work. In the course of the embryonal development the number of the cell types increase. This lead to an increase in the number of the bonds and to an increase on the energy spent for their realization. Therefore, the diapause at the early stages of embryogenesis, when the number of the cell types is not great, requires less energy, than the diapause at the adult stage.

The evolutionary process had an energy component. The more primitive the animal, the lower the power of its metabolism. The primitive invertebrates are not able to secure all the integrative bonds of the adult individual during the seasonal deterioration of the environment when their metabolism is disturbed. They had nothing to do but to diapause at the embryonal stages, although this diminishes their chances to compete successfully

A possibility of increasing complexity of the resting stages, of their "getting adult" emerges in the process of evolution along with the growth of the energy reserve of an individual. This possibility is realized by selection of those advantages which an individual gets if it starts to utilize the environment resources earlier than the others at the beginning of a favourable season. "Getting adult" of the resting stages is secured not only by the height of organisation, but also by some other causes, since it occurs at different levels in the different phylogenetic lines. For example, only primitive invertebrates such as rotifers Bdelloidea, crustaceans Cyclopoida and Ostracoda, nematods and oligochaetes pass into resting state at the adult or larval stage. But in some highly organized invertebrates, such as insects, embryonal diapause is observed.

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Effect of sub-optimal temperature on male sterility of the cotton leafworm (Spodoptera littoralis)

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We investigated the patterns of sperm release from the testes of the cotton leafworm, *Spodoptera littoralis*, a moth which produces an unusually high number of sperm bundles. A clear rhythm of sperm release persisted in a constant temperature of 25°C, in both the light-dark cycle (daily rhythm) as well as in continuous darkness (circadian rhythm). These data suggest that the rhythm of sperm release is controlled by an intrinsic circadian oscillator located in the reproductive system. The rhythmic release of nucleated (euperine) sperm was lost and significantly reduced when the pupae were kept for 4–6 days at a lowered temperature of 16°C, before adult emergence. The resulting males were sterile. In a further study it was shown that in optimal conditions glycoproteins were rhythmically synthesized and released from the upper vasa deferential (UVD) epithelium into the lumen. The peak of glycoprotein secretion coincided with the maximum presence of sperm in the UVD. At the lower temperature both rhythms observed were lost. The results obtained in this study extended significantly our previous report (Bebas, et al. 2001).

References

Bêbas, P., Cymborowski, B., Giebultowicz, J.M. Circadian rhythm of sperm release in males of the cotton leafworm, *Spodoptera littoralis*: in vivo and in vitro studies. *J. Insect Physiol*. 2001 (in press).

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Elimination ways of heavy metals in social food chain of red wood ant colonies

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The elimination ways of heavy metals in social food chain of red wood ant of *Formica* s. str. (*Hymenoptera, Formicidae*) colonies was assessed by carrying out feeding experiments with $CdCl_2$ (500 mg $CdCl_2$ in honey) in 1990–1992 in Finland and in two test series in Estonia (1993–1999). In the experiments honey solution polluted with cadmium three hierarchically different nests was tested in red wood ant colonies, isolated from one another: 1) an entirely independent colony isolated from the settlement, 2) a mother nest, 3) a daughter nest. The mother and the daughter nests belonged to different supercolonies having no contact with one another. An independent control nest was chosen in the same settlement for comparison.

All analyses indicated the highest Cd content in the foragers (6…9 mg/kg) of the control nest and in the foragers, inside workers and reserve ants of the Cd polluted colony (40...60 mg/kg), reflecting respectively the natural pollution background of the forest community and ant colony pollution level in the experimental nest. High Cd content in all foragers and inside worker groups of the experimental nests obviously caused disturbances in metabolic processes, resulting in disorders in the formation and accumulation of store substances. The stable and higher content of pollutants in outside workers in comparison with other animals enables us to use of red wood ants in environment bioindication.

The lowest level in the larvae, pupae and in sexuals respectively 0,03…0,1 and 0,05…0,2 mg/kg. The Cd level of the sexuals remains, in contrast, near the low level of the pupae and larvae during the first year in experimental nests.

We discovered three groups of elimination ways in social food chain and compensation mechanisms of social homeostasis which contribute to the decrease in bioaccumulation of Cd in the colony’s food chain and facilitate inactivation and elimination of metals in red wood ant colonies: I. Physiological elimination and inactivation of Cd in metabolic pathways on the organism level. II. Behavioural acts in the social food chain on the colony level. III. Social homeostasis and behavioural acts on the supercolony and settlement levels compensate the lack of queens, reserve workers, nurses, inside workers and the brood in the polluted nest in the course of internest exchange.

The particularly low level of metal compounds in the brood and in the sexuals gives evidence of the ability of a red wood ant colony to protect them against poisons that occur in the colony’s food chain through biofiltering. The self-regulating superstructures of red wood ants, as supercolonies and federations, can essentially diminish the environmental detrimental effect on the colony. In the case of continuous and high environmental pollution, all the nests being in similar conditions, entire populations begin to vegetate and in the end they perish, because the internest compensation mechanisms cannot make up for the loss of store ants and queens caused by heavy pollution load.

Temperature influence on Lampronia capitella Cl. feeding

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The insects activity rhythm is interrelated with the environmental factors. Taking into account the classification of insects according to the daily activity rhythm suggested by A.S. Danylevsky we can refer *Lampronia capitella* Cl. to the group of insects that feed with an equal intensity during the day. First of all, it is due to the fact that food surpluses are characteristic of *L. capitella* Cl. growth. They are developed in the food substratum (bud or berry).

To ascertain the temperature influence on *L. capitella* Cl. feeding, we compared the *L. capitella* Cl. development in natural conditions and in laboratory at various air temperatures. In laboratory the experiment was carried out for 7 days at an air temperature of 25°C, humidity of 70–75% and for a 10 hours daytime. In natural conditions the experiment was performed for more then 13 days at the average daily temperatures of 9.7°C, 14.3°C and 15.1°C. The Caterpillars were weighed just when they were out of a bud, so in natural conditions at an air temperature of 9.7°C the caterpillars of the second age were weighed not twice but one time during the first two days of their development.

The caterpillars of the first age were not examined. While studying the intensity of feeding of the larvae of the second, third and fourth ages, it was found out that the larvae of the fourth age were the most active and consequently they make more harm than those of the second and third ages. To make the most precise assessment of the voracity of the caterpillars of different ages we counted the coefficient of voracity of each of them. So for the caterpillars of the fourth age it is 34.5%, third age – 25.4%, second – 12.7%.

To ascertain the temperature influence on *L. capitella* Cl. voracity we compared the daily consumption of food be the caterpillars of different ages. The data we got showed that when the temperature rose the intensity of feeding increased.

Thus at an air temperature of 25°C the caterpillars of the second age had on the average about 7 mg of food. At an air temperature of 8.3°C the caterpillars of the same age had 5.7 mg of food a day. At an air temperature of 25°C the caterpillars of the third age had 10.5 mg of buds, while at 15.4°C they ate 9.5 mg of food. The caterpillars of fourth age had 13 mg of food a day at a temperature of 25°C, at 17.8°C they ate 10.2 mg of buds a day.

So the digestion coefficient of the caterpillars developed in the steady laboratory conditions is higher than of the caterpillars developed in the changing natural conditions. Besides, the daily digestion coefficient of the caterpillars developed in the laboratory grew according to the ages. As for the caterpillars grown in the natural conditions this coefficient lowered. At an air temperature of below 25°C the nutrients are digested worse, consequently the caterpillar s development cycle prolongs, and as a result, the harmfulness of *L. capitella* Cl. increases.

The rhythms of external gas exchange and heartbeats during the state of thanatosis evoked by external stimuli in adult Colorado potato beetle Leptinotarsa decemlineata (Say)

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For the determination of standard metabolic rate and other respiratory parameters the insect has to be voluntarily motionless. However, it is often a serious problem how to achieve the immobility of an adult insect in an insect chamber of a respirometer. The adults of Colorado potato beetle (CPB) are very active at room temperatures, and sporadically occurring periods of immobility are usually too short for measuring their standard metabolic rates and respiratory patterns.

There have been proposed several methods for restraining an individual insect during respirometric and other measurement, e.g. by the use of anaesthetics, or by holding the insect under water for some time. Many insects respond to a sudden and brief stimulus by passing abruptly into a state of more or less complete tonic immobility – called thanatosis or death feigning. One of the possibilities for immobilizing adult CPB and other coleopterous insects is to evoke the state of thanatosis by external stimuli.

To immobilize the adult CPB we used the mechanical stimuli: the shaking of the insect chamber against the bottom of a thermostat three times with the intervals of 2 seconds. After the shaking the moving activity stopped immediately, and we regarded the state of immobility lasting 3–16 minutes as thanatosis. The beetles waked abruptly from the thanatosis, as the abrupt beginning of spontaneous muscular contractions saw it, and at this time the new stimuli were applied to evoke a following period of death feigning. The adults of CPB did not habituate to the shaking at least during two hours.

Standard metabolic rate and other respiratory parameters in beetles were recorded by means of an electrolytic respirometer or by a flow-through respirometer (CO_2 analyser). Both the mentioned respirometric methods were combined with an optical actography, based on the irradiation of the insect with infra-red light. The mentioned infrared optical method allowed recording the active body movements, but also the rhythmic movements of body tissues, e.g. heartbeats, that are externally imperceptible. All the measurements were made at 20°C in full darkness in diapausing and active adults of CPB raised from the larvae collected near Tartu (Estonia) from a local population.

During thanatosis the adult CPB displayed clear cycles of discontinuous gas exchange while no extraordinary muscular contractions occurred. The cyclic gas exchange did not periodically alternate with tracheal ventilation by abdominal pumping movements, as it was common in CPB while voluntarily motionless. The comparison of standard metabolic rates and heartbeat patterns between the beetles in the state of death feigning and these that are voluntarily motionless did not reveal any significant differences.

We concluded that thanatosis, evoked by external stimuli, is an appropriate state for measuring the standard metabolic rates and other respiratory parameters, but also heartbeats, during the diapause and active life of adult CPB.

Effect of temperature on the developmental rate and life table parameters of the greenbug, Schizaphis graminum (Rondani) (Homoptera: Aphididae)

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The effectiveness of four constant temperatures on the developmental rates and some life table parameters of the greenbug, *Schizaphis graminum* (Rondani) which reared on corn leaves was studied. Data revealed that the duration period of the nymphal stage was 11.52, 8.13, 6.22 and 4.31 days and the pre-viviparity period was 2.01, 0.74, 0.45 and 0.41 days at constant temperatures of 15, 20, 25 and 29°C, respectively. Temperature threshold for the development of the nymphal stage was 8.82°C and the thermal units necessary for the development was 90.05 day-degrees (DD).

Life table parameters were as following: The reproduction rates (Ro) were 11.53, 30.81, 45.25 and 40.66; mean generation time (GT) was 23.67, 21.35, 13.28 and 12.67 days ; population doubling time (DT) of the greenbug was 6.91, 4.23, 2.44 and 2.38 ; intrinsic rate of increase (rm) was 0.104, 0.157, 0.284 and 0.2.89 and finite rate of increase (λ) was 1.105, 1.171, 1.331 and 1.335 at 15, 20, 25 and 29°C, respectively.

Number of generations of the greenbug which could develop in one season on corn plants under Assiut conditions was about 21.8 generations.

Strategies of freeze tolerance in adult of sunn pest bug (Eurygaster integriceps Put.): Winter profile of natural population

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The sunn pest bug (*E. integriceps*) is a serious pest of wheat and to lesser extent barley in the West Asia and Near East. The pest causes losses of 20 to 70 percent and damage can reach 100 percent if control measure is not applied (Miller and Morse 1996). *E. integriceps* have migratory habits, only small part of the life cycle takes place in the cereal fields. The adults spend the summer, autumn and winter in the mountains, in aestivation and hibernation state, respectively. The present study was conducted to elucidate the cold hardiness mechanism of *E. integriceps.*

Adults were collected from fields (Karaj-Iran) and mountains of Ateshgah Karaj located in the central part of Iran from June to March 1999–2000. Adults were collected randomly, and daily temperature was recorded regularly in natural condition in the altitude of 2300 m from sea level. Supercooling point (SCP) of the whole body was measured by the method of Somme (1964). Each insect was placed in contact with a thermocouple connected to two-channel temperature recorder (Testo 650). The tip of thermocouple was kept in a fixed position on the body surface of insect, located inside a narrow glass tube, and cooled in a freezer (-40°C, Bosch). Specimens were cooled gradually about 1°C/min. The SCP was determined, as the temperature at which a rapid increase in temperature occurred due to the release of the latent heat of fusion (lee, 1989).

The SCP was observed at lowest degree (-14.47°C) during summer of 1999. Since cessation of feeding cause considerable increase in supercooling capacity, as was observed by Cannon and Block (1988) in microarthropods. SCPs of adults arise progressively from a mean of -12.9°C on November to -6.7°C on January and stabilized at -5.9°C during remainder of the winter. SCPs of adult were consistently above the corresponding outdoor temperature minima such that adult undoubtedly remained in a freeze state throughout the winter. The overwintering sites are usually covered by snow for four months and adults often are wetted from either rainfall or snow –melt. Therefore, freezing of surface water, as was observed in samples, may inoculate freezing of the insects. It is well established that wetting on insect increases its SCP. Since the minimum temperature under natural condition is reached to -13°C or lower in January, it may be concluded that wet insects are freeze tolerant. However, further studies are necessary to determine the survival of *E. integriceps* both in laboratory and its natural overwintering habitats.

The SCP of 242 adults in different weight and size was measured during late autumn and winter in altitude of 2300 m. There was no significant correlation between SCP and weight, and size. Indicating that these factors may not affect SCP of the whole body.

Utilization of lipid for flight and reproduction in Spodoptera litura (Lepidoptera: Noctuidae)

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Although the common cutworm, *Spodoptera litura*, a serious pest of many vegetables and crops in East Asia, has been believed to engage in migration, essentially no research on its flight activity has been carried out. The present research was undertaken to elucidate the characteristics of migration that are related to flight energy and reproduction. As it is generally accepted that long distance migratory insects primarily utilize triacylglycerol (TG) as their flight energy source, we focussed on analyzing the physiological condition of adults, in particular the TG level and its fatty acid composition.

Tethered flight experiments demonstrated that three-day old male moths could fly more than 20 hrs, and were estimated to be able to fly for two days, judging from the level of TG remaining in the body after the flight. Among eight identified fatty acids composing the adult TG, the ratios of the following unsaturated fatty acids, oleic acid (18:1), linoleic acid (18:2) and linolenic acid (18:3), gradually declined with longer flight duration. On the other hand, the TG levels of ten-day old non-flown males, reared only on water, were the same as those of three-day old males after 12 hr flight, but the ratios of these unsaturated fatty acids in TG remained nearly unchanged. These results suggest that the unsaturated fatty acids in TG are mainly used as flight energy sourse.

As ovarian development in females of this species occurs shortly after adult emergence, long-distance migratory capacity has been regarded as highly unlikely. In fact, ovarian development was completed within three days after adult emergence and females laid eggs thereafter. During this three day period, TG levels and the ratio of unsaturated fatty acids in TG in the ovary increased and eventually occupied most of the abdomen, despite a nearly constant level of the total amount of TG and the ratio of unsaturated fatty acids in TG in the abdomen. This fact suggests the transfer of TG from the fat body to the ovary. However, we could demonstrate a high flight activity in three-day old females with full grown ovaries by tethered flight. In fact, some of the females could mate and lay fertile eggs even after 12 hours flight, and the number of eggs laid was not markedly reduced compared to non-flown control individuals. These results suggest that the TG deposited in the ovaries are utilized as a flight energy source and the females conduct reproduction using residual TG after flight. Thus, we conclude that both females and males of *S. litura* have long-flight capacity and a sufficient energy source in the form of TG adapted for this purpose.

As *S. litura* adults use for their activities nutrients in the fat body that are mostly accumulated by the larvae feeding on host plants, flight activity is expected to be largely influenced by the quantity and quality of unsaturated fatty acids in TG during larval stage. Results showing higher flight activity in adults that feed on host plants with a higher content of unsaturated fatty acids during the larval stage are presented.

Photoperiodic and temperature control of diapause induction and colour change in Nezara viridula (Heteroptera) at the edge of the species' range in Central Japan

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Nezara viridula is an important pest with a worldwide distribution that continues to colonize new areas. In Central Japan, the northern limit of distribution was reported to lie in Wakayama Prefecture in early 1960s. Our field observations in 1998–2000 in Osaka (located further to the north) showed that this species had become common there. Seasonal adaptations that accompany range expansion were studied in the laboratory.

Nymphal growth in this species was reported to be controlled by photoperiod (Ali & Ewiess, 1977). In Osaka population, at 20°C, nymphal period was significantly shorter under 10L:14D and 16L:8D than under intermediate photoperiods. At 25°C, in contrast, nymphal period was slightly shorter under intermediate conditions (the difference was significant in females only). Thus, it is unlikely that nymphs retard growth under summer long-day conditions when temperature is high, but some photoperiod-mediated acceleration of nymphal growth might take place in autumn when temperature is moderate and photoperiod is shorter.

Nezara viridula has an adult diapause controlled by a long-day type photoperiodic response, and this diapause is associated with a change of body colour from green to russet. Difference in incidence of diapause between sexes was small in most regimes. At 20 and 25°C and in both sexes, photoperiodic responses were similar and had threshold values falling between 12L:12D and 13L:11D suggesting that a response of diapause induction is thermostable within this range of temperature, and daylength plays a leading role in induction of diapause. Precopulation and preoviposition periods were significantly longer under near-critical regimes than under long-day ones.

Short-day and near-critical photoperiods induced a change in body colouration from green to russet within about 30 days at 20°C and 20 days at 25°C. Proportions of russet individuals were similar in both sexes and coincided or a little exceeded those of diapause individuals. Rates of colour change were higher under 10L:14D than under 13L:11D suggesting that colour change is strongly associated with photoperiodic induction of diapause.

Results indicate that *N. viridula* has extended its distribution range northwards in Japan. However, it remains unclear if the species has become established in the region or flies annually from southern overwintering sites. Photoperiodic response of diapause induction suggests that the species can enter diapause in Osaka in September, early enough to ensure successful overwintering. A variation of photoperiodic response recorded in the experiment may be explained by heterogeneity of population conditioned by either recent colonization or annual immigration.

Two types of time–temperature relationship in chill survival quantification

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To compare the levels of cold hardiness between two species, populations or treatments, we should look for survival (mortality rate) at several temperatures and several exposure times. The necessity of using several experimental conditions arises from the possibility (demonstrated in several insect species by Nedvěd 1998) that a species A seems to be more cold hardy than species B in one experimental condition, but less hardy in other condition.

The resulting series of values (*e.g.* half lethal times (Lt_{50}) or lethal temperatures (LT_{50})) in each species shows a global relationship (trend) between the exposure time and temperature. Fitting this data series by an appropriate equation (curve) allows predicting values in conditions in which no measurement was performed, and subsequently to compare the cold hardiness level between species in diverse studies with different exposure conditions used.

Moreover, the form of equation that fits best the particular data represents an important information about the nature of cumulating of injurious chilling (the dose – *e.g.* degree days). Till now published data allow including the particular species into one of two distinct groups (defined as cold injury subclasses in Nedvěd 2000b).

Casagrande & Haynes (1976) found the first type in the chrysomelid *Oulema melanopus* there is a linear relationship between log (Lt_{50}) and the second power of the difference between the experimental temperature and a specific temperature limit (theoretical upper threshold). We found this relationship also in the bug *Pyrrhocoris apterus* (Kalushkov & Nedvěd 2000), and in a tenebrionid beetle *Alphitobius diaperinus* (unpublished, collaboration with Vernon, Salin, and Renault). While the former two species are relatively cold hardy temperate insects, the latter is a sensitive tropical species.

In other animals (temperate collembolan *Orchesella cincta*; Nedvěd *et al*. 1998; tropical beetle *Stenotarsus rotundus*; Nedvěd 2000a; tropical cockroach *Nauphoeta cinerea*, unpublished), there is a linear relationship between reciprocal lethal time (rate of dying, $r=1/Lt_{50}$) and the difference between the experimental temperature and a specific temperature limit (upper limit of the cold injury zone – ULCIZ).

Again, this type is present in both temperate and tropical insect species, and thus, the nature of how the chilling dose is cumulated represents a difference in some basic underlying injury mechanisms, not in the overall level of cold susceptibility related to the geographical origin of those insects. These two distinct types of cumulating of cold injury dose define two subclasses of the SNOW WHITE cold injury class – with types *Oulema* and *Orchesella*.

Changes of supercooling points during ontogenesis and dormancy in two species of Calliphora blowflies

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Calliphora vicina R.- D. and *C. vomitoria* L. are widely distributed Holarctic species. In northern breadths both species overwinter as postfeeding (wandering) larvae, but *C. vicina* forms diapause whereas *C. vomitoria* remains nondiapause. Being freeze intolerant, larvae of both species do not survive at the temperatures below supercooling points (SCP). Diapausing *C. vicina* larvae better endure long stay in cold than active ones. The SCP dynamics and supercooling point variation during *C. vicina* ontogenesis were studied in conditions favourable for hibernation (4–11°C). The measurements were carried out by cuprum-constantan thermocouple.

The lowest SCP are correlated with non-feeding stages: eggs (-27.5°C) and puparium (-21°C). The sharp SCP decrease in new-born larvae occurs after the feeding begins and remains at a low level up to the end of the feeding period. The average SCP values vary that time from -7 to -9°C, being 1–2°C lower in *C. vicina* compared to *C. vomitoria*. The gut cleaning in *C. vomitoria* larvae is accompanied by cold hardiness increase by approximately 3°C. The SCP changes were not registered at that period in *C. vicina*. The long cooling of examined species wandering larvae influenced differently on their cold hardiness. Two month delay of *C. vomitoria* puparization at 4°C has not changed their SCP. As to *C. vicina*, first month diapausing pronymphae's SCP doesn't differ from that of feeding larvae and then fell down to certain degrees. At 4°C the cold hardiness increase has take place approximately a week earlier, than at 11°C. However SCP average values were similar at both temperature regimes. The *C. vicina*'s the diapause formation occurs during a month after feeding termination. This period is remarkable also by a high level of oxygen consumption and strong blockage of pupal development. It is possible to assume that the cold hardiness increase during *C. vicina* diapause is caused by endogenous processes and is included in the diapause program. Despite lack of diapause in *C. vomitoria*, the wandering larvae of both species have similar SCP values. Weak cold resistance of hibernating larvae is compensated by their high mobility (migration deep in the soil) that allowed these species to occupy northern regions.

SCP dynamics during *C. vicina* metamorphosis was found to be essentially the same in other Diptera studied previously. Dramatic SCP reduction (up to -21°C) coincides with pupal molting. Beginning of imaginal development is accompanied by cold hardiness decrease, however before the adult fly eclosion cold hardiness reaches again a maximum characteristic to pupal molting stage.

Some constituents of population response to climate changes in malaria mosquito, Anopheles messeae Fall.

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Up to date, all the scenarios forecasting quantitative response of malaria mosquitoes to climate warming have been mostly based on speculations upon experimental data concerning the relations between temperature and some mosquito biological traits (Jetten, Takken, 1994; Martens, 1997). Ecological surveillance of *An. messeae* populations was conducted in suburbs of Ekaterinburg in 1973–1997, with 20–22 biological parameters being recorded throughout each season and a long series of data on this species was obtained for the first time.

As it has been shown (Nikolaeva, 1997), due to an increase in local temperature and precipitation for the last 20 years annual population density of adult mosquitoes has increased to 9,2–16,4 times. For each of 25 years 24 variables (12-for average month temperature and 12-for month precipitation) were analysed to estimate response function for mosquito density, and multiple regression was developed. According to regression coefficients, from 70 to 86% of population density variation in time must be attributed to the joint effects of two factors. The evidence was obtained for a strong influence of these factors on adult population density during autumn (October–November) and spring (March–April) which seemed to be critical time for survival of wintering females. A direct influence of climate warming involved significant changes in seasonal rhythms, as well as in survival rates and reproductive activity of females. Thus, since the middle 80's a shift to 1–2 months toward later dates was recorded for female mosquitoes leaving for hibernation. In 1995, the numerous females were recorded at experimental cattle shed until December, taking blood meals but not developing the ovaries. Such a situation is regarded as typical for anopheline species in Central Asia. At the same decade, a shift to 3–4 weeks toward early dates of termination of winter diapause has taken place in spring, so increasing a season of active life to 1,5–2,5 months.

Recorded since late 80's an increase in summer temperatures was followed by the increase in longevity, reproductive age of females and total population fecundity. Dissections of females for their age grading have shown that in warm seasons in 90's females completed up to 4 gonotrophic cycles, while in earlier decades they usually completed up to 2 cycles. In 1994–1996, the marking of 1,000 females with fluorescent powder and daily checking them up at experimental resting place confirmed conclusions about an increase in longevity of the females and developmental rates of follicles at higher temperature in June–July to 1.5–2.0 times. The recorded changes in response to increased environmental temperatures were consistent with experimental data but a magnitude of response was essentially higher.

Synchronous pupation in spring controlled by a circannual rhythm in the varied carpet beetle, Anthrenus verbasci (Coleoptera: Dermestidae)

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Under natural conditions, adults of *Anthrenus verbasci* emerge in April and reproduce in May. Blake (1959) reported a circannual rhythm in pupation in a British population of this species, and recently we confirmed it in a population of Osaka, Japan (ca. 35°N). When larvae were reared under LD 12:12 at various constant temperatures, the pupation showed circannual rhythm at about 40 weeks intervals, and therefore temperature compensation was shown to some extent. Moreover, under alternations of LD 16:8 and LD 12:12 at various constant periods, pupation occurred about 23 weeks after transfer from a long-day to a short-day photoperiod in most cases. Therefore, it is concluded that the timing of pupation in *A. verbasci* is controlled by a circannual rhythm and its zeitgeber is a change in photoperiod. A decrease in the photophase induces a phase shift to about 23 weeks before pupation. In the present study, larvae within a week after hatching were reared under natural conditions from May or June 1996. Most of the larvae pupated synchronously in April 1997, but some larvae did not pupate in this period. A few of these larvae pupated as the second group in April 1998. When larvae were reared under natural daylength at 20°C from June 1997, some of them pupated as the first group in February 1998. Some of the remaining larvae pupated as the second group in February 1999. Under natural conditions, low temperatures probably delayed pupation until April. Then, larvae were reared under various constant photoperiods at 20°C. Under LD 12:12 and LD 13:11, larvae pupated synchronously about 26 weeks after hatching and 40 weeks after the first pupation group. Under LD 16:8 also, the periodic pattern was observed, although pupation in the first group occurred about 20 weeks later than that under LD 12:12 and LD 13:11. Moreover, under LD 14:10, LD 15:19 and LD 16:8 the pupation was less synchronously than LD 12:12 and LD 13:11. Therefore, there is a distinctive critical daylength between 13 and 14 h. The daylength of 13.5 h corresponds to the natural length in late-August days including twilight at 35°N. Therefore, synchronous pupation in spring in *A. verbasci* can be explained as follows: Larvae probably respond to the decrease in daylength crossing the critical value in late August and the circannual rhythm shifts to the phase about 23 weeks before pupation. Then, the gate to pupation opens in the next February, but pupation occurs synchronously in April because of low temperatures in February and March.

Relationship between mosquito attack activity and air temperature and relative humidity

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The impact of air temperature and relative humidity on mosquitoes attacking humans was assessed during three seasons in the zone of Messoyakha-Norilsk (Dudinsky District, Krasnoyarsk Territory) pipeline construction. Measurements were conducted in three localities: Levinskiye Peski settlement (62°24′N and 36°09′E), Messoyakha settlements (30 km west) and Fakel settlement situated between those at the same latitude. The station in Levinskiye Peski settlement was situated 150 km from the Yenisei River bank in a biotope characteristic of the lower Yenisei. The stations in settlements Fakel and Messoyakha represented typical transpolar tundra. The most common mosquito species were *Aedes hexodontus* Dyar (approximately 86%) and *Aedes punctor* Kyrbi (approximately 9%). Mosquito counts were carried out using "Berezantsev bell" on even dates one hour before sunset and after sunset on all count points. Wind velocity, air relative humidity and temperature, illumination and atmospheric pressure were registered at the moment of counts. A total of 500 counts were made, of which 450 were processed mathematically. More than 19,000 mosquitoes were caught.

All results of counts plotted on a graph show an area of a definite configuration restricted from the top by a curve drawn by the maximum values, which expresses functional relationship of mosquito activity and the studied factors.

Using only the maximal values for analysis we artificially stabilized other factors on optimal values. Defining of functional relationship comprised selecting an equation in the general form and defining of parameters of this equation by experimental points of reference as was recommended by Vygodsky (1966) and Bronstein (1964).

A curve characterizing relationship of activity of mosquito attack and air relative humidity is described by the equation:

$$Y_1 = C_1 e^{kx}$$

where Y_1 is the number of mosquito attacks in the form of natural logarithm; x – relative air humidity or temperature; C_1 and k defined parameters of the curve.

In the final variant the equation describing the impact of relative humidity on attack activity is presented as follows:

$$Y_1 = 4.95\, e^{0.054x}$$

Relationship between mosquito attack and temperature is described by two curves. The first one characterizing attack activity at a temperature of ≥19°C:

$$Y_3{}^1 = 8150e^{-0.18x}{}_3$$

The second curve characterizes activity of attack within the interval 7–19°C:

$$Y^2{}_3 = 2.23e^{0.6x}{}_3$$

Data presented suggest relationship between mosquito *Aedes* attack activity and relative humidity within the interval of 75–100% as well as air temperature within the interval of 7–21°C.

Life cycle of decorated cricket, Gryllodes supplicans Walk., in a laboratory culture

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Insects provide a convenient object for investigations in all divisions of modern biology. A comparative, evolutionary and ontogenetic approaches are used to study mechanisms of animal behavior. Insect behavior changes with age. Different stages of development are characterized by different behavioral complexes. Consequently, applied and fundamental investigations need a detailed description of insect ontogeny as well as knowledge of biology, ecology of the object and features of the development of behavior.

Life cycles of insects maintained in stable conditions and used in laboratory investigations have been explored far not adequately. The goal of our work was to study the life cycle of *Gryllodes supplicans* and add a new species to the list of model objects.

Animals were kept in groups, pairs and singly in a climatic chamber. Classification of the imago stage periods and investigation of the behavioral reaction complexes were carried out by an “open field” method. Statistical analysis was performed using “Statistica” program kit.

Under conditions of laboratory maintenance the life cycle is polyvoltine, homodynamic, non-diapaused. Eggs are represented by a single “generation” and develop during 41 days. Egg-laying dynamics is individual, depends on the number of copulations. The cricket has 10 larval ages totally lasting for 110.5 days. The length of larval ages does not depend on the culture density. The general duration of imago life under maintenance conditions given is 38 days for a mating male and 63.5 days for a mating and egg-laying female. The overall life cycle length in the cricket *Gryllodes supplicans* is 229 days “from egg to egg”. A male starts singing at day 5 (3–9) after the imaginal molt. The initiation of reproductive behavior in female occurs on day 14 (10–21), a female starts laying eggs next day after mating. The total productivity of one female is 548 (461–833) eggs of which 3.7% develop to the imago stage.

The most typical complexes of behavioral reactions in crickets characterize reproductive, territorial and defense behavior. At various stages of the imaginal ontogeny different behavioral complexes dominate: a concealment and avoidance reactions dominate in the prereproductive period; copulative (males and females), reproductive (egg-laying by females), territorial (calling and aggressive) behavior dominate in the reproductive period of the imaginal ontogenesis; a concealment reaction dominates in the postproductive period.

Germ cell death in the testes of the wax moth, Galleria mellonella, during larval diapause

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Diapause is a special form of dormancy developed by many arthropods including insects, which enables them to survive a lack of food and adverse climatic conditions. It is common knowledge, that during larval and pupal diapause of Lepidoptera, spermatogenesis discontinues providing uninterrupted partial differentiation of germ cells, which lyse before spermatozoa are formed. The lysed cells are continuously replenished by newly formed primary spermatocytes stemming from the germarium of testicular follicles. Even though the degeneration of sperm cell is a common feature, the character of this process remains unknown. Thus, the present study was carried out to elucidate: (1) whether the spermatogenesis in the wax moth is discontinued during larval diapause and, (2) whether cells lysis is preceded by changes in the structure of nuclear material following the programmed cell death. We used the TUNEL method as a marker of apoptosis, which allowed us to identify DNA fragmentation accompanied by distinct changes, seen in the cell as chromatin condensation observed through electron microscopy. Here we present that during the diapause of the wax moth spermatogenesis discontinues, and, in all investigated larvae kept at 18°C throughout a period of 3 months, late spermatocytes and spermatids are absent from the testes. The spermatocytes, which are developmentally advanced, enter the stage preceding the first meiotic metaphase and then degenerate in the process restricted to several characteristic events. Firstly, we observed nuclear envelope disruption, an aberrant nucleus containing heterochromatic bodies seen as an electron-dense material, and finally the lysis of whole cells. The histochemical study demonstrates that all of these processes are of an apoptotic character. The transfer of diapausing individuals from 18° to 30°C brakes the diapause and renews spermatogenesis, thus finally causing a decrease in the total number of dying cells. Breaking of the diapause was asynchronous among all examined larvae, so some individuals already showed metaphase, while in others spermatocyte degradation was still observed, even 5 days after the transfer to 30°C.

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Emergence phenology and the life cycles of Diptera (Insecta) inhabiting the shallow water zone of lakes: Comparison of the data for three latitudes

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Ecology of the most taxa of aquatic and semiaquatic Diptera is poorly known. In this study, the populations of Diptera except for Chironomidae was investigated in 1996–2000 on 3 pairs of small lakes in the North-West of Russia: the northern group (66° 21'N 33° 35'E; Loukhi Distr. of Karelia), the central group (60°18'N 29°17'E; Vyborg Distr. of Leningrad Prov.), the southern group (56°12'N 28°40'E; Sebezh Distr. of Pskov Prov.). At every lake, the littoral zone to the water depth of 1–1.5 m and the zone of water line were considered. Faunal composition, abundance, seasonal dynamics and habitat distribution of non-chironomid Diptera immatures were studied. To obtain the emerging imagines 3 techniques were used: vial rearings of separate larvae and pupae, laboratory rearings from substrata, emergence traps.

The seasonal emergence patterns were ascertained for 68 species of 16 families (22 spp. belong to Ceratopogonidae, 11 spp. – to Limoniidae). The main results are:

1) The period of emergence of Diptera elongates from the northern lakes to the southern ones. In the first case, adult emergence occurs mainly from the latter half of June to the end of July. At the other lakes, emergence lasts from May to early October, tendency to the mass emergence in the first part of summer diminishes, and the species emerging only in late summer–autumn occur. For the most of species on the northern lakes, the emergence timing coinciding with the first warm period of a season may be treated as an adaptation to the harder conditions of hypoarctic zone, where the temperature instability (e.g., early cold spell) can terminate the emergence.

2) The periods of emergence of the same abundant species elongate at the more southern lakes as compared to the lakes located to the north (for the asynchronous development or increase of the number of generations).

3) At the northern lakes, all common species are uni- or semivoltine. At the lakes of central group, 5–7 of 22 common species are probably bi- or polyvoltine. At the southern lakes, more than 15 of 45 common species seem to be bi- or polyvoltine.

4) The most of species at all the lakes hibernates as larvae. At the central and southern lakes the species hibernating also or mainly in the pupal stage are observed (mainly in the zone of water line).

5) The number of littoral-inhabiting species pupating and emerging within the littoral zone (i.e. not migrating to the zone of water line) increases from the northern to the southern lakes. This tendency is primarily associated with presence of more dense and wide stands of littoral vegetation, as the development of many dipterans not migrating before the pupation takes place only in this habitat. Among them, the taxa developing on emergent plants (phytophages, such as Hydrellia; root-piercing detritophages – Notiphila and some Erioptera), and other dwellers of vegetated lake littoral (Anopheles, Dixella, Oplodontha, etc.). Besides, 4 species of Palpomyiinae (Ceratopogonidae) pupate in littoral stands with high quantity of plant remains near the water surface, while on the other sites their larvae migrate to the water edge.

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Physiological and genetical variability in populations of Schizaphis graminum Rond. (Homoptera: Aphididae)

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Acceptability of host plants is one of the basic environment-forming factors determining microevolution processes in populations of the greenbug (*Schizaphis graminum* Rond.). Intraspecific forms of the insect differ in virulence, i.e., in physiological ability to overcome plant resistance. Genetic mechanisms of *S. graminum* interaction with wheat and sorghum are explained by the "gene-for-gene" relations: each host gene responsible for resistance corresponds to the specific insect gene responsible for virulence. The possibility of adaptation to a plant leads to the necessity to study variation of the insect for determination of the pest population boundaries, direction and range of migrations. In 1993–2000 polymorphism in the Krasnodar population of *S. graminum* was estimated by frequencies of virulence phenotypes (biotypes), which were identified using five sorghum samples with genes for resistance Sgr1–Sgr6. In total 11 aphid phenotypes were identified. The most typical clones for the Krasnodar population are those heavily injuring variety Sarvasi (Sgr1), widely used in breeding, and samples with genes for resistance Sgr3, Sgr4. The structure of diversity (frequency of certain phenotypes and share of rare phenotypes) during the years of the study was different. Significant differences of the Krasnodar and Saratov greenbug populations in 1999 for frequency of virulence phenotypes indicates the possibility of existence of more or less isolated populations in the European part of Russia. The European populations of the insect were shown to be relatively isolated from the Asian populations (Uzbekistan, Kazakhstan). The genes for resistance in samples k-9436 (Sgr5) and k-1362 (Sgr5 + Sgr6) are effective only against the European aphid populations, and that of the cultivar Sarvasi (Sgr1) – against Asian ones. It has been determined that greenbug biotypes, capable to injure resistant varieties, are formed (at least, frequently) before their commercial cultivation, and the genetic uniformity promotes distribution of aphid clones with specific virulence.

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Antifreeze proteins from fish and insects studied by differential scanning calorimetry and nanoliter osmometry

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The polar oceans are either in the winter (Arctic) or year round (Antarctic at high latitudes) at about -1.9°C, the freezing point of seawater. During these periods the seas are covered with ice. Typical marine teleosts have a melting point of -0.5 to -0.9°C thus they are in the cold periods supercooled by 1°C or more. Any contact with the ice by the fish would therefore lead to freezing. The Antarctic notothenioid *Dissostichus mawsoni* lives at 300–500 m where the temperature is -1.9°C. At least eight size classes of antifreeze glycoproteins (AFGP's) are found in the blood of *D. mawsoni* ranging from 2.6 kDa to 34 kDa.

Antifreeze proteins inhibit the growth of ice crystals by interaction with specific crystal faces on the ice crystals thus giving rise to a separation of the melting point and the freezing point. Antifreeze proteins show the expected colligative effect on the melting point but depress the freezing point 200–300 times more than expected on a colligative basis. This is called "thermal hysteresis" or "the antifreeze effect" (Cheng & DeVries 1991).

It has been observed that AfGP 1–5 are more efficient in inhibiting ice growth than AFGP 6–8. Also a small initial ice growth is observed when the temperature is decreased in an AFGP 1–5 solution containing a minute polycrystalline ice crystal. In the present investigation solutions of AFGP 1–5, 1–8 and 7 & 8 was studied by differential scanning calorimetry (DSC). Two exotherms were found in the AFGP 1–5 and 1–8 solutions whereas in the 7&8 solution only a "disturbance" of the ice growth was observed.

Differential calorimetry on solutions of thermal hysteresis proteins from the common meal worm *Tenebrio molitor* showed a clear thermal hysteresis but not the small initial ice growth observed in the AFGP 1–5 solutions.

Reference

Cheng, C.C. & DeVries, A.L. (1991) The role of antifreeze glycopeptides and peptides in the freezing avoidance of cold-water fish. Pp. 1–14 In "Life under extreme conditions" (G. di Prisco, ed.), Springer-Verlag, Berlin Heidelberg.

Freeze tolerance in the earthworm Dendrobaena octaedra

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The freeze tolerance and the underlying biochemical defence mechanisms in the earthworm *Dendrobaena octaedra*, were investigated.

Survival after exposure to subzero temperatures was analysed in *D. octaedra* from three climatic regions (Denmark, Finland and Greenland). Freeze tolerance showed variation between the different populations of *D. octaedra*. Worms from the northern populations (Finland and Greenland) had a higher freeze tolerance than worms from the southern population (Denmark). 100% of the Finnish worms survived a temperature of –2°C, 90% survived a temperature of – 4°C and 70% survived – 6°C. 70% of the greenlandic worms survived – 2°C, 60% survived – 4°C and 30% survived – 6°C. The mortality of the Danish worms was generally high, 60% of the survived – 2°C, only 10% survived – 4°C and non survived a temperature of – 6°C.

In the Finnish population, freezing led to the production of high concentrations of glucose reaching values much higher than controls (103 mg / g DW vs. 2 mg / g DW), but glycerol levels were not elevated after freezing. The Danish and Greenlandic populations had substantially lower glucose levels after freezing than the Finnish populations (17 mg / g DW vs. 103 mg / g DW) or dead individuals did not produce glucose. This probably causes the lower freeze tolerance of these two populations.

It was determined if freezing had an influence of the reproduction of the earth worms. After warming to summer temperatures (15°C), survivors of freezing produced viable cocoons.

Egg retention in Trichogramma: something between learning and diapause

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It is well known that insects are capable of modifying oviposition behaviour and oogenesis in a response to environmental conditions. These modifications form a continuum of steps – from learning to reproductive diapause.

The object of our study, *Trichogramma,* is a minute egg parasitoid. We have demonstrated that *Sitotroga cerealella* eggs were accepted for oviposition by certain *Trichogramma principium* females, while other wasps of the same strain delay parasitization or totally refuse to parasitize the same host. These >refusing= females carried a high number of mature ovarian eggs, they moved actively, and even might incidentally contact the host, but the usual sequence of behavioural reactions resulting in parasitization was interrupted at the stage of arrestment and host recognition, suggesting that refusal to oviposit may be considered as egg retention. Less than a half of ovipositing females started oviposition during the first two days of the experiment, while the rest of ovipositing females showed a delay of parasitization ranging from 2 to 10 days of contact with the host. Thus, parasitization by a group of simultaneously emerged wasps was almost uniformly distributed over 8–10 days which suggests that the refusal to oviposit in an immediately available host may benefit risk-spreading.

As for *Trichogramma* females that accepted *S. cerealella* eggs, they appeared to maintain the tendency to parasitize when sequentially offered new portions of the host eggs. This "parasitization state" was stable both in the presence of a host and under host deprivation extended up to 8 days, and even when preferred and usually rejected host ages or species were sequentially offered. As a result, *T. principium* females more often accepted less preferred host eggs when previously offered a more preferred host. In most studied cases of learning, experience with a given host species either does not influence the level of affinity for other hosts or acceptance of a low-quality host decreases if a high-quality (preferred) host was previously encountered. This suggests that the stability of the parasitization state is based on endocrine mechanisms. Then, refusal to oviposit may be considered as a specific state when not oogenesis, but oviposition behaviour is subject to neurohormonal regulation.

Thus, the studied phenomenon shows certain properties peculiar to learning: it is manifested in behaviour (not in oogenesis); it is determined by the immediate environment (not by anticipatory token stimuli); neither reduced activity nor increased longevity nor resistance to environmental extremes were revealed. On the other hand, separation of females into ovipositing and refusing is of "all-or-none" type, similar to that into active and diapaused, and "parasitization state" is practically irreversible (while learning usually induced reversible gradual changes).

Endogenous variations in maternal effect of photoperiod on the progeny diapause in Trichogramma embryophagum

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A laboratory study was carried out on photoperiodic control of prepupal diapause in the egg parasitoid *Trichogramma embryophagum* Htg. To ensure maximum genetic uniformity, all experiments were conducted with one isofemale parthenogenetic strain. The maternal generation was reared at 20°C and 8 photoperiods (L:D = 3:21, 6:18, 9:15, 12:12, 15:9, 18:6, 21:3 and 24:0 h). The maternal influence on the tendency to diapause in the progeny was estimated by rearing of the daughter generation at 15°C in the dark. Experiments revealed a long-day type response based on maternal influence on the progeny prepupal diapause. Comparative analysis of photoperiodic responses in successive laboratory generations reared under constant conditions revealed significant endogenous fluctuations in the tendency to diapause. The maximum rate of progeny diapause (20–45%) was recorded at day length of 12 and 15 h, the estimated threshold photophase ranged from 6 to 10 h (left threshold) and from 16 to 17 h (right threshold). Thus, the left threshold day-length was very variable, while the right threshold day-length kept relative constancy. A possible reason is that the right threshold is subjected to stabilizing selection in the natural conditions, while the left threshold zone is a selectively neutral character revealed only in laboratory experiments.

Experiments with individual females sequentially offered with new portion of host eggs demonstrated that the probability of progeny prepupal diapause significantly depends on the maternal age. In these experiments, maternal females were reared and kept at 20°C and L:D=18:6; the progeny was reared at 15°C in the dark. At these conditions, only a small proportion of progeny prepupae diapaused. The percentage of prepupal diapause was maximal (ca 15%) in the progeny eclosed from the eggs laid during 1st–2nd days of maternal life. Then the proportion of diapausing progeny decreased to 0–5% at 10th–12th days of *T. embryophagum* female life and then slightly increased in 14–18 days old females.

We conclude that endogenous factors (maternal age and variation in generation sequence) play an important role in maternal influence on progeny diapause, particularly in the neighbourhood of threshold temperature and photoperiodic conditions.

Diapause in the predatory bug Geocoris punctipes (Heteroptera: Geocoridae)

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The predatory bug *Geocoris punctipes* (Say) is an important natural enemy in numerous crop systems in the southern United States. Efforts to conserve this predator are focussed on developing appropriate overwintering habitats and relay crops to encourage successful overwintering in or near target crop fields and colonization of these fields. We have been studying the overwintering biology of *G. punctipes* to better understand its response to abiotic conditions and the timing of diapause induction and termination so that we can synchronize appropriate resources with the dynamics of the bug. Like many predatory heteropterans, *G. punctipes* overwinters as an adult in reproductive diapause. Diapause is induced in fall by short photoperiods and is maintained by persistent short photoperiod. Diapause response and intensity vary with latitude, with northerly populations (N38° 04', W84° 29') having a shorter critical photoperiod (L:D 13.2:10.8) and a greater incidence of diapause (>80% diapause at peak) than more southerly populations (N31° 28', W83° 31'; critical photoperiod of L:D 12.4:11.6), and peak incidence of 42%). In a southern population (south Georgia, USA), diapause development proceeds throughout the fall, and diapause is terminated in the population at the end of December. Throughout the fall, diapause intensity, as reflected by pre-oviposition periods of bugs transferred into the laboratory from the field, steadily declines until diapause is terminated in mid-winter. Subsequent reproduction is likely suppressed by low temperatures that occur through most of January and at least part of February and March. Nymphs are occasionally encountered in the field prior to April, but are found much more regularly beginning in April.

Seasonal adaptations in Lithosiidae (Lepidoptera)

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Lithosiidae is a rather small family of Lepidoptera, which has often been considered as subfamily in Arctiidae. More than 1000 species is known in world fauna and there are near 50 species of lithosiid moths in Russia. They inhabit mainly in tropical forests and feed on Lichenes. This species overwinters usually as larvae, and more seldom as pupa. A. S. Danilevskii (1961) reported that larval diapause of *Lithosia griseola* is controlled by photoperiodic reaction (PhPR) of long day type. Information concerning photoperiodic adaptations in other species of Lithosiidae are not found in literature.

M. Koch (1955) noted that species of this family produced as a rule only one generation in Europe. Accordingly our observations in forest-steppe zone of Russia (50°N) they have one generation also. This suggestion is based on only one clear defined peak of moths flight activity, which is observed either in the beginning of summer (*Lithosia sororcula*), or in the end of it (*Miltochrista miniata, Lithosia lurideola*). Is the univoltine seasonal cycle of temperate litosiids a result of obligatory diapause or such seasonal path is determined by any external factors? The answer on this question might be received after experimental investigation some most usual species of this family, which has not been studied until now. The experiments was carried out under temperatures 20 and 25°C in different photoperiods from L:D=12:12 to L:D=18:6, with an interval between variants of day length 1 hour.

Lithosia lurideola Zinck. The diapause is formed irrespectively of the environmental conditions. In all photoperiodic modes caterpillars stopped a feed after reaching III–IY stage, and did not moult on the following stage. In such state they remained before colds.

Lithosia sororcula Hufn. Pupal diapause is controlled by PhPR of long day type which precisely becomes apparent in 24°C. Some pupae were active under photoperiodic conditions L:D=17:7 and L:D=18:6, however their maximum amount did not exceed 50%. In 20°C pupae enter diapause under all photoperiodic conditions. In short day the acceleration of development of caterpillars was exhibited.

Miltochrista miniata Forst. The larval diapause in III–IY stages is determined by photoperiodic conditions. Critical day length in 20°C is nearest to 16 h 30 min. and 15 h 30 min. in 24°C.

Thus, only univoltine seasonal cycle of *L. lurideola* is a result of forming obligatory larval diapause. The diapause in *M. miniata* and *L. sororcula* is controlled by photoperiodic conditions. However in the correspondence with the experimentally determined parameters of PhPR the short day for them occurs already after July 20, and the caterpillars practically develop under the short day conditions throughout large part of life. This fact causes univoltine seasonal cycle in this species despite of availability PhPR and facultative diapause.

Trophic diapause and its adaptive role in the annual cycle of eurybiontic species of lady beetles (Coleoptera, Coccinellidae)

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Together with winter diapause of adults, a so-called trophic diapause is typical for many predatory species of lady beetles. It is found most frequently in the regions with distinct dry and hot seasons. The occurrence of trophic diapause in species inhabiting tropical regions appeared surprising. This diapause has been revealed by Semyanov in two lady beetle species: *Leis dimidiata* (Fabr.) and *Harmonia sedecimnotata* (Fabr.) collected in the Southeastern China, somewhat to the south of the Tropic of Cancer (environs of Guangzhou). In spite of strong differences in climate, the above mentioned regions both possess a single common feature – the annual depressions in aphid abundance. Evidently, trophic diapause is not induced by climatic factors but by the absence of aphids serving as food. The induction of trophic diapause in beetles is accompanied by strongly decreased metabolism and by changes in behaviour: the thigmotaxis appears and the beetles move into shelters forming groups. In this condition beetles can stay without protein food for a long time.

The induction of trophic diapause in lady beetles is usually accompanied by gradual resorption of ovaries. A subsequent termination of the diapause needs some time for maturation; the duration of this period is equal to that observed after emergence of beetles from pupae or after overwintering. In *L. dimidiata* no complete resorption of ovaries occurs in a similar situation; secondary oocytes remain for at least three months. Therefore, even after three months of trophic diapause, the duration of pre-oviposition period is only about three days.

An adaptive significance of this phenomenon is evident: during a depression of aphid abundance females retain the ability to restart oviposition very rapidly after reappearance of aphids. In other words, a period between the beginning of feeding on aphids and oviposition becomes as short as possible, significantly increasing a probability for the successful development of larvae before the next possible depression in aphid abundance.

Respiration and water-gas exchange in trombiculid mites (Acariformes: Trombiculidae)

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Trombiculid mites (chiggers) (order Acariformes, suborder Actinedida) are unique soil-dweller arthropods which never come up to the soil surface. The integument of the active post-larval instars, deutonymphs and adult mites completely lacks pigment granules and is provided with a cover of protective tightly situated long setae (neotrichia). Moreover, these mites appear to be devoid of the tracheal system. In this study, the analysis of the integument functioning of deutonymphs and adult mites *Hirsutiella zachvatkini* (Schluger, 1948), *Euschoengastia rotundata* (Schluger, 1955) and *Leptotrombidium orientale* (Schluger, 1948) is proposed using data of both scanning and transmission electron microscopy, and observations on living mites in a laboratory.

The integument of the active deutonymphs and adult mites is built up of a very specific epithelial tissue. The soft body walls of these instars form deep folds and are provided with long branched mechanoreceptoric setae which protect integument from damage by soil particles. Dense cover of setae determines water repelling properties of the integument and retention of air above the surface of the cuticle for respiration. It also results in small value of surface to volume ratio furthering conservation of water in organism. Thus, neotrichia in trombiculid mites functions as a typical plastron and is thought to be as a quite physiologically effective structure.

The setae are situated in round setae pits provided with a clear procuticle with curved pore canals and poorly distinguished lamellae, and narrow epicuticle. The setae pits are surrounded with wave-like folds possessing short tight ridges on the surface formed by epicuticle. In contrast to the cuticle of the seta pits, the cuticle of lateral folds is built up of electron-dense homogeneous substance, which gradually substitute clear cuticle of the former. The underlain epithelial tissue is formed of separately scattered hypodermal cells, which do not represent a uniform integral layer, and also of large polymorph, so called “intraepithelial cells”, without nuclei and other organelles except few ribosomes and some oval homogeneous inclusions without surrounding membrane. The cytoplasm of these cells is of different electron density. In particular, at the tip of the lateral folds these cells often look optically empty and are supposedly filled with metabolic and sorption water. In general, the integument of deutonymphs and adult mites being intensively folded, and having many setae, functions as a quite specific organ system retaining a particular air volume above cuticle and, due to the absence of tracheae, plays a role in providing the necessary air-water balance and successful respiration of the large long-living adult trombiculid mites, especially in the unfavourable environmental conditions such as seasonal floods, rain, etc. Moreover, the lateral integumental folds with epicuticular ridges, electron-dense cuticular substance and intraepithelial cells filled with metabolic and sorption water are thought to function as a real air gills which selectively absorb and transport of oxygen from the outside to the inner tissues and organs. Thus, plastron in the form of neotrichia and the integumental folds seems to function in close physiological unity providing for the effectiveness of respiration and water balance in the soil inhabiting mites such as representatives of the family Trombiculidae. This investigation is supported by grant N 00-04-48885 from the Russian Foundation for Fundamental Researches.

Cold tolerance of the Antarctic springtail Gomphiocephalus hodgsoni

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Cold tolerance of the springtail *Gomphiocephalus hodgsoni* (Collembola: Hypogastruridae) was studied at Cape Bird, Ross Island, Antarctica (77°13'S, 166°26'E). Microclimate temperatures indicate a highly seasonal thermal environment, with winter minima <-39°C. Snow cover significantly buffers both minimum temperatures and cooling rates. *G. hodgsoni* survives low temperatures by avoiding freezing. Mean low group supercooling points (SCPs) ranged from -35.4°C in October to -28.3°C in January. The lowest SCP measured was -38.0°C. The high SCP group was very small, making up only 18% of the population in January. In October, *G. hodgsoni* had a very high glycerol content (>80 µg/mg dry weight), although this declined rapidly to low levels (c. 7–10 µg/mg dry weight) in January. Quantities of glucose and trehalose were low during October, but steadily increased throughout the summer. Haemolymph osmolality was exceptionally high (about 1600 mOsm/kg) at the end of November, but this rapidly declined to approximately 500 mOsm/kg by late December. The presence of thermal hysteresis proteins was indicated by both osmometry on haemolymph samples and recrystallisation inhibition studies of springtail homogenates. There was a strong relationship between glycerol content and SCP, but the relationship between haemolymph osmolality, SCP and carbohydrates is uncertain.

Why are there so many freeze tolerant insects in the Southern Hemisphere?

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Insect cold tolerance strategies have traditionally been categorised as either freeze tolerant or freeze avoiding. Although there have been recent attempts to create sub-categories within this dichotomy, the reasons why one strategy or the other is adopted remain elusive. Several authors have recently observed that freeze tolerance appears to be more common among insects in the Southern Hemisphere than in the Northern Hemisphere. Insect habitats in the Southern Hemisphere differ from those in the Northern Hemisphere largely as a result of oceanic influence. In addition, El Niño Southern Oscillation (ENSO) events result in inter-year variability of a very high magnitude. We assert that the unpredictability of these Southern Hemisphere habitats means that cold tolerance must be a year-round phenomenon, and that the likely presence of gut nucleators makes freeze tolerance the most likely strategy of cold tolerance within existing biochemical and phylogenetic constraints.

The casebearers life cycles (Lepidoptera, Coleophoridae) of Volgo-Ural region

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On the base of the data obtained, main types of Coleophoridae of the Volgo-Ural area life cycles are given below.

I. Larva feeds in summer and (or) autumn, overwintering full-feed, pupates and imago appears in summer *(Ecebalia vestianella)*.

II. Larva feeds in summer and (or) autumn, overwintering on different stages of development, then it feeds, pupates and imago appears in summer *(Casignetella directella)*.

III. Biannual cycle, including two winter diapauses, divided or associated with larva`s aestivation *(Sistrophaeca siccifolia)*.

IV. Cycle of bivoltine species *(Aporiptura ochroflava)*.

V. Larva feeds in summer, aestivates, feeds in autumn, overwintering in diapause full-feed, then it pupates and imago appears in summer *(Klinzigedia phlomodella)*.

VI. Larva feeds in summer, aestivates and moves into winter diapause, then it pupates, imago appears in spring *(Multicoloria vicinella)*.

VII. Larva overwinters in diapause, then it can feed or pupates, imago appears in summer *(Perygra alticolella)*.

Besides, life cycles of casebearers species *Casignetella niveistrigella* from Zhiguli reserve of Samara province (south declivities of mountains), from environs N. Bannovka of Saratov province (south declivities of chalky mountains) and Kalmykia (hills of Ergeni) were explored. The cognate life cycle was observed in all these places. The young larvae hatches in middle-August, feeds on the leaves of *Gypsophila fastigiata* and *G. juzepczukii* and overwinters in diapause. In the spring it appears, feeds to the June, then it pupates, moths comes up in the end of June and in July.

This life cycle is greatly distinguished from “plain-type” of cycle of Coleophoridae, which we observed in environs of the Saratovka river of Saratov province. The young larva feeds from the June, becomes full-feed in September and overwinters in diapause. In the spring a larvae does not eat, it pupates, moth comes up in May.

After the displacement of larvae from N. Bannovka in the conditions, as on the Saratovka river (average day temperature 28–34°C, night temperature 18–22°C, moderate insolation, which allows feeding-plant to develop from the June to the September) annual cycle of this moth goes back to the “plain-type”.

We expect, that in extreme conditions for the given species from investigated places, they have changed type of the annual cycle. This cycle is adapted to the great overfall of average day temperatures (t = 37–43°C) and night temperatures (t = 15–20°C), as well as to the high insolation, that destroyed the leaves of feeding-plants during the “hot” summer.

Multiple aspects of insect cold hardening: A case study of Pyrrhocoris apterus (Heteroptera)

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The family of Pyrrhocoridae includes some 300 species distributed mainly in Palaeotropics. Only *Pyrrhocoris apterus* (L., 1758), and a few others, were able to colonize the temperate region. What are the prerequisites allowing such an expansion of their territory? We study physiological traits/adaptations involved in winter survival. In the Czech republic, *P. apterus* adults overwinter inside/under the layer of litter where temperature fluctuations are well buffered, nevertheless, the minima may reach -10 to -15°C for a few days during exceptionally cold spells. Earlier studies identified some of the critical aspects of successful overwintering: entering the state of reproductive diapause; two-step down-regulation of ice-nucleators; accumulation of polyols during cold acclimation and; restructuring of membrane phospholipids (Hodková and Hodek, 1997; Hodková et al., 1999; Košťál and Šlachta, 2001).

On the poster, we are presenting a detailed overview of those and of some additional aspects (energy reserves, metabolic suppression, respiration, enzymatic activities, water balance, osmoregulation, ionic concentrations), which are likely to be involved in overwintering. We hope to get insight into the complexity of physiological adjustments by comparing diapausing and non-diapausing insects that either were or were not cold acclimated, by comparing different geographic populations of *P. apterus* and by comparing different species of the family Pyrrhocoridae.

References

Hodková M., Hodek I. (1997). Temperature regulation of supercooling and gut nucleation in relation to diapause of *Pyrrhocoris apterus* (L.) (Heteroptera). *Cryobiology* 34, 70–79.

Hodková M., Šimek P., Zahradnickova H., Novakova O. (1999). Seasonal changes in the phospholipid composition in thoracic muscles of a heteropteran*, Pyrrhocoris apterus. Insect Biochemistry and Molecular Biology* 29, 367–376.

Košťál V., Šlachta M. (2001). Variation in cold hardiness during overwintering of *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *Acta Societatis Zoologicae Bohemicae,* in press.

Regulations of induction and termination of diapause in Orthosia stabilis (Lepidoptera, Noctuidae)

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The noctuid moth *O. stabilis* is univoltine throughout of its area. In this connection, it is interesting to investigate nature of prolonged dormant inducing in the beginning of summer and mechanism controlling its induction . T h e investigation of diapause inducing factors was carried out by traditional methods. Larvae were reared in two temperatures 20°C and 24°C and day lengths from 12 to 18 hours of light per day with one hour intervals. The adult imagines was not registered in all variants. As a result we have concluded that diapause in this species has obligatory character.

In order to determine the diapausing stage of *O. stabilis* we have taken samples on the 10, 20, and 30 day after pupation. It was turned out that formation of diapause took place between 10 and 20 days of pupa development and in fact diapausing stage of this species is pharate imago in pupal cuticle.

The role of temperature and day length in termination of prolonged diapause of *O. stabilis* was studied. At first larvae were reared in 24°C (or 20°C) and corresponding photoperiodic regimes, then, after pupation, insects from 24° C were transferred in 20°C and the same photoperiodic regimes where they remained during 30 days. Next, insects from all variants were influenced on low temperature (6.5°C and darkness) during 1–2 months. Finally they were returned in 20°C and initial photoperiodic regimes, according of experimental scheme. The control groups of insects were reared in constant temperature 20°C and short (12 h) and long (18 h) day.

In control variants diapause was not interrupted in a single insect. In experimental groups after two months of influence of low temperature adult were appeared only in short day (13–14 h) variants and did not flew out in long day (16–18 h) ones. Photoperiodic sensitivity of pharate imago *O. stabilis* was only found after two months of keeping them in low temperature. PhPR of reactivation has a short day character. In case, when larva were reared in 20°C and short day (12 h. light in day) flight of moths was observed even after one month of low temperature influence and passed more intensively.

So, univoltine seasonal cycle of *O. stabilis* is determined by obligate diapause in pharate imago. The photoperiodic sensitivity in pharate imago was manifested only after low temperature influence. Photoperiodic response for diapause termination has the short day character. For successfully activation of diapausing imago of *O. stabilis* combination of temperature and day length is required.

A significance of seasonal life history and population age structure of insects for coevolution of their parasites in the arctic zone

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The investigation of chalcidoid parasitic species community ("cenon") on the birch soft scale (BBS), *Eulecanium douglasi* Sulc, in geographical aspect revealed the increase of parasitic species richness at high latitudes in comparison with that at middle latitudes. This phenomenon contradicts the generally acknowledged decrease of biodiversity from the south to the north. Our study shows that its cause is a hemicyclism, i.e. biennial life cycle of BSS in the Hypoarctic. An intrinsic property of hemicyclism is a possibility of differentiation of the individuals into opposite seasonal life histories. It is a cause of the formation of two BSS population fractions here – both main and alternative ones. A heterochronization of seasonal development of different host individuals created a ground for a segregation of ecological niches of parasitic species infesting individuals of either one or both host population fractions. As a result, the age structure heterogeneity of host population under the hypoarctic conditions causes the increase of species richness in the cenon which becomes more saturated by parasitic species than the same cenons under more southern conditions in plane boreal forest of Europe: 10 and 5 species accordingly.

Our data have something in common with those got by Kukal and Kevan (1987) in the High Arctic of Canada where the age structure heterogeneity of population of the moth, *Gymaephora groenlandica* (Wocke), as we think, determines the high effectiveness of its parasites in regulation of host population.

Transformation of leaf litter in the gut of soil dipteran larvae (Diptera: Bibionidae)

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Dipteran larvae may consume an important part of annual litter fall and produce faecal pellets, which may form an important part of fermentation horizon of some forest soils. The changes of leaf litter during the passage through the gut influence soil forming in the forest. We investigated parameters of feeding biology of soil Diptera larvae *Bibio pomonae* Fabricius, 1775 and *Penthethria holosericea* Meigen, 1818.

Guts of both species consist of foregut, with valvula cardiaca producing peritrophic membrane, midgut, with two long gastric caeca, and short hindgut. The secretory cells prevailed in anterior and posterior midgut wall and in the gastric caeca. The macromolecules are enzymatically attacked in alkaline midgut inside peritrophic membrane. The following steps of digestion take place in ecto-peritrophic space, mainly in neutral gastric caeca. Gut conditions and tests of enzyme activities indicated the utilization of proteins and lipids, mono- and disaccharides and starch.

Despite assimilation efficiency of larvae feeding at leaf litter was relatively high and cell walls of leaf litter changed its microstructure during gut passage, no cellulolytic activity in gut was recorded *in vitro*. The absence of cellulases and high mortality on sterile filter paper indicated that larvae may use enzymes of microbial origin or obtained the energy by predation on cellulolytic microorganisms. Presence of cellulolytic microorganisms in the gut supported microbial origin of cellulases.

The comparison of phospholipid fatty acids profile confirmed the difference of microbial communities of endo- and ecto-peritrophic space. High number of bacteria was observed in the caeca of *P. holosericea*. It supported the existence of special gut microflora in ecto-peritrophic space. The caecal microflora is similar to hindgut one. However, no parts of the hindgut specialized for microbial fermentation and no methane production were observed.

Selective microbivory of *P. holosericea* and decrease of bacteria numbers in alkaline part of midgut supported the possibility of predation of ingested microorganisms. However the lysozyme showed neutral pH optimum.

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Cold adaptation of digestive enzymes in springtails: Testing of isoenzyme hypothesis

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Temperature dependence of activities of amylase isoenzymes was investigated in arctic springtails *Onychiurus arcticus* (Collembola: Onychiuridae). The material was obtained from laboratory culture reared in British Antarctic Survey (Cambridge, England). Specimens were maintained at 5°C for two weeks before homogenisation. Homogenates of single animals were analysed for α-amylase isoenzymes using cellulose acetate electrophoresis (Hebert and Beaton, 1993). The electrophoretically separated amylolytic isoenzymes were resuspended in Britton-Robinson buffer and the suspension was added to the chromolytic substrate for amylase activity determination (see Šustr and Block, 1998) at 20 and 35°C.

Four isoenzymes of amylase (I, II, III, IV) were detected. Separated bands I and III had higher relative activity than II and IV. Activity of all separated isoenzymes increased with temperature between 20 and 35°C. Higher temperature coefficients (Q_{10} as well as E_a calculated from Arrhenius plot) showed bands I and IV. It was hypothesised that changes in ratio between activities of I+IV and II+III may be responsible for previously observed changes of temperature dependence of amylolytic activity due to temperature acclimation (Šustr and Block, 1998). The future testing of the hypothesis will require an experiment with two (warm and cold acclimated) groups of animals and testing of individual variability in isoenzyme composition of amylase.

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References

Hebert P.D.N, Beaton M.J. (1993) Methodologies for allozyme analysis using cellulose acetate electrophoresis: A practical handbook. (Revised edition.) Helena Laboratories, Beaumont, Texas.

Šustr V., Block W. (1998) Temperature dependence and acclimatory response of amylase in the High Arctic springtail *Onychiurus arcticus* (Tullberg) compared with the temperate species *Protaphorura armata* (Tullberg). J. Insect Physiol. 44, 991–999.

Effects of photoperiod and temperature in the maternal and current generations on the induction of larval diapause in Lucilia sericata (Diptera: Calliphoridae)

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The blow fly *Lucilia sericata* shows a facultative diapause in the third-instar larva after cessation of feeding. In this study, the effects of photoperiod and temperature in the maternal and current generations on the induction of larval diapause were examined. Insects were reared from eggs in four combinations of two photoperiods, LD 16:8 and LD 12:12, and two temperatures, 25 and 20°C. Eggs laid by these insects were transferred to ten combinations of two photoperiods, LD 16:8 and LD 12:12, and five temperatures, 25, 20, 17.5, 15 and 12.5°C. Newly formed puparia were counted daily after the larvae ceased feeding.

No larvae entered diapause when insects were kept under the combination of a long-day photoperiod and a high temperature throughout the maternal and current generations. Some larvae entered diapause when either photoperiod or temperature in the current generation was changed to short-day or low temperature. Moreover, when the current generation was kept under short-day and low temperature conditions, diapause incidence was higher than those under the former conditions. When maternal conditions were changed, diapause incidence showed a similar tendency. Furthermore most larvae entered diapause when both maternal and current generations were kept under short-day and low temperature conditions. Therefore, photoperiod and temperature in both maternal and current generations influenced the induction of diapause.

Nymphal period differences found in four pure lines generated by successive selections for specific wing-form and body-colour in the brown planthopper, Nilaparvata lugens (Homoptera: Delphacidae)

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N. lugens adults exhibit wing dimorphism, i.e., long-winged macropters and short-winged brachypters. Although it has been generally accepted that increasing nymphal density induces more long-winged and darker coloured adults with longer nymphal periods, the four pure lines which have been generated by successive selections for specific wing-form and body-colour predominantly exhibited the selected characteristics in a broad range of densities: blackish brachypterous (BB), blackish macropterous (BM), yellowish brachypterous (YB) and yellowish macropterous (YM) pure lines. When 150 nymphs were reared at 25° under 16L–8 D photoperiod in a columnar cage (i.d., 5.4 cm ; height, 22.0 cm) with rice seedlings, the average female nymphal period was ca. 14 days for BB, 15 days for BM and YB, but 16 days for the YM pure line, while the male nymphal period was 0.5–1 day shorter for each of the respective lines, regardless of the expressed wing form. Under these conditions, adult emergence started to occur one day earlier in blackish pure lines (BB, BM) than in yellowish pure lines (YB, YM), but variations in nymphal period were greater in the brachypterous pure lines (BB, YB) than in the macropterous pure lines (BM, YM). Thus, genes regulating wing-form and body colour were suggested to be involved in the regulation of nymphal developmental rate. In F_1 progenies of BB x YM, nymphal period was ca. 15 days in females (sex chromosome type, XX), corresponding to the middle value between the two pure lines, while that of males (sex chromosome type, XY) was ca. 13.5 days, similar to that of BB. This strongly suggests that duration of the nymphal period is controlled by criss-cross inheritance and the regulatory genes are at least on the X sex chromosome. The meaning of the presence of the regulatory genes is discussed.

Impact of exposure of Coccinella septempunctata L. (Col., Coccinellidae) to extreme temperatures on their life cycles

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Analysis of data shows that temperature impact on the physiological processes of *Coccinellidae* has been studied fairly well for temperatures close to optimum and relatively insufficiently for extreme temperatures. It is for this reason that we conducted a study of how extreme temperatures affect discrete stages of the life cycles in *Coccinellidae (Coccinella septempunctata).*

The *Coccinellidae* selected for our experiment at the end of their vegetation period fed on artificial food under laboratory conditions precluding the diapause. In April (the time when *Coccinellidae* come out of the diapause under natural conditions) the experimental beetles switched to feeding on aphids (*Aphis pomi* Deg.) and were subjected for an hour to an extreme temperature 44°C RH 60%. Beetles of the control group were taken from their wintering grounds after they had come out of the diapause at the end of April and were kept like the experimental beetles under optimum conditions of 22–24°C RH 50%.

It was observed that experimental *Coccinellidae* mated 3 days earlier than those of the control group. However, their oviposition began 17 days earlier. The fertility of an experimental female beetle as compared to one of the control group decreased on average by one third. During experimentation mortality reached 27%, and in the control group it amounted to 21%. The cycle of life of the experimental beetles was 3 to 7 days shorter than that in the control group.

Then the experimental beetles of the first generation were kept under three sets of conditions: the first group (OK_1) was kept at a temperature of 30°C RH 50% without exposure to extreme temperature, the second group (OK_2) was kept at temperatures 22–34°C RH 50–60% and was exposed to extreme temperature of 44°C for 15 minutes, and the third group (OK_3) was kept at a temperature of 30°C RH 50% and was exposed to extreme temperature of 44°C for one hour. The experimental beetles and those of the control group had the same food regimen. Oviposition in both groups occurred at the same time. The average fertility of the female beetles of OK_1, OK_2 and OK_3 was 791, 542 and 157 eggs respectively, and that in the control group was 300 eggs with 30, 50, 72 and 34% of all eggs lost respectively. Oviposition in OK_1, OK_2 and OK_3 lasted for 25, 17 and 11 days respectively, and that in the control group lasted for up to 45 days. The gas exchange of the imago and larvae of the III–IV ages (OK_1) was higher than that of the imago (OK_2) and larvae of the III–IV ages. The cycle of life of the *Coccinella septempunctata* of the second generation under different conditions ranged between 17 and 20 days.

Conclusion: exposure of *Coccinellidae* to extreme temperatures in certain conditions they are kept under is stimulatory to the development of *Coccinellidae* of the second generation, whereas recurrent exposure of *Coccinellidae* of this generation to extreme temperatures oppresses their activity at the various stages of their development.

Desiccation resistance strategies of woodlice

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Resistance to dry conditions at RH close to 0% was measured in five Oniscidean species (*Armadillidium vulgare*, *Cylisticus convexus*, *Oniscus asellus*, *Porcellio scaber* and *Trachelipus ratzeburgi*). Water content, transpiration rate, and survival time were compared among these species and between 'summer' acclimated (SA) and 'winter' acclimated (WA) groups. There were three distinct strategies of survival. Prior to desiccation, water content (% of total body weight) was lower in the WA than in the SA groups of all species except *O. asellus*. Water content of *O. asellus* prior to desiccation was similar in WA and SA groups but they differed in transpiration rate. It was lower in the SA individuals that were more resistant to desiccation, i.e. they survived longer in experimental conditions of dehydration. In the other four species there was no interspecific difference between WAs and SAs in transpiration rate. WAs of the most drought resistant species (*A. vulgare* and *P. scaber*) tolerated greater desiccation (i.e. water content was lower in the time of death) then their SAs. SAs of these species contained more water both prior to desiccation and in the time of death than other species in our study. On the other hand, WAs of *C. convexus* and *T. ratzeburgi* survived desiccation to a similar level of water content as their SA groups (which was similar to WAs of *A. vulgare* and *P. scaber*). Therefore WAs of *C. convexus* and *T. ratzeburgi*, containing less water prior to desiccation, died earlier. Relative water loss (transpiration rate related to surface) was the only parameter that showed the level of drought hardiness and was highly negatively correlated with survival time. Neither the presence/number of tracheal invaginations on pleopods nor the body shape, usually considered to be characteristics of woodlice more adapted to terrestrial life, correlated with resistance to desiccation.

The effect of thermoperiods on the photoperiodic induction of larval diapause in the satin moth, Stilpnotia salicis L.

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Satin moth occurs in two ecological strains in Hungary. Its bivoltine strain inhabits primarily the so-called warm-summer regions while its monovoltine strain is typical of areas having relatively cool summers. Irrespective to genetic factors, the facultative larval diapause of satin moth is determined mainly by daily photoperiods. Our previous studies have revealed considerable differences in diapause response between larval populations belonging to the two ‘ecotypes’ of *S. salicis*. In present investigations our aim was to study the influence of daily thermoperiods on the diapause induction of this species.

Young larvae of a bivoltine *S. salicis* strain were reared in jars and fed regularly with willow (*Salix*) leaves. Small stripes of corrugated paper served as hiding sites for second instar larvae (resting in small cocoons) when they entered diapause. The insects were kept in a temperature room at constant 23°C and LD 19:5 photoperiod. In another chamber a constant thermoperiod of TC 19 (25°C) : 5 (15°C) was in function in combination with a photoperiod of LD 19:5. The percentage of diapausing L_2 larvae was registered in each experimental group.

At constant 23°C and LD 19:5 photoperiod young larvae of the bivoltine *S. salicis* strain entered diapause in 27.0% of the population. If a thermoperiod were also used in ‘natural’ synchroneity with the photoperiod, the percentage of diapausing larvae increased up to 98.5%. On the contrary, if the scotophase started 2.5 hours before the beginning of the cryophase, the ratio of diapausing individuals was low (14.9%) again. Thus it can be pointed out that the ambient temperature prevailing during the scotophase influences significantly the diapause determination in satin moth larvae. Moreover, it was also demonstrated that the first few hours of the scotophase were especially susceptible to thermal effects.

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The changes of chill coma temperatures in the annual cycle of ants of the genus Myrmica

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The publications devoted to the study of chill coma temperatures (CCT) are almost entirely absent in the ant literature. Nevertheless, such data may be of special interest when considering cold-shock resistance of ants and their adaptation to boreal and subarctic climates. This is why we began this work using 6 species of ants belonging to the genus *Myrmica*: *M. rubra, M. ruginodis, M. rugulosa, M. lobicornis, M. scabrinodis* and *M. sulcinodis*.

The ant colonies were collected in several places near St. Petersburg (ca. 60° N) as well as in Chupa, Karelia (66°15' N) and near Belgorod (50°30' N) in early summer and kept in laboratory in plastic nests at two experimental regimes: (1) constant “summer” conditions of long (22 h) days and 20°C, (2) a rough simulation of natural conditions, i.e. the “summer” conditions (regime 1) until September, then short (12 h) days and the temperature decreasing from 20°C to 10°C in several steps during 6–7 weeks, then the “overwintering” at 5°C in darkness for 3–4 months, and then the summer conditions again. Three ant colonies were used for each species and population. The CCT of 30 workers from each colony was measured each 6–8 weeks the whole year round. The ants were chilled in a micro-freezing camera at a rate of about 1°C per minute and the temperature at which a cold stupor began was determined.

No definite and significant differences in mean CCT were found between species and geographical populations studied. At the same time an apparent annual cycle of CCT variation was revealed in these ants. In summer season the mean values of CCT were about 1–2°C while from autumn to early spring the mean CCT were between -1 and -2°C. A rather sharp decrease of mean CCT values was observed during August and an increase occurred in March–April. Surprisingly, quite similar annual cycles of CCT variation were observed both under"natural" (regime 2) and constant (regime 1) conditions. We discuss the possible endogenous nature of this annual cycle of CCT variation in worker ants and its ecological importance.

New light on photoperiodic time measurement in the spider mite Tetranychus urticae

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The question whether the photoperiodic clock in insects and mites is either a circadian oscillator (or a complex of circadian oscillators) or a non-circadian hourglass has not yet been solved. Arguments in favour of the circadian clock hypothesis are mainly, if not exclusively, based on kinetic (light/dark) experiments. Evidence based on the photoreceptor pigments involved has not been considered up till now. Available evidence shows that in insects the photoreceptor pigments for photoperiodism and circadian entrainment are not the same, which forms a strong indication that photoperiodism and circadian rhythmicity are separate phenomena in insects, based on different molecular mechanisms. Experiments with orange-red light of >580 nm indicate that also in the spider mite *Tetranychus urticae* different photoreceptor pigments are involved in photoperiodic induction of diapause and entrainment of circadian rhythmicity, i.e. the Nanda-Hamner rhythm. The outcome of the above experiment corroborates the earlier conclusion that photoperiodic time measurement in the spider mite is not circadian-based (Veerman and Vaz Nunes, 1987). A non-clock role is suggested for the Nanda-Hamner rhythm in the photoperiodic induction of diapause in this mite (Veerman, 2001).

References

Veerman, A., 2001. Photoperiodic time measurement in insects and mites: A critical evaluation of the oscillator-clock hypothesis. Journal of Insect Physiology (in press).

Veerman, A., Vaz Nunes, M., 1987. Analysis of the operation of the photoperiodic counter provides evidence for hourglass time measurement in the spider mite Tetranychus urticae. Journal of Comparative Physiology 160A, 421-430.

Prolonged diapause as an element of Chrysopa dorsalis Burm. (Neuroptera: Chrysopidae) life cycle

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In many occasions insects are known to remain in diapause for more than one year especially in unpredictable habitats. Nevertheless ecophysiological features as well as environmental factors responsible for induction, maintenance and termination of prolonged diapause are still poorly understood.

Studying seasonal adaptations in green lacewing *Chrysopa dorsalis* from Belgorod Province (50°N, 36°E) we have found that in the forest-steppe zone two generations may be produced. However from 76 to 100% of the first generation prepupae enter diapause, about 40% of them having obligate diapause. Neither natural thermoperiods nor increasing day length stimulated non-diapause development. In the rest photoperiod and temperature control the seasonal development pathway.

A part of *Ch. dorsalis* prepupae required two or three years to complete diapause. Prolonged diapause seems to be a permanent element of life cycle of this species, although a quota of prepupae that remained in diapause after the first winter varied from 40% in 1995 to 4% in 1998. Positive correlation (R=0, 87) was found between the number of such individuals and the number of deposing prepupae in the first generation. There were no differences concerning the larvae development rate and the prepupae weight between individuals, which had one-year diapause or prolonged one. On the other hand, weight loss due to dehydratation and respiration during first winter were lower in prepupae with prolonged diapause. Because the offspring from eggs laid by single females collected in the field at the same time emerged in successive years and a tendency to enter long-term diapause was not inherited a conclusion is made that the individual variation in the rate of horotelic processes seems to be a physiological basis of prolonged diapause. On the other hand, environmental factors, such as high temperature during induction and low humidity in the next spring can stimulate long-term diapause.

Prepupae exhibited high cold tolerance soon at the beginning of diapause without low temperature treatment. Their supercooling points (SCPs) were in the range of –15 to –21°C. After the morphogenesis resumed in spring SCP increased up to –7.7°C, whereas SCPs were as low as at the beginning of diapause in prepupae remained in long-term diapause. Their supercooling capacity remained at the high level (-17.4°C) even when diapausing prepupae were held at a temperate temperature during 27 weeks before the second winter. Thus in *Ch. dorsalis* cold hardiness is a component of diapause program.

In the forest-steppe zone an occurrence of *Ch. dorsalis* is restricted by artificial coniferous plantings. Probably, prolonged diapause increases polymorphism in local populations and gives the guarantee to survive in unpredictable conditions.

The importance of microhabitat and microclimate for the colonization and survival of polar arthropods

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On a global scale, species diversity decreases with increasing latitude from temperate regions to the poles. On a local scale, species diversity is controlled by the age and stability of the site, the degree of isolation, microclimate and other factors. The harsh terrestrial environment of the Antarctic, and its isolation from other continents, accounts in part for the reduced flora and fauna compared with the Arctic, which offers a greater diversity of habitats for colonization. The faunas of sub-Antarctic islands such as South Georgia are much richer in species than the Antarctic continent and although some species are endemic, others are common to neighbouring continents, whilst a few species have been introduced by human activities.

As environmental conditions become more severe with increasing latitude, the selection of a microhabitat which offers an ameliorated microclimate compared to the surrounding area becomes essential for many species. In polar regions, such places are confined to areas close to melt streams or sheltered areas of ground which are snow free for at least a few months each year. At Rothera, on the Antarctic Peninsula (67°34'S, 66° 08'W) soil temperatures in winter regularly fall to –15°C despite a 20 cm layer of snow. In the summer at this latitude, the soil surface temperature can fall by 3°C h^{-1} necessitating a rapid cold-hardening response by active microarthropods (Worland & Convey, in press). Ultimately, where conditions are more extreme, mites have been found to take refuge in fine cracks in rocks. Here, even the colour of the rock has been found to be an important factor as dark rocks absorb more solar radiation than light ones, resulting in an increased mean daily temperature and providing an extended season for development by animals taking shelter in them.

Arthropods are more diverse than any other animal group and are found in almost any terrestrial environment where life can exist, including hot and cold deserts. Their small size and the naturally high solute concentration of their body fluids, makes it inevitable that they will supercool, providing a pre-adaptation mechanism to survive low temperatures by avoiding freezing.

This paper examines the microclimate of polar land habitats, which appear to have been preferentially selected by microarthropods. Environmental factors which are likely to affect the overwinter survival of microarthropods under severe conditions such as snow accumulation, insulation by plant material, moisture availability and the length of the growing season are examined. The difference in climate between neighbouring land masses and Antarctica and the dispersal of arthropods between them, is also considered.

Reference

Worland M.R., & Convey P.C. in press: Rapid coldhardening in Antarctic microarthropods. *Functional Ecology*.

Thermo- and hydropreference reactions of jumping spiders Evarcha arcuata (Clerck 1757) and Evarcha falcata (Clerck 1758) (Araneae, Salticidae) in South Ural

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The most important abiotic factors that essentially affect the physiological state of poikilotherm species are basically temperature and humidity the attitude of these species to these factors has carefully been studied, but data concerning the reaction of spiders towards them are not sufficient.

For the purpose of studying the reaction of two species of Salticidae to the hydrothermal factor, there was performed an experiment determining their thermo- and hydropreference. All the measurements were taken using standard methods. Only adult species were used in the experiment. To determine the reaction to the thermal factor, we considered a daily range of spiders scattering in thermograde and dynamics changing of thermopreference during the season. The research took place in Chelyabinsk region in Ilmen reserve in the permanent establishment Miassovo during the summer of 2000.

Seasonal and daily rhythms of thermopreferencial reactions of *E. arcuata* and *E. falcata* coincide with appropriate changes of the temperature in places of their residence which points to the presence of inner factors: the physiological state of a spider and the specific type of thermopreference. During the entire season species *E. falcata* were observed to be moving to warmer places of the thermograde (29.9±1.08°C). *E. arcuata* were seen to choose colder places (26.9±0.91°C). Females and males of these two species prefer different temperatures: *E. arcuata* 27.5°C and 26.3°C, *E. falcata* 27.7°C and 32.2°C accordingly. Thus, *E. falcata* is a more thermophilic species than *E. arcuata*. Average quantities of the range of *E. arcuata* (7.2°C) and *E. falcata's* (6.3°C) scattering do not differ considerably ($T=0.35<t_{st}$, $P=0.05$), the norm of reaction of these two species to the thermal factor being approximately identical. Still the range of scattering is different when speaking about male and female individuals. It is 7.7°C with *E. arcuata* females, 6.6°C with males; 8.4°C with *E. falcata* females and 4.2°C with males. Thus, there can be observed a tendency towards a more exacting attitude of male individuals to the thermal factor (especially that concerns *E. falcata*). This phenomenon can be accounted for by the fact that this is females that are responsible for reproduction and protection of descendants, females being more flexible to the thermal factor.

Daily and seasonal reactions to relative air humidity of these two species are not so evident as those towards temperature. An average quantity of the preferred humidity does not differ much it is 47.5% with *E. falcata*, 44.8% with *E. arcuata* ($T=-1.21<t_{st}$, $P=0.05$). Behavioural reactions towards humidity, which is a mechanism of maintaining a necessary level of organism watering, point to the fact that these two species of Salticidae do not depend much on this factor (in the area of research); that allows to consider them mesophiles.

Effects of host plant quality on overwintering success of the leaf beetle Chrysomela lapponica (Coleoptera: Chrysomelidae)

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I investigated effects of variation in host plant quality on adult feeding and overwintering success of the willow feeding leaf beetle, *Chrysomela lapponica.* Beetles of the summer generation were fed in the laboratory on host plants, *Salix borealis*, originating from (a) site with low-density populations of *Ch. lapponica*, (b) site with outbreak density of *Ch. lapponica*, © post-outbreak site (five plants per site, 20–25 beetles per plant). Each beetle individual (347 in total) was weighed (I) immediately after hatching, (ii) next day after beetles stopped feeding (iii) after hibernation, before beetles started feeding. Duration of pre-overwintering feeding was recorded, and the rate of weight gain calculated. Beetle mortality was assessed on plant-specific level before and after overwintering. The detected variation in beetle characteristics was explained by the differences between sites, whereas within-site variation in plant quality was minor or non-existent. Beetles fed on plants from low-density and peak-density sites demonstrated similar performance, whereas on plants from post-outbreak site beetles fed longer and gained higher weight, but demonstrated higher weight loss and higher mortality during hibernation. All studied characteristics were explained by the total carbon content in the host plant foliage. Since carbon concentration was higher in plants from post-outbreak site, the discovered effects may be linked with increase in carbon-based defensive compounds, which could be induced by herbivore damage during an outbreak. Herbivore-induced decrease in host plant quality observed in post-outbreak sites (delayed inducible resistance, DIR) was earlier found to increase larval mortality and thus contribute to the decline in population density of *Ch. lapponica* (Zvereva et al. 1997). Results of the current study suggest that DIR can also disturb accumulation of nutritive reserves and thus increase mortality of adult beetles during hibernation, enhancing post-outbreak density decline.

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