Entomol Gener	25(4): 255-264	Stuttgart 2001-10	ISSN: 0171-8177

EGT-Nr 1.041 IV

Environmental Control of Voltinism of the Stinkbug Graphosoma lineatum in the Forest-Steppe Zone (Heteroptera: Pentatomidae)

DMITRY L MUSOLIN & AIDA H SAULICH

Received: 2001-06-16 / 2001-08-11 Accepted: 2001-08-13

MUSOLIN D L [Natl Agr Res Center Hokkaido Region, Sapporo 062-8555, Japan] & SAULICH A H [Biol Res Inst, St.Petersburg State Univ, Peterhof, St.Petersburg 198904, Russia]: **Environmental Control of Voltinism in the Stinkbug Graphosoma lineatum in the Forest-Steppe Zone (Heteroptera: Pentatomidae).**- Entomol Gener **25**(4): 255-264; Stuttgart 2001-10. - [Article]

An experimental study under quasi-natural conditions in the forest-steppe zone was conducted to clarify the seasonal cycle of *Graphosoma lineatum* Linnaeus 1758 (Heteroptera: Pentatomidae), a species with a facultative adult winter diapause. It was demonstrated previously that if adults of a new generation emerge in the middle of July all ♀♀ enter diapause, and thus this species produces only 1 generation per year. In the present study, the emergence of adults was artificially shifted to the end of May–2nd half of June what resulted in reproduction in 69-71% ♀♀. These results supported the possibility that at least a part of the local population of *G lineatum* can produce 2 generations per year in the forest-steppe zone of Russia in particularly warm years. The environmental conditions and peculiarities of the biology of *G lineatum* that can promote bivoltinism are discussed, and the seasonal cycle of the species is compared with those of other Heteroptera with facultative adult winter diapause from the forest-steppe zone.

Key words: *Graphosoma lineatum* Linnaeus 1758 – diapause – dormancy – Russia - voltinism – seasonal cycle

MUSOLIN D L [Natl Agr Res Center Hokkaido Region, Sapporo 062-8555, Japan] & SAULICH A H [Biol Res Inst, St.Petersburg State Univ, Peterhof, St.Petersburg 198904, Russia]: **Environmental Control of Voltinism in the Stinkbug Graphosoma lineatum in the Forest-Steppe Zone (Heteroptera: Pentatomidae).**- Entomol Gener **25**(4): 255-264; Stuttgart 2001-10. - [Article]

Для выяснения структуры сезонного цикла *Graphosoma lineatum* Linnaeus, 1758 (Heteroptera: Pentatomidae), вида с факультативной имагинальной диапаузой, были проведены экспнрименты в природных условиях в лесо-степной зоне (Белгородская область России). Ранее было показано, что если клопы нового поколения линяют на имаго в середине июля, то все самки формируют диапаузу и, таким образом, этот вид развивается только в 1 поколении в год. В новом эксперименте окрыление имаго было искуственно сдвинуто к концу мая - второй половине июня, в результате чего 69-71 % самок приступили к размножению. Эти результаты подтверждают возможность того, что, как минимум, часть популяции *G lineatum* может развиваться в 2 поколениях в лесо-степной зоне в особенно теплые годы. Обсуждаются температурные условия и особенности биологии *G lineatum*, способствуюшие бивольтинному сезонному развитию. Сезонный цикл вида сравнивается с сезонными циклами других полужесткокрылых с факультативной имагинальной зимней диапаузой из лесо-степной зоны.

0171-8177/01/0025-0255 $ 2.50

Для выяснения структуры сезонного цикла *Graphosoma lineatum* Linnaeus 1758 (Heteroptera: Pentatomidae), вида с факультативной имагинальной диапаузой, были проведены экспернименты в природных условиях в лесо-степной зоне (Белгородская область России). Ранее было показано, что если клопы нового поколения линяют на имаго в середине июля, то все самки формируют диапаузу и, таким образом, этот вид развивается только в 1 поколении в год. В новом эксперименте окрыление имаго было искуственно сдвинуто к концу мая - второй половине июня, в результате чего 69-71 % самок приступили к размножению. Эти результаты подтверждают возможность того, что, как минимум, часть популяции *G lineatum* может развиваться в 2 поколениях в лесо-степной зоне в особенно теплые годы. Обсуждаются температурные условия и особенности биологии *G lineatum*, способствуюшие бивольтинному сезонному развитию. Сезонный цикл вида сравнивается с сезонными циклами других полужесткокрылых с факультативной имагинальной зимней диапаузой из лесо-степной зоны.

1 Introduction

Graphosoma lineatum Linnaeus 1758 is a common phytophagous stinkbug widespread in the Palearctic region. In the spring, adults feed on various trees and shrubs, but soon move on various species of wild and cultivated Umbelliferae, seeds of which are the principal food resource for this species.

G lineatum has been reported to produce 1 generation in southern Sweden [57°N; LARSSON 1989], 1 or 2 generations in Ukraine [44.5-52.5°N; PUCHKOV 1961, 1987] and in Kazakhstan [41-55.5°N; ASANOVA & ISKAKOV, 1977], and 2 complete generations in the Crimea [44.5-46°N; ARNOL'DI 1948] and in southern France [43.5°N; NGUYEN BAN 1964]. The species overwinters at the adult stage, and diapause was demonstrated to be controlled by the long-day type photoperiodic response [POPOV 1971, MUSOLIN & SAULICH 1995, NAKAMURA et al 1996]. It was also shown that *G lineatum* exhibits a recurrent photoperiodic response and remains sensitive to photoperiodic conditions during reproduction and diapause [MUSOLIN & MAYSOV 1998] as well as after diapause termination [NAKAMURA et al 1996].

Previously, the temperature requirements of different life stages in the Belgorod (Russia) population of this species and a photoperiodic response at 24 and 28°C were reported by MUSOLIN & SAULICH [1995]. The critical day-length of the photoperiodic response was shown to be temperature-dependent in this species, and the threshold value was 17 h 15 min at 24°C and 15 h 45 min at 28°C. Moreover, photoperiodic conditions influenced the duration of nymphal period: at 24°C, nymphs grew quicker under short-day conditions than under long-day conditions. Also, sum of effective temperatures required for one complete generation was evaluated at approximately 325 degree-days, and it was suggested that this species could produce 2 generations in warmer years in this region. However, it turned out to be very difficult to discriminate generations in the field by usual phenological observations, because adults of *G lineatum* are characterized by the long life-span and extended oviposition period and they were constantly recorded in the region from mid-May till late autumn [unpublished].

Special experimental procedures for clarification of voltinism patterns in insects were proposed by DANILEVSKY [1961] and has been successfully used in experiments with several insect species [e.g: GORYSHIN et al 1986, SAULICH et al 1994, TERAOKA & NUMATA 1995, VOLKOVICH 1998]. The techniques involve rearing several series of insects (usually from eggs to the stage that can enter diapause) under quasi-natural conditions and commencement of series throughout the season with a particular time interval (e.g, every 10 days).

The previous experiment using this method showed that even if nymphs of *G lineatum* hatch from the eggs as early as mid-June, emerged adults would enter diapause [MUSOLIN & SAULICH 1996].

In the present study, insects from the same population were used, and also adults were reared under quasi-natural conditions, but artificially shifted ecdysis to the very beginning of the summer. On the basis of these findings, the seasonal development of this species in the forest-steppe zone will be discussed here, and the seasonal cycle of *G lineatum* will be compared with those of some other Heteroptera with facultative adult winter diapause from this region.

2 Material and methods

Adults of *G lineatum* were collected in the field in the "*Forest on the Vorskla River*" nature reserve (Belgorod region of Russia, the forest-steppe zone, 50°38′N, 35°58′E) in late August / early September 1995. Insects were kept in the dark at a temperature of 7 ± 2°C, and in early spring were transferred to the conditions of 18 h light : 6 h dark photoperiod [18L:6D] at 28 ± 1°C. The eggs obtained after termination of diapause in adults and then hatched nymphs were kept under room conditions (around 16L:8D and 20°C). On May 25, 1996, nymphs of various ages (ranged between 2nd and 5th, last, instar) were transferred to quasi-natural conditions in the nature reserve. Adults that emerged between May 25 and June 30 were grouped into 3 series: those that emerged (1) before June 10, (2) between June 11 and June 20, and (3) between June 21 and June 30.

Nymphs were reared in transparent plastic containers measuring 100×250×150 mm with 2 openings 80 mm in diameter for aeration covered by gauze. Water and a mixture of dry seeds of cultivated dill and coriander and wild *Conium maculatum, Pastinaca sylvestris,* and *Anthriscus sylvestris* were supplied as food. When available in the field, leaves and umbels (flowers and fresh seeds) of the same species were added. After emergence, adults were kept in pairs (♂ and ♀) in plastic Petri dishes 100 mm in diameter, the lids of which had openings 50 mm in diameter for aeration covered by gauze. Food was checked and replenished every other day. Commencement of oviposition was recorded daily. ♀♀ that did not start to lay eggs on day 40 after adult ecdysis were dissected and their physiological status was determined based on the state of the gonads and fat body: those without mature eggs or vitellogenic oocytes in the ovarioles and with a well-developed fat body were considered to be in diapause.

Both nymphs and adults were kept in a specially modified meteorological booth. The shelf on which the Petri dishes with insects were kept was about 130 cm above the ground. Only the northern side of the booth was open and the insects inside the booth were sheltered from direct sunlight and rain. The temperature in the booth was recorded with a daily thermograph and checked using min and max thermometers.

3 Results and Discussion

The results of the study are presented in **Fig 1** along with those of the previous experiment. In 1995, eggs were obtained from adults collected in the field at the end of May, and 1st nymphs hatched on June 7. Adults emerged between July 15 and August 10 and all ♀♀ entered diapause. Similarly to these bugs, none of the ♀♀ from the later series commenced oviposition and all were judged to be in diapause [MUSOLIN & SAULICH 1996]. In 1996, the emergence of adults was artificially shifted to the earlier part of the season (by rearing of nymphs under room conditions before the beginning of the field experiment), and as a result, from 69-71% of ♀♀ were non-diapause in three experimental series.

At the time of adult emergence from the first series from 1995, the natural day-length was around 16 h 30 min (including half of civil twilight) and decreased day after day. Mean ambient temperature was below 20°C and remained low during the following weeks.

As shown in the previous laboratory experiment, such a day-length induces diapause in 75% of ♀♀ even at temperature of 24°C [MUSOLIN & SAULICH 1995]. Lower temperature and perhaps also decreasing day-length promoted diapause induction resulting in diapause in 100% of ♀♀ of all series from 1995.

In 1996, the emergence of adults coincided with the period of increasing and the longest (17 h 07 min) day-length. Ambient temperature was not unusually high, but gradually increased from mid-June to mid-July. This combination of environmental conditions resulted in a high incidence of non-diapause development (reproduction): 69% of ♀♀ from the first series started oviposition in 25.2 ± 3.61 days (mean ± S.E.) after adult emergence (Fig 1). Incidence of non-diapause ♀♀ was also high in 2 later series from 1996 and the preoviposition period in these series amounted to 31.8 ± 1.78 and 30.9 ± 2.04 days, respectively.

The results of these experiments demonstrated that while a univoltine pattern of seasonal development is a principal one for *G lineatum* in the region, some part of the population can potentially produce 2 generations per year in the forest-steppe zone: most of ♀♀ from the series from 1996 were non-diapause and laid their first eggs in the middle of June that corresponded the beginning of the second series from 1995. As shown in 1995, the insects hatched at least before mid-July have enough time to complete nymphal development, emerge as adults and prepare for overwintering.

These results, however, raise the question under which circumstances this species can realize this potential ability to produce the second generation. It is obvious that reproduction before overwintering in *G lineatum* is possible only if adults emerge when days are the longest and temperature is high. It seems probable that in unusually warm years overwintered adults can start reproduction in the middle of May. Progeny of these ♀♀ will complete nymphal development and molt into adults in the 2nd half of June. As shown in the series of 1996 of the experiment, ♀♀ emerged at this time are mostly non-diapause and these ♀♀ can produce 2nd generation.

Recently, it was suggested that temperature might be one of the most important environmental factors and cues that influence seasonal development of insects (and, particularly, heteropterans) in the temperate zone in spring [MUSOLIN & SAULICH 1999].

The results presented above suggested that high spring and early summer temperatures can promote early resumption of development and reproduction of the bugs from the overwintered generation as well as growth, maturation and reproduction of their progeny. This acceleration of seasonal development may result in a shift from a uni- to bivoltine seasonal pattern, at least in a part of the species population in a particularly warm years (**Fig 2**).

As mentioned, *G lineatum* is closely associated with Umbelliferae species. The seeds of these plants ripen already in May, remain available to nymphs and adults throughout the whole season and thus do not restrict seasonal development of *G lineatum* as it is known in some other species of Heteroptera [NAKAMURA & NUMATA 1997, 1998, 1999, MUSOLIN & SAULICH 1999].

Moreover, Umbellifera usually produce seeds only in sunny and open forest edges, meadows and gardens where ambient temperature is higher than in the surrounding microhabitats, at least at daytime. It seems to be a strong factor that could promote reproduction in the early-emerged individuals.

It also was shown in the laboratory experiment that the longer was the photophase under which ♀♀ were kept, the shorter was the preoviposition period in these ♀♀ [MUSOLIN & MAYSOV 1998]. It may also promote reproduction in early individuals and diapause in those that emerge later.

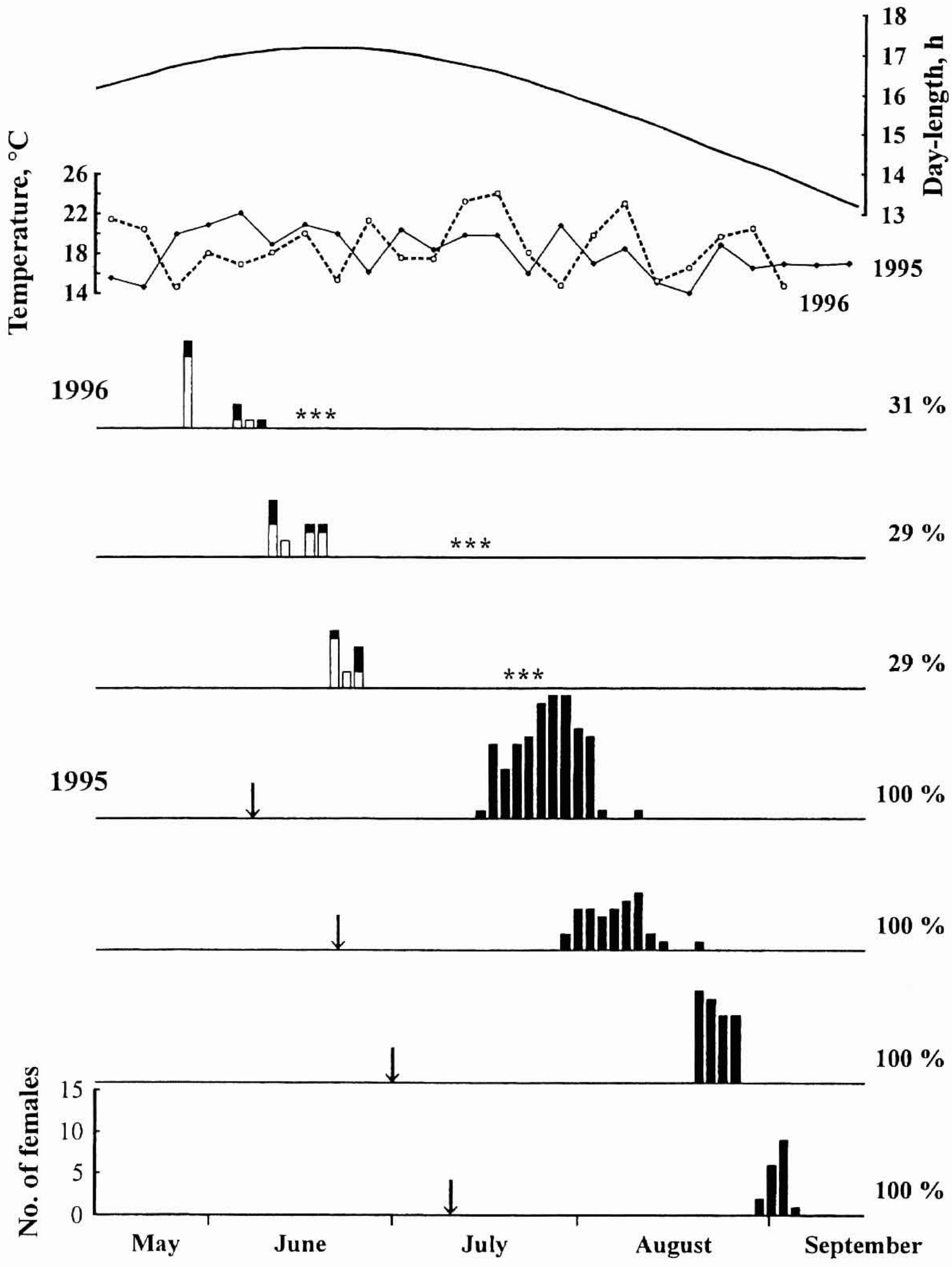

Fig 1: Induction of adult diapause in *Graphosoma lineatum* Linnaeus 1758 under quasi-natural conditions in 1995 and 1996 [Heteroptera: Pentatomidae].- Each —— represents an experimental series (data for 1995 are partly from MUSOLIN & SAULICH 1996). ↓↓↓ dates of hatching of the nymphs in 1995. **Histograms** show emergence and physiological state of ♀♀: non-diapause (○○) or diapause (●●); the incidences of diapause in ♀♀ of each series are shown as %. *** the beginning of oviposition. —— natural day-length including half of civil twilight (after SHARONOV 1945). Temperature was calculated as mean for 5-day periods in the experimental meteorological booth. n = 14-102.

In the two-generation seasonal scheme, reproduction period of the 1st generation would be short (**Fig 1** and **2**): in the series from 1995, mid-July environmental conditions induced diapause in 100% of newly emerged f ♀♀. Most non-diapause ♀♀ in 1996 ceased oviposition by mid- or the end of July and this coincided with our latest records of egg batches in the field [unpublished]. As shown previously, both field-collected and laboratory-reared bugs continued to lay eggs for several months if kept under long-day conditions and favorable temperatures, but terminated oviposition soon if transferred to short-day conditions [NAKAMURA et al 1996, MUSOLIN & MAYSOV, unpublished].

Graphosoma lineatum has a recurrent photoperiodic response and remains sensitive to photoperiodic conditions during reproduction and diapause [MUSOLIN & MAYSOV 1998; unpublished] as well as after diapause termination [NAKAMURA et al 1996]. Thus it was supposed (but still not proved experimentally) that if some ♀♀ did not completely realize their reproductive potential, they could enter diapause, overwinter and continue reproduction the next year [NAKAMURA et al 1996].

Adult diapause is perhaps the most common type of winter diapause in many Heteroptera families and is apparently dominant in temperate Pentatomoidea (93% of the species in Central Europe: HERTZEL 1982) and in terrestrial predatory true bugs from the temperate zone (76.7% of 57 species studied to date and reviewed by RUBERSON et al 1998). It is quite clear that incorporation of facultative, environmentally controlled, diapause into life cycle makes seasonal development of the species more flexible and allows taking advantages in utilization of the seasonally variable resources by producing more than one generation per year and entering diapause shortly before the actual deterioration of the environmental conditions. On the other hand, facultative nature of diapause does not necessarily imply bi- or multivoltinism [TAUBER & TAUBER 1976, 1977, CANARD & GRIMAL 1988, SAULICH & VOLKOVICH 1996; for review in Heteroptera: SAULICH & MUSOLIN 1996].

Flexible voltinism patterns dependent on year-to-year weather fluctuations have been shown at least in two other Heteroptera species. The populations studied of both *Lygaeus equestris* (Lygaeidae) and *Aquarius remigis* (Gerridae) are primarily univoltine, but favorable environmental conditions may promote appearance of partial second generations [SOLBRECK & SILLÉN-TULLBERG 1981, SOLBRECK 1991, BLANCKENHORN 1994]. In respect to *L equestris*, SOLBRECK [1991] especially emphasized importance of spring and summer temperature, amount of snow in previous winter and total number of sunny hours in spring as the factors that determined appearance of the 2nd generation.

Seasonal development of 2 other Heteroptera species with a facultative photoperiodically induced reproductive winter diapause has been studied in the forest-steppe zone using experimental protocols similar to those used in our experiments with *G lineatum*.

Thus, *Pyrrhocoris apterus* (Pyrrhocoridae) is sensitive to photoperiodic conditions from the fourth nymphal instar, while last several days of the final (5th) instar seem to be a principal period of photoperiodic sensitivity when photoperiodic conditions change from long-day to short-day [HODEK 1971, SAULICH et al 1994]. The species can produce 1 or 2 generations per summer season and it was supposed that both of these types of seasonal development could be realized in the same year: early bugs of the new generation commence reproduction, while those emerging later in the season enter diapause [SAULICH et al 1994].

In another heteropteran, *Arma custos* (Pentatomidae), adult stage seems to be one principally sensitive to photoperiodic signals, and day-length conditions during nymphal stages had little or no effect on diapause induction [SAULICH & VOLKOVICH 1996].

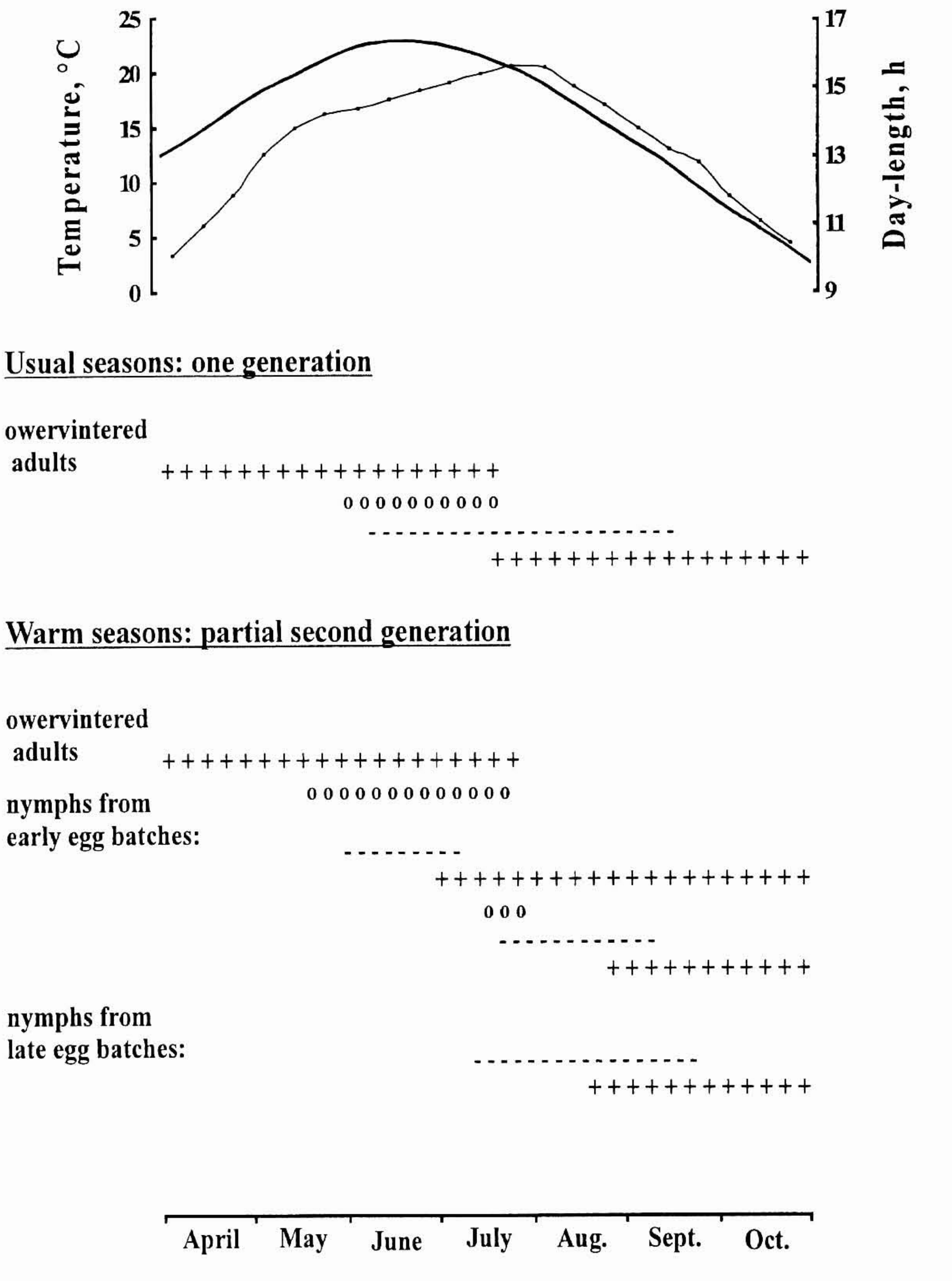

Fig 2: Schematic representations of possible scenarios of seasonal development of *Graphosoma lineatum* Linnaeus 1758 in usual and warm seasons in Belgorod region (Russia, the forest-steppe zone, 50 °N, 36 °E). +, adults; **o**, eggs; -, nymphs. ▬ natural day-length (after BECK 1980); —•—•— mean 10-day air temperature (after KARAUSHEVA 1980). See text for details.

This species normally produces 1 generation in the forest-steppe zone (and most probably in other parts of its natural range), although diapause was shown to be facultative, and a combination of long photophase (longer that 15-16 h) and high temperature (29-30°C) determined non-diapause development in most bugs in the laboratory. An artificial shift of adult emergence from the end of July (as it takes place in the field) to the end of June induced reproduction in only 37% of the ♀♀ reared under quasi-natural conditions [VOLKOVICH & SAULICH 1994, SAULICH & MUSOLIN 1996].

It seems likely that while *G lineatum* usually produces only 1 generation per year in the forest-steppe zone, the tendency towards diapause and, thus, to univoltinism in this species is not as strong as in *A custos*, although much more favorable conditions are required for *G lineatum* than for *P apterus* to induce reproduction and promote a two-generation seasonal pattern in the region.

4 References

ARNOL'DI KV [1948]: On biology of some pentatomid bugs in the Crimea, with a reference to their population dynamics.- Dokl Akad Nauk SSSR **60:** 173-176; Moskwa / USSR (in Russian).

ASANOVA RB & ISKAKOV BV [1977]: Harmful and useful Heteroptera of Kazakhstan.- Kainar, Alma-Ata / Kazakhstan, USSR (in Russian).

BECK SD [1980]: Insect photoperiodism. 2nd ed.- Academic Press, New York / USA.

BLANCKENHORN WU [1994]: Fitness consequences of alternative life histories in water striders, Aquarius remigis (Heteroptera: Gerridae).- Oecologia **97:** 354-365; Berlin / Deutschland.

CANARD M & GRIMAL A [1988]: Insect photoperiodism: various ways of regulating univoltinism in lacewings (Planipennia: Chrysopidae).- Experientia **44:** 523-525; Basel / Schweiz.

DANILEVSKY AS [1961]: Photoperiodism and seasonal development of insects.- Leningrad State University Press, Leningrad / USSR (in Russian) [Translated into English by J JOHNSON assisted by N WALOFF as DANILEVSKII AS [1965]: Photoperiodism and seasonal development of insects.- Oliver and Boyd, Edinburgh / United Kingdom].

GORYSHIN NI, VOLKOVICH TA, SAULICH AH & SHAHOVA NN [1986]: Experimental analysis of seasonal development of the Colorado potato beetle, Leptinotarsa decemlineata Say, in the forest steppe-zone. II. Field experiments and phenological observations.- Zool Zh **65:** 528-539; Moskwa / USSR (in Russian, English Summary).

HERTZEL G [1982]: Zur Phänologie und Fortpflanzungsbiologie einheimischer Pentatomiden-Arten (Heteroptera).- Entomol Nachrichten und Berichte **26:** 69-72; Leipzig / Deutsche DR.

HODEK I [1971]: Sensitivity of larvae to photoperiods controlling the adult diapause of two insects.- J Insect Physiol **17:** 205-216; Oxford / United Kingdom.

KARAUSHEVA AI [1980]: Features of climate and weather in the nature reserve "Forest on the River Vorskla", Belgorod region.- Trans Leningrad State Univ **9:** 29-39; Leningrad / USSR (in Russian, English Abstract).

LARSSON FK [1989]: Female longevity and body size as predictors of fecundity and egg length in Graphosoma lineatum L. (Hemiptera, Pentatomidae).- Dtsch Ent Z, N F **36:** 329-334; Berlin / Deutschland.

MUSOLIN DL & MAYSOV AV [1998]: Perception of photoperiodic information during the induction and termination of diapause in stinkbug Graphosoma lineatum L. (Heteroptera, Pentatomidae). In: MEDVEDEV GS et al (eds): The problems of entomology in Russia. Proceedings of XI Congress of Russian Entomological Society (St. Petersburg, 23-29 Sept. 1997). **2:** 44. Nauka, St. Petersburg / Rossija (in Russian).

MUSOLIN DL & SAULICH AH [1995]: Factorial regulation of the seasonal cycle of the stinkbug Graphosoma lineatum L. (Heteroptera, Pentatomidae). 1. Temperature and photoperiodic responses.- Entomol Obozr **74:** 736-743; St.Petersburg / Rossija (in Russian, English Summary) [Translation in Entomol Rev 1996 **75:** 84-93; Lanham, MD / USA].

MUSOLIN DL & SAULICH AH [1996]: Photoperiodic control of seasonal development in bugs (Heteroptera).- Entomol Obozr **75**, 489-506; St.Petersburg / Rossija (in Russian, English Summary) [Translation in Entomol Rev 1996 **76:** 849-864; Lanham, MD / USA].

MUSOLIN DL & SAULICH AH [1999]: Diversity of seasonal adaptations in terrestrial true bugs (Heteroptera) from the temperate zone.- Entomol Sci **4:** 623-639; Tokyo / Nippon.

NAKAMURA K, HODEK I & HODKOVÁ M [1996]: Recurrent photoperiodic response in Graphosoma lineatum (Heteroptera: Pentatomidae).- Eur J Entomol **93:** 519-523; České Budejovice / Česko.

NAKAMURA K & NUMATA H [1997]: Seasonal life cycle of Aelia fieberi (Hemiptera: Pentatatomidae) in relation to the phenology of its host plants.- Ann Entomol Soc Am **90:** 625-630; Lanham, MD / USA.

NAKAMURA K & NUMATA H [1998]: Alternative life cycles controlled by temperature and photoperiod in the oligophagous bug, Dybowskyia reticulata.- Physiol Entomol **23:** 69-74; Oxford / UK.

NAKAMURA K & NUMATA H [1999]: Environmental regulation of adult diapause of Graphosoma rubrolineatum (Westwood) (Heteroptera: Pentatatomidae) in southern and northern populations of Japan.- Appl Entomol Zool **34:** 323-326; Tokyo / Nippon.

NGUYEN BAN J [1964]: Étude de la biologie de Graphosoma lineata (Hemipteroïde Scutellerinae).- Bull Soc Histoire Nature Toulouse **99:** 325-340; Toulouse / France.

POPOV GA [1971]: Rearing of bugs (Hemiptera, Pentatomidae) for the cultures of egg parasites of Eurygaster integriceps.- Bulletin Vsesojuznogo Nauchno-issledovatelskogo Instituta Zashiti Rasteniy (VIZR) **19:** 1-10; Leningrad / USSR (in Russian).

PUCHKOV VG [1961]: Stink bugs. The Fauna of the Ukraine. Vol **21** (1).- Inst of Zool, Acad of Sci of the Ukrainian SSR, Kiev / Ukraina, USSR (in Ukrainian).

PUCHKOV VG [1987]: Order True bugs – Hemiptera. In: VASILIEV VP (ed): Pests of agricultural plants and forests. Vol **1** Pest nematodes, mollusks, arthropods: 279-305.- Urozhay, Kiev / Ukraina, USSR (in Russian).

RUBERSON JR, KRING T J & ELKASSABANY N [1998]: Overwintering and the diapause syndrome of predatory Heteroptera. In: COLL M & RUBERSON JR (eds): Predatory Heteroptera: Their ecology and use in biological control: 49-69.- Thomas Say Publications in Entomology, Entomological Society of America, Lanham, MD / USA.

SAULICH AKH & MUSOLIN DL [1996]: Univoltinism and its regulation in some temperate true bugs (Heteroptera).- Eur J Entomol **93**: 507-518; České Budejovice / Česko.

SAULICH A KH & VOLKOVICH TA [1996]: Univoltinism and its control in insects.- Entomol Obozr **75:** 244-258; St.Petersburg / Rossija (in Russian, English Summary) [Translation in Entomol Rev 1996 **76:** 205-217; Moskwa / Rossija.

SAULICH AH, VOLKOVICH TA & NUMATA H [1994]: Control of seasonal development by photoperiod and temperature in the linden bug, Pyrrhocoris apterus in Belgorod, Russia.- Zool Sci **11:** 883-887; Tokyo / Nippon.

SHARONOV VV [1945]: The tables for calculation of natural illumination and visibility. - Acad Sci of the USSR, Moskwa-Leningrad / USSR (in Russian).

SOLBRECK C [1991]: Unusual weather and insect population dynamics: Lygaeus equestris during an extinction and recovery period.- Oikos **60:** 343-350; Lund / Sverige.

SOLBRECK C & SILLÉN-TULLBERG B [1981]: Control of diapause in a "monovoltine" insect, Lygaeus equestris (Heteroptera).- Oikos **36:** 68-74; Lund / Sverige.

TAUBER MJ & TAUBER CA [1976]: Environmental control of univoltinism and its evolution in an insect species.- Can J Zool **54:** 260-265; Ottawa / Canada.

TAUBER MJ & TAUBER CA [1977]: Adaptive mechanisms underlying univoltinism in insects.- Proc XII Internat Conference (1976) of International Society for Chronobiology: 639-642.- The Publishing house Il Ponte, Milan / Italia.

TERAOKA T & NUMATA H., 1995: Induction of adult diapause in a parasitoid wasp, Ooencyrtus nezarae under natural conditions.- Entomol Exp Appl **76:** 329-332; Dordrecht / Koninkrijk der Nederlanden.

VOLKOVICH TA [1998]: Environmental control of seasonal cycles in green lacewings (Neuroptera, Chrysopidae) from the forest-steppe zone of Russia.- Acta Zool Fenn **209:** 263-275; Helsinki / Suomi.

VOLKOVICH TA & SAULICH AH [1994]: The predatory bug Arma custos: photoperiodic and temperature control of diapause and coloration.- Zool Zh **73:** 26-37; Moskwa / Rossija (in Russian, English Summary) [Translation in Entomol Rev 1995 **74:** 151-162; Lanham, MD / USA].

Acknowledgements: We are grateful to Professor H Numata (Osaka City University) and Dr K Nakamura (Okayama University of Science) for critical reading of this manuscript. This research was partly supported by the Russian Foundation of Basic Research (Leading Scientific Schools project # 00-15-97934), Federal Programs *Biodiversity* and *Integration* for A.S., and the Ministry of Education, Science, Sports and Culture of Japan (Grant-in-Aid for STA Fellows) for D.M.

Authors' Addresses – Anschriften der Verfasser: Dr Dmitry L Musolin, Entomology Laboratory, Department of Agro-Environmental Sciences, National Agricultural Research Center for Hokkaido Region, 1 Hitsujigaoka, Sapporo 062-8555, Hokkaido, Nippon.

E-mail: musolin@.affrc.go.jp

Д-р Аида Саулич, Лаб. энтомологии, Биологический НИИ Санкт-Петербургского государственного университета. Ораниенбаумское шоссе, 2, Старый Петергоф, Санкт-Петербург 198904, Россия.

E-mail: **Saulich@AS1061.spb.edu**

* * *