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Phenology of the 28-spotted potato ladybird beetle *Henosepilachna vigintioctomaculata* in the south of the Russian Far East

Abstract
Relevance. The 28-spotted potato ladybird beetle, Henosepilachna vigintioctomaculata, causes severe damage to plants of the Solanaceae family in the south of the Russian Far East. Today the application of chemicals is the main method for protecting crops against the potato ladybird beetle. This leads not only to the eradication of the pest, but also to the pollution of agricultural ecosystems and the emergence of potato ladybird beetle populations that are resistant to pesticides. A study on the seasonal cycles of the development of the potato ladybird beetle may help to devise new methods for controlling this pest.
Methods. We conducted laboratory experiments to study the developmental timing ofa potato ladybird beetlepopulation. The number of eggs was counted, and then the eggs were placed in Petri dishes. The number of emerged larvae was recorded on a daily basis. The hatched larvae were transferred to glass containers (hereafter rearing cages) in batches of 10. We recorded the dates of the transition from one immature developmental stage to another notingthe simultaneity of these transitions. At the onset of the pupal stage, the date was recorded and food was withdrawn from the rearing cages. Scientific observations were carried out on the emergence ofyoung beetles. Field research on the phenology of the potato ladybird beetle was conducted at afield site of 40 m^2. The timing of the following events was recorded: the emergence of the adult beetles from diapause, the colonization of the potato field, the beginning and the end of oviposition, the emergence of the larvae and the pupae, the flight of the new insect generation.
Results and conclusion. Our laboratory experiment on the immature developmental stages of the potato ladybird beetle revealed that the egg stage was 4-5 days in duration, the larval stage was 16-17 days and the pupal stage was 4-5 daysunder optimal conditions. We also observed deviations from the mean values, which could be conditioned by external factors. For instance, the duration of embryonic development depended either on humidity or on the time range of hatching from one egg mass. The observed deviations of the developmental timing of the larvae and the pupae were most probably due to the quantity and quality of the available food, and the presence of secondary metabolites and glycoalkaloids in it. The field research on thephenology of the potato ladybird beetle showed that there was only one generation in 2020, but two generations in 2021. After comparing climatic conditions in 2020 and 2021, we concluded that *Henosepilachna vigintioctomaculata* can produce two generations during dry and hot years.
Keywords: the 28-spotted potato ladybird beetle, phenological development, immature developmental stages, ontogeny

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Фенология картофельной коровки *Henosepilachna vigintioctomaculata* на юге Дальнего Востока

Резюме
Актуальность. На юге Дальнего Востока ощутимый вред растениям семейства Пасленовых (Solanaceae) наносит картофельная коровка Henosepilachna vigintioctomaculata. В настоящее время основным средством борьбы с картофельной коровкой является химическая обработка посадок, что приводит не только к уничтожению вредителя, но и к загрязнению агроэкосистем и появлению устойчивых к пестицидам популяций картофельной коровки. Изучение сезонных циклов развития картофельной коровки может помочь в разработке методов борьбы с ней.
Методика исследования. Для изучения сроков развития популяции картофельной коровки проводятся лабораторные эксперименты. Подсчитанные яйца помещали в чашки Петри, ежедневно фиксировали появление личинок. Отродившихся личинок пересаживали в стеклянные сосуды по 10 особей. При переходе с одной преимагинальной стадии на другую фиксировалась дата и кучность смены возраста. С наступлением фазы куколки фиксировалась дата, из садков убирался корм. Велись наблюдения за выходом молодых жуков. Полевые исследования по фенологии картофельной коровки проводились на стационарном участке 40 кв. м. Отмечались сроки выхода взрослых особей из диапаузы, заселение ими посадок картофеля, начало и конец откладки яиц, сроки появления личинок и куколок, лёт молодого поколения.
Результаты и заключение. В ходе лабораторного эксперимента при изучении преимагинальных стадий развития при оптимальных условиях было установлено, что стадия яйца длится 4-5 суток, стадия личинки 16-17 суток, куколки 4-5 суток. Также были выявлены отклонения от средних значений, которые связаны с внешними факторами. Так увеличение срока эмбриогенеза зависит от влажности либо от растянутости сроков отраждения из одной яйцекладки. Отклонение сроков развития личинок и куколок, скорее всего, связано с количеством и качеством пищи, содержанием в ней содержанием в ней продуктов вторичного обмена и гликоалкалоидов. При изучении фенологии в полевом эксперименте было установлено, что в 2020 году картофельная коровка дала одну генерацию, а в 2021 – две. Сравнивая климатические условия 2020-2021 годов можно предположить, что в более сухие и жаркие года *Henosepilachna vigintioctomaculata* дает два поколения.
Ключевые слова: картофельная коровка, фенология развития, преимагинальные стадии, онтогенез

Introduction

Physiological responses of living organisms to temperature have been generating considerable interest in scientific literature for more than a hundred years. The main discussion focuses on the metabolic theory of ecology (MTE), where body temperature and body weight are fundamental factors that determine the rate of central life processes, namely metabolism, development, reproduction, population growth, species diversity and even the rate of ecosystem processes such as phenology and population dynamics [1]. For cold-blooded organisms, including insects, the impact of the interrelationship between temperature of their surroundings and their development, survival, reproduction ranges from a daily or even an hourly effect on some individuals to the seasonal patterns of phenology [2][3], population dynamics [4][5], and species distribution [6][7][8]. Models that are aimed at predicting how temperature will impact these processes should consider the non-linear character of thermal responses [7,9,10] and their intraspecific and intrapopulation variation.

Intraspecific variation in development rates among individuals in a population [11] affectsthe observed distribution of phenological events in these populations. Thermal responses are often distributed asymmetrically. They can thus change the timing of life stage transitions [12] and influence its demographic consequences. In this regard, it is necessary to constantly monitor the processes occurring in insect populations in general and in phytophagous insectpopulations in particular.

There are contradictory data on the number of generations, population dynamics and the phenology of the 28-spotted potato ladybird beetle in Primorsky krai despite the fact that *Henosepilachna vigintioctomaculata* is a widespread pest of agricultural crops in the south of the Russian Far East.

The study on the potato ladybird beetle has always received much attention. For instance, Gusev G.V. [19] and Antipova L.K. [20] considered the potato ladybird beetle to be a new species in the fauna of the Russian Far East. By contrast, Kurentsov A.I. [21] noted that H. vigintioctomaculata is a typical representative of the Manchurian fauna, whose habitat includes mixed conifer forests and temperate broad-leaf forests. After inspecting a collection of potato ladybird beetles from different locations in Primorskykrai, Ivanova A.N. [22] reached the conclusion that the potato ladybird beetle is an indigenous species of the Russian far-eastern fauna.

Many researchers report the presence of the potato ladybird beetle in several districts of Khabarovsky krai, Amur and Sakhalin oblast and the Jewish autonomous oblast [15][16][17]. This insect is also found in Korea, north-eastern and central China, Japan, India, Vietnam and Nepal [18][19]. The expansion of thehabitat range of the potato ladybird beetlecan be explained by an increase in the area of land under potato cultivation and by a change in preferences of this phytophagous for a new food source plant. In 1964, the habitat range of the potato ladybird beetle encompassed all districts of Primorsky krai, also Khabarovsky krai, the Jewish autonomous oblast, Amur oblast, the southern districts of Sakhalin Island and the south of the Kuril Islands [23,24,25].

The time when adult beetles emerge from diapause depends on climatic and weather conditions in a particular location. The emergence from diapause starts at +11°C +15°C and the peak ofactivity is observed at +20°C. This coincides with the time when the Asian bird cherry, *Padus asiatica* (Kom.) and the Ussurian pear, *Pyrrus ussuriensis* (Maxim.), begin to blossom. After the emergence from diapause, the potato ladybird beetle can be found on such plants as spikenard, oak, hazel, birch and jasmine. Then it moves to common weeds in fields (e.g. field sowthistle, *Sonchus arvensis* L., and black nightshade, *Solanum nigrum* L.). After weeds, adult beetles start to feed on potato, also cucumber and tomato, on leaves of common bean, soybean, marrow and squash [26,27,28].

Potato ladybird beetles are polygamous and mate several times during summer. Females that were inseminated earlier in autumn and spring can start oviposition without additional mating [17]. Overwintered females have a small volume of fat body. In spring, with an increase in temperature, they start to feed intensively and grow fat incessantly. Intense oviposition begins approximately on the 25th day after hibernation termination and the fat body volume decreases [29]. The potato ladybird beetle begins to oviposit from the end of the first ten-day period of June. Its egg masses are compact and usually contain 15-30 eggs, rarely from 50 to 70 eggs. One female can lay 200-500 eggs in average. The potato ladybird beetle oviposits predominantly on the undersides of potato leaves or on weeds, such as common dayflower, *Commelina communis* L., couch grass, *Agropyron repens* L., field sowthistle, *Sonchus arvensis* L., and field bindweed, *Convolvulus arvensis* L. [30].

Embryonic development depends on temperature and humidity and lasts usually from 6 to 10 days under the conditions of Primorsky krai but its duration can be 4-5 days in some cases. Under laboratory conditions, the duration of this stage is 7-9 days at 21-22˚C and 75-80% humidity, but 4-6 days at 23-25 ˚C. Larval cohorts stay close to each other at first and begin to crawl away in 2-3 days. Larvae molt through 4 instars and develop from 20 to 24 days. The development of larvae lasts 24 days at 19-20˚C and 20 days at 20-22 ˚C. The pupal stage is 6-9 days in duration [29][30].

Oviposition takes place over a long period of time, i.e. from the first ten-day period of June to the beginning of August. For this reason, young beetles continue to emerge until mid-September. This can create a wrong impression of a higher number of generations. For example, Vulfson R.I. [26] and Ivanova A.N. [22] suppose that the potato ladybird beetle produces one generation. By contrast, Panyukhov G.A., Bosenko L.I. [29], Simakova T.P. [30] identify 2 generations.

Young beetles migrate from potato fields to other crops (cucumber, eggplant, tomato) when potato is harvested in the end of August. In September, when there are no usual fodder plants for the potato ladybird beetle, this pest starts to feed on woody plants, which grow around potato fields. Young beetles move to overwintering sites in the second part of September. According to Ivanova A.N. [22], ladybird beetles do not fly deep into the taiga and do not cluster at their overwintering sites. They prefer to disperse in leaf litter at a density of 0.1-1.5 beetles per 1 m2 not far away from potato fields, or they can stay under old potato stems and leaves in the fields.

To study the patterns of changes in insect population size, it is advisable to use logic models, which are based on the understanding of how a population responds to changes in various environmental and biological factors. According to systems theory, all biological systems are formed by subsystems [31]. The systems of a lower order serve as components to the systems of a higher order, thus the state of the former affects the latter. A study on the individual role of ecological and biological factors in insect population dynamics from the perspective of systems theory can help to discover the ecological mechanisms of changes in population structure and to provide rationale forthe optimization of pest control measures against phytophagous insects [32].

Methods

A laboratory colony of *Henosepilachna vigintioctomaculata* (Motschulsky) was formed in 2019. Adult ladybird beetles were collected at different locations in Primorskykrai. For the introduction into the insectarium culture, we collected adult beetles, egg masses and larvae in their natural habitats: on linden, *Tilia amurensis*, bird cherry, *Padus asiatica*, potato, *Solanum tuberosum*, tomato, *Solanum lycopersicum*, and eggplant, *Solanum melongena*. To maintain polymorphism of the lines, adult beetleswere collected in nature in 2020 and 2021andthen introduced into the culture.

Standard methods for maintaining and propagating insect cultures were used to optimize environmental parameters, population density and food supply [33]. When creating the laboratory population, we considered the parameters of minimum mortality, minimum change in forms and maximum fecundity. To achieve an ecological optimum, the culture was stabilized. This excluded uncontrollable factors and seasonal fluctuations. The dynamics of daily and seasonal temperatures and humiditywas also excluded. The insects developed in the rearing cages at 26 ± 1.05 ˚C and at 75-80 % humidity. These conditions were maintainedduring both day and night. The photoperiod was set to 18 h light / 6 h dark.The rearing cageswere placed on stands with timer delay. The racks were equipped with the grow lights Quantum line ver. 1 (lm281b + pro 3000K + SMD 5050, 660 nm) (Samsung, Japan). The split system Rovex RS-07MST1 / RS-07MST1 (Aux Air, China) kept the temperature constant. The aerator AceLine TFSL-6 (China) was usedfor aeration, which was an element of the microclimate. Humidity was controlled by POLARIS PUH 9105 IQ (China). The laboratory insects were reared on leaves of potato variety Smak, which was grown in soil in a culture room at 26 ± 1.5 ˚ C and 75-80 % humidity with a 18-h photoperiod. We selected egg masses with more than 25 eggs for the experiment. The egg masses were reared in Petri dishes on filter paper, which was moistened with autoclaved distilled water when necessary. We examined the egg masses twice a day until the emergence of the larvae. Scientific observations were carried out during the incubation period to determine the mortality rate and thesimultaneity of the larval emergence. We selected active light-yellow larvae with dark satae, showing no symptoms of an infection and having the percentage of emergence close to 100 % [33][34]. The larvae were transferredin batches of 10 to 80 ml glass containers, which were covered with cotton cloth. Fresh leaves of potato variety Smak served as a forage plant and were provided to the larvae every day. We recorded the duration of the larval stage and the timing of each molting and transition to the next instar. The pre-pupal stage began when the larvae stopped feeding and became less active. After the pre-pupa was attachedto the surface of a container or to the filter paper, the pupation started. We recorded the begging of the stage of the pupa, which differed morphologically from the pre-pupa, and determined the duration of this stage [35][36].

Field research on the phenology of the potato ladybird beetle was conducted on a 40 m2field site in Timiryasevskij settlement, Ussuriysk district, Primorsky krai. The records were made twice a week.The timing of the following events was recorded: the emergence of the adult beetles from diapause, the colonization of the potato field, the beginning and the end of oviposition, the emergence of the larvae and the pupae, the flight of the new insect generation.

Results and discussion

Sixty-six egg masses were described in our research. The mean number of eggs per one mass was 26. The hatched larvae were divided in 110 families: 10 larvae in each family. The study on the immature developmental stages of the potato ladybird beetle revealed that the egg stage was 4-5 days in duration, the larval stage was 16-17 days and the pupal stage was 4-5 days (Figure 1). The standard deviation was ± 1.59 at the egg stage but we also identifiedseveral egg masses, whose developmental time increased to 11-12 days. This could be conditioned either by an insufficient moisture content of the filter paper, which might have increased the duration of the larval emergence, or by a wide time range of hatching from one egg mass (which is the norm for most of the insect populations) [33]. At the larval stage, two groups of the larvae were

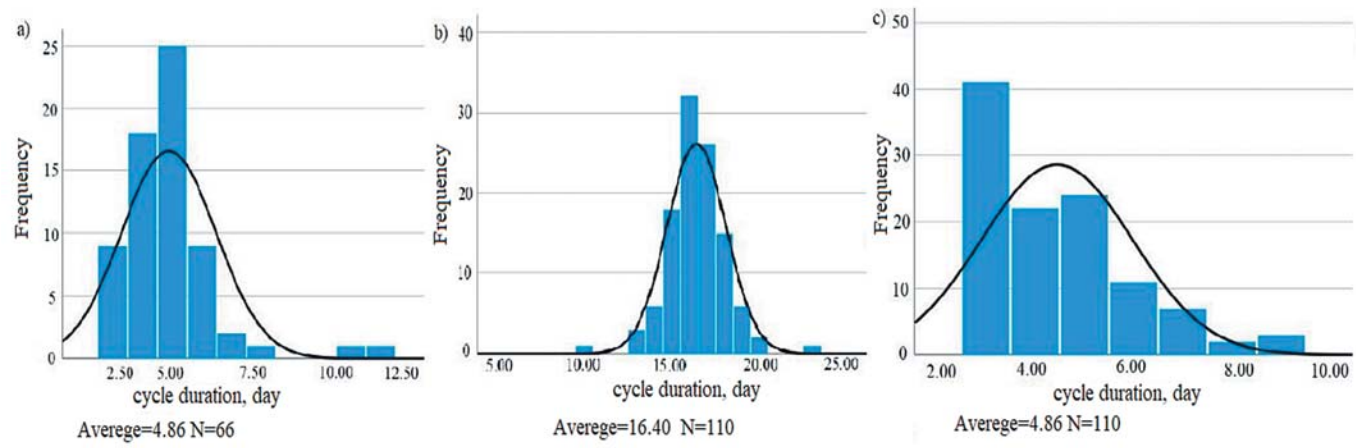


Рис. 1. Сроки развития преимагинальных стадий развития картофельной коровки. а) стадия яйца b) стадия личинки c) стадия куколки (IBM SPSS StatisticsSubscription)
Fig. 1. The developmental time of the potato ladybird beetle at different immature stages: a) egg stage, b) larval stage, c) pupal stage (IBM SPSS Statistics Subscription)

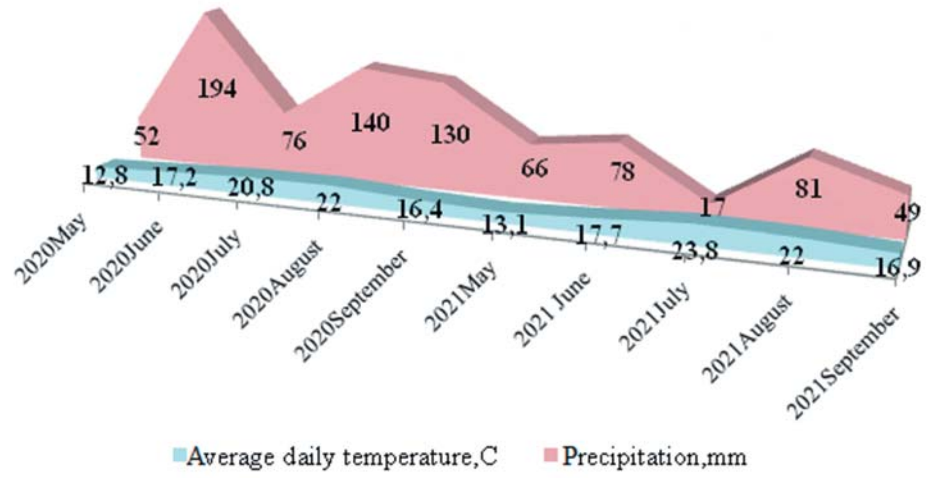


Рис. 2. Среднесуточные показатели температуры и среднемесячные показатели количества осадков в 2020-2021гг (по данным агрометеостанции пос. Тимирязевский)
Fig.2. Daily mean temperatures and monthly precipitation amounts in 2020-2021 (according to the agrometeorological station in stl. Timiryazevskij)

identified, the development time of which was significantly shorter or longer compared to the average values obtained for this stage. Presumably,the quality and quantity of the food were responsible for it (the amount of nutrients, the availability of secondary metabolites, in particular glycoalkaloids). At the pupal stage, the developmental time also increased, which could be explained by the amount of the nutrients that were consumed by the insects at the larval stage.There are data on the influence of forage plants on the duration of the ontogeny of the 28-spotted potato ladybird beetle [37,38]. Moreover, analogous correlations were discovered for other insect species. For example, the turnip sawfly,(*Athalia colibri* Christ.) when feeding on immature cabbage, develops from a young larvae to an adult insect in 18 daysat 28˚C and in 35.6 days at 17.7 ˚C. Although when the turnip sawfly feeds on mature cabbage at the same temperatures, it needs 22 and 39.3 days respectively to fully develop [39]. The influence of food on the development was discovered for the spongy moth (*Porthetria dispar* L.), the grape phylloxera (*Phylloxera vastatrix,* Planch) and Aphis laburni [40, 41, 42, 43].

The laboratory experiment allowed determining the timing and duration of different developmental stages of the potato ladybird beetle at constant temperature and humidity. Climatic conditions are rarely so stable in nature. For this reason, we conducted a field experiment and a study on the stages of ontogeny under the conditions of changeable environmental factors.

When conducting field research, environmental factors such as temperature and precipitation amounts should be considered. They can significantly affect the timings of phenology and ontogeny in general. After comparing daily mean temperatures and monthly precipitation amounts in 2020-2021 (Figure 2), the conclusion can be reached that the year 2020 was cold and rainy. This affected the duration of the ontogenetic stages and the timings when the adult beetlesemerged from diapause and oviposited.

Таблица 1. Фенология развития картофельной коровки в Приморском крае (п. Тимирязевский) в 2020 году
Table 1. Phenology of the development of the potato ladybird beetle in Primorskykrai (stl. Timiryazevskij) in 2020

Months (I-XII) / ten-day periods (1-3)																		
V			VI			VII			VIII			IX			X			XI-IV
1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	-
◘	◘	●	●	●	●	●	●	●										
				○	○	○	○											
				■	■	■	■	■										
						□	□	□	□									
								●	●	●	●	●	●	◘	◘	◘	◘	◘
								○	○	○	○							
									■	■	■	■						

Legend. ● – active adult beetles; ◘– adult beetles in diapause; ○ – egg; ■ – larva; □ –pupa

In 2020, the first potato sproutsappeared on May 20th. The synchronous emergence of the potato ladybird beetle from diapause was recorded on May 23d (Table 1). The colonization of the potato field was observed during the first and the second ten-day period of June. After colonizing the potato field, the overwintered adult beetles started to oviposit. The larvae of the first generation were observed from the second ten-day period of June to the third ten-day period of July. The pupae could be found from the first ten-day period of July to the first ten-day period of August. The young beetles of the second generation were observed from the third ten-day period of July to the second ten-day period of September. A part of the second-generation beetles laid eggs, which hatched later. The larvae began to die in the first ten-day period of September. The adult beetles started to prepare for diapause from the second ten-day period of September. They began to feed on woody plants, whichgrew near the potato field.

In 2021, the synchronous emergence of the potato ladybird beetle from diapause was recorded on May18-20th (Table 2). The first potato sprouts appeared on May 19th. The first signs of the insect damage that was caused by the potato ladybird beetle were observed on May 20-21st. The first egg masses were found during the second ten-day period ofJuneafter the additional feedingphase. The larvae of the first generation could be observed from the end of the second ten-day period of June. The synchronous pupation of the larvae took place during the second and third ten-day period of July. The emergence of the second beetle generation was recorded from the third ten-day period of July to the first and the second ten-day period of August. The young beetles of the second generation oviposited until the first ten-day period of September inclusive. The emergence of the young beetles of the third generation was recorded during the third ten-day period of August. The egg masses and the larvae of the first and the second instar were also observed during this period. Daily mean temperatures started to decrease (17°C) from the end of the second ten-day period of September. For this reason, the developing larvae died, the adult beetles were preparing to enter diapause and moved from the potato fields to nearby forests.

After comparing the phenology of the potato ladybird beetle in 2020 and 2021, we reached the conclusion that the potato ladybird beetle hadtwo generations in 2021. Presumably, the potato ladybird beetle produces more than one generations in hot summers. We could also observe the second and the third generations overlapping. This can create a wrong impression of a higher number of generations. This issue requires further research.

There is a vast amount of foreign literature on the phenology of the potato ladybird beetle and its closely related species. Kohji Hirano made a significant contribution. His works provide an opportunity to compare the life cycles of the potato ladybird beetle in Primorsky krai and Japan. According to Hirano, the potato ladybird beetle has two generations in Japan. Moreover, the phenology of this phytophagous insect is similar to the phenological data that we obtained in 2021 (Table 3) [44].

Unfortunately, we could not find foreign literature on the period in question, though a comparison of climate features in Japan and Primorsky krai showed that the weather conditions of these two regions are very similar with only minor humidity fluctuations (Fig.3).

Thus, the conclusion can be reached that the potato ladybird beetle can have two generations per year in warm climate regions. Although physical environmental factors jointly affect

Таблица 2. Фенология развития картофельной коровки в Приморском крае (п. Тимирязевский) в 2021 году
Table 2. Phenology of the development of the potato ladybird beetle in Primorsky krai (stl. Timiryazevskij) in 2021

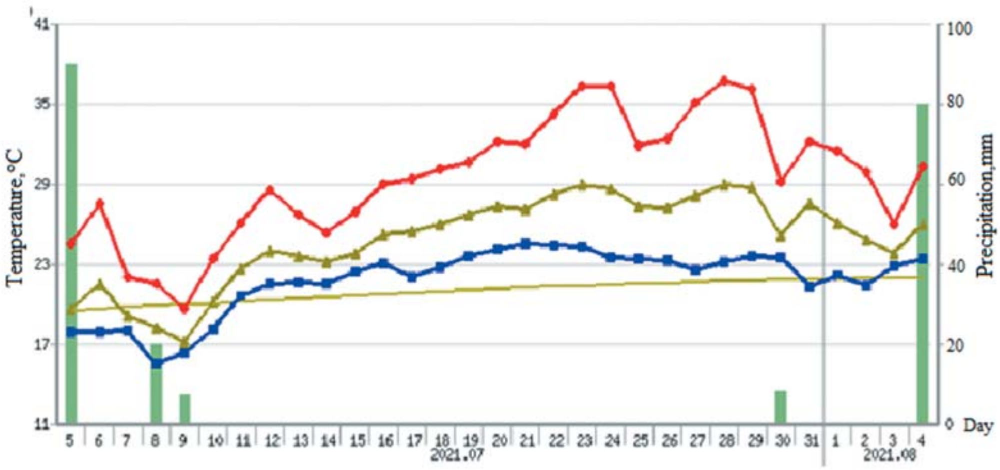
Months (I-XII) / ten-day periods (1-3)																		
V			VI			VII			VIII			IX			X			XI-IV
1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	-
◘	◘	●	●	●	●	●	●											
				○	○	○	○											
				■	■	■	■	■										
						□	□	□	□									
								●	●	●	●	●	●	◘	◘	◘	◘	◘
									○	○	○	○						
									■	■	■							
										□	□							
										●	●	●	●	◘	◘	◘	◘	◘
											○							
											■	■						

Legend. ● – active adult beetles; ◘ – adult beetles in diapause; ○ – egg; ■ – larva; □ –pupa

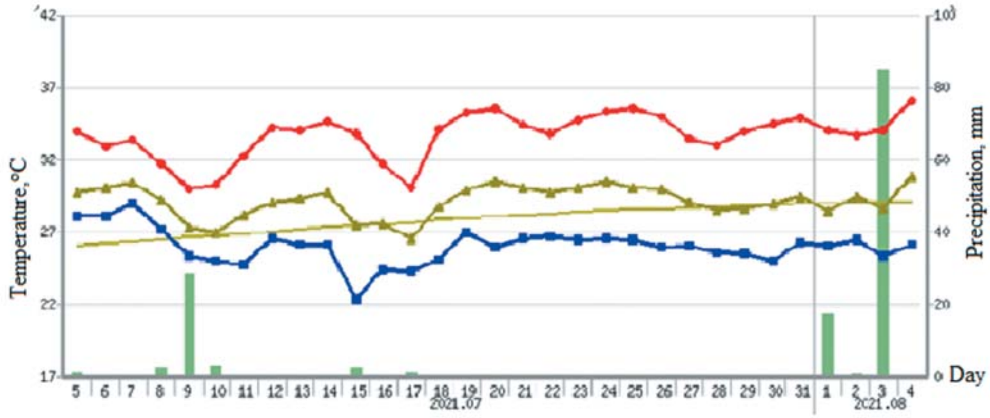
Таблица 3. Фенология развития картофельной коровки в Японии, Fujimaki (Hirano, 1995)
Table 3. Phenology of the development of the potato ladybird beetle in Japan, Fujimaki (Hirano, 1995)

Months (I-XII) / ten-day periods (1-3)																		
V			VI			VII			VIII			IX			X			XI-IV
1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	-
◘	◘	●	●	●	●	●	●											
				○	○	○	○											
				■	■	■	■	■										
						□	□	□	□									
								●	●	●	●	●	●	◘	◘	◘	◘	◘
									○	○	○	○						
									■	■	■							
										□	□							
										●	●	●	●	◘	◘	◘	◘	◘
											○							
											■	■						

Legend. ● – active adult beetles; ◘– adult beetles in diapause; ○ – egg; ■ – larva; □ –pupa



A



B

Рис. 3. Месячная вариация метеорологических элементов
в Фудзимаки и Тимирязевском(А –Тимирязевский, В –Фудзимаки)
Зеленая, красная и синяя линии показывают среднемесячные значения среднесуточной, максимальной и минимальной температуры, соответственно. Зелёные столбики показывают месячное количество осадков и месячную продолжительность солнечного сияния, соответственно (по данным Японского метеорологического агентства [45]).
Fig. 3. Monthly variation of meteorological elements in Fujimaki and Timiryazevskij(A- Timiryazevskij, B –Fujimaki)
The green, red and blue lines indicate monthly averages of daily mean, maximum and minimum temperatures, respectively. The green bars show monthly precipitation amounts and monthly sunshine durations, respectively (according to Japan Meteorological Agency [45]).

insects, the individual impact of each factor differs. Insects are poikilotherms and their body temperature depends largely on the temperature of their surroundings. Environmental temperatures determine the metabolic rates of insects, also their development rates, longevity and fertility, the number of their generations, their feeding rate and behavioral responses [46]. The effect of temperature is inseparable from the influence of humidity.

Temperature has both a direct and an indirect effect on a population and its viability.When temperature values deviate rapidly from the ecological optimum, it directly affects individuals in a population and causes death. The indirect effect occursmainly through fodder plants [47]. This is conditioned by impossibility to satisfy the ontogenetic needs of a species and by changes in the character of hygrothermal factors in the optimum zone [48].

Additionally, climate variability has increased over the last decades and will continue to do so according to projections. This will lead to an increase in the duration, intensity and frequency of extreme climatic events [49][50], which may significantly affect functions of ecosystems [51][52][53]. For example, an increase in day length combined with extreme heat led to a reduction in the diversity of bumblebees [54], which are important pollinators of agricultural crops [55][56]. A recent meta-analysis of weather events in the wild showed that high resistance was rare among populations and many of them could not recover after exposure to severe weather events despite the fact that many species had compensatory mechanisms for mitigating negative consequences [57].

Climate variables can produce a synergistic effect, which is greater than additive effect of each separate variable on the environment [58,59] and thus creates “ecological surprises” when the decline of a population is extreme [60]. Although an ecological response to extreme climatic events is often negative (e.g. reduction in population size), such consequences can be minor [61], and some climatic variables can also be antagonistic, which leads to a positive ecological response [62]. For this reason, the prediction of ecological responses to climatic events requires the understanding of mechanisms regulating these processes. Therefore, our data can be useful for predicting changes in population size for the potato ladybird beetle. It is logical to assume that a higher number of pest generations may facilitate the accumulation of this pest in an ecosystem. In consequence, a higher number of beetles will enter diapause (a considerable part of femalescan be inseminated in autumn). This may trigger a pest population outbreak in spring causing severe damage to potato crops during sprouting.

As for other negative factors, which affect the population size of the phytophagous insect (scarce food resources, a low nutritional value of forage plants during drought periods), a higher number of generations allows the pest to maintain a sufficient population size. This demonstrates the ecological plasticity of the phytophagous insect under the unstable conditions of monsoon climate in its habitat.

In conclusion, our research is the first step towards understanding how the interrelation between processes, which depend on density, and abiotic variations affects population dynamics. This interrelation is also an example of a model that describes phenological responses to temperature. The model predicts the patterns of changes in population size. Such predictions can be verified by census data. We showed that this scheme, which was parametrized by empirical data on the events of the life cycle, could reflect complex dynamics observed under field conditions.

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