Effect of increased ambient temperature on seasonal generation number in *Lucilia sericata* (Diptera, Calliphoridae)

Maksym V. Makaida, Oleksander Y. Pakhomov, Viktor V. Brygadyrenko*

Oles Honchar Dnipro National University, Gagarin av., 72, Dnipro, 49010, Ukraine

Abstract

Makaida, M.V., Pakhomov, O.Y., Brygadyrenko, V.V., 2021. Effect of increased ambient temperature on seasonal generation number in *Lucilia sericata* (Diptera, Calliphoridae). *Folia Oecologica*, 48 (2): 191–198.

Global climate change and, specifically, rising temperatures, may increase the number of generations of necrophagous insects. The common green bottle fly *Lucilia sericata* (Meigen, 1826) (Diptera, Calliphoridae) ranks among the most important cosmopolitan necrophagous insects that utilize corpses and cause myiasis in farm animals and humans. Based on the data simulations, the use of accumulated degree-hours enables to calculate the number of generations of this forensically important species of blowfly with a greater accuracy than before, considering short-term increases of temperature at the boundary of the cold and warm seasons. The number of generations of *L. sericata* has increased from 7.65 to 8.46 in the Ukrainian steppe zone over the last 15 years, while the active developmental period of this species has increased by 25 days due to earlier start in spring. The average temperature increase of 1 °C increased the number of generations of *L. sericata* by 0.85. With a global climate change following the Representative Concentration Pathway (RCP) 4.5 scenario (average temperature increase of 2.4 °C), adopted by the Intergovernmental Panel on Climate Change, by 2100 the number of generations of *L. sericata* in a simulated ecosystem will increase by 2.0 to 9.0 generations per year.

Keywords

blowly, climate change, forensic entomology, generations, model, post-mortem interval

Introduction

Global warming affects plant and animal communities across all climatic zones (Burda and Koniakin, 2019; Baranovski et al., 2020). Insect species with southern ranges move northward, where they find themselves in unsuitable climatic conditions at certain stages of their ontogenesis, although the average annual temperatures do not necessarily differ from those of their original range (Avtaeva et al., 2019; 2020; 2021). Inconsistencies with the habitat conditions in a new range affect various environmental characteristics. This can cause changes in the morphology and physiology of species (Shulman et al., 2017; Komlyk and Brygadyrenko, 2019). Changes in the ranges of certain insect species with which humans frequently come into contact, such as flies of the Calliphoridae family, can also have implications for human wellbeing.

Determination of post-mortem interval (PMI) – time elapsed from the time of death to the discovery of the body, lies at the basis of modern forensic entomology (Greenberg,

*Corresponding author:
e-mail: brigad@ua.fm

1991; Catts, 1992; Amendt et al., 2006). Advances in forensic entomology are of a great importance in ecological practice, since the utilization speed of dead organic materials in an ecosystem is essential for the rapid elimination of human pathogenic microorganisms (Greenberg, 1991; Catts, 1992; Amendt et al., 2006). The rate of utilization of a corpse is important in reducing the likelihood of an epidemic spread of species from the genera *Clostridium*, *Bacillus*, *Pseudomonas*, *Proteus*, *Klebsiella* and many others (Zazharskyi et al., 2019). Processes of decomposition and utilization of corpses in anthropogenically transformed and urbanized ecosystems are valuable in protection and optimization of recreational resources (Amendt et al., 2004; Hwang and Turner, 2009).

The rate of development of most forensically important arthropod species directly depends on the ambient temperature, making it the most crucial factor in determining PMI (Kamal, 1958; Grassberger and Reiter, 2001; Amendt et al., 2006). The basis for determining the relationship between the ambient temperature and the rate of development of a given arthropod species is the ADD indicator – the sum of effective temperatures required to reach the corresponding stage of development. This indicator is characteristic for each species (Amendt et al., 2006). For greater precision, modern studies tend to use ADH – sum of effective temperature in hours, rather than in days, allowing the time of death to be determined more accurately (Catts, 1992; Wang et al., 2020).

Turchetto and Vanin (2009) mention the expansion of the range of Diptera necrophages, which was first discovered in Italy, however, changes in the development and number of generations of Diptera necrophages are still poorly studied. Existing research shows that global warming changes the total number of insects, the composition of their communities, activity and life cycles. All this combined dramatically affects the usage of necrophagous insects for determining the post-mortem interval (Turchetto and Vanin, 2009).

Upper and lower development thresholds of a particular species of arthropod in a particular development phase are essential indicators in forensic entomology. Despite slight discrepancies in the data in the literature, this indicator is also a constant (Catts, 1992; Amendt et al., 2006; Tarone et al., 2011). The effect of temperature on the decomposition rate of a corpse is a crucial element that determines the efficiency of the necrophage – food resource system (Amendt et al., 2006). Reduction of ambient temperature below the lower development threshold (LDT) for a particular stage of development of an insect induces diapause. Besides the ambient temperature, the start and end of the diapause period are also controlled by daylight duration (Tachibana and Numata, 2004).

Lucilia sericata (Meigen, 1826) (Diptera, Calliphoridae) is one of the most widespread necrophages of human and animal corpses. It is found in all climatic zones worldwide: from the equator to the Arctic Circle (Amendt et al., 2006). Throughout its range, the species dominates insect communities of necrobionts and acts as one of the most important carriers of infectious and parasitic diseases (Baron and Colwell, 1991; Pearse and Peucker, 1991). In addition, the larvae of this fly are capable of developing under the skin of sheep and humans, causing the development of severe myiasis (Pearse and Peucker, 1991). The influence of global climate change on the number of generations of this species has not yet been studied. Therefore, the purpose of this article is to assess the effects of climate change on the development of *L. sericata* and the number of generations produced per season.

Materials and methods

Two approaches were used in this study: calculation of ADD – the sum of effective daily temperatures and ADH – the sum of effective hourly temperatures. Data for simulation of climatic changes was provided by the weather Web service (https://www.rp5.ua) These data includes hourly temperature readings on Gubinikha meteorological station in 2005–2020 (Dnepropetrovsk region, Ukraine, 48.8096°N, 35.2591°E).

The beginning of *L. sericata* development was defined as the first day during which the temperature exceeded LDT for at least three hours and the subsequent cold period did not exceed three days. The end of the development period was defined as the last day during which ambient temperatures exceeded LDT for at least three hours and the subsequent cold period exceeded three days. These values were determined empirically to exclude short-term temperature rises during the cold period, which did not induce active development (Tachibana and Numata, 2004; Pitts and Wall, 2005; Roe and Higley, 2015).

The value of 9 °C, derived by Marchenko (2001), was chosen as LDT. It is based on the most fundamental studies and is geographically closest to the ecosystem we modeled – the vicinity of the Gubinikha meteorological station (Dnepropetrovsk region, Ukraine, 48.8096°N, 35.2591°E). We used 3 ADD and ADH values presented in the literature to calculate our assessment of ADH and ADD values changing throughout 2005–2020 (Table 1) (Marchenko, 2001; Cervantès et al., 2017; Wang et al., 2020). However, in the process of modelling the influence of increased temperature on the number of generations we have used ADH value provided by Wang et al., (2020). It is based on the most recent research and provides the most accurate results due to native use of ADH calculation.

As the points of reference for the evaluated temperature increases, the IPCC-adopted models were used: RCP 1.9, RCP 2.6, RCP 4.5, RCP 6, RCP 8.5. We used the most probable average temperature increases in the conditions of increase in the carbon concentration in the corresponding scenario (i.e. 1.5 °C, 2 °C, 2.4 °C. 2.8 °C, 3.4 °C) (Van Vuuren, 2011; Collins et al., 2013).

The average hourly temperature for 16 years (2005–2020) at the Gubinikha station (140,544 values) was used as the starting point of our assessment. Average temperature for each hour of the year was then incrementally increased by 0.2 °C per simulation to emulate average rise in temperature. ADH and ADD sums were calculated for each model (Fig. 3). A line chart was used to demonstrate the relationship between average temperature increase and number of generations calculated for the corresponding model.

Table 1. Effect of temperature on the development of *L. sericata* in the steppe zone of Ukraine (2005–2020)

Year	Average temperature (°C)	Development period				ADD	ADH	Number of generations		
		Start date	End date	Duration (days)	Duration (% of year)			by Marchenko, 2001	by Cervantès et al., 2017	by Wang et al., 2020
2005	8.6	04.04.2005	17.11.2005	227	62.2	1,706	41,722	8.40	7.62	6.93
2006	8.6	29.03.2006	16.11.2006	232	63.6	1,640	40,327	8.12	7.37	6.70
2007	10.3	19.03.2007	16.11.2007	242	66.3	1,841	45,469	9.15	8.31	7.55
2008	9.5	08.03.2008	07.12.2008	274	74.9	1,612	39,837	8.02	7.28	6.61
2009	9.6	29.03.2009	29.11.2009	245	67.1	1,678	41,288	8.31	7.55	6.85
2010	10.2	20.03.2010	29.11.2010	254	69.6	1,996	48,998	9.86	8.95	8.13
2011	8.7	26.03.2011	05.11.2011	224	61.4	1765	42,976	8.65	7.85	7.14
2012	10.0	03.04.2012	09.11.2012	220	60.1	2,180	52,900	10.65	9.67	8.78
2013	10.1	31.03.2013	11.11.2013	225	61.6	1,780	43,587	8.77	7.97	7.24
2014	9.7	06.03.2014	11.11.2014	250	68.5	1,818	44,984	9.05	8.22	7.47
2015	10.2	09.03.2015	13.11.2015	249	68.2	1,819	44,495	8.96	8.13	7.39
2016	9.3	01.03.2016	10.11.2016	254	69.4	1,716	41,720	8.40	7.62	6.93
2017	10.0	01.03.2017	14.11.2017	258	70.7	1,729	42,830	8.62	7.83	7.11
2018	9.9	31.03.2018	08.11.2018	222	60.8	2,020	49,224	9.91	9.00	8.17
2019	10.7	05.03.2019	15.11.2019	255	69.9	1,878	46,110	9.28	8.43	7.66
2020	10.9	03.03.2020	10.11.2020	252	68.9	1,861	46,152	9.29	8.43	7.66

ADD – accumulated degree-days, the sum of effective temperatures in the days required to complete the development of an individual from the moment of oviposition to its emergence as an adult; ADH – accumulated degree-hours, the sum of effective temperatures in the hours required to complete the development of an individual from the moment of oviposition to its emergence as an adult.

Results

Increased ambient temperature caused by global climate change leads to an increase in the number of generations in *L. sericata* during a year (Table 1). From 2005 to 2020, the number of generations of this species increased from 7.65 to 8.46 in the steppe zone of Ukraine. At the same time, the beginning of the development period during 2005–2020 shifted from April 4 to March 3 during 2005–2020. The end of the development period remained practically unchanged (November 17 and November 10 respectively). Thus, the development period increased from 227 to 252 days (from 62.2 to 68.9% of the total year length).

Other approaches to measuring the sum of effective temperatures (Fig. 1 and 2) provided different time periods suitable for the development of *L. sericata*. The use of hourly data (ADH) allows one to determine the beginning and end of the development period more accurately. For average temperatures for 2005–2020 (Fig. 1), the transition of the average daily temperature through LDT (9 °C) was observed at April 6 in spring and October 18 in autumn. Repeated transitions through 9 °C during the year were not observed. By applying the hourly approach these dates shifted to March 31 and October 31, respectively (i.e., the development season of the species is considerably lengthened). With this approach, a short-term decrease in temperature below the LDT is observed between October 25 and October 29 with a subsequent increase in daytime temperatures above the LDT.

The inter-annual variability was higher when we analyzed a particular year (Fig. 2). For example, in 2019 the average daily temperature exceeded LDT three times (Fig. 2a) before steadily exceeding it from April 22 onward. Hourly temperature jumps above 9 °C were observed from March 5: however, the night temperature dropped below 9 °C until May 11. In 2019, the period of short-term transitions of the average daily temperature below LDT began from September 20, while when using hourly measurements, this period began on September 19. During autumn of 2019 (Fig. 2b) three short-term (in duration 9–20 days) periods of the temperature rising above LDT were observed: September 20–October 6, October 9–October 29 and November 4–November 15 (when using daily temperatures) and September 18–October 6, October 10–October 25 and November 4–November 13 (when using hourly temperatures). Thus, in a particular year in the spring and autumn the development of additional generations of *L. sericata* can be observed.

With an 1 °C increase in average temperature in a given ecosystem, the number of *L. sericata* generations observed increases by 0.85 (Fig. 3). Interestingly, despite the abrupt transition of temperatures through the LDT, the correlation between generations and an increase in the average temperature is very close to a linear function ($R^2 = 0.9986$) in 30 simulations (an increase in the average annual local temperature by 6 °C with a step of 0.2 °C). According to the baseline scenario (RCP 4.5), proposed by the Intergovernmental Panel on Climate Change (IPCC), the global

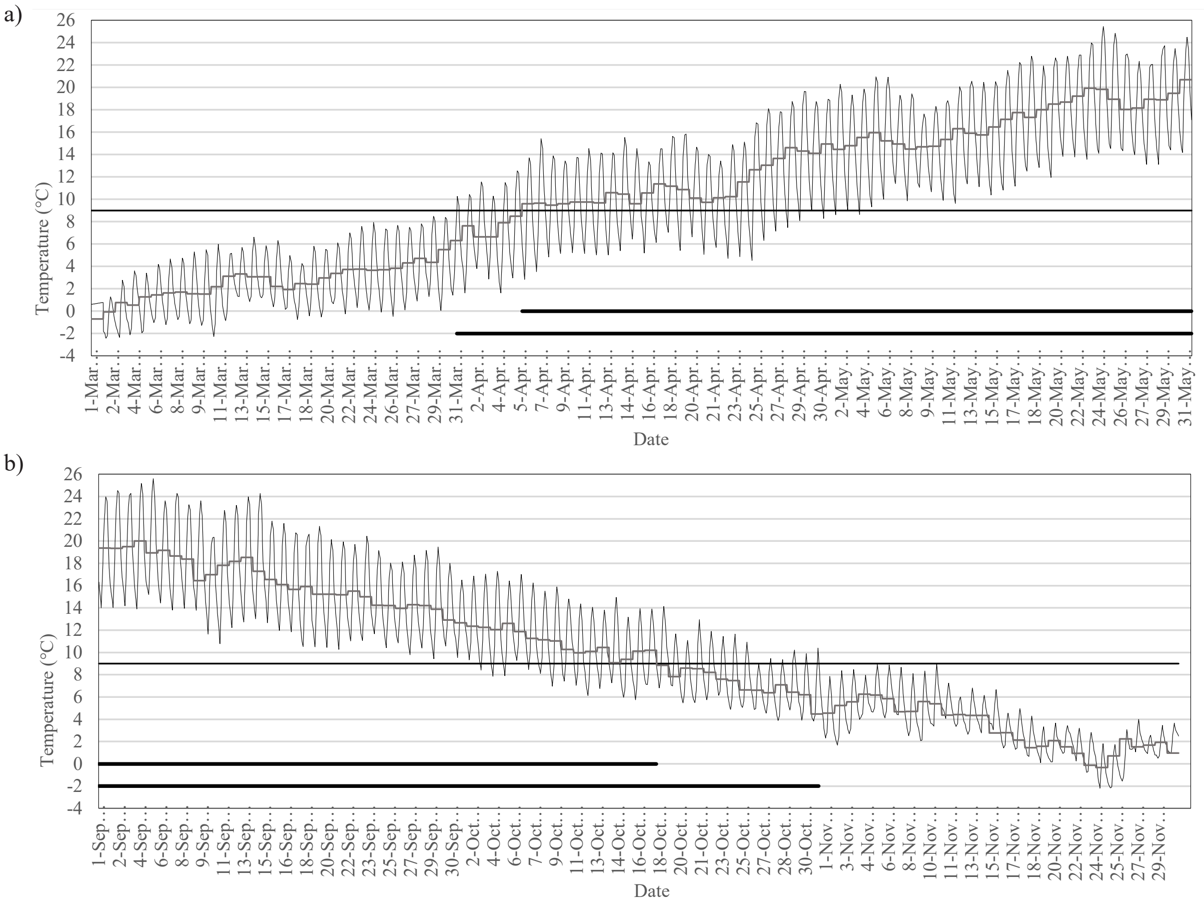


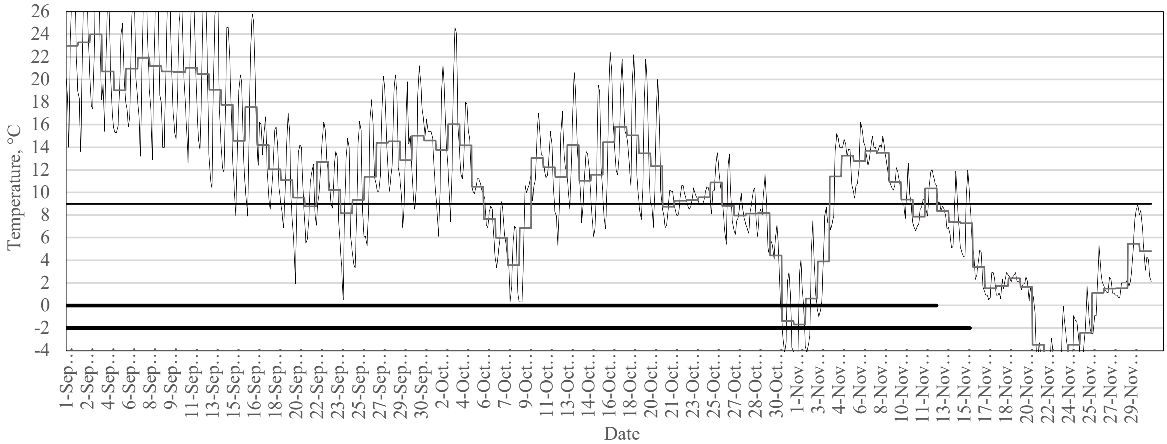
Fig. 1. Dynamics of the autumn and spring hourly (continuous black curve) and average daily (grey stepped line) temperature based on data from Gubinikha meteorological station during the period 2005–2020: a) spring, b) autumn; the black horizontal line marks the lower development threshold (LDT), which in L. *sericata* is 9 ° C; the black line at 0 °C shows the developmental period of L. *sericata* based on hourly temperatures; the black line at –2 ° C shows the developmental period of *L. sericata* based on the average daily temperatures

average temperature will increase by 2.4 °C, which means that the number of *L. sericata* generations will increase by 2.0 to 9.0 per year in the steppe zone of Ukraine.

The effect of the increase of air temperature on the development rate of *L. sericata* can be demonstrated by evaluating the monthly changes in the number of generations (Table 2). Thus, the start of the active development period in March is possible with the global warming scenario at RCP 2.6 (average temperature increase of 2 °C) and above, otherwise it will begin in April, which will affect the total number of generations and the speed of utilization of dead bodies in the early spring. The end of the active development season in November is also possible only if global warming develops according to the RCP 2.6 or higher scenario. The monthly number of generations in the hottest months of the year exceeds 2.0 with the development of global warming according to the RCP 6.0 (average temperature increase of 2.8 °C) or higher scenario.

Discussion

Ecological niche characteristics includes temperature, humidity, lighting mode and some other factors. This study does not consider lighting mode and precipitation (Gallagher et al., 2010). LDT of *L. sericata* is +9 °C, according to Marchenko (2001) (location: Kaunas, Lithuania), +9.19 °C, according to Wang et al. (2020) (location: Suzhou, China), + 8.6 °C, according to Cervantès et al. (2017) (location: Rosny sous Bois, France), +8.0 °C, according to Reibe et al. (2010) (location: Vienna, Austria), +9.0 °C, according to Niederegger et al. (2010) (location: Jena, Germany). Divergence of LDT in different geographic populations of the same species can be caused by methodological differences in the experiments and genetic variations between the populations. Further inconsistencies may have been introduced because of unintentional use of closely related species in older sources as several species are virtually indistinguishable without DNA sequencing. Additionally, a certain level of inaccuracy may have been introduced due to various differences in the methodology itself, such as food being fed to larvae in chunks of different sizes, focusing on certain temperature ranges rather than the full spectrum, etc. Larval mass of this species in a rabbit cadaver *Oryctolagus cuniculus* Linnaeus, 1758, weighing 1.3–2.5 kg, has a temperature exceeding the ambient temperature by 20 °C and more (Turner and Howa)



b)

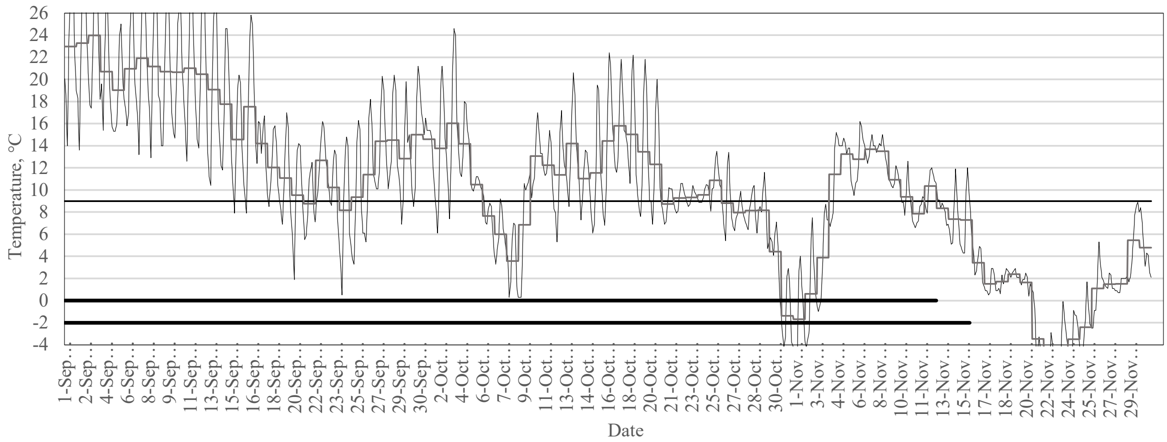


Fig. 2. Dynamics of the spring and autumn variations in hourly (continuous black curve) and daily average (grey stepped line) temperatures based on data from observations of the Gubinikha meteorological station in 2019: a) spring, b) autumn; the black horizontal line marks the lower development threshold (LDT), which in L. *sericata* is 9 °C; the black line at 0 °C shows the developmental period of L. *sericata* based on hourly temperatures; the black line at –2 °C shows the developmental period of L. *sericata* based on the average daily temperatures

ard, 1992; Charabidze et al., 2011). Thus, geographic and possibly genetic differences in populations will have a much weaker impact on the development of the larvae than the size of the animal corpses that *L. sericata* feeds on.

Climate changes cause changes in the start and end of the activity of various arthropod necrophages, a shift in these periods can lead to changes in the seasonal succession of necrophagous invertebrates, the decomposition processes themselves, and displacement of the insects' activity periods relative to each other. It will cause problems for environmental and forensic science (Turchetto and Vanin, 2009). Under laboratory conditions, all developmental stages of *L. sericata* show high resistance to low temperatures, but in field conditions emergence of larvae from the diapause is less than 1% due to the effects of unaccounted factors, including natural predators, insufficient nutrition pre-pupation and presence of toxic substances in soil (Pitts and Wall, 2005). Therefore, temperature variations and prolongation of the development period in spring will have little effect on the total number of flies of this species in natural ecosystems in spring. However, in autumn, when the local temperature rises, the number of flies will change more markedly than in spring. Further increases in summer temperatures will most likely impact flies insignificantly outside of ADT accumulation, as they have a high upper development threshold, which will not be reached in most regions of the world. Extreme weather events like heat waves will negatively impact them, but, as they are unpredictable, taking them into account in the model is not feasible.

Global climate changes lead to an increase in local temperatures in different seasons. These changes will undoubtedly affect the populations of necrophages, and *L. sericata* in particular. Existing models of climate change scenarios predict an increase in global temperatures by several degrees in different geographic locations, which will increase the number of generations of *L. sericata* to varying degrees in different parts of the range of this species: from equatorial populations to those living in the Arctic Circle. Quantitative changes in temperature may vary depending on geographic location. In contrast, the regression model of increase in the number of generations was prepared based on local data to obtain a universal regression equation, which allows one to make a direct connection between the rise in average temperatures and an increase in the number of generations per year to 0.85 with an increase in the local temperature by 1 °C.

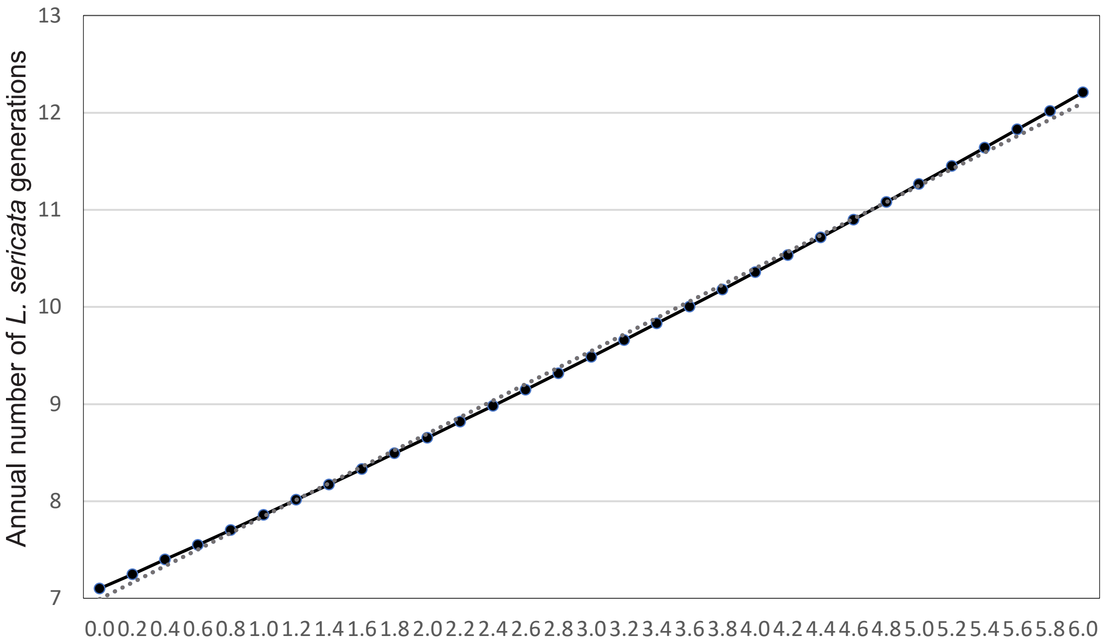


Fig. 3. Dependence of the number of L. *sericata* generations per year on the average temperature increase at the local observation point: the solid black line connects the simulation results (dots mark every 0.2 °C) based on average hourly temperature for 16 years (2005–2020) at the Gubinikha weather station, the dashed grey line illustrates the resulting linear regression equation.

Table 2. Monthly change in the number of *L. sericata* generations according to different global warming scenarios

Month	Average number of generations in observation period (2005–2020)	RCP 1.9	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
January	0.00	0.00	0.00	0.00	0.00	0.00
February	0.00	0.00	0.00	0.00	0.00	0.00
March	0.00	0.00	0.01	0.01	0.02	0.05
April	0.29	0.36	0.45	0.49	0.53	0.69
May	1.00	1.12	1.24	1.29	1.34	1.53
June	1.43	1.55	1.67	1.72	1.77	1.95
July	1.65	1.78	1.90	1.95	2.00	2.18
August	1.65	1.78	1.90	1.95	2.00	2.19
September	0.90	1.03	1.14	1.19	1.24	1.42
October	0.18	0.24	0.33	0.37	0.41	0.57
November	0.00	0.00	0.01	0.01	0.02	0.05
December	0.00	0.00	0.00	0.00	0.00	0.00
Total	7.10	7.87	8.65	8.98	9.32	10.63

Conclusion

We revealed linear regression between the annual number of *L. sericata* generations and the average temperature increase in the modelled ecosystem. Our results show that it is possible to predict the change in generations at a given ecosystem using the derived regression equation. Quantitative measurement of the development speed of *L. sericata* with ADH provides more accurate data by counting in short-term warming periods in the autumn and spring. We suggest that similar models could be created for other Diptera, which play a significant role in local necrofauna communities.

Acknowledgements

This work was supported by the Ministry of Education and Science of Ukraine (grant 0120U102384).

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Submitted March 7, 2021
Accepted June 16, 2021