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**INFLUENCE OF TEMPERATURE ON VIABILITY
AND DEVELOPMENT OF *HETERAKIS GALLINARUM*
(NEMATODA, HETERAKIDAE) EGGS**

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Influence of Temperature on Viability and Development of *Heterakis gallinarum* (Nematoda, Heterakidae) Eggs. Yevstafieva, V., Omelchenko, O., Melnychuk, V., Nagorna, L., Petrenko, M., Shaferivskiyi, B., Kravchenko, S., Suprunenko, K., Sheiko, S., Karysheva, L., Burda, T., Syzonenko, N., Savenkova, O. & Liulka, V. — Pinworms of the genus *Heterakis* Dujardin, 1845 parasitize a wide range of hosts, including a number of species of domestic and wild birds. These nematodes are ecologically adapted to the climatic conditions of many geographical zones, which contributes to their widespread distribution. The aim of the work was to investigate the influence of different temperature regimes at laboratory conditions on the growth, development and viability of eggs isolated from the gonads of female nematodes *Heterakis gallinarum* Schrank, 1788. The conducted studies established that, depending on the cultivation temperature, nematode eggs developed from 6 to 56 days, and their survival rate was from 67.7 to 83.7 %. The temperature of 25 °C was the most favourable for the development of *H. gallinarum* eggs, the development lasted 12 days and the highest number of eggs with motile infective larvae was formed (83.7 %). It was found that the period of egg development in cultures gradually decreased with increasing temperature: it was 56 days at 15 °C, 18 days at 20 °C, 12 days at 25 °C and 6 days at 30 °C. The survival rate of *H. gallinarum* eggs gradually increased with increasing temperature in regimes of 15 °C, 20 °C and 25 °C to 67.7 %, 80.7 % and 83.7 %, respectively. At a temperature of 30 °C, egg survival decreased slightly to 78.7 %. It was found that the development of *H. gallinarum* eggs from the zygote stage to the formation of motile infective larvae, depending on the temperature regime of cultivation, is accompanied by a decrease in egg length by 4.9–5.4 %, an increase in egg width by 4.1–7.6 % and a thinning of the shell by 9.5–28.6 %. Under different temperature regimes, the morphometric parameters of eggs during their development differ in terms of their length, width and shell thickness.

Key words: *Heterakis gallinarum*, histomoniasis, embryogenesis, temperature regime, nematode eggs, survival rate.

Introduction

Temperature is one of the most important environmental variables that determine the distribution and abundance of many species of animals including parasitic nematodes. Each of their species is characterized by the presence of a temperature niche, characterized by a certain optimum and range of tolerable temperatures (Pandey, 1972; David et al., 1983; Leathwick, 2013; Zalewski et al., 2022). Threshold temperatures tend to limit the reproduction and development of most species, especially during their embryonic and post-embryonic developmental stages, when survival depends on environmental temperature (Beveridge et al., 1989; Yevstafieva et al., 2020; Yevstafieva et al., 2021). At a critically high temperature, the death or survival rate of helminth eggs and larvae occurs (Gamboia, 2005; Knapp-Lawitzke et al., 2016). At much lower temperatures, as a rule, their development period extends, sometimes with a decrease in the survival of nematode eggs and larvae (Azam et al., 2012; Kafle et al., 2018).

All physiological mechanisms of adaptation of parasites to the action of abiotic factors appeared in the process of their evolution, which is considered as adaptation to a successive series of environments (Aleuy & Kutz, 2020). The temperature of the environment is a physical factor that limits both the number and the geographical distribution of parasites. These mechanisms include: adaptation, which enables the preservation of structure and function at the cellular level with a strong increase or decrease in temperature; preservation of the population under extreme environmental temperature change, such as natural selection of phenotypes with high resistance to strong environmental temperature change, etc. (Brunner & Eizaguirre, 2016; Turner et al., 2021; Santos & Ebert, 2022). This determines the relevance of studying the mechanisms of adaptation of parasitic nematodes to changes in environmental temperature during their exogenous development.

Climate change may influence the occurrence, infection rates and geographical distribution of parasites, including helminths, directly affecting their distribution in the environment, particularly at the egg and larval stages. In biologically diverse nematodes, including geohelminths, climate warming contributes to an increase in the range of distribution, colonization of new hosts, and modification of their development cycles. Moreover, the researchers point out the dependence of parasite metabolism and the speed of their development cycles on temperature. This is especially true for parasites whose developmental stages are present in the external environment (Morley & Lewis, 2008; Kim et al., 2012; Okulewicz, 2017; Blum & Hotez, 2018).

In the case of parasitic geohelminths, the survival of eggs outside the host's body depends on environmental conditions. The egg shell is one of the most stable biological structures that provides a high degree of protection for the developing embryo (Meng et al., 1986; Mahmoud, 2002). However, temperature affects its maturation, survival, size, and embryogenesis. At high temperature, embryos in nematode eggs slow down their activity, fall into a thermal stupor and may die (Vežgajić et al., 2016). Depending on the species of nematodes, the optimal temperature regime for their embryogenesis varies (McCallister & Schmidt, 1984).

Heterakis gallinarum Schrank, 1788 is one of the most common parasitic nematodes of the digestive tract of domestic chickens in most countries of the world (Wongrak et al., 2014; Amundson et al., 2016; Elshahawy et al., 2021). Due to the fact that parasites develop directly, without the participation of intermediate hosts, females are very fertile (producing approximately 34,000 to 86,000 eggs per lifetime), and their exogenous stages of development are quite resistant to adverse external factors, there is a rapid spread of histomoniasis among susceptible birds, especially when they have access to outdoors or to the pen's floor (Fine, 1975; Daş & Gauly, 2014; Belete, 2016). Temperature also affects the exogenous development of histomoniasis. In particular, during daily temperature cycles from lower to higher temperatures (from 12 to 22 °C), the incubation period of *H. gallinarum* shortens (Saunders et al., 2000). Other authors studied the effect of temperature ranging from 10 to 35 °C on the development of *H. gallinarum* eggs and established that the duration of their embryogenesis decreases from 78 to 6 days with increasing temperature (Clapham, 1933, 1934; Osipov, 1957, 1958). Also, there is a report where the shortest development period of *H. gallinarum* eggs was 4 days at a temperature of 33 °C (Roberts, 1937).

The aim of the work was to investigate the influence of different temperature regimes at laboratory conditions on the growth, development and viability of eggs isolated from the gonads of female *H. gallinarum*.

Material and Methods

Experimental research was conducted at the Laboratory of Parasitology of the Poltava State Agrarian Academy (Ukraine) during 2023. The collection of *H. gallinarum* nematodes was carried out by the method of complete helminthological dissection of the colons of slaughtered chickens. In laboratory, eggs were obtained from the gonads of *H. gallinarum* females and washed into Petri dishes (not less than 100 eggs per dish). Each individual culture of eggs was cultivated at four different temperatures: 15 °C, 20 °C, 25 °C and 30 °C until the appearance of a motile infective larva in the egg. The degree of development, morphological changes and the internal structure of the embryo were determined in experimental egg cultures every 2–4 days, depending on the temperature regime. The number of eggs at each stage of development, eggs that stopped in development and were destroyed were counted. Experimental cultivation of *H. gallinarum* eggs was carried out in triplicates.

The morphometric parameters of *H. gallinarum* eggs during their growth and development were studied using the ToupView version × 64 program, 4.10.17015.20200426 (Hangzhou ToupTek Photonics Co., Ltd, China). Photomicrographs were taken using a digital camera SIGETA M3CMOS 14000 14.0 MP (China).

Standard deviation (SD) and average values (M) were calculated. Significance of difference between average values in the studied *H. gallinarum* eggs was established using one-way analysis of variance and F-test for 95 % confidence level.

Results

In the process of cultivation of *H. gallinarum* eggs from the zygote stage (fig. 1, a) to the formation of a motile infective larva (fig. 1, b), their development time and survival depended on the temperature regime.

The development of *Heterakis* eggs was the longest and lasted 56 days at a temperature of 15 °C. In this case, the lowest number of eggs developed to the stage of the motile infective larva — 67.7 ± 1.5 % (fig. 2).

The zygote stage lasted for 36 days of cultivation, the number of eggs at this stage gradually decreased from 100 % to 10.3 ± 4.0 %. The stage of cleavage and formation of blastomeres lasted for 4–44 days of cultivation, by the 28th day their number increased from 8.0 ± 2.0 to 30.7 ± 4.5 %. Starting from the 32nd day, the number of eggs at the stage of cleavage and the formation of blastomeres gradually decreased and on the 44th day it was 5.3 ± 3.5 %. The stage of formation of a non-infective larva lasted from 24 to 52 days. By the 40th day their number increased from 4.0 ± 2.0 % to 40.0 ± 3.6 %, after which it decreased and by the 52nd day comprised 5.7 ± 2.1 %. Motile infective larvae were detected in eggs during 36–56 days of cultivation, their number gradually increased from 9.0 ± 1.7 to 67.7 ± 1.5 %. Stoppage in the development and death of eggs was registered as early as on the 12th day of cultivation (4.3 ± 5.0 %), gradually increasing until the 52nd day and remained at the level of 32.3 ± 1.5 % until the 56th day.



Fig. 1. Eggs of *Heterakis gallinarum* isolated from the gonads of female nematodes, during experimental cultivation: a — zygote stage; b — the stage of formation of a motile infective larva.

At a temperature of 20 °C, the development of *H. gallinarum* eggs occurred faster and lasted 18 days. The level of survival of eggs increased; on the 18th day 80.7 ± 2.5 % of eggs were at the stage of motile infective larva (fig. 3).

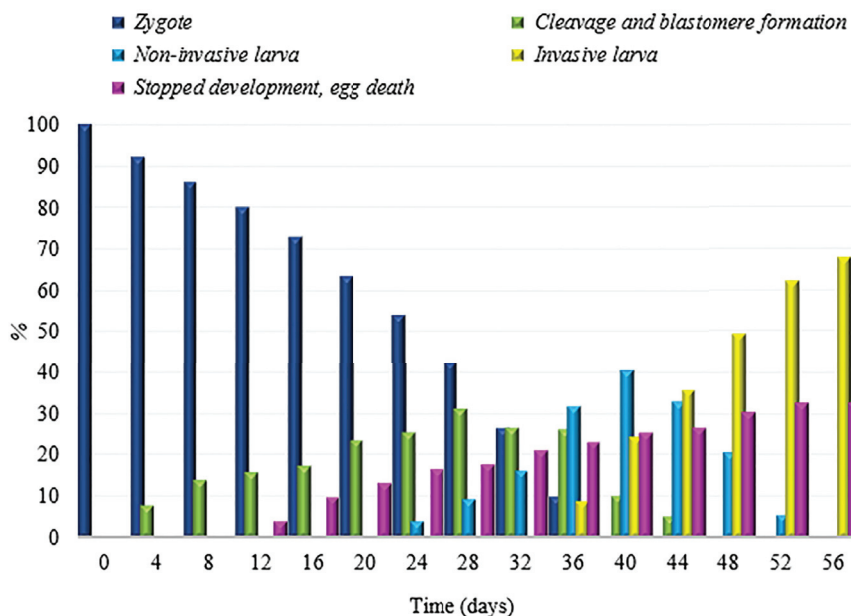


Fig. 2. Indicators of development and survival of *Heterakis gallinarum* eggs during cultivation in laboratory conditions at a temperature of 15 °C.

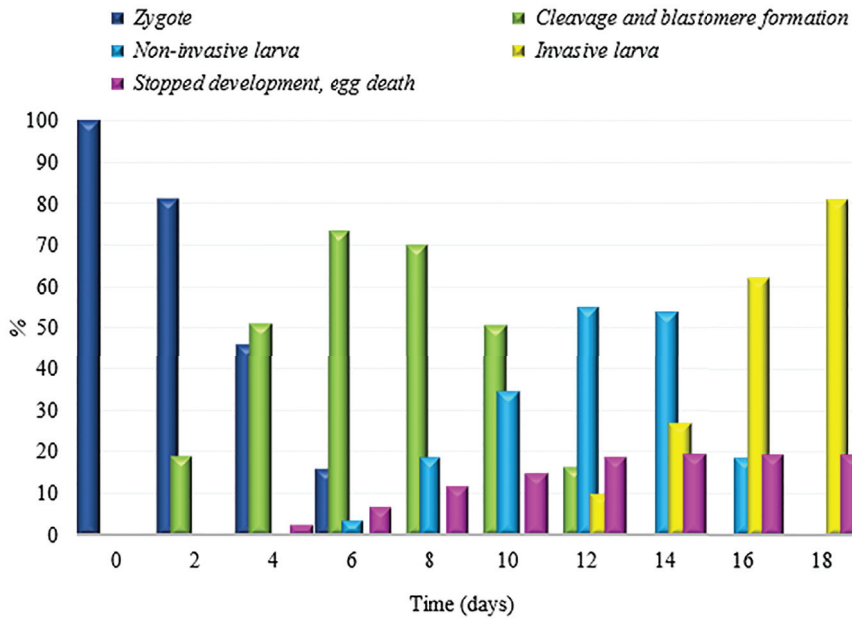


Fig. 3. Indicators of development and survival of *Heterakis gallinarum* eggs during cultivation in laboratory conditions at a temperature of 20 °C.

The zygote stage lasted for 6 days of cultivation, the number of eggs at this stage gradually decreased from 100 % to 16.3 ± 5.1 %. The stage of cleavage and formation of blastomeres lasted for 2–12 days of cultivation, by the 6th day its number increased from 19.1 ± 3.6 to 73.3 ± 7.4 %. Starting from the 8th day, the number of eggs at this stage decreased and by the 12th day it was 16.7 ± 6.0 %. The stage of formation of a non-infective larva lasted from 6 to 16 days. By the 12th day their number increased from 3.7 ± 3.1 % to 54.7 ± 4.2 %, subsequently decreasing to 18.7 ± 2.3 % by the 16th day. Motile infective larvae were detected in eggs during 12–18 days of cultivation, their number gradually increased from 10.3 ± 2.9 % to 80.7 ± 2.5 %. Stoppage in development and death of eggs was registered as early as on the 4th day of cultivation (2.7 ± 1.2 %), gradually increased until the 14th day and remained at the level of 19.3 ± 2.5 % until the 18th day.

At a temperature of 25 °C, the development of *H. gallinarum* eggs was even faster than at a temperature of 20 °C, and lasted 12 days. Moreover, under this temperature regime, the largest number of eggs with a motile infective larvae was observed, 83.7 ± 3.1 % (fig. 4).

The zygote stage lasted for 4 days of cultivation, the number of eggs at this stage gradually decreased from 100 % to 26.0 ± 2.6 %. The stage of cleavage and formation of blastomeres lasted for 2–8 days of cultivation, by the 4th day their number increased from 23.7 ± 5.0 % to 58.7 ± 5.9 %. From that point, their number decreased and by the 8th day it was 6.0 ± 2.1 %. The stage of formation of a non-infective larva lasted from 4 to 10 days. By the 8th day their number increased from 11.7 ± 3.1 % to 58.7 ± 2.1 %, after which it decreased to 13.7 ± 3.8 % by the 10th day. Motile infective larvae were detected in eggs during 8–12 days of cultivation, their number gradually increased from 24.0 ± 3.5 % to 83.7 ± 3.1 %. Stoppage in development and death of eggs was recorded starting from the 4th day of cultivation (3.7 ± 1.5 %), it gradually increased until the 10th day and remained at the level of 16.3 ± 3.1 % until the 12th day.

At a temperature of 30 °C, the development of *H. gallinarum* eggs was the most rapid, occurring in 6 days. However, the number of eggs with motile infective larvae was lower (78.7 ± 1.5 %) than during cultivation at a temperature of 25 °C (fig. 5).

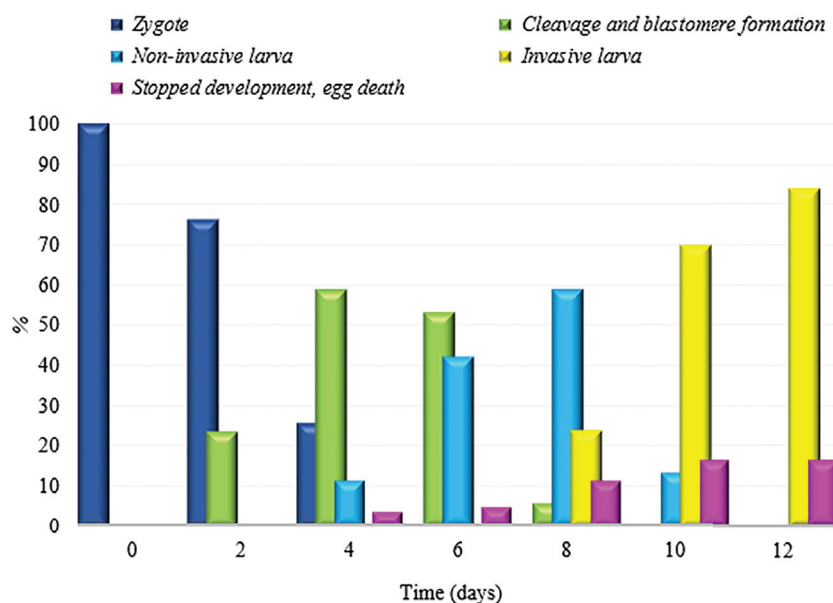


Fig. 4. Indicators of development and survival of *Heterakis gallinarum* eggs during cultivation in laboratory conditions at a temperature of 25 °C.

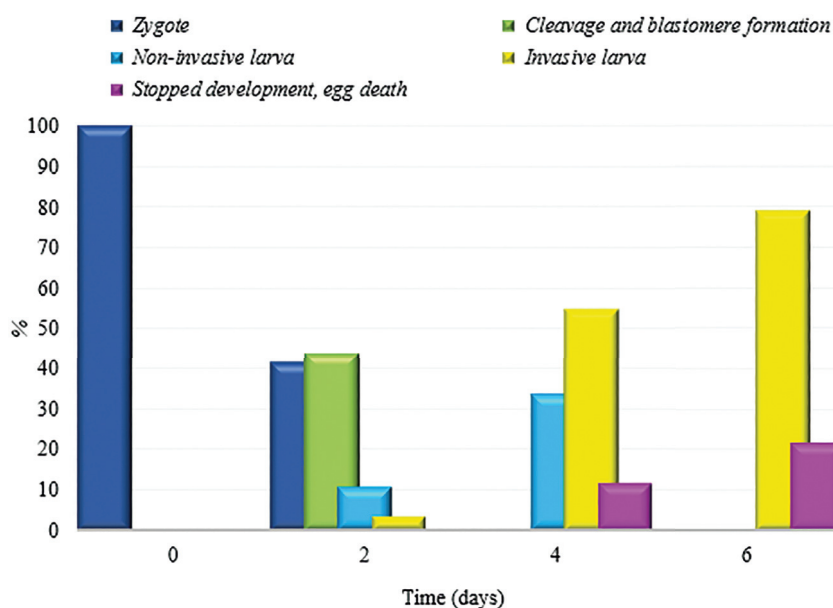


Fig. 5. Indicators of development and survival of *Heterakis gallinarum* eggs during cultivation in laboratory conditions at a temperature of 30 °C.

The zygote stage lasted for 2 days of cultivation, the number of eggs at this stage gradually decreased from 100 % to 41.7 ± 3.1 %. The stage of cleavage and formation of blastomeres was observed at day 2, their number was 43.7 ± 4.2 %. The stage of formation of a non-infective larva lasted from 2 to 4 days, and the number of eggs at this stage increased from 11.0 ± 2.0 % to 33.3 ± 1.5 %. Motile infective larvae were detected in eggs during 2–6 days of cultivation, their number gradually increased from 3.7 ± 1.2 % to 78.7 ± 1.5 %. Stoppage in development and death of eggs was registered from the 4th day of cultivation (11.7 ± 2.1 %), the number of such eggs gradually increased until the 6th day to 21.3 ± 1.5 %.

When determining the morphometric parameters of *H. gallinarum* eggs during their development, changes in the length and width of the eggs, the thickness of their shell, as well as changes in these parameters depending on the temperature of cultivation were revealed (fig. 6, a, b, c).

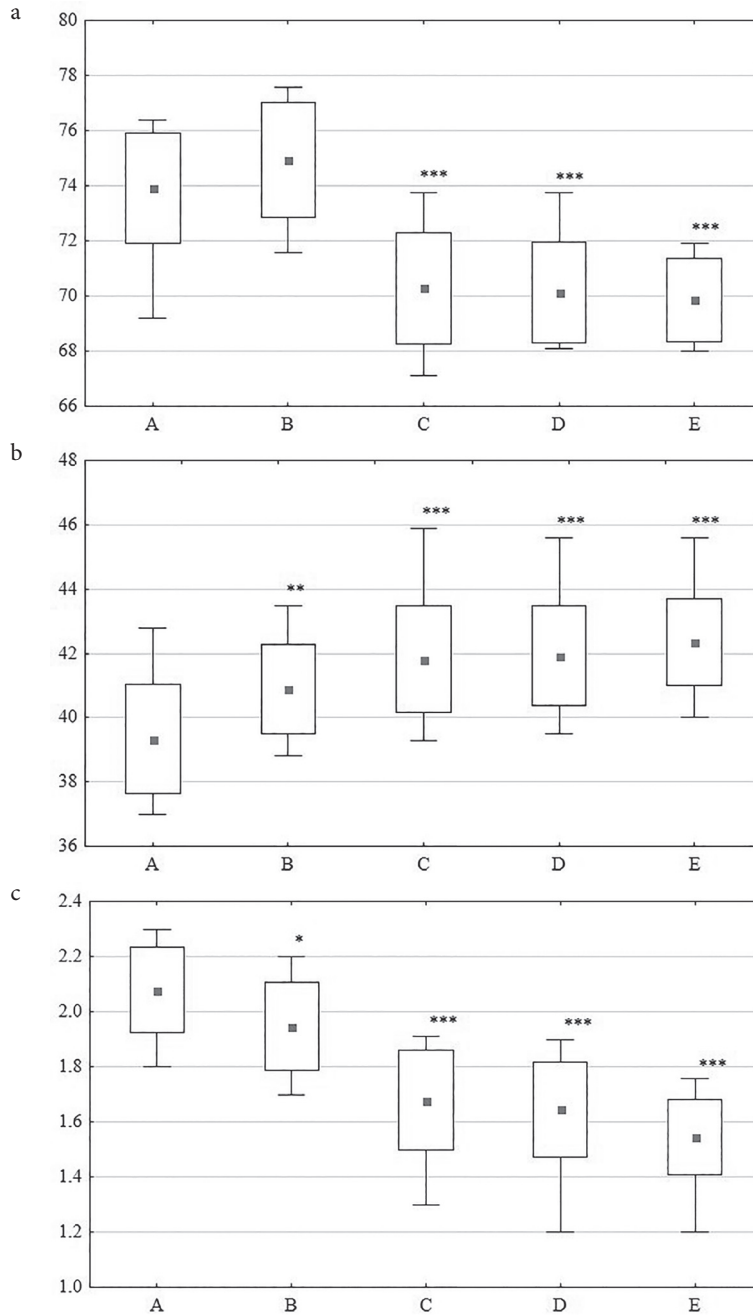


Fig. 6. Morphometric indicators of *Heterakis gallinarum* eggs during cultivation: a — egg length, b — egg width, c — shell thickness (μm); A — zygote stage; B — motile infective larva stage at 15 °C; C — motile infective larva stage at 20 °C; D — the stage of a motile infective larva at 25 °C; E — the stage of a motile infective larva at 30 °C; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ — relative to indicators of eggs at the zygote stage; the small square in the centre corresponds to the median, the lower and upper limits of the large rectangle correspond to the first and third quartiles, respectively, the vertical segment line directed up and down from the rectangle corresponds to the minimum and maximum values ($n = 15$).

Thus, at a temperature of 15 °C, the length of eggs with motile infective larvae slightly increased by 1.6 % ($75.1 \pm 1.9 \mu\text{m}$) compared to that value in eggs at the zygote stage. At a temperature of 20 °C, the length of such eggs decreased by 4.9 % ($70.3 \pm 2.0 \mu\text{m}$, $P < 0.001$), at 25 °C — by 5.1% ($70.1 \pm 1.8 \mu\text{m}$, $P < 0.001$), and at 30 °C — by 5.4 % ($69.9 \pm 1.5 \mu\text{m}$, $P < 0.001$). The width of eggs with motile infective larvae was greater at 15 °C by 4.1 % ($40.9 \pm 1.4 \mu\text{m}$, $P < 0.01$), at 20 °C by 6.4 % ($41.8 \pm 1.7 \mu\text{m}$, $P < 0.001$), at 25 °C by 6.6 % ($41.9 \pm 1.6 \mu\text{m}$, $P < 0.001$), and at 30 °C by 7.6 % ($42.3 \pm 1.3 \mu\text{m}$, $P < 0.001$) compared to similar indicators in eggs at the zygote stage. The shell in eggs with motile infective larvae was thinner compared to egg shell at the zygote stage at a temperature of 15 °C by 9.5 % ($1.9 \pm 0.2 \mu\text{m}$, $P < 0.05$), at 20 °C by 19.1 % ($41.8 \pm 1.7 \mu\text{m}$, $P < 0.001$), at 25 °C by 23.8 % ($1.6 \pm 0.2 \mu\text{m}$, $P < 0.001$), and at 30 °C by 28.6 % ($1.5 \pm 0.1 \mu\text{m}$, $P < 0.001$).

Therefore, we found that with an increase in temperature from 15 °C to 30 °C, the development time of *H. gallinarum* eggs gradually decreases before the formation of infective larva, and their survival rate increases with an increase in temperature from 15 °C to 25 °C. At a temperature of 30 °C, the survival rate of the eggs is slightly reduced. In particular, at a temperature of 15 °C, 66.7 % of eggs with a motile infective larva were formed in 56 days, at a temperature of 20 °C, development lasted for 18 days and 80.7 % of eggs included infective larvae, at a temperature of 25 °C, development lasted for 12 days, and the egg viability was 83.7 %, and at a temperature of 30 °C, development lasted 6 days and 78.7 % of eggs were at the infective larva stage. Therefore, according to the conducted research, the optimal temperature for the development of *H. gallinarum* eggs in laboratory conditions is a temperature of 25 °C, at which the viability rate and the formation of infective eggs is the highest.

Discussion

There is an indication of a significant spread of histomoniasis caused by the protozoan *Histomonas meleagridis* (Smith, 1895) and transmitted by *H. gallinarum* among birds in many countries of the world (Wongrak et al., 2014; Amundson et al., 2016; Elshahawy et al., 2021). Researchers note that one of the factors of such prevalence of the pathogen is its high resistance at exogenous stages of development to adverse environmental factors, including temperature (Saunders et al., 2000; Kaufmann et al., 2011). Therefore, it is relevant to study the influence of different temperature regimes in laboratory conditions on the growth, development and viability of eggs isolated from the gonads of female nematodes *H. gallinarum*.

Similar data were obtained by other authors who noted that at a temperature of 26 °C, eggs become infective in 14–17 days, at 10–15 °C in 78 days, 12.9–21.7 °C — 29 days, 20 °C — 15 days, 21–27 °C — 10 days, 30 °C — 7 days, 35 °C — 6 days (Clapham, 1933, 1934; Osipov, 1957, 1958). At the same time, another author experimentally established that the optimal temperature for the development of *H. gallinarum* eggs is 33 °C, at which the formation of infective eggs takes place within 4 days (Roberts, 1937).

We also obtained data on changes in the morphometric parameters of *H. gallinarum* eggs during their development from the zygote stage to the stage of formation of a motile infective larva, taking into account the temperature regime. It was found that the development of eggs is accompanied by a significant decrease in their length (by 4.9–5.4 %, $P < 0.001$), an increase in their width (by 4.1–7.6 %, $P < 0.01$... $P < 0.001$) and a thinning of their shell (by 9.5–28.6 %, $P < 0.05$... $P < 0.001$). Moreover, with increasing temperature, these changes in the parameters of the width, length of the eggs, and the thickness of their shell were more significant. The change in the size of *Heterakis* eggs during their development was also confirmed in our previous study (Yevstafieva et al., 2018): at a cultivation temperature of 27 °C there was a slight decrease in the length of the eggs (by 2.7 %) and an increase in their width (by 2.2 %).

Therefore, the temperature of external environment significantly affects the development time of *H. gallinarum* eggs, their survival and size, which is confirmed by experimental studies in laboratory conditions.

Conclusion

Experimental studies showed that temperature affects the growth, development and survival of *H. gallinarum* eggs isolated from the gonads of female nematodes. The most optimal temperature for their development is 25 °C, at which the formation of motile infective larvae under laboratory conditions takes 12 days and the survival rate is 83.7 %. At lower temperatures (20 °C and 15 °C), the development time of *H. gallinarum* eggs increased to 18 and 56 days, respectively, and their survival rate decreased to 80.7 % and 66.7 %, respectively. When the incubation temperature was increased to 30 °C, the development time of the eggs was the shortest, 6 days, and the survival rate decreased to 78.7 %. The exogenous development of *H. gallinarum* eggs from the zygote stage to the stage of formation of a motile infective larva in the egg is accompanied by morphometric changes characterised by a decrease in egg length (by 4.9–5.4 %), an increase in egg width (by 4.1–7.6 %) and thinning of the shell (by 9.5–28.6 %). The extent of these changes depends on the temperature at which the eggs are cultivated.

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