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Comparison of Rhopalosiphum padi (L.), Metopolophium dirhodum Walk. and Sitobion avenae F. apterae exules Development and Reproduction Parameters

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Abstract

Rhopalosiphum padi (L.), Sitobion avenae F. and Metopolophium dirhodum Walk.—demonstrating that R. Padi has an advantage in population growth: significantly higher fecundity ($F = 5.92$; $p = 0.02$ and $F = 10.13$; $p = 0.003$) and shorter longevity ($F = 7.88$; $p = 0.000$ and $F = 4.50$; $p = 0.04$) with a shorter time from birth until the start of reproduction ($F = 45.6$; $p = 0.000$ and $F = 36.2$; $p = 0.000$), higher intrinsic rate of natural increase rm ($F = 36.06$; $p = 0.000$ and $F = 23.48$; $p = 0.000$) and a shorter population doubling time (DT) ($F = 35.59$; $p = 0.000$ and $F = 21.45$; $p = 0.000$). We show that adult aphids go through reproduction and post reproduction periods, with interruptions in reproduction constituting a reproduction rhythm. Our data suggests that interruptions in reproduction are determined by adult ovulation potential as well as embryo numbers and maturation rate. We also establish correlation between fecundity and development parameters, including reproduction rhythm, for the three aphid species.

Disciplinary: Agricultural Science

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1 Introduction

Rhopalosiphum padi (L.), *Sitobion avenae* F. and *Metopolophium dirhodum* Walk. are considered the most destructive pests of cereal crops (Descamps & Chopa, 2011; Honek et al., 2018; Gandrabur, 2019). These three species often cohabit in farming ecosystems, causing a complex effect on plants. The key factor in their success at exploiting host plants is their unique ability—

common to all species, including those with the bisexual type of reproduction—to rapidly increase in numbers through parthenogenesis and viviparity (Le Trionnaire et al., 2008; Uematsu & Shibao,2018; Loxdale et al., 2020).

Aphids exhibit very complex and highly variable intraspecific population dynamics (Dixon & Kindlmann, 1998), which can be seen as a representation of a genetic (endogenous) population development programme in variable environmental (exogenous) conditions. The genetic programme determines the unique properties and adaptability limits of the population, determined by the clonal composition, changes of ontogenetic morphs and type of reproduction during the life cycle. In the current conditions created by climate change and anthropogenic impact on the environment, researchers are now focusing on the emerging risk of increased aphid populations and damage, given that they are prone to outbreaks of mass reproduction (Ma & Ma, 2012). To date, a large number of mathematical models of aphid population dynamics have been established (Kindlmann et al., 2007; Duffya et al., 2017). However, none of them offer reliable predictions that could be used in commercial farming, which is due to the sharp fluctuations in aphid abundance (Kindlmann & Dixon, 2010; Park et al., 2017). Aphid developmental features, including endogenous reproductive rhythms specific to the individuals that make up the population, are still poorly understood. This is despite the fact that both their "desire" to increase abundance (strategy) and the means that they use to achieve it (tactics) are phylogenetically coded reserves of adaptations.

The relationships between the three aforementioned aphid species are considered non-competitive due to their topical specificity on plants. *R. padi* colonizes all plant organs. *S. avenae* feeds mainly on the spikelet and spikelet internode, while *M dirhodum* feeds on the two upper leaves (Vickerman & Wratten, 1979; Honek et al., 2006; Bokina, 2009; Gandrabur, 2019). A comparative study of the development of these aphid species during the early stages of cereal organogenesis, when a primary infestation occurs, has not yet been presented.

The aim of our work was to identify species-specific and general characteristics of *R. padi*, *M. dirhodum* and *S. avenae* apterae exules development, including their chronological rhythmic changes in reproduction.

2 Materials and Methods

The work was carried out with holocyclic populations of *R. padi*, *M. dirhodum* and *S. avenae* that occur near St. Petersburg. 20 clones of each aphid species were used. *R. padi* and *M. dirhodum* clones were collected from the primary aphid hosts, *S. avenae* — in grain farming ecosystems of different districts of the Leningrad region. The clones were kept in covered pavilions under equal habitat conditions, in separate isolated vessels. Only soft spring wheat of Leningradskaya 6 variety, with 10 plants sown in each vessel was used as the aphid host plant. The wheat was infested during the emergence of the 3rd leaf. We placed one nymph per vessel at the same time. There was no influence of population density, entomophage presence, plant diseases or feeding limits on aphid development. The following developmental parameters were measured for all 20 individuals from each clone: each nymph instar duration, prematurity period duration, time from maturation to the

start of reproduction, time from birth to the start of reproduction, total reproduction period duration, post-reproduction period duration, longevity and total fecundity. Based on experimental data, we calculated the following life table parameters: R_o (average fecundity of one female at 100% survival of females from nymph for the first reproductive period, equal to the time from birth to starting of reproduction—T); $r_m = (\ln Ro) / T$ (intrinsic rate of natural increase for quick estimation); $DT = \ln 2 / r_m$ (population doubling time) (Wyatt & White, 1977; Leather & Dixon,1984; Maia et al., 2000; Descamps & Chopa, 2011).

Additionally, daily reproduction dynamics parameters were also measured for 10 individuals from each clone: total number of days of continued reproduction, number of interruptions in reproduction, the total number of days during interruptions in reproduction, average interruption duration between nymph cohorts, the average time to produce a nymph cohort time to produce the first nymph cohort, daily changes in the number of born nymphs, number of nymphs on the first day of reproduction, reproductive and live females.

The temperature during the experiment (July 31 to October 8), is presented according to https://world-weather.ru/pogoda/russia/pushkin/september-2020/ (fig. 1).

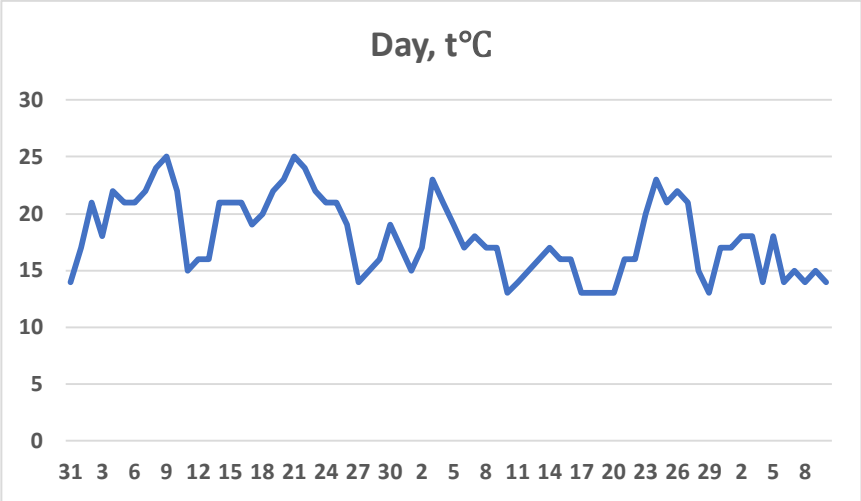

Figure 1: Daily temperature for the duration of the experiment: July 31 to October 8.

Statistical processing of experimental data was carried out using regression analysis and one-factor analysis of variance (Fisher's test) in Statistica.

3 Results

We have identified the differences in *R. padi*, *M. dirhodum* and *S. avenae* development parameters when fed on Leningradskaya 6 variety (Table 1).

During the experiment, daytime temperatures stayed above zero and varied between 25°C and 13°C (Figure 1). Aphid development from birth to maturity occurred in the first ten days of August at average daily temperatures of 21.3±0.76°C (Figure 1). We recorded considerably faster development of *R. padi*, especially in third instar nymph, and slower development of *M. dirhodum*, especially in fourth instar nymph. The shortest time from birth to start of reproduction was observed in *R. padi*, with the longest time in *M. dirhodum* (Table 1). The reproductive period

duration was significantly longer in *S. avenae*, and no significant difference was observed between *R. padi* and *M. dirhodum* (Table 1). A significantly shorter longevity coupled with higher fecundity was observed in *R. padi*. No differences in the duration of the post-reproduction period of the three aphid species or in the longevity or total fecundity in *S. avenae* and *M. dirhodum* have been proven. (Table 1). *R. padi* had a significant advantage in life table parameters, although the three aphid species did not differ significantly in R_o values (Table 2).

Table 1: Development parameters (Xmean ± SE) for apterae exules of *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi*

Aphid species		Duration of the periods before reproductions, days						Duration of imaginal periods, days			Longevity, days	Total fecundity, nymphs
		nymph instars					from birth to the start of reproduction	from maturation to the start of reproduction	reproduction	post reproduction		
		1st	2nd	3rd	4th	total						
Sitobion avenae (1)		2.1±0.18	1.9±0.22	2.2±0.13	2.5±0.14	8.6±0.15	9.4±0.11	0.85±0.11	32.1±1.50	9.7±0.94	51.4±1.67	43.3±2.12
Metopolophium dirhodum (2)		2.8±0.14	2.1±0.16	1.7±0.15	2.9±0.10	9.5±0.21	10.0 ± 0.26	0.45±0.15	27.1±1.31	11.1±1.39	48.0±2.08	41.6±1.96
Rhopalosiphum padi (3)		2.3±0.11	1.8±0.12	1.2±0.09	2.4±0.15	7.7±0.16	8.2±0.14	0.50±0.114	26.6±0.58	8.2±0.85	43.0±1.10	49.9±1.70
The results of one-way ANOVA (Fisher's test) investigating development parameters for Sitobion avenae, Metopolophium dirhodum and Rhopalosiphum padi apterae exules												
Factor (aphid species)		Fisher's values										
1 - 2*	F	12.7	0.84	5.22	5.63	13.2	3.86	4.50	6.30	0.65	1.67	0.328
	p	0.010	0.365	0.028	0.023	0.001	0.057	0.040	0.016	0.427	0.204	0.57
2 - 3	F	8.33	2.28	8.33	7.54	45.3	36.2	0.068	0.10	1.85	4.50	10.13
	p	0.006	0.139	0.006	0.009	0.000	0.000	0.795	0.754	0.182	0.040	0.003
1 - 3	F	2.11	0.04	35.2	0.24	14.3	45.6	4.87	11.5	0.54	7.88	5.92
	p	0.154	0.843	0.000	0.627	0.001	0.000	0.033	0.002	0.479	0.000	0.02

Note: * aphid species parameters are compared using numbers: *S. avenae* (1) - *M. dirhodum* (2), etc.

Table 2: Life Table parameters (mean ± SE) for apterae exules of *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi*.

Aphid species		Ro	rm	DT
Sitobion avenae (1)		22.9±1.21	0.3305±0.0057	2.109±0.038
Metopolophium dirhodum (2)		24.7±1.63	0.3222±0.0116	2.206±0.082
Rhopalosiphum padi (3)		24.9±1.09	0.3917±0.0083	1.785±0.039
The results of one-way ANOVA (Fisher's test) investigating development parameters for Sitobion avenae, Metopolophium dirhodum and Rhopalosiphum padi apterae exules				
Factor (aphid species)		Fisher's values		
1 - 2*	F	1.21	0.41	1.141
	p	0.277	0.526	0.292
2 - 3	F	0.029	23.48	21.45
	p	0.870	0.000	0.000
1 - 3	F	1.52	36.06	35.59
	p	0.226	0.000	0.000

Note: * comparison of aphid species parameters is similar to Table 1.
R_o— a net reproductive rate equal to female; r_m— the intrinsic rate of natural increase; DT— population doubling time.

By determining the daily fecundity for individual females of each aphid species throughout the reproductive period, we identified fluctuations in the number of offspring (Fig. 2), associated not only with the females' age but also with the reproductive rhythm, expressed in interruptions between nymph cohorts (Table 3).

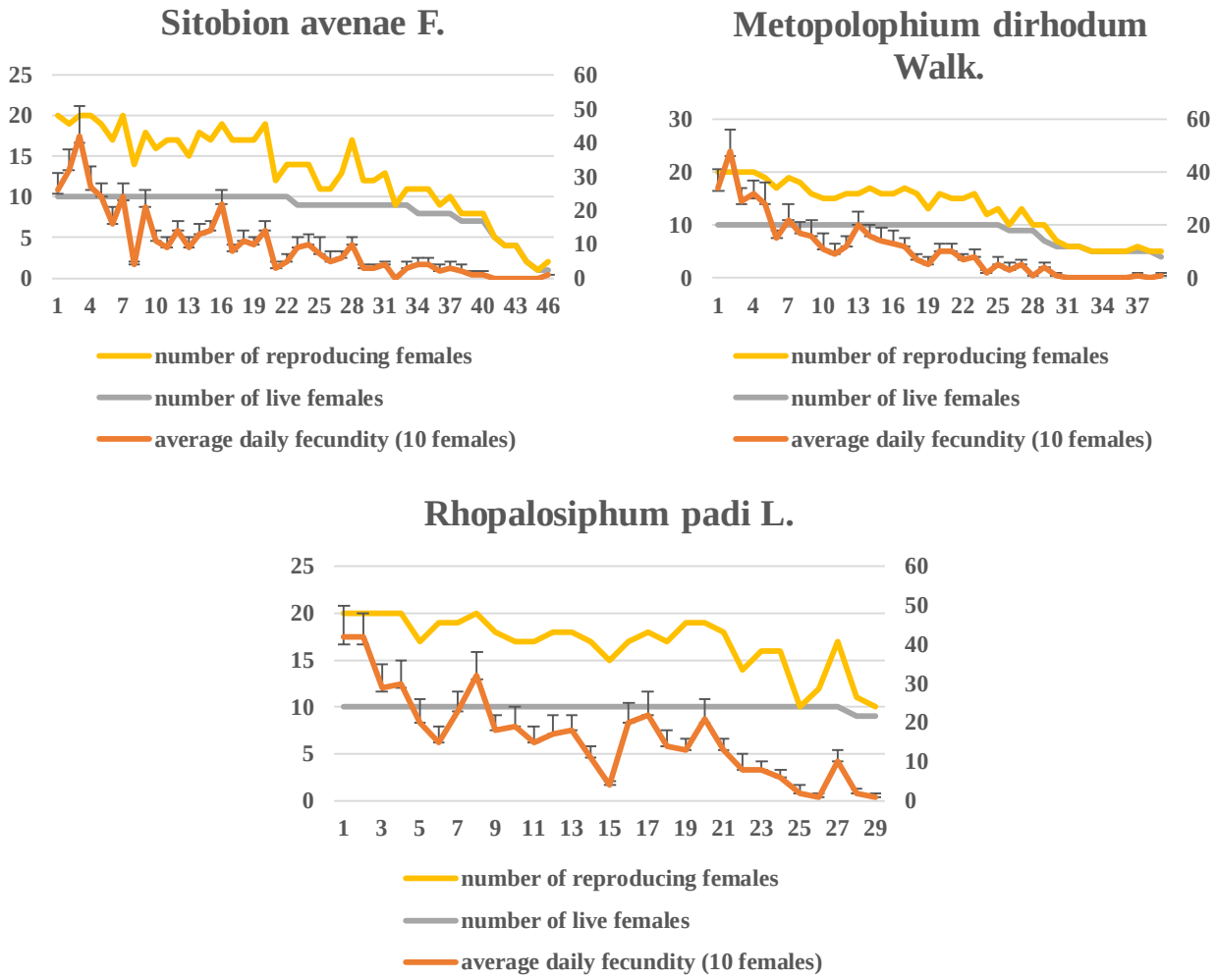

Figure 2: Daily fecundity (10 ♀), number of reproducing and living ♀ for apterae exules of three aphid species (a, b and c).

Note: deviations are expressed as the minimum (down) and maximum (up) number of nymphs for one ♀ on a given day.

Table 3: Reproduction rhythm for apterae exules of *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi* ($\bar{X} \pm SE$).

Aphid species	Fecundity/total reproduction period	Reproduction period						
		total number of days in interruptions	total number of continued reproduction days	number of interruptions in reproduction	duration of interruption between nymph cohorts	time to produce a nymph cohort		number of nymphs on the first day of reproduction
						the first cohort	average	
Sitobion avenae (1)	1.37±0.09	10.8±1.84	21.2±1.60	6.3±1.00	1.90±0.37	6.9±1.06	3.26±0.33	2.6±0.45
Metopolophium dirhodum (2)	1.63±0.16	9.2±1.62	17.5±0.81	4.8±0.76	2.19±0.39	8.1±0.96	3.58±0.56	3.4±0.56
Rhopalosiphum padi (3)	1.86±0.11	6.2±0.63	20.1±0.80	3.8±0.39	1.69±0.16	8.5±1.19	4.48±0.48	4.2±0.66

The results of one-way ANOVA (Fisher's test) investigating development parameters for Sitobion avenae, Metopolophium dirhodum and Rhopalosiphum padi apterae exules									
Factor (aphid species)		Fisher's values							
1 - 2*	F	2.057	0.99	4.28	1.28	0.28	0.66	0.25	1.23
	p	0.1687	0.333	0.053	0.272	0.602	0.427	0.620	0.282
2 - 3	F	1.36	2.695	5.27	1.26	1.36	0.068	1.48	0.86
	p	0.2595	0.102	0.034	0.276	0.258	0.697	0.240	0.369
1 - 3	F	11.96	6.83	0.38	4.95	0.28	0.95	4.42	3.97
	p	0.0028	0.0176	0.545	0.039	0.603	0.342	0.050	0.062

Note: *comparison of aphid species parameters is similar to Table 1.

In *R. padi,* the duration of the reproduction period and the number of nymphs in the first cohort were significantly higher, while the number of interruptions in reproduction and the total number of days during interruptions in reproduction were significantly lower compared to *S. avenae*. Among the aphid species under consideration, the total number of days of continued reproduction was the lowest in *M. dirhodum,* possibly driven by the shorter reproductive period than in *S. avenae* and lower fecundity than in *R. padi*. Thus, *R. padi* had a significant advantage over *S. avenae* and *M. dirhodum* in average reproductive rate (fecundity / total reproduction period). In turn, *S. avenae* and *M. dirhodum* did not differ significantly, although *M. dirhodum* performed worse in total days of continued reproduction.

Regression analysis of experimental data allowed us to establish relationships between various aphid development parameters (Table 4).

Table 4: Results of the correlation analysis of *Sitobion avenae, Metopolophium dirhodum* and *Rhopalosiphum padi* (L.) apterae exules development parameters.

Factors		Regression equations	n	r	r2	p
Total fecundity	continued reproduction period	y=8.89+0.24*x	30	0.676	0.457	0.00004
	average time to produce a nymph cohort	y=1.1868+0.0579*x	30	0.4089	0.1672	0.0249
	rm	y=0.1872+0.0036*x	60	0.6587	0.4339	0.0000
	total number of days during interruptions	y=16.4326-0.1652*x	30	-0.3342	0.1117	0.0711
Fecundity/total reproduction period	number of interruptions in reproduction	y=11.2306-3.8682*x	30	- 0.6189	0.3831	0.0003
Total reproduction period	longevity	y=16.5317+1.081*x	60	0.7759	0.6020	0.000
	number of interruptions in reproduction	y= -5.083+0.3547*x	30	0.8364	0.6996	0.0000
	total number of continued reproduction days	y=8.8056+0.381*x	30	0.6266	0.3927	0.0002
rm	time to produce the first nymph cohort	y= -3.6849+33.355*x	30	0.5112	0.2614	0.0039
	number of nymphs on the first day of reproduction	y=-4.7111+23.4885*x	30	0.6647	0.4418	0.00006
Postreproduction period	longevity	y=-10.0235+0.4109*x	60	0.6745	0.4550	0.000

Note: DT—population doubling time; r_m—intrinsic rate of natural increase (for quick estimation).

Aphid fecundity was found to be significantly positively correlated with the total number of continued reproduction days, the average time to produce a nymph cohort and r_m, and negatively correlated with DT; no correlation was found with the number of interruptions in reproduction and longevity. There was a very weak positive correlation between total fecundity and total reproduction period ($r = 0.27$; $p = 0.04$), and a trend toward a negative correlation with the total

number of days during interruptions in reproduction. As opposed to total fecundity, the average reproductive rate negatively correlated with the number of interruptions in reproduction and did not correlate with the total number of days in continued reproduction. At the same time, the total reproduction period in high and medium degrees positively correlates with longevity, the number of interruptions in reproduction and the total number of days of continued reproduction. Correlation analysis of r_m parameters showed that they are positively correlated with—in addition to the aforementioned parameters—total fecundity, the number of nymphs on the first day of reproduction and the time to produce the first nymph cohort. The duration of the post-reproduction period was positively correlated with aphid longevity.

4 Discussion

A significant number of researchers have studied cereal aphid development parameters under different conditions, including temperature, host plants, entomophages, fertilizers, climate change and other environmental factors influencing these insects' abundance and survival in farming ecosystems (Powell & Bale, 2006; Bale & Hayward, 2010; Descamps & Chopa, 2011; Saska et al., 2016; Hu et al.,2015; Karami et al., 2016; Park et al., 2017; Yang et al., 2019). However, identifying and comparing species-specific patterns of aphid interspecific and intraspecific relationships remains a challenge. This is due to the fact that existing data is highly heterogeneous, obtained with different ontogenetic morphs of species from different geographic populations under non-comparable environmental conditions.

In this work, three aphid species were studied under equivalent environmental conditions with limited exposure to external factors. Only apterae exules were used.

Analysing our experimental results, we put them in the general context of development parameters reported by others for the studied species' apterae exules fed on optimal samples of wheat, barley, or maize at 20-22°C.

The maturation rates we measured for the three aphid species (Table 1) are largely consistent with our data for other clones of these species and with reports of other authors. Thus, the shortest period from birth to adult moult was observed in *R. padi*, while the longest in *M. dirhodum* Additionally, nymphal development stages I and/or IV were generally reported to be the longest in all aphid species (Dean, 1974a; Cannon,1984; Asin & Pons, 2001; Özder, 2002; Razmjou et al., 2011; Karami et al., 2016; Vereshchagina & Gandrabur, 2016; Peng et al., 2017; Park et al., 2017; Yang et al., 2019), which is consistent with our results.

In all three species, we found higher longevity (Table 1) than reported by other authors (Asin & Pons, 2001; Taheri et al., 2010), but *R. padi* proved to have significantly shorter longevity than *M. dirhodum* or *S. avenae*, a difference that has been noted in other works.

The number of authors, like us, report a shorter reproductive period in *R. padi* than in *S. avenae*, but—in contrast to our results—longer in *S. avenae* than in *M. dirhodum* (Dean, 1974a; Asin & Pons, 2001).

The aphid fecundity values we observed (Table 1) do not exceed their known variability (Dean, 1974a; Asin & Pons, 2001).

A post-reproduction period has been observed in aphids (Auad et al., 2009; Park et al., 2017). In our experiments, the post-reproduction period was observed in all species. However, its duration did not differ significantly, despite it lasting 16–23 days in individual females. It has been suggested that during the post-reproduction period—at least in gall-forming aphid species—females perform a function of protecting against enemies (Uematsu et al., 2018). If so, this function, selected during phylogeny, may have persisted in now free-living species with gall-forming ancestral forms as well as in species that cause deformation on primary hosts (e.g. *R. padi*). Supporting contact communication and food optimisation through extraintestinal digestion may also be part of the *responsibilities* of such females.

R. padi, *M. dirhodum* and *S. avenae* life table parameters also reflect the high phenotypic plasticity of aphids. The R_o parameters we identified for all species were generally lower than those reported by other authors (Taheri et al., 2010; Gao et al., 2012; Karami et al., 2016; Saska et al., 2016; Fadl, 2017; Park et al., 2017; Peng et al., 2017) and did not differ significantly between the species, probably due to the generally low aphid fecundity (Tables 1, 2). At the same time, the observed r_m (Table 2) could significantly differ or be close to the results of other authors. In our experiments, DT of *R. padi* and *M. dirhodum* was slightly shorter than that reported by other authors (Asin & Pons, 2001; Karami et al., 2016; Saska et al., 2016; Park et al., 2017) with a significantly shorter time for *R. padi* than the other two species (Table 2).

Thus, *R. padi* exhibited a number of statistically significant differences that give it an advantage in increasing population abundance. It is reasonable to suggest that with *R. padi*'s higher reproduction speed and volume, it's material and energy costs of embryo production and nutritional requirements will also be higher than in *S. avenae* and *M. dirhodum*. Therefore, although it is not competing with the other two species for a preferred location on the plant (Bokina, 2009; Honek et al., 2006; Gandrabur, 2019), there may be an implicit dominance of *R. padi* in *capturing* and altering assimilate transport.

As demonstrated above, in all three aphid species fecundity is realized in portions. This rhythm can be primarily attributed to the functioning of aphid reproductive apparatus.

In our observations, the first marked decrease in the number of reproductive offspring occurred in *R. padi* on day 5 of reproduction and on day 6 in *M. dirhodum* and *S. avenae*, apparently due to their longer maturation time. By the end of this period, three females of each species had ceased reproduction (Fig. 2 a, b, c). Subsequently, no clear trend was observed in the variation of the daily number of reproductive females in these species, but females of *R. padi* were the first to complete the reproduction (Fig. 2 a, b, c).

Aphid reproductive rhythm is shaped by the total number of embryos, ovulation rate and embryo maturation time (Leather & Wellings, 1981). Even without further ovulation in adulthood, aphids can maximize their fecundity by having many embryos at the very early stages of

development of each ovariole when moulting to the adult stage (Dixon & Dharma, 1980 a, b). This is confirmed by the positive correlation—observed by us in the three aphid species—between r_m and the time to produce the first nymph cohort as well as between r_m and the number of nymphs on the first day of reproduction. Interruptions in reproduction vary according to the adults' ability to ovulate and embryo maturation rate.

We have identified common relationships in the reproduction patterns of the three aphid species (Table 4). It was shown that total fecundity, firstly, does not correlate with longevity and, secondly, correlates very weakly with the duration of the total reproduction period, despite a proven statistical correlation between the latter. Perhaps, the lack of correlation in the first case is driven by the positive correlation between longevity and the post-reproduction period, when nymphs are no longer born. The second case is connected to the structure of the reproduction process, in particular, the correlation between fecundity and the total number of days of continued reproduction as well as between fecundity and the average time to produce a nymph cohort (Table 4). Naturally, higher fecundity results in a higher r_m and lower DT.

5 Conclusion

Based on individual development and life table parameters of *R. padi*, *S. avenae* and *M. dirhodum*, we clearly demonstrate that *R. padi* has a statistically proven advantage in population growth. This advantage results in *R. padi*'s high food consumption, limiting the feeding of the other two species when they cohabit, despite differences in their distribution on the plant.

It is established that *R. padi*, *S. avenae* and *M. dirhodum* reproduce rhythmically with nymph birth (1-16 days), interruptions in reproduction for a number of days (1-8), and a post-reproduction period (2-23 days).

New correlations between fecundity and intrinsic rate of natural increase (r_m) as well as with the reproduction rhythm have been identified. Fecundity correlates with the total number of days of continued reproduction, the total number of days during interruptions in reproduction, the average time to produce a nymph cohort; r_m correlates with the time to produce the first nymph cohort and the number of nymphs on the first day of reproduction. A correlation between the average reproduction rate and the number of interruptions in reproduction is shown.

Analysis of experimental data shows that reproduction rhythm is determined by the possibility of adult ovulation as well as embryo numbers and their maturation rate.

Aphid population growth patterns, which are independent of population density, can be used to improve plant protection models and programmes.

6 Availability of Data and Material

Data can be made available by contacting the corresponding author.

7 Conflict of Interest

The authors declare that there is no conflict of interest, either existing or potential.

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