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COMPARATIVE ANALYSIS OF FECUNDITY IN RELATED AMPHIMICTIC *APORRECTODEA CALIGINOSA* AND APOMICTIC *A. TRAPEZOIDES* EARTHWORMS, AND THE PROBLEM OF REPRODUCTIVE ADVANTAGES OF PARTHENOGENETIC ANIMALS

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Comparative Analysis of Fecundity in Related Amphimictic *Aporrectodea* caliginosa **and Apomictic *A. trapezoides* Earthworms, and the Problem of Reproductive Advantages of Parthenogenetic Animals. Mezhzherin, S. V., Chayka, Yu. Yu., Kokodiy, S. V., Tsyba, A. A.** — The comparative analysis of fecundity and fertility was studied experimentally for the amphimictic *Aporrectodea caliginosa* diploid and the close parthenogenetic *A. trapezoides* triploid earthworms during two seasons. The individual fecundity of cocoons at is significantly higher in the parthenogenetic species than in amphimictic one. Fertility is in contrast lower in the parthenogenetic species, which results in leveled parameters of the reproductive potential. A generalization and analysis of the available data on the comparative fecundity of representatives of different animal groups shows that the automatic increase in fecundity in same-sex organisms due to the exclusion of males cannot be considered a universal rule providing biological progress and the ecological advantage of parthenogenetic organisms. This explanation is not suitable for hermaphroditic organisms. In addition, in some cases, parthenogenetic reproduction is accompanied by reduced fertility and even reduced fecundity.

Key words: parthenogenesis, fecundity, earthworms, biological press

Introduction

The relationship of apomictic and amphimictic reproduction in biological evolution remainsy one of the unresolved issues of modern biology. The logic of the evolutionary transition from asexual to sexual reproduction is not completely clear, and the most important and obscure points of interest are the meaning of irreversible rejection of hermaphroditism and the transition to obligate bisexual reproduction. In the evolutionarily most advanced groups, in particular Cephalopoda, Arthropoda and Chordata, the hermaphroditism is present only as sporadic pathologies, and the rare situations of asexual reproduction are either random event (monozygotic twins), or a useful device (polyembryony).

Parthenogenesis is the sexual reproduction by unfertilized eggs (Cuellar, 1977; Suomalainen et al., 1987), which holds a special place in the reproductive system of higher animals. This mode of reproduction should be considered secondary in relation to amphimixis, and therefore a progressive method of sexual reproduction. Parthenogenesis is believed to provide short-term benefits. Several types of parthenogenesis are known. One of the most common forms of parthenogenesis is associated with the formation of organisms with an allopolyploid structure of the genome (Suomalainen et al., 1987). They originate from interspecific crosses, which result in the formation of polyploid same-sex hybrids, in which the gametogenesis occurs without the reduction divisions. The first-generation hybrids, usually females, produce diploid gametes, which are fertilized by the spermatozoa of males of parental species. That leads to the formation of triploids that can multiply by parthenogenesis (Suomalainen et al., 1987). The tetraploids appear in the following hybridizations. In some groups, like earthworms (Mezhzherin et al., 2017), even octoploids can be found.

The alloploid parthenogenetic species and biotypes are found in almost all large taxa of freshwater and terrestrial animals of the Holarctic. The exception is birds and mammals. In the case of mixed populations, parthenogenetic specimens are usually not inferior in abundance to parental species, and in a situation of isolation from parental species, their populations are no less numerous. They are capable of large-scale expansion, subsequently occupying the territories and landscapes that are not suitable for amphimictic species (Cuellar, 1977; Suomalainen et al., 1987). What is the reason for the success of same-sex parthenogenetic specimens? Many researchers have now agreed upon their high reproductive potential at the population level as the key factor (Williams, 1975; Cuellar, 1977; Maynard Smith, 1978; Suomalainen et al., 1987; Dawson, 1995; Gibson et al., 2017). In the initially hermaphroditic organisms, the absence of spermatogenesis probably allows to focus the life potential of individuals on egg production. In the initially bisexual organisms, the absence of males allows at the population level to save up resources intended for their production. Thus, ceteris paribus, the parthenogenetic populations should theoretically be more prolific than amphimictic.

Nevertheless, this seemingly logical assumption remains only a hypothesis which is not supported by sufficient evidence. Especially when it comes to the hermaphroditic groups of animals in which parthenogenesis is especially common. The idea that the energy saved up in the event of rejection of spermatogenesis in these primitive animals can be used to increase the production of oocytes and to enhance the reproductive potential is purely theoretical and does not take into account several circumstances. First of all, this concerns the quality of ameiotic eggs and the viability of parthenogenetic offspring. Specific experiments have shown that the level of egg production in planarians of the family Dugesiidae (Weinzierl et al., 1999) and oligochaetes of the family Tubificidae (Poddubnaya, 1984) is initially equal or higher compared to the related amphimictic forms. However, the survival of hermaphroditic offspring is much lower. A steady decrease in individual fecundity is also characteristic of some parthenogenetic insects (Roth, 1974; White, Contreras, 1979) and gynogenetic fish (Kokodiy, 2016; Mezhzherin et al., 2017; Przybyl et al., 2019). At the same time, there is a number of data of the opposite nature, confirming the real possibility of increasing the reproductive potential in populations of parthenogenetic organisms primarily due to the same-sex population structure (Weeks, 2005; Crummett, Wayne, 2009; Tada, 2013; Schall, 1981; Schlupp et al., 2010, etc.). The inconsistency of the data indicates a limited explanation for the evolutionary success of parthenogenetic organisms based only on their reproductive advantages. A better explanation requires both additional research and theoretical analysis and synthesis of available data on comparative fecundity. Particular attention should be paid to earthworms, in which parthenogenesis is very common, and data on comparative fecundity are not available. The aims of our work were to conduct a comparative analysis of the fecundity of the close amphimictic and apomictic earthworm species of the genus *Aporrectodea* in laboratory conditions, and to generalize and subsequently analyze materials on the comparative fecundity of similar groups of animals.

Material and methods

A comparison of the individual fecundity of parthenogenetic and amphimictic earthworms under controlled conditions was carried out on two closely related species of *Aporrectodea* Orley, 1885. *A. caliginosa* (Savigny, 1826) has a diploid genome and an amphimictic reproduction system. It is the most widespread species of the open landscapes of the forest and forest-and-steppe zones of Europe. *A. trapezoides* (Dugés, 1828) is parthenogenetic, has a triploid genome and a more southerly distribution. Most likely, this allopolyploid species occurred as a result of hybridization of *A. caliginosa* with an unknown species of that genus (Mezhezherin et al., 2018). In the forest-steppe zone, the ranges and habitats of the species overlap (Perel, 1979).

The study was conducted over two seasons. In 2018, 30 mature earthworms were used as the material for the study. Ten of them were *A. trapezoides* and 20 were identified as *A. caliginosa*. The earthworms were kept in pairs. The sample of *A. trapezoides* was taken in the first half of April from the Belichi housing district in Kyiv (50.45955, 30.35166), and the sample of *A. caliginosa* was collected in the vicinity of Baranivka village (50.29639, 27.67111) of Zhytomyr Region.

In 2019, fecundity was analyzed in 27 *A. trapezoides* and 42 *A. caliginosa* specimens. The parthenogenetic earthworms were kept one specimen per container, and the amphimictic were kept in pairs. Earthworms were collected in the first half of April from three places in Zhytomyr Region: near Stanishovka village (50.21982209, 28.72116799), in the district of Maryanovka, Zhytomyr city (50.28711826, 28.70536566) and from Radomyshl town (50.50361, 29.24611).

An original technique was developed to culture earthworms of the genus *Aporrectodea* (Chayka, Vlasenko, 2019). The technique allows a satisfyingly correct evaluation of the number of cocoons and juvenile forms kept in small containers. Optimum soil moisture and a completely nutritive diet were previously selected to do that. The earthworms were kept without light at room temperature in well-ventilated plastic containers with a volume of 0.33 l. The soil used for cultivation was taken directly from the collection site and pre-sieved through a zoological sieve. The experiments started in mid-April and ended in late summer to early autumn, when the breeding intensity faded away, and the parental specimens were not viable in a number of containers. The number of cocoons and juvenile individuals was counted by sieving the substrate every 5–10 days depending on the intensity of reproduction. The removal of young earthworms was not carried out. Fecundity parameters were calculated per one mature adult. Two parameters were used, which reflect the mean number of cocoons or larvae produced by one specimens during the reproductive season. The mean group score is based on the mean numbers of cocoons and juveniles counted on a particular day. An individual assessment is based on the summarized counts of cocoons and juveniles in each container, carried out over the entire period of the study. In containers containing two worms, individual fecundity was assessed as the mean value obtained for two parental specimens. Situations when an individual *A. caliginosa* remained in the container were not taken into account.

Results

The process of laying cocoons in individual specimens began in 2018 on 20th day of experiment, and in 2019 on the 8th day of experiment, simultaneously in two species. The larvae appeared later in 2018 after 20 days, and in 2019 after 40 days from the start of the experiment, also at the same time in containers with *A. caliginosa* and *A. trapezoides*. Reproduction peaked in June. In July, the number of produced cocoons decreased; in August, despite stable humidity and high temperature, reproduction almost stopped (fig. 1, 2).

Counts of the number of cocoons showed that the individual fecundity of A. *trapezoides* was significantly higher than that of *A. caliginosa*. The results obtained in different seasons and with different calculation methods showed that the mean number of cocoons per specimen in the parthenogenetic species is significantly higher than in the amphimictic species (table 1). Notably, the cocoons of different species did not differ in size, shape and color. Dissection showed that *A. caliginosa* cocoons contained one embryo, whereas in *A. trapezoides* their number ranged from one to two.

The greatest degree of discrepancy in the fecundity levels of earthworm species is observed in a period of maximum breeding intensity. In most counts, conducted during this period, differences in the number of cocoons per individual were statistically significant (table 2). At the beginning and at the end of the season, when the number of laid cocoons is minimal, differences in fecundity are almost absent (fig. 1, 2).

Table 1. Mean number of cocoons per specimen in amphimictic *A. caliginosa* and parthenogenetic *A. trapezoides* earthworms in culture conditions

Year	Statistical parameters	Mean number of cocoons per one parental specimen			
		Mean group assessment		Individual assessment	
		A. caliginosa	*A. trapezoides*	*A. caliginosa*	*A. trapezoides*
2018	M ± SE	0.27 ± 0.04*	1.16 ± 0.16*	0.25 ± 0.04*	1.18 ± 0.18*
	n	7	7	79	34
2019	M ± SE	2.51 ± 0.44	3.05 ± 0.6	2.47 ± 0.12**	3.07± 0.14*
	n	15	15	324	415

Note. M ± SE — mean value and standard error, n — number of counts for group assessment and the number of individual assessments. *Differences are significant at $p < 0.001$.

Table 2. Comparative analysis of individual fecundity assessed as cocoon laying in two earthworm species during maximal productivity

Date	*A. trapezoides*	*A. caliginosa*
	M ± SE	M ± SE
June 04, 2019	6.46 ± 0.41**	4.57 ± 0.45**
June 11, 2019	6.96 ± 0.52*	5.10 ± 0.51*
June 17, 2019	6.70 ± 0.50*	5.10 ± 0.51*
June 26, 2019	5.70 ± 0.55	4.38 ± 0.46

Note. M ± SE — mean value and standard error. Differences are significant at: $^*p < 0.05$, $^{**}p < 0.01$.

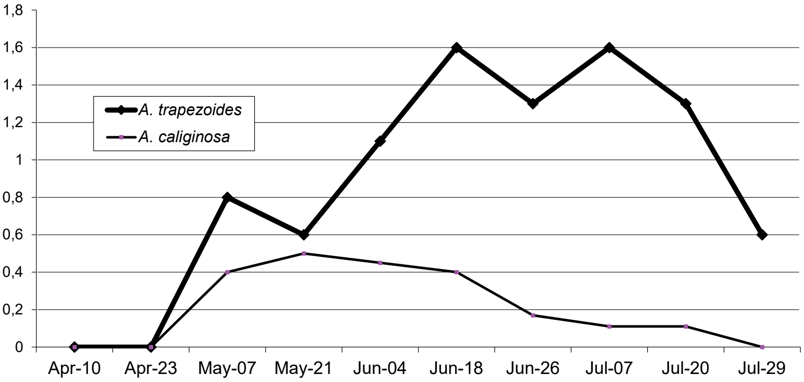

Fig. 1. Mean number of cocoons per one mature specimen in close parthenogenetic (*A. trapezoides*) and amphimictic (*A. caliginosa*) earthworm species during the reproduction season of 2018.

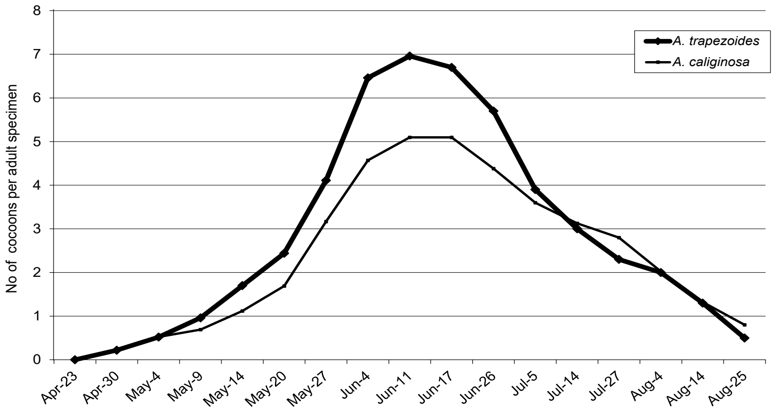

Fig. 2. Mean number of cocoons per one mature specimen in close parthenogenetic (*A. trapezoides*) and amphimictic (*A. caliginosa*) earthworm species during the reproduction season of 2019.

Fertility levels depend not only on the earthworm species, but also on the population from which they are taken. Nevertheless, in all cases, specimens of the parthenogenetic species produce a greater number of offspring (table 3).

Comparison of two species by the mean number of juvenile specimens, calculated per parent specimen, yielded significant differences between amphimictic and apomictic worms

Table 3. Mean number of cocoons per parental individual in two species of earthworms of different populations in 2019

Samples	*A. caliginosa*		*A. trapezoides*	
	M ± SE	n	M ± SE	n
Stanishevka	2.58 ± 0.19*	96	3.11 ± 0.15*	384
Maryanovka	3.20 ± 0.19	160	3.46 ± 0.61	16
Radomyshl	1.53 ± 0.17	80	1.97 ± 0.33	32

Note. *Differences significant at $p < 0.05$.

Table 4. Mean number of juvenile specimens per one parent in amphimictic *A. caliginosa* and parthenogenetic *A. trapezoides* earthworms in culture conditions

Year	Statistical parameters	Mean number of juvenile specimens per parent specimen			
		Mean group assessment		Individual assessment	
		A. caliginosa	*A. trapezoides*	*A. caliginosa*	*A. trapezoides*
2018	M ± SE	0.760 ± 0.045	1.271 ± 0.210	0.77 ± 0.084*	1.221 ± 0.157*
	n	7	7	63	34
2019	M ± SE	1.092 ± 0.171	1.258 ± 0.210	1.071 ± 0.02	1.249 ± 0.099
	n	10	10	198	415

Note. Statistica parameters are same as in table 1. *Iifferences significant at $p < 0.05$.

in only one case out of four comparison options (table 4). Moreover, these differences were at the lowest level of significance. The reason for the lack of differences at the level of juvenile specimens is most likely the relatively low survival rate of *A. trapezoides* in the early stages compared to *A. caliginosa*.

Discussion of results

Summarizing the study results, it can be unequivocally stated that the parameters of individual fecundity based on counts of the number of deposited cocoons are higher in the parthenogenetic triploid species *A. trapezoides* than in the amphimictic diploid *A. caliginosa*. At the same time, at the level of juvenile specimens, the reproductive potential is leveled. That is associated with the relatively low viability of *A. trapezoides*, which is quite possibly caused by artificial conditions. In any case, this means that meiosis is not always the most effective way to produce gametes in animals, and amphimixis is not the most effective form of reproduction. The mitotic gamete production and apomixis may well replace them.

The findings on the comparative fecundity of genetically close amphimictic and apomictic species of earthworms are consistent with the results of similar studies conducted on other groups of hermaphroditic invertebrates. For example, the study on planarians of the *Schmidtea polychroa* group (Weinzierl et al., 1999) and two species groups of oligochaetes of the Tubificidae family (Poddubnaya, 1984). In the first case, the fecundity is initially higher, compensated by the low fertility of cocoons and offspring. In the second case, with the initially equal fecundity of amphimictic and parthenogenetic worms, the latter also have a sharp decrease in the survival of offspring during the life cycle. In primitive hermaphrodite animals, where parthenogenesis is very common, this means that, ceteris paribus, apomixis not only does not lead to a greater reproductive potential, but also limits it compared to similar amphimictic species.

Nevertheless, the increase in reproductive potential in animal species with obligate parthenogenetic is undeniable. An increased production of oocytes at the population level can be noted for most primarily bisexual animals (table 5). That increase is achieved, first of all, due to the absence of males. This fact is evident in the gastropod mollusks *Campeloma limum* (Crummett, Wayne, 2009) and *Pomatopyrgus antipodarum* (Schreiber et al., 1998), among insects in *Clitarchus hooker* sticks (Morgan-Richards, Trewick, 2010) and in *Scepticus insularis* weevils (Tada, Katakura, 2013). Among vertebrates, a similar situation occurs in cyprinids of the *Poecilia formosa* groups (Schlupp et al., 2010) and *Poeciliops*is monacha–*lucida* (Weeks, 2005), the salamander species complex *Ambystoma tigrinum* (Bogart et al., 1987) in lizards of the genera *Cnemidophorus* and *Aspidoscelis* of the family Teidae (Schall, 1981; Newton et al., 2016), in geckos *Heteronotia binoei*, Gekkonidae (Kearney, Shine, 2005), in Caucasian lizards of the genus *Darevskia*, Lacertidae (Darevsky, 1967) of the order Squamata. In all these cases, the fecundity of parthenogenetic allopolyploids does not exceed that of the parent or close amphimictic species. Due to the absence of males, the allopolyploids are most likely to achieve a greater reproductive potential.

There are proven exceptions to that rule. Thus, in parthenogenetic cockroaches of the *Pycnoscelus indicus–surinamensis* group (Roth, 1974) and the grasshopper *Warramba virgo* (White, Contreras, 1979), parthenogenetic females are characterized by reduced fecundity, which, however, does not affect their ecological success.

Table 5. Comparative analysis of fecundity, fertility and reproductive potential of populations of parthenogenetic species (forms) with related amphimictic species

Species / Group of species	Fecundity and Fertility	Reproductive potential	Literary issues
	Turbellaria, Dugesiidae		
Schmidtea polychroa	Same-sex forms have higher fecundity of cocoons and low fertility	<	Weinzierl et al., 1999
	Oligochaeta, Lumbricidae		
Aporrectodea caliginosa–trapezoides	Parthenogenetic species have a greater number of cocoons with lesser survival of juveniles	=	This article
	Oligochaeta, Naididae		
Tubifex tubifex	With an equal number of cocoons, a sharp decrease in survival in parthenogenetic forms during the life cycle	<	Poddubnaya, 1984
Limnodrilus hoffmeisteri	With an equal number of cocoons, a sharp decrease in survival in parthenogenetic forms during the life cycle	<	Poddubnaya, 1984
	Gastropoda, Viviparidae		
Campeloma limum	Parthenogenetic forms are more prolific	>	Crummett, Wayne, 2009
	Gastropoda, Hydrobiidae		
Pomatopyrgus antipodarum	An equal fecundity	>	Schreiber et al., 1998
	Insecta, Blattoptera, Blaberidae		
Pycnoscelus indicus–surinamensis	Fecundity in parthenogenetic species is below than amphimictic one	<	Roth, 1974
	Insecta, Orthoptera, Morabitidae		
Warramba virgo	With an equal number of clutches, parthenogenetic forms have a half number of eggs	<	White, Contreras, 1979
	Insecta, Coleoptera, Curculionidae		
Scepticus insularis	Parthenogenetic forms are more fertile	>	Tada, Katakura, 2013
	Insecta, Phasmatodea, Phasmatidae		
Clitarchus hooker	An equal fecundity	>	Morgan-Richards, Trewick, 2010
	Actinopterygii, Cyprinodontiformes, Poecilidae		
Poecilia formosa–latipina–mexicana	An equal fecundity	>	Schlupp et al., 2010
Poeciliopsis monacha —lucida	An equal fecundity	>	Weeks, 2005
	Actinopterygii, Cypriniformes, Cyprinidae		
Carassius auratus–gibelio	Fecundity in parthenogenetic species is lower by 30 %	=	Kokodiy, 2016; Przybyl et al., 2019
	Actinopterygii, Cypriniformes, Cobitidae		
Cobitis elongatoides–taenia–tanaitica	Fecundity in parthenogenetic species is lower by 30–40 % , and tetraploids by 70–80 %	=	Mezhzherin et al., 2017
	Amphibia, Caudata, Ambistomatidae		
Ambistoma tigrinum complex	An equal fecundity	>	
	Reptilia, Squamata, Teiidae		
Cnemidophorus	An equal fecundity	>	Schall, 1981
Aspidoscelis	An equal fecundity	>	Newton et al., 2016
	Reptilia, Squamata, Gekkonidae		
Heteronotia binoei	An equal fecundity in nature	>	Kearney, Shine, 2005
	Reptilia, Squamata, Lacertidae		
Darevskia	An equal fecundity		Darevskiy, 1965

Note. The reproductive potential of populations of parthenogetic species: greater (>), less () and equal (=), compared with related amphimictic species.

A special situation occurs in gynogenetic polyploid cyprinids of the families Cobitidae and Cyprinidae. In triploid hybrid fish of the *Cobitis elongatoides– taenia– tanaitica* group, the production of eggs is less by one third than in individuals of the diploid parent species (Mezhzherin et al., 2017), and in tetraploid fish, the egg production is only 20 % of the diploid level. The reason for the decrease in fertility is a sharp increase in the size of eggs in polyploids. A similar situation was also observed in triploid fish of the *Carassius auratus–gibelio* group, whose gynegenetic females, as shown by studies in Ukraine (Kokodiy, 2016) and Poland (Przybyl et al., 2019), also increased egg size and, accordingly, reduced individual fecundity. This means that, taking into account the 30–40 % ratio of males in populations, the reproductive potential of the gynogenetic representatives of these species groups is close to the level of amphimictic.

It should also be noted that high fecundity rates of parthenogenetic forms may not reflect the real reproductive potential of the population, since the survival of clonal offspring is often lower than that of amphimictic. Special studies on this problem have not been conducted for most objects, although available data, for example, on *Poecilia formosa* show (Hubbs, Schlupp, 2008) that survival in the early stages of the development of a hybrid gynogenetic form is not different from that of a parent species.

Thus, the hypothesis that the transition from bisexual to same-sex reproduction should automatically lead to an increase in the reproductive potential of populations of parthenogenetic species is not supported by specific studies on comparative fecundity. This means that the hypothesized rule is not universal and can not be extended to different systematic groups. First, it is in principle not suitable for hermaphroditic organisms, among which parthenogenesis is widespread. Second, in some cases there is a decrease in the fecundity of same-sex species or forms compared with similar bisexual species. Third, in some systematic groups, there is a low fertility of parthenogenetic offspring. This situation is more likely an exception, but it gives every reason to believe that the postulated increase in reproductive potential in unisexual species compared with bisexual species is not a universal rule, but as a particular mechanism of evolutionary success. Most likely, there are several factors that determine the evolutionary advantage of parthenogenetic organisms, allowing them to numerically dominate in joint populations with specimens of the amphimictic species or to occupy vast areas inaccessible to close amphimictic species.

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