

## Assortative mating in Gastropoda: A meta-analysis

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The term ‘assortative mating’ denotes situations when the choice of a mating partner is nonrandom and the phenotypes across mate pairs are correlated, either positively or negatively. Assortative mating has been registered as a particular type of behaviour in many taxa of animals, including various vertebrate and invertebrate species. The aim of this study is to conduct a meta-analysis of published data concerning assortative mating in various taxa of Gastropoda. In total, we found 36 published peer-reviewed papers that consider the size-assortative mating in Gastropoda. 32 species belonging to different taxonomic groups of this class were studied, which provided 58 cases for further analysis. The range of estimates of the strength of assortment between individuals for species included into our meta-analysis (46 cases) is very wide: from  $-0.155$  (*Brephulopsis cylindrica*) to  $+0.966$  (*Veronicella sloanii*). Integrally, for the studied species of Gastropoda, the average weighted estimate of the strength of assortment between the sizes of copulating individuals was  $0.381 \pm 0.014$ . It revealed that virtually all the points representing individual studies form a funnel-shaped dispersion on a scatterplot that lies along the line representing the estimate of the generalized mean  $r_{gen} = 0.343$  and uniformly fill the funnel-shaped space between the lines of 95% confidence interval of the correlation coefficient for a given sample size adjusted for the overall mean. The distribution of the estimates of the correlation coefficient between copulating individuals among the various gastropod species has a shape close to the normal distribution (Kolmogorov-Smirnov's  $d = 0.061$ ;  $P > 0.20$ ). Moreover, most estimates are concentrated within a range from 0.2 to 0.6. We found that the probability of obtaining reliable estimates of the correlation coefficient between the sizes of copulating individuals is dependent upon the number of pairs used in the analysis (binary logistic regression:  $\chi^2 = 8.92$ ;  $df = 1$ ;  $P = 0.0028$ ). It can be argued that the existence of the negative size-assortative mating in Gastropoda has not yet been proved. On the other hand, if only statistically significant cases of size-assortative mating are considered (37 cases out of 58, or 63.7%), the average weighted estimate of the strength of assortment between sizes of copulating mollusks is  $0.439 \pm 0.015$  (95% confidence interval: 0.409–0.468). If we consider the mating system and the environment simultaneously, the positive size-assortativity is most pronounced among the gonochoristic snails living in the aquatic environment ( $0.448 \pm 0.021$ ) while among the aquatic hermaphroditic species it is the weakest ( $0.315 \pm 0.028$ ). Terrestrial hermaphrodites (land snails and slugs) take the middle position. The numerous examples of the assortative mating with respect to different morphological traits, either quantitative or qualitative, have been described in various species of aquatic and land snails.

**Keywords:** mollusks; nonrandom mating; shell traits; reproductive strategy.

### Introduction

Assortative mating (AM) is used to describe a variety of patterns of nonrandom mating. In the speciation literature, assortative mating is treated as a mechanism of pre-mating reproductive isolation between distinct species or divergent populations. In the behavioural literature, assortative mating has been used to describe a particular form of mate choice in which individuals select mates on the basis of phenotypic similarity to themselves. More generally, assortative mating can be defined as a pattern of nonrandom mating, without making specific assumptions regarding its behavioural mechanism or evolutionary role. Adopting this general view, assortative mating can be measured as a correlation between the values of a homologous phenotypic or genotypic trait across members of mated pairs. Assortative mating may be either positive, implying a tendency to mate with phenotypically similar individuals, or negative (also called disassortative), implying the converse (Jiang et al., 2013).

AM has been registered as a particular type of behaviour in many taxa of animals, including various vertebrate and invertebrate species (Ridley, 1983; Janicke et al., 2019; Rios Moura et al., 2021). Among mollusks, proven examples of AM are known in marine (Erlandsson & Rolán-Alvarez, 1998; Pal et al., 2006; Wada, 2017) and freshwater (Staub & Ribi, 1995; Koene et al., 2007) species belonging to actively moving animals with relatively complex behaviour, i.e. to the cephalopods and gastropods. The importance of this phenomenon for the better understanding of speciation processes and maintaining of intraspecific polymorphism in aquatic mollusks has repeatedly been discussed (Erlandsson & Rolán-Alvarez,

1998; Pickles & Graham, 1999; Takada & Rolán-Alvarez, 2000; Boulding et al., 2017). Though there is a wealth of records or studies concerned with AM in land snails, these data remain rather contradictory. In most cases, a random pattern of mating, in respect of both body size and shell banding pattern has been reported (Wolda, 1963; Baur, 1992), although there are studies which proved the reality of AM in this group (Johnson, 1982; Asami et al., 1998; Kimura et al., 2015; Kramarenko & Kramarenko, 2019). Theoretically, the potential adaptive significance of AM for terrestrial gastropods is obvious, since the choice of a larger mate would enhance the reproductive success of hermaphroditic animals. In land snails and slugs, ‘female’ fecundity (number of clutches, clutch size, and egg size) usually positively correlates with the shell size (Kramarenko, 2013).

Detecting the presence and causes of AM is important because this mating pattern is usually accompanied by sexual selection and thus may have a profound impact on the genetics and demographics of populations (Crespi, 1989). Mate preference is fundamental to biological questions linking ecology, phenotypic evolution, and the genetic basis for mating traits, yet our capacity to measure mate preference and study its consequences in natural systems is highly limited. Much of what we know and the predictions we are able to make about evolutionary processes involving mate preference stem from theoretical models, laboratory studies, and simulations, with less emphasis on field studies. This is because in most, if not all cases, it is impossible to directly measure mate preference in the wild (Clancey et al., 2022).

Assessments of the environmental factors that influence life-history traits are commonly limited by the spatial and temporal extent of most

research. Studies conducted at one or two study sites for one or two years offer little potential to assess variation expressed across broad landscapes over many years. Recent advances in the use of meta-analysis offer some relief from this limitation. Meta-analysis enables one to derive a quantitative summary of data from multiple studies and to assess variation over time and space (Dreitz et al., 2001).

Meta-analysis is one of many ways to summarize, integrate, and interpret selected sets of scholarly works in the various disciplines. It applies to research studies that produce quantitative findings, that is, studies using quantitative measurement of variables and reporting descriptive or inferential statistics to summarize the resulting data. Meta-analysis can be understood as a form of survey research in which research reports, rather than people, are surveyed (Lipsey & Wilson, 2000). The aim of this study is to

conduct a meta-analysis of published data concerning AM in various taxa of Gastropoda. The 'Discussion' section contains also a short overview of studies of AM in the current malacological literature, with emphasis on methodological aspects of this research.

### Literature search

To determine the pattern of occurrence of AM across Gastropoda and to reveal whether there are any differences among taxonomically and ecologically distinct groups of this class, the meta-analysis of published sources was carried out. The study has been based on bibliographic searches through three large online databases – Google Scholar, Web of Science Core Collection, and Scopus (Table 1).

**Table 1**

Data from literature sources used to conduct a meta-analysis of size-assortative mating among different gastropod species

Species	Taxonomic group	MS <sup>1</sup>	Bio <sup>2</sup>	n	r <sub>p</sub>	P	Source
<i>Lymnaea stagnalis</i> (L., 1758)	Basommatophora	herm	wat	55	-0.027	0.842	Koene et al. (2007)
<i>Physa acuta</i> Draparnaud, 1805	"	"	"	68	0.092	0.226	Graham et al. (2015)
<i>P. acuta</i>	"	"	"	46	-0.020	> 0.050	Ohbayashi-Hodoki et al. (2004)
<i>Physa gyrina</i> (Say, 1821)	"	"	"	149	0.529	< 0.001	deWitt (1996)
<i>Radix auricularia</i> (L., 1758)	"	"	"	128	0.350	< 0.001	Yu et al. (2016)
<i>Radix lagotis</i> (Schrank, 1803)	"	"	"	71	0.420	< 0.001	Yu & Wang (2013)
<i>R. lagotis</i>	"	"	"	102	0.420	< 0.001	"
<i>Siphonaria capensis</i> Quoy & Gaimard, 1833	"	"	"	17	0.480	0.040	Pal et al. (2006)
<i>S. capensis</i>	"	"	"	15	0.510	0.030	"
<i>Buccinanops globulosus</i> (Kiener, 1834)	Caenogastropoda	gono	"	104	0.476	< 0.001	Avaca et al. (2012)
<i>Cerithidea rhizophorarum</i> (Adams, 1855)	"	"	"	100	0.057	> 0.050	Takeuchi et al. (2007)
<i>Cypraea annulus</i> L., 1758	"	"	"	27	-0.094	> 0.050	Katoh (1989)
"	"	"	"	39	0.021	> 0.050	"
<i>Echinolittorina malaccana</i> (Philippi, 1847)	"	"	"	228	0.570 <sup>4</sup>	< 0.001	Ng et al. (2016)
"	"	"	"	40	0.520	< 0.010	"
<i>Echinolittorina radiata</i> (Eydoux & Souleyet, 1852)	"	"	"	49	0.670 <sup>4</sup>	< 0.001	"
<i>Littoraria flava</i> (King & Broderip, 1832)	"	"	"	-	0.390	< 0.050	Cardoso et al. (2007)
<i>Littoraria arduiniana</i> (Heude, 1885)	"	"	"	286	0.536	< 0.001	Ng & Williams (2012)
<i>Littoraria melanostoma</i> (Gray, 1839)	"	"	"	184	0.423	< 0.001	"
<i>Littorina littorea</i> (L., 1758)	"	"	"	49	0.079 <sup>4</sup>	> 0.200	Saur (1990)
"	"	"	"	19	0.126	0.620	Erlandsson & Johannesson (1994)
"	"	"	"	22	0.528	0.001	"
"	"	"	"	22	0.147	0.520	"
<i>Littorina neglecta</i> Bean, 1844	"	"	"	30	0.184	< 0.050	Johnson (1999)
<i>Littorina saxatilis</i> (Olivier, 1792)	"	"	"	40	0.430 <sup>4</sup>	< 0.010	Saur (1990)
"	"	"	"	10	0.867 <sup>4</sup>	< 0.010	Hull (1998)
"	"	"	"	10	0.945 <sup>4</sup>	< 0.010	"
"	"	"	"	18	0.764	< 0.001	Erlandsson & Rolan-Alvarez (1998)
"	"	"	"	20	0.745	< 0.001	"
"	"	"	"	333	0.520	< 0.001	Johannesson et al. (1995)
<i>Littorina subrotundata</i> (Carpenter, 1864)	"	"	"	146	0.182	0.029	Zahradnik et al. (2008)
<i>Nodilittorina radiata</i> (Eydoux & Souleyet, 1852)	"	"	"	281	0.296	< 0.001	Ito & Wada (2006)
<i>Olivella biplicata</i> (Sowerby, 1825)	"	"	"	197	0.350 <sup>5</sup>	0.001	Edwards (1968)
<i>Viviparus ater</i> (De Cristofori & Jan, 1832)	"	"	"	308	-	< 0.050	Staub & Ribic (1995)
<i>Alderia modesta</i> (Loven, 1844)	Opisthobranchia	herm	"	122	-	< 0.050 <sup>3</sup>	Angeloni (2003)
<i>Aphysia californica</i> (Cooper, 1863)	"	"	"	108	0.190	0.050	Angeloni et al. (2003)
"	"	"	"	47	0.240	0.098	Pennings (1991)
"	"	"	"	83	-0.007	0.910	"
<i>Aphysia kurodai</i> (Baba, 1937)	"	"	"	89	0.210	< 0.050	Yusa (1996)
<i>Aphysia vaccaria</i> Winkler, 1955	"	"	"	190	0.130	0.008	Angeloni & Bradbury (1999)
<i>Bulla gouldiana</i> Pilsbry, 1895	"	"	"	24	-	> 0.050 <sup>3</sup>	Chaine & Angeloni (2005)
<i>Felimare zebra</i> (Heilprin, 1889)	"	"	"	148	0.608	< 0.001	Crozier (1918)
<i>Arianta arbustorum</i> (L., 1758)	Stylommatophora	"	land	35	0.245	0.160	Baur (1992)
<i>Bradybaena pellucida</i> Kuroda & Habe, 1953	"	"	"	44	0.500	< 0.001	Kimura et al. (2015)
<i>Brephulopsis cylindrica</i> (Menke, 1828)	"	"	"	60	0.543	< 0.001	Vychalkovskaya (2011)
"	"	"	"	50	-0.155	0.284	Kramarenko & Kramarenko (2019)
"	"	"	"	70	0.140	0.331	"
"	"	"	"	50	-0.078	0.592	"
<i>Helix pomatia</i> L., 1758	"	"	"	83	0.190	0.090	Baur (1992)
<i>Succinea putris</i> (L., 1758)	"	"	"	87	-	> 0.050	Jordaens et al. (2005)
<i>Veronicella sloanii</i> (Cuvier, 1817)	"	"	"	50	0.966	< 0.001	Clarke & Fields (2013)
<i>Xeropicta derbentina</i> (Krynicki, 1836)	"	"	"	73	0.419	< 0.001	Kramarenko & Kramarenko (2019)
"	"	"	"	71	0.404	< 0.001	"
"	"	"	"	149	0.276	< 0.001	"
"	"	"	"	193	0.377	< 0.001	"
"	"	"	"	393	0.366	< 0.001	"
"	"	"	"	100	0.285	< 0.010	"
"	"	"	"	359	0.194	< 0.001	"

Notes: 1 – MS: mating system (herm – hermaphroditic species; gono – gonochoric species); 2 – Bio: biotope (wat – aquatic or freshwater biotopes; land – land biotopes); 3 – binary logistic regression model; 4 – Spearman's or Kendall's rank correlation coefficient; 5 – linear regression analysis.

We focused on English-written articles appeared in peer-reviewed journals, and excluded conference papers and other publications without peer-review. Keywords used for the search included ‘assortative mating’ or ‘mate choice’ and ‘snails’ or ‘Gastropoda’.

In total, we found 36 published peer-reviewed papers that consider the size-assortative mating in Gastropoda. 32 species belonging to different taxonomic groups of this class were studied, which provided 58 cases for further analysis. Our sample is significantly larger in comparison with those used in two previous studies, namely in Jiang et al. (2013), who analyzed 8 cases of AM in gastropods, and in Graham et al. (2015), who undertook a meta-analysis of size-assortative mating in hermaphrodite animals, with 22 cases belonging to Gastropoda included.

### Meta-analysis

The funnel plot method (Egger et al., 1997) was used as a graphical test to detect a possible bias in published papers.

One may distinguish two principal groups of factors that determine the size-assortative mating in gastropods: a) factors related to observational and statistical design that may bias the results – sample size, choice of conchiometric characters, statistical method(s) used for the null-hypotheses testing; and b) the biological properties of the studied species (or groups of species) that promote the emergence of AM under natural conditions. Of the second group, we considered two important biological characteristics of snails – the mating system (hermaphroditism vs. gonochorism), and their environment (aquatic vs. terrestrial). In addition, we took into account the taxonomic position of the species included into the meta-analysis and divided them among four groups corresponding to the four higher taxa: Basommatophora (limnic and marine pulmonate snails), Opisthobranchia (marine branchiate snails), Caenogastropoda (marine and limnic branchiate snails), and Stylommatophora (terrestrial pulmonate snails).

We hypothesized that the degree of selectivity in mate choice in respect of body size is a species-specific trait in Gastropoda, not affected significantly by external factors such as sampling date or sampling locality. To test this assumption, we estimated the variation in assortativity indices (the strengths of the assortment –  $r_p$ ) for each species of Gastropoda included into our database.

When comparing different species (or groups of species), the original values of the correlation coefficients ( $r_p$ ) were transformed into z-estimates by means of Fisher’s z transformation. These estimates were subsequently used to determine the significance of the intergroup differences based on the variance analysis algorithm (i.e. calculating the  $Q_B$  and  $Q_W$  values) proposed by Lipsey & Wilson (2000). In addition, for each group of species, the mean weighted z-score and its statistical error ( $\bar{z} \pm S\bar{z}$ ), as well as the 95% confidence interval ( $z_L$ – $z_U$ ) were calculated:

$$\bar{z} = \frac{\sum_{i=1}^k Z_i \cdot (n_i - 3)}{\sum_{i=1}^k (n_i - 3)} \quad (1)$$

$$S_{\bar{z}} = \frac{1}{\sqrt{\sum_{i=1}^k (n_i - 3)}} \quad (2)$$

$$z_L = \bar{z} - 1,96 \cdot S_{\bar{z}}, \quad (3)$$

$$z_U = \bar{z} + 1,96 \cdot S_{\bar{z}}, \quad (4)$$

where  $n_i$  –  $i$ th sample size;  $k$  – number of objects in a given group.

The Q-values that were used to test the homogeneity of the  $z_i$  estimates in the group were calculated using the formula:

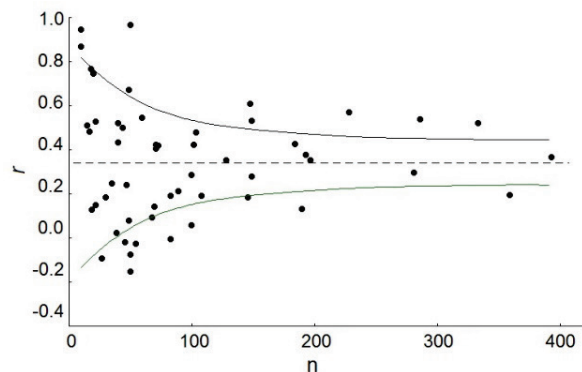
$$Q = \sum_{i=1}^k [(z_i - \bar{z})^2 \cdot (n_i - 3)] \quad (5)$$

It is known (Lipsey & Wilson, 2000) that this value has  $\chi^2$ -distribution with  $k-1$  degrees of freedom.

### Estimating the strength of assortment

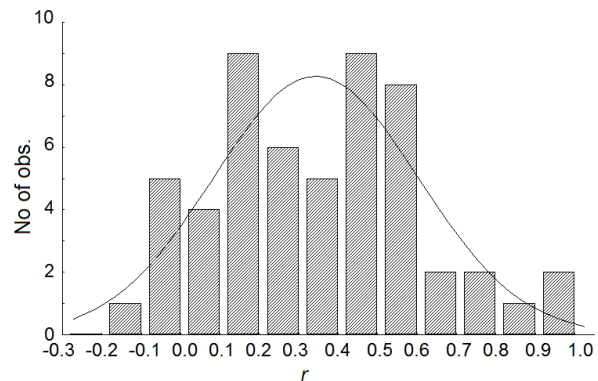
We checked our set of publications for possible bias by means of the funnel plot method. It revealed that virtually all the points representing individual studies form a funnel-shaped dispersion on a scatterplot that lies along the line representing the estimate of the generalized mean  $r_{gen} =$

0.343 (a test based on the linear regression model:  $a = 0.342 \pm 0.054$ ,  $P < 0.001$ ;  $b = 0.000002 \pm 0.000395$ ,  $P = 0.997$ ), and uniformly fill the funnel-shaped space between the lines of 95% confidence interval of the correlation coefficient for a given sample size adjusted for the overall mean (Fig. 1). It confirms the lack of serious bias in the data used in our meta-analysis.



**Fig. 1.** Funnel plot of relationship between the correlation coefficient values ( $r$ ) and number of pairs ( $n$ ) analyzed in studies devoted to size-assortative mating in Gastropoda: the dashed line corresponds to the general mean ( $r_{gen} = 0.343$ ); the two bold curves correspond to the 95% confidence interval for  $r$  adjusted for the general mean

The distribution of the estimates of the correlation coefficient (or its analogs) between copulating individuals among the various gastropod species has a shape close to the normal distribution (Kolmogorov-Smirnov’s  $d_{KS} = 0.061$ ;  $P > 0.20$ ). Moreover, most estimates are concentrated within a range of about 0.4, from 0.2 to 0.6 (Fig. 2).



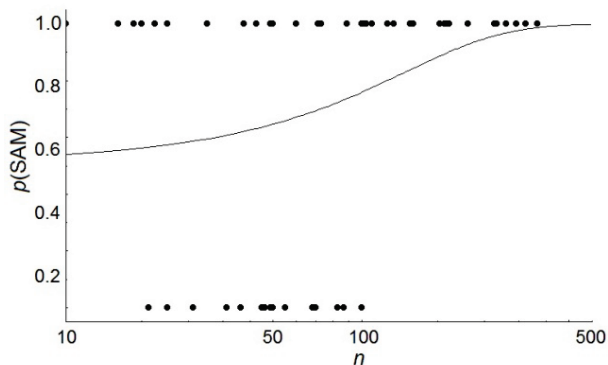
**Fig. 2.** Histogram of distribution of estimates of the correlation coefficient ( $r$ ) between sizes of copulating individuals in varied species of Gastropoda included into meta-analysis: Kolmogorov-Smirnov  $d_{KS} = 0.061$ ;  $P > 0.20$ ); the theoretical curve of normal distribution is added

We found that the probability of obtaining reliable estimates of the correlation coefficient between the sizes of copulating individuals is dependent upon the number of pairs used in the analysis (logistic regression:  $\chi^2 = 8.92$ ;  $df = 1$ ;  $P = 0.0028$ ). Despite the fact that reliable estimates of the correlation coefficient have already been found at  $n = 10$ , when 50 pairs are included in the analysis, the probability that AM will be detected is 65%, after inclusion of 100 pairs – 76%, and 150 pairs or more – exceeds 84% (Fig. 3).

The range of estimates of the strength of assortment between individuals for species included into our meta-analysis (46 cases) is very wide: from  $-0.155$  (*B. cylindrica*; Kramarenko & Kramarenko, 2019) to  $0.966$  (*V. sloanii*, a terrestrial slug; Clarke & Fields, 2013). Integrally, for the studied species of Gastropoda, the average weighted estimate of the strength of assortment between the sizes of copulating ( $\bar{z} \pm S\bar{z}$ ) individuals was  $0.381 \pm 0.014$ .

It is characteristic that out of six instances of a negative correlation between the sizes of copulating individuals, neither of them was significant. The average weighted estimate only for negative correlation coefficients is  $-0.055 \pm 0.058$  (95% confidence interval:  $-0.169$ – $0.060$ ). Using

this estimate, the null hypothesis cannot be rejected since the confidence interval includes zero. Thus, it can be argued that the existence of the negative size-assortative mating in Gastropoda has not yet been proved. On the other hand, if only statistically significant cases of size-assortative mating are considered (37 cases out of 58, or 63.7%), the average weighted estimate of the strength of assortment between sizes of copulating mollusks is  $0.439 \pm 0.015$  (95% confidence interval: 0.409–0.468).



**Fig. 3.** Logistic regression of relationship between probability of size-assortative mating ( $p_{(SAM)}$ ) and the number of pairs included into analysis ( $n$ ):  $\chi^2 = 8.92$ ;  $df = 1$ ;  $P = 0.0028$  (semi-log graph)

The mating system (hermaphroditism vs. gonochorism) significantly influences the strength of assortment in the mating partner choice among different species of mollusks ( $Q_B = 16.896$ ;  $df = 1$ ;  $P < 0.001$ ). The gonochorist taxa demonstrate the higher strength of assortment as compared to the hermaphrodites ( $0.448 \pm 0.021$  and  $0.332 \pm 0.018$ , respectively).

The environmental characteristics of gastropods, on the contrary, had no significant effect on the degree of AM (for aquatic species:  $0.399 \pm 0.017$ ; for terrestrial species:  $0.345 \pm 0.024$ ;  $Q_B = 3.301$ ;  $df = 1$ ;  $P = 0.069$ ).

If we consider the mating system and the environment simultaneously, the positive size-assortativity is most pronounced among the gonochorist snails living in the aquatic environment ( $0.448 \pm 0.021$ ), while among the aquatic hermaphroditic species it is the weakest ( $0.315 \pm 0.028$ ). In general, there are significant differences ( $Q_B = 17.595$ ;  $df = 2$ ;  $P < 0.001$ ) in the strength of assortment among the three studied groups of gastropods (Table 2).

**Table 2**

The strength of size-assortative mating in three groups of Gastropoda differing in their reproductive systems and environment

Group	$k$	$\bar{Z} \pm S\bar{z}$	95% CI
Aquatic gonochorists	17	$0.448 \pm 0.021$	0.406–0.490
Terrestrial hermaphrodites	15	$0.345 \pm 0.024$	0.298–0.392
Aquatic hermaphrodites	15	$0.315 \pm 0.028$	0.260–0.370
$Q_B = 17.595$ ; $df = 2$ ; $P < 0.001$			

Notes:  $k$  – number of cases analyzed;  $\bar{Z} \pm S\bar{z}$  – the arithmetical mean of z-transformed estimates and its statistical error; 95% CI – 95% confidence interval for z-transformed estimates;  $Q_B$  – homogeneity test between groups.

The taxonomic position of mollusks influences the strength of size assortment as well ( $Q_B = 20,059$ ;  $df = 3$ ;  $P < 0,001$ ). The Caenogastropoda demonstrate the most pronounced positive size-assortativity ( $0.448 \pm 0.021$ ), whereas opisthobranchs are least inclined to select their sexual partners in respect of their body size ( $0.271 \pm 0.039$ ). The intermediate values of  $\bar{Z}$  estimates were found among the Basommatophora and Stylommatophora ( $0.359 \pm 0.040$  and  $0.345 \pm 0.024$ , respectively).

We were able to find the necessary ( $n \geq 3$ ) number of independent estimates of the strength of assortment, obtained either for different populations or at different times, only for five species of Gastropoda (Table 3).

As expected, the species-specific estimates of the strength of the size-assortative mating were significantly different between themselves ( $Q_B = 54.825$ ;  $df = 4$ ;  $P < 0.001$ ). The maximum strength of this reproductive behaviour pattern was found in a marine snail *Littorina saxatilis* ( $0.630 \pm 0.049$ ). On the other hand, this species demonstrates a significant intraspecific variability in the estimates of the strength of AM in respect of body

size ( $Q_W = 18.653$ ,  $P = 0.002$ ); it was also true for *Brephulopsis cylindrica* ( $Q_W = 18.837$ ;  $P < 0.001$ ).

**Table 3**

Assessment of the strength of size assortative mating in some species of gastropods

Species	$k$	$\bar{Z} \pm S\bar{z}$	95% CI	$Q_W (P)$
<i>L. littorea</i>	4	$0.196 \pm 0.100$	0.000–0.392	3.659 ( $P = 0.301$ )
<i>L. saxatilis</i>	6	$0.630 \pm 0.049$	0.534–0.727	18.653 ( $P = 0.002$ )
<i>A. californica</i>	3	$0.133 \pm 0.066$	0.003–0.262	2.487 ( $P = 0.288$ )
<i>B. cylindrica</i>	4	$0.152 \pm 0.068$	0.019–0.285	18.837 ( $P < 0.001$ )
<i>X. derbentina</i>	7	$0.323 \pm 0.028$	0.269–0.377	10.306 ( $P = 0.112$ )
$Q_B = 54.825$ ; $df = 4$ ; $P < 0.001$				

Notes:  $k$  – number of cases analyzed;  $\bar{Z} \pm S\bar{z}$  – the arithmetical mean of z-transformed estimates and its statistical error; 95% CI – 95% confidence interval for z-transformed estimates;  $Q_W$  – homogeneity test within groups;  $Q_B$  – homogeneity test between groups.

### Assortative mating based on shell traits in Gastropoda

The positive correlation between sizes of mating partners was observed in 39 instances (or 67.2%) out of 58 included into our meta-analysis, whereas all known cases of the negative correlation appeared non-significant. Remarkably, the examples of the positive size-assortative copulation have been observed in all higher taxa and all ecological groups of Gastropoda included into our study. The average weighted estimate of the strength of assortment between sizes of copulating mollusks is  $0.439 \pm 0.015$  (95% confidence interval: 0.409–0.468). Results of meta-analysis by Janicke et al. (2019) confirms a finding that animals typically mate assortatively (global Pearson correlation coefficient:  $r = 0.36$ ; 95% confidence interval: 0.19–0.52). And species richness was not significantly related to the strength of assortative mating across all animal families and traits.

In the majority of case studies, the Pearson's correlation coefficient has been chosen as the most 'natural' measure to reveal size-assortative mating and to estimate its strength (Amqvist et al., 1996; Jiang et al., 2013). However, other statistical methods are quite applicable for this purpose. For instance, Kimura et al. (2015), in their study of AM in the land snail *Bradybaena pellucida*, used the intraclass correlation coefficient ( $r_i$ ) calculated on the basis of ANOVA (Kramarenko & Kramarenko, 2019). Saur (1990), Hull (1998), and Ng et al. (2016) preferred the rank correlation coefficients (Spearman's or Kendall's) as more robust to outliers. Edwards (1968), in a study of AM in the marine caenogastropod *Olivella biplicata*, used the linear regression coefficient to assess the relationship between sizes of males and females taken in courting pairs.

On the other hand, some researchers (Angeloni, 2003; Chaîne & Angeloni, 2005) applied the logistic regression of relationship between probability of mating and the differences in size between courting snails to reject the hypothesis of a random choice of the sexual partner. However, such method is more applicable for laboratory conditions when the individuals are given the opportunity to choose among potential partners. Baur (1992) conducted a similar experiment while studying AM in two species of terrestrial gastropods, *Arianta arbustorum*, and *Helix pomatia*. This author divided the experimental animals into three size cohorts (large, medium, and small) and used Pearson's chi-square test to test the probability of formation of pairs consisting of partners of different size. An analogous approach (with only two size cohorts, large and small) was applied by Koene et al. (2007) and Jordaens et al. (2005) in their experiments on the selectivity of partner choice in the aquatic basommatophoran *Lymnaea stagnalis* and the amphibious mollusk *Succinea putris*. Sometimes, the age cohorts are analyzed instead of groups of snails of different size. For instance, Tomiyama (1996) formed two cohorts, of young and old snails, in a study of AM in the land snail *Achatina fulica*.

The use of the non-parametric permutation criteria represents another option (Kramarenko & Kramarenko, 2019). Among others, such an approach was followed by Pal et al. (2006) in their analysis of size-assortative copulation in hermaphroditic sea limpets (*Siphonaria capensis*).

The range of traits served as proxies for the body size of mollusks is rather wide. In non-shelled animals, such as sea hares (*Aplysia*), it may be the body mass or body volume (Pennings, 1991; Angeloni & Bradbury,



1999). In shell-bearing snails, the shell volume is also used (Baur, 1992; Ng & Williams, 2012; Kimura et al., 2015), but simpler measures like absolute shell height or width remain most popular.

The assessments of the strength of the size-assortative mating depend on which conchometric variables are used as “proxies” for the shell size (Kramarenko & Kramarenko, 2019). A similar situation was observed in a study of size-assortative mating in the nudibranch snail *Felimare zebra* (Crozier, 1918). In this species, the body lengths of the copulating partners proved to be highly correlated ( $r = 0.608$ ;  $P < 0.001$ ), while the use of the body volume did not give a significant relationship ( $r = 0.135$ ;  $P = 0.28$ ).

Of the qualitative traits potentially determining the reproductive selectivity of gastropods, three have been studied most often: ecotypic identity, shell banding polymorphism, and chirality (direction of shell coiling).

AM in respect of the ecophenotypic variation was studied mostly in the Littorinidae, a family of the marine intertidal gastropods (Perini et al., 2020). Many species of this family consist of two sympatric intraspecific ecotypes differing from each other both phenotypically and ecologically. For example, within *Littorina saxatilis* of Galicia (Spain), two ecotypes have been delineated (Johannesson et al., 1995): SU-morph (mollusks with smooth shell surface and without pigmented bands), and RB-morph (ridged shell surface bearing pigmented bands). The two ecotypes occur sympatrically in stony biotopes alongside the shores of Spain and demonstrate clear positive AM with respect to morphs – the values of the Yule’s V index varied from 0.55 to 1.00 (the mean value was 0.77). The null-hypothesis of random mating was rejected in 10 cases out of 12, thus showing that the snails refuse to mate with a partner of a contrasting morph (Rolán-Alvarez et al., 1999).

Two intraspecific ecotypes were delineated within populations of *L. saxatilis* in West Sweden (Janson, 1982): E(xposed)-ecotype (small snails with fragile shells inhabiting wave-swept rocky surfaces devoid of crabs) and S(heltered)-ecotype (larger snails with thick shell walls present in boulder shores where crabs are abundant). The two ecotypes are potentially able to interbreed but due to strong positive AM, the gene flow between the two groups is impeded (Johannesson et al., 2008).

In England, the populations of *L. saxatilis* also are represented by two ecotypes called H- and M-morphs. The former includes snails with thin and ridged shell surface and wide aperture, living at low depths, whereas another morph is characterized by thick globose shells with smooth ribs, the snails inhabit moderate depths (Hull et al., 1996). Though positive AM was recorded in both ecotypes, it was more strongly expressed in snails of the M-morph (Pickles & Graham, 1999). Under laboratory conditions, an M-population showed complete assortative mating to type, irrespective of the density of H- and M-females, whereas at low densities the H-males did occasionally mate with M-females (Hull, 1998).

A similar situation was found in other littorinid species, *Littorina brevicula*, inhabiting Japan (Kyushu Island). The two morphotypes, S-type (slender shell) and G-type (globose shell), exhibit positive AM, however, its strength depends on depth: the two ecotypes mated assortatively in the upper shore, but not in the mid shore (Takada & Rolán-Alvarez, 2000).

Two mechanisms of the AM formation have usually been discussed as possible explanations for the cases described above. First, it has been hypothesized that the spatial distribution of individuals of different morphs may be non-random (Johannesson et al., 1995; Rolán-Alvarez et al., 1999). Another explanation is that the copulation of pairs consisting of individuals of the same ecotype is longer and less frequently interrupted than in mating of snails of contrasting morphs (Hollander et al., 2005).

In many groups of animals, species exhibiting AM with respect to colour variation (body, fur or feather colouration) are known. Such examples have been documented among vertebrates – in mammals (Hedrick et al., 2016), birds (Rull et al., 2016), reptiles (Pérez de Lanuza et al., 2016), amphibians (Gade et al., 2016), and fishes (Martin, 2013). Similar cases were found among invertebrates, including sea urchins (Calderón et al., 2010) and insects (Van Den Berg et al., 1984).

In mollusks, however, random mating with respect to shell colouration and banding pattern has usually been reported (Schilder, 1950; Schmetter, 1950; Lamotte, 1951; Wolda, 1963). Our own data (Kramarenko & Kramarenko, 2019) do not contradict this – the null-hypothesis of random mating in relation to shell phenotype in *Xeropicta derbentina* was rejected

in 2 cases out of 7. The two proven cases of AM in this snail were caused by a deficiency of pairs made up of individuals of contrasting morphs, i.e. the positive assortativity has been observed.

Rolán-Alvarez & Ekendahl (1996) have described an example of the negative AM (disassortativity) with respect to colour variations in a marine littorinid gastropod, *Littorina fabalis*. This pattern of the mate choice is regarded as the main mechanism of the maintenance of the shell colour polymorphism in this snail (Rolán-Alvarez et al., 2012). All species and populations of the subgenus *Neritrema* (*Littorina fabalis*, *L. obtusata*, *L. saxatilis*) show a systematic tendency towards negative assortative mating when shell colour is grouped in the broad categories ‘light’ and ‘dark’. Moreover, a more detailed analysis of each colour separately suggests that shell colour may not be the main target of assortative mating, but perhaps a physically-linked trait to the real target of selection (Gefæll et al., 2021).

In many taxa of gastropods, the intraspecific polymorphism in regard to shell chirality is known. Meisenheimer (1912) was, probably, the first author to suppose that the difference in direction of shell coiling in land mollusks may represent a serious obstacle to their successful copulation. Since 1912, this consideration had repeatedly been confirmed by the students of Stylommatophora (Janssen, 1966; Clarke & Murray, 1969).

The first experimental evidence of the reality of the positive AM with respect to shell chirality was obtained for the land snail species *Partula suturalis* (family Partulidae). In Johnson’s (1982) experiments, of 34 pairs of *P. suturalis* consisting of individuals with shells of the same coiling direction, successful mating was registered in 15 cases (44%), whereas among 26 pairs formed of snails with contrasting chirality only three pairs (12%) managed to mate. The same was true for another land snail, *Bradybaena similis*, – the pairs consisting of similar partners were able to copulate in 33 cases out of 38 (87%), while the mating success of pairs of contrasting morphs was much lower – 4 cases out of 23, or 17% (Asami et al., 1998).

In both cases, the null-hypothesis of random mate choice was rejected and the existence of the positive assortativity was proven.

Remarkably, reproductive success may be different in individuals of contrasting chirality. In the freshwater basommatophoran *Lymnaea stagnalis*, left-coiled snails may fertilize the dextral conspecifics but the opposite is not true (Koene & Cosijn, 2012).

A negative AM with respect to coiling direction has been reported in at least one case. As Schilthuizen et al. (2007) have shown, in *Amphidromus inversus*, a South-East Asian tree snail species, dextral and sinistral individuals tend to copulate more frequently than expected by chance, and the deficiency of pairs consisting of the same morph is observed. This mechanism was invoked to explain why this snail species demonstrates a rare phenomenon of antisymmetry when dextral (D) and sinistral (S) individuals occur sympatrically in nearly equal proportions (Schilthuizen et al., 2007).

## Conclusion

The positive correlation between sizes of mating partners was observed in 39 instances (or 67.2%) out of 58 included into our meta-analysis, whereas all known cases of the negative correlation appeared non-significant. Remarkably, the examples of the positive size-assortative copulation have been observed in all higher taxa and all ecological groups of Gastropoda included into our study, and both in dioecious and gonochoristic species. However, this conclusion should be taken with caution, since the absolute number of gastropod species which have been studied in this respect is negligible as compared to the total number of extant species in this group. One may predict theoretically that, since there is a positive relationship between body size and fecundity in snails, different clades of these animals should independently develop AM as a reproductive strategy. Our data give some empirical support for this prediction. The selective importance of size-assortative mate choice is highly probable.

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