

# Assortative mating by size: a meta-analysis of mating patterns in water striders

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## Summary

Assortative mating by size is a common mating pattern that can be generated by several different behavioural mechanisms, with different evolutionary implications. Assortative mating is typically associated with sexual selection and has been regarded as an attribute of populations, species, mating systems or even higher order taxa. In most animal groups, however, appropriate analyses of assortative mating at these different levels are lacking and the causes and forms of assortative mating are poorly understood. Here, we analyse 45 different population level estimates of assortative mating and non-random mating by size in seven confamilial species of water striders that share a common mating system. A hierarchical comparative analysis shows that virtually all the variance within the clade occurs among samples within species. We then employ meta-analysis to estimate the overall strength of assortative mating, to determine the form of assortative mating and to further assess potential differences among species as well as the probable causes of assortative mating in this group of insects. We found overall weak but highly significant positive assortative mating. We show that analyses of the degree of heteroscedasticity in plots of male versus female size are critical, since the evolutionary implications of 'true' and 'apparent' assortative mating differ widely and conclude that the positive assortative mating observed in water striders was of the 'true' rather than the 'apparent' form. Further, within samples, mating individuals were significantly larger than non-mating individuals in both males and females. All of these non-random mating patterns were consistent among species and we conclude that weak positive assortative mating by size is a general characteristic of those water strider species that share this mating system. We use our results to illustrate the importance of distinguishing between different forms of assortative mating, to discriminate between various behavioural causes of assortative mating and to assess potential sources of interpopulational variance in estimates of assortative mating. Finally, we discuss the value of using meta-analytic techniques for detecting overall patterns in multiple studies of non-random mating.

**Keywords:** assortative mating; sexual selection; meta-analysis; genetic variation; non-random mating; Gerridae

## Introduction

Assortative mating by size, or homogamy, is typically defined as a positive correlation between the sizes of mates within a population or sample (reviews in Ridley, 1983; Crespi, 1989). Assortative mating has received a great deal of attention from theorists and empiricists and is one of the most common mating patterns in nature. It is usually investigated within the context of sexual selection because of its link to non-random mating success (Arak, 1983; Ridley, 1983). Assortative mating has profound evolutionary consequences, because it typically promotes the maintenance of genetic variation within populations and may enable population divergence and

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speciation, under many circumstances (Crow and Felsenstein, 1968; Partridge, 1983; Ridley, 1983; Crespi, 1989; Williams and Sarkar, 1994). Assortative mating has been analysed at several different levels, reflecting the fact that properties of populations, species, higher order taxa and/or mating systems may actually cause assortative mating (Ridley, 1983; Crespi, 1989).

Crespi (1989) stressed that the apparently simple pattern of assortative mating may actually describe more than one distinct relationship between male and female sizes and each relationship may result from more than one distinct mechanism. Distinguishing among mechanisms has proved difficult even in the more well-studied species (e.g. in gammarids: Dick and Elwood, 1993; Ward, 1993; Ward and Porter, 1993). In a comparative analysis, Crespi (1989) concluded that assortative mating in arthropods has multiple causes, that no single process is necessary and that any of several processes is sufficient. Distinguishing among patterns and causal pathways for each pattern requires two lines of investigation. First, detailed studies of the pattern of assortment and other components of non-random mating by size and, second, mechanistic studies of the components of mating and their contribution to non-random mating by size. The current study is concerned with the first line of investigation.

### **Patterns of assortative mating and their causes**

What we will refer to as 'true' assortment is described by a linear relationship between male and female sizes where observations are symmetrically distributed around the regression line. This is what is normally meant by assortative mating. In contrast, there may be 'apparent' assortment where a positive regression results from increased or decreased variance in male size with increased female size (Fig. 1b and c), rather than a true linear relation (Crespi, 1989). This will be the case only if the strength of any large or small male mating advantage is related to the size of the mate (not to be confused with size advantages which are general and not related to the size of the mate; cf. below). This type of relative large male advantage will occur if large males are able to mate with all females, while small males are restricted to mate primarily with small females (Fig. 1b) (for an example, see Christy, 1983). Alternatively, such relative small male advantage will occur if small males are able to mate with all females, while large males are restricted to mate primarily with large females (Fig. 1c). We show that the distinction between true and apparent assortative mating is critical, because these forms have different evolutionary implications (see discussion). This, however, requires information about the residuals of the relationship describing assortative mating and we suggest a statistical procedure for evaluations of such relationships. Unfortunately, such information is rarely given and often plots of male and female size are not even shown (but see Christy, 1983; Reid *et al.*, 1994). Therefore, many cases of assortative mating may actually be of the apparent rather than true form.

A number of different mechanisms may result in true assortative mating. Following Crespi (1989), the causes of true assortative mating may be broadly classified into three categories: (1) mate choice, (2) mate availability and (3) mating constraints (Table 1). Based on these alternative mechanisms, it is possible to generate predictions about the pattern of large or small individual mating advantage, as measured by the mean size of mating individuals divided by that of non-mating individuals of each sex (hence, 'size ratios'). Mate choice will produce true assortative mating if individuals of one sex tend to choose large mates, provided that it is combined with intrasexual competition within the choosy sex in which there is large size advantage or if both sexes choose large mates (Crespi, 1989). Irrespective of which sex exercises mate choice, we would expect assortative mating to be associated with size ratios larger than 1 in both sexes, because of the combined effects of mate choice and intrasexual competition.

Some forms of size-differential mate availability may also result in true assortative mating. A relatively greater availability of large females will do so if it is combined with large male

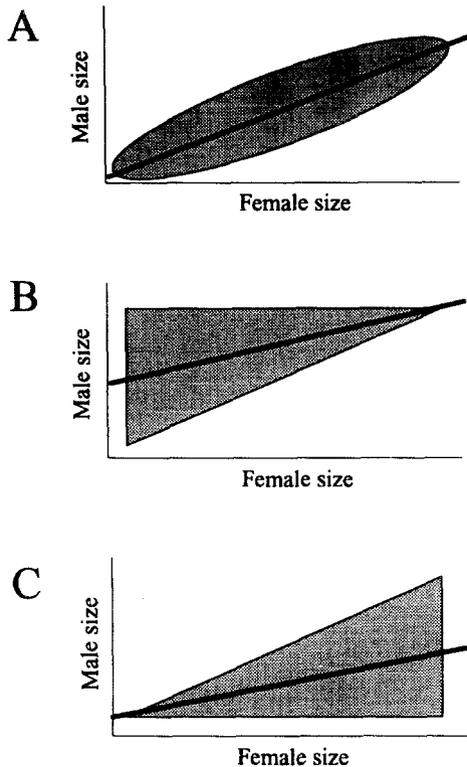


Figure 1. Three forms of assortative mating. The true form (a) is distinguished by a linear relationship between the sizes of mating males and females, where observations are distributed symmetrically around the regression line. The apparent forms (b and c) are recognized by linear relationships between male and female size where observations are delineated by a triangle around the regression line (heteroscedasticity).

advantage in intrasexual competition for females or female choice of large males. Size-related female availability may arise for a variety of reasons (see Crespi, 1989). In any case, mating males will be larger than non-mating males and mating females will tend to be larger than non-mating females as a result of increased availability. Similarly, true assortative mating may also result from the size-differential availability of both sexes resulting from temporal or spatial covariation of the sizes of males and females. For example, microhabitat characteristics may segregate individuals by size (Ward and Porter, 1993). In these cases, there is no obvious reason to expect size ratios different from 1 in either sex.

Finally, true assortative mating will result if there is some constraint that limits pairing to those that achieve some relative fit (e.g. Brown, 1993). These constraints may result from either physical or energetic barriers. For example, mismatched pairs may have difficulties during courtship, copulation or mate guarding. If true assortative mating is caused by such constraints, there is again no obvious reason to expect size ratios different from 1 in either sex.

#### **A case study – assortative mating in water striders**

Water striders (Heteroptera: Gerridae) form an ecologically rather homogenous family of predatory/scavenging bugs, inhabiting water surfaces of aquatic habitats (Spence and Andersen,

Table 1. Summary of the various hypotheses for assortative mating (after Crespi, 1989) and some of their predictions

Hypothesis	Predictions			
	Form of assortative mating under field conditions	Assortative mating under laboratory conditions	Male size ratio	Female size ratio
1. Mate choice (with intrasexual competition)				
(a) Male choice	True	Yes	> 1	> 1
(b) Female choice	True	Yes	> 1	> 1
2. Mate availability				
(a) Female availability	True	No/Yes	> 1	> 1
(b) Temporal or spatial covariation	True	No	≈ 1	≈ 1
3. Constraints	True	Yes	≈ 1	≈ 1
4. Male size advantage related to the size of the mate				
(a) Relative large male advantage	Apparent	Yes	> 1	< 1
(b) Relative small male advantage	Apparent	Yes	< 1	> 1
Observed pattern	True	Yes	> 1	> 1

Size ratios refer to the mean size of mating individuals divided by the mean size of non-mating individuals.

1994). In most species, the basic mating scheme can be described as follows (see Rowe *et al.*, 1994; Spence and Andersen, 1994; Arnqvist, 1995 for reviews). Matings are initiated by males who lunge at and attempt to grasp females. Females are typically reluctant to mate and thus try to dislodge males by struggling vigorously. If the male is able to subdue the female, copulation follows. Copulation is followed by a guarding period of variable duration where the male rides passively on the back of the female. Matings are usually terminated with a post-mating struggle initiated by the female. Both sexes mate multiply and matings are typically prolonged by the mate guarding phase. This description of water strider mating behaviour is considered the plesiomorphic mating system within the family (type I, *sensu* Arnqvist, 1995) and is directly applicable for all species included in the current analysis.

There appears to be a tendency toward positive assortative mating in water striders. However, correlation coefficients are rarely significant for single samples and a great deal of variation exists in the strength and sign of correlations within and among populations (Foster and Treherne, 1982; Fairbairn, 1988; Arnqvist, 1989, 1992c). To our knowledge, only two significant single-sample observations have been published (Fairbairn, 1988). This may reflect a general trend within the clade towards weak assortative mating combined with inadequate sample sizes and/or strong environmental effects or reflect significant differences among species in mating patterns. In an analysis of mating patterns in three species of water striders, Fairbairn (1988) found evidence for assortment in *Aquarius remigis* but not in *Gerris comatus* or *Gerris buenoi*. However, no statistical comparison among species was carried out. Assortative mating in her populations was weak and there was a high degree of variability in correlation coefficients between samples in each species. Since weak assortative mating cannot be detected if the sample size is not very large, Fairbairn (1988) suggested that samples should be combined within species and analysed with analysis of covariance or that sample sizes should be drastically increased. Crespi (1989) has criticized the former technique because combining samples collected under different environmental conditions potentially obscures real differences among samples. The latter technique will often

be impractical and limited, since several hundred pairs may be required to characterize only a single population.

Rubenstein (1984) suggested that there may only be apparent assortative mating in water striders. He argued that a relative large male mating advantage would produce a weak pattern of apparent assortative mating (see Fig. 1b), but provided no supportive data. Two mechanisms have been suggested to account for true assortative mating in water striders. First, based on the framework provided by Ridley (1983), Fairbairn (1988) suggested that the male choice of large females, in combination with large male advantage in intrasexual competition, was responsible for assortative mating. Although mating females were larger than non-mating females in this and in other studies (Fairbairn, 1988; Krupa and Sih, 1993), there is no direct evidence of male choice of large females in water striders. Moreover, a relatively large size of mating females cannot be taken as evidence for male choice of large females, since such a pattern can arise for a number of alternative reasons (Table 1). Second, Crespi (1989) noted that water strider individuals of different species and larval instars tend to segregate spatially by size (Spence, 1981; Nummelin *et al.*, 1984). If such size-related differences in habitat use occurs also within each sex in a given population (Rubenstein, 1984), spatial covariation in size between mates may be responsible for assortative mating.

Discussions of assortative mating in our model system have thus paralleled those of more general treatments of the problem: it is not clear whether weak assortative mating is a general characteristic of water strider mating systems, whether it is of the true or apparent form, if it is limited only to certain species or its causal basis. These ambiguities are characteristic of much of this field of study (Ridley, 1983; Crespi, 1989). In the current paper, we analyse a large and unique set of data on non-random mating patterns in a suite of water strider species. Our main goal is to detect and characterize weak mating patterns within the clade. Even though assortative mating is a population-level phenomenon, we suggest that the behavioural processes that cause assortative mating in populations within this clade are likely to be specific to their common mating system rather than in being species specific. We first use a hierarchical comparative analysis of variance to identify the relevant level of analysis and then employ meta-analysis to analyse our data. Meta-analysis refers to a set of statistical procedures that is designed to combine and compare the results of several independent studies in a joint analysis (Hedges and Olkin, 1985; Hunter and Schmidt, 1990; Rosenthal, 1991; Rosenthal and Rosnow, 1991; Cooper and Hedges, 1994). Meta-analysis has only recently attracted attention among and been employed by evolutionary ecologists (Järvinen, 1991; Gurevitch *et al.*, 1992; VanderWerf, 1992; Gurevitch and Hedges, 1993; Poulin, 1994; Tonhasca and Byrne, 1994), but has already proven extremely useful for quantitative summaries of research domains in our field (see Arnqvist and Wooster, 1995 for an introduction). In our analysis, 45 population-level data sets from seven different species are analysed jointly to determine both the strength and form of assortative mating and the size ratios of mating and non-mating individuals. We show that meta-analysis is a powerful method for the purpose of detecting and studying large-scale patterns of non-random mating such as weak assortative mating. Further, we use the pattern of non-random mating to distinguish among the various forms and the potential causes of assortative mating.

## Methods

Our database includes 45 samples of assortative mating from seven different water strider species on three continents. The total number of mating pairs in this database is 1630 (see the Appendix). Twelve of the data sets have been obtained from the literature and the remaining 33 are new. The seven species share a common mating system (see above). The basic sampling method for each of

these 45 data sets was identical; each population was scanned for mating pairs which were captured with hand nets. The body lengths of individual males and females were thereafter measured, either with an ocular micrometer or Vernier calipers (as in Fairbairn, 1988; Krupa and Sih, 1993). In 25 of the data sets, samples of single individuals were also collected. In these cases, the intent was to capture all single individuals present at the sample site or to sample approximately the same number of single individuals of each sex as those sampled when mating.

For each sample, the Pearson correlation coefficient ( $r_p$ ) of male and female body lengths in mating pairs was used as a measure of assortative mating. To assess the magnitude and shape of triangularity of this relationship (Fig. 1b and c), an index of heteroscedasticity was obtained for each data set by the following procedure (see Zar, 1984, p. 288). The male body length was regressed on the female body length. The absolute value of male residuals generated in this regression were thereafter correlated with the female body length, using Spearman rank correlation ( $r_s$ ). This index of heteroscedasticity will be  $< 0$  if there is a relative large male advantage (Fig. 1b) and  $> 0$  if there is a relative small male advantage (Fig. 1c). In the meta-analysis described below, these two correlation coefficients are used as measures of effect size for the degree of assortment and heteroscedasticity, respectively. The term 'effect size' in meta-analysis refers to a general, common measure of the statistical magnitude of an effect in a particular study or sample. Correlation coefficients are common measures of effect size, since they possess many of the properties desired of a measure of effect size in meta-analysis (see Hedges and Olkin, 1985; Rosenthal, 1991; Cooper and Hedges, 1994).

Since phylogenetic relationships and unequal representation within the clade could potentially bias our analysis, we first performed a nested analysis of variance on the data in our database (Sokal and Rohlf, 1981). This analysis describes the distribution of variance among samples by partitioning the total variance in the database into components representing each of the nested hierarchical taxonomic levels in a clade and, thus, provides an objective criterion for which level should be used for analysis (see Harvey and Pagel, 1991). Both the estimate of assortative mating and the index of heteroscedasticity were subjected to such analyses.

Since our comparative analysis revealed no role of taxonomic affiliation within the clade (see results section), we analysed population level mating patterns in a meta-analysis. The meta-analysis considers each sample (population) of assortative mating as an observation, as opposed to regarding each single mating within a sample as an independent observation. As we show, this approach may be statistically more powerful in detecting weak assortative mating and in distinguishing among patterns of non-random mating than more traditional methods of analysing such data, provided a sufficient meta-sample of data sets is available. The data are also analysed to determine further if species exhibit differences in mating patterns and to determine if other metrics associated with species and samples affect these patterns.

When combining multiple studies to elucidate overall trends, some studies may provide more reliable estimates than others due to larger sample sizes. One of the major features of meta-analysis is that it allows us to account for the reliability of different estimates by giving greater weight to large samples compared to small samples. Prior to our calculation of weighted mean assortative mating ( $r_p$ ) and weighted mean index of heteroscedasticity ( $r_s$ ), all correlation coefficients were transformed to Fisher's  $Z_r$ . To find the weighted means of Fisher's  $Z_r$ , we used the following equation:

$$\bar{Z}_r = \frac{\sum(n_j - 3)Z_{rj}}{\sum(n_j - 3)} \quad (1)$$

where  $n_j$  is the sample size in sample  $j$  (Rosenthal, 1991). Weighted means of Fisher's  $Z_r$  were then converted back to weighted mean correlation coefficients as (Rosenthal and Rosnow, 1991; Cooper and Hedges, 1994):

$$\bar{r} = \frac{e^{2\bar{Z}_r} - 1}{e^{2\bar{Z}_r} + 1} \quad (2)$$

To test whether these weighted mean correlations (effect sizes) were significantly different from zero, 95% confidence intervals were computed (Shradish and Haddock, 1994). We also performed an omnibus test of the null hypothesis (weighted Stouffer procedure; Rosenthal, 1991), by converting the one-tailed  $p$  values of each individual sample into a standard normal deviate  $Z$  (positive in sign for positive effect sizes and negative in sign for negative effect sizes), weighting each  $Z$  by the sample size and then combining the weighted  $Z$ s to find the overall weighted  $Z$  as follows:

$$\text{weighted } Z = \frac{\sum(n_j - 3)Z_j}{\sqrt{\sum(n_j - 3)^2}} \quad (3)$$

The weighted  $Z$  was then converted back to obtain a two-tailed  $p$  value (see Rosenthal, 1991).

Meta-analysis also allows assessments of whether the included observations are drawn from a pool with a common distribution (Hedges and Olkin, 1985; Hunter and Schmidt, 1990). In our case, differences among taxa within the clade with regards to patterns of assortative mating or the degree of heteroscedasticity might introduce potential biases. In addition to the nested hierarchical analysis of variance described above, we further tested directly for species level effects. First, we assessed the heterogeneity of Fisher's  $Z_r$ s with a chi-square-based test statistic:

$$\chi^2(k - I) = \sum \left[ \left( n_j - Z_{rj} - \bar{Z}_r \right)^2 \right] \quad (4)$$

where  $k$  is the total number of samples (Rosenthal, 1991). This test thus weights each observation by the sample size and it represents a valid meta-analytic test of the null hypothesis that the meta-sample is statistically homogenous. Second, following tests of normality, we also performed standard unweighted ANOVAS of species effects on assortative mating and the index of heteroscedasticity using Fisher's  $Z_r$  transformed correlation coefficients for comparative purposes (Hedges and Olkin, 1985).

Various forms of dependence between studies can cause bias in meta-analysis (Hunter and Schmidt, 1990; Cooper and Hedges, 1994; Arnqvist and Wooster, 1995), much as in conventional statistics (Hurlbert, 1984). In our analysis, a potential source of bias, beyond taxonomic affiliation (see above), could be caused by systematic dependencies among samples collected at the same geographical locality. To evaluate the potential role of any such bias, we also performed all of the above analyses using only one effect size from each population/site and species (see the Appendix). We used the weighted mean correlation coefficient and the mean sample size among samples from each site and species in these analyses. Analysing pooled data from each subgroup in this way is conservative, since it significantly decreases the power of the meta-analysis (Hunter and Schmidt, 1990).

To assess whether our estimate of assortative mating in a population was associated with species or sample metrics, we performed weighted correlations between the degree of assortment and six different factors. These were the index of heteroscedasticity of the sample, the male size ratio in the sample, the female size ratio in the sample, coefficient of variation of male size in the

sample, the coefficient of variation of female size in the sample, and the species' sexual size dimorphism. Correlation coefficients were transformed to Fisher's  $Z$ , prior to these analyses and each case were given the weight  $w_i = n_i - 3$ , where  $n_i$  is the within-study sample size of the  $i$ th case (Hedges and Olkin, 1985; Cooper and Hedges, 1994).

To compare the size of mating versus non-mating individuals in each population, a size ratio was estimated as the mean body size of mating individuals divided by the mean body size of single individuals in each of the 25 data sets where matched samples of single and mating individuals were available (see the Appendix). A size ratio  $\geq 1$  thus implies that mating individuals are larger than single individuals. To generate effect sizes from these size ratios, differences in size between mating and non-mating individuals were tested with  $t$ -tests within each data set. The  $t$ -values from these tests were then transformed into absolute values of Pearson correlation coefficients by the formula (Rosenthal, 1991; Kirby, 1993):

$$|r| = \sqrt{\frac{t^2}{t^2 + (N-2)}} \quad (5)$$

These correlation coefficients were then signed (Kirby, 1993), i.e. given a positive sign for size ratios  $> 1$  and a negative sign for size ratios  $< 1$  and used as our measure of effect size of the size ratio between mating and non-mating individuals. The weighted average effect sizes were thereafter computed according to Equations 1 and 2, and the significance of these effect sizes were tested with the weighted Stouffer method (Equation 3). Finally, for the purpose of comparison, we also tested the null hypothesis of  $H_0$ : size ratio = 1 directly with unweighted standard  $t$ -tests on the actual size ratios (see the Appendix). All statistical analyses reported in this paper were performed with the SYSTAT statistical package (Wilkinson, 1987; Kirby, 1993).

## Results

The nested analyses of variance showed no role of taxonomic affiliation within the clade in affecting mating patterns (Table 2). Virtually all of the variance in our database could be attributed to variance among samples within species. Thus, these hierarchical analyses strongly suggest the population (sample) as the appropriate level for analysis (Harvey and Pagel, 1991) and therefore validate our further analyses.

Weak positive assortative mating is a general characteristic of the populations analysed in the current analysis. Although there was considerable variation among samples (correlation coefficients ranged from  $-0.200$  to  $0.516$ ; Fig. 2a), the weighted mean correlation coefficient  $r_p =$

Table 2. Hierarchical partitioning of the variance components for variation in mating patterns in water striders

Among: Within:	Samples Species	Species Subgenera	Subgenera Genera	Genera Family
Variance component	$\sigma_{sa\{sp\}}^2$	$\sigma_{sp\{su\}}^2$	$\sigma_{su\{ge\}}^2$	$\sigma_{ge\{fa\}}^2$
Assortative mating ( $r_p$ )	98.6	1.4	0.0	0.0
Index of heteroscedasticity( $r_s$ )	99.1	0.9	0.0	0.0

Values represent the percentages of total variance accounted for at successive hierarchical levels. Variance components were estimated in a three-level nested analysis of variance with unequal sample sizes (Sokal and Rohlf, 1981; Harvey and Pagel, 1991).

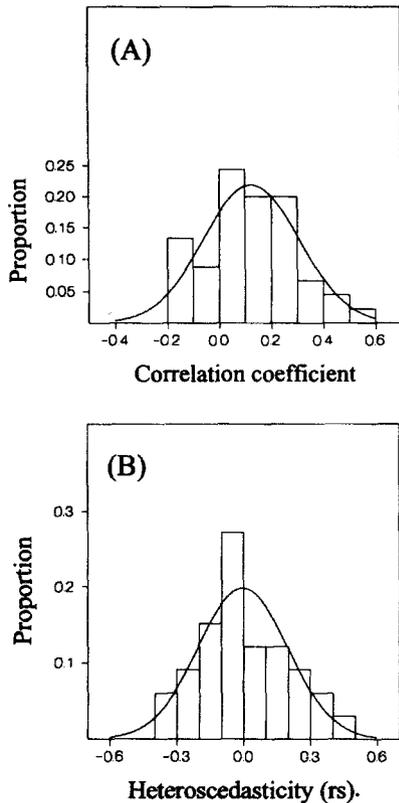


Figure 2. Frequency distributions of (a) Pearson correlation coefficients ( $n = 45$ ) describing the relationship between male and female size (our measure of assortative mating) and (b) Spearman correlation coefficients ( $n = 33$ ) describing heteroscedasticity (our index of the form of assortative mating; see text).

0.115 is highly significantly different from zero (see the Appendix) ( $95\%$  C.I.:  $0.064 \leq 0.115 \leq 0.166$ ). As expected, variation among single population estimates was clearly related to sample size (Fig. 3a). Single sample estimates of assortative mating tended to converge on the mean value as sample size increases, which validates the use of weighted analysis (see Fig. 3a: Spearman rank correlation between  $n$  and  $|(r_p - 0.123)|$ ;  $r_s = -0.329$ ,  $n = 45$ ,  $p < 0.05$ ). Assuming a true  $r_p$  of 0.12 for populations within the clade, a sample size of 429 mating pairs would be required to generate a statistical power of 0.8 in single-sample estimates at a probability level of  $\alpha = 0.05$  in one-tailed tests (the corresponding sample size in two-tailed tests is 544 pairs) (Cohen, 1988). Mean species values of assortative mating ranged from 0.048 to 0.215, but there were no indications of differences in assortative mating between species either in the weighted test of homogeneity ( $\chi^2 = 37.63$ ,  $df. = 44$ ,  $p > 0.5$ ) or in the unweighted one-way analysis of variance ( $F = 0.678$ ,  $df. = 6$ ,  $p > 0.5$ ; Fig. 4a). The distribution of Fisher's  $Z_r$  transformed estimates of assortative mating did not differ from a normal distribution (Kolmogorov–Smirnov test,  $n = 45$ ,  $p = 0.99$ ) (Fig. 2a).

There was no general trend for triangularity in the relationship between male and female body lengths in mating pairs. Indices for heteroscedasticity ranged from  $-0.326$  to  $0.516$ . The weighted mean index of heteroscedasticity was 0.011, which did not differ significantly from zero (see the

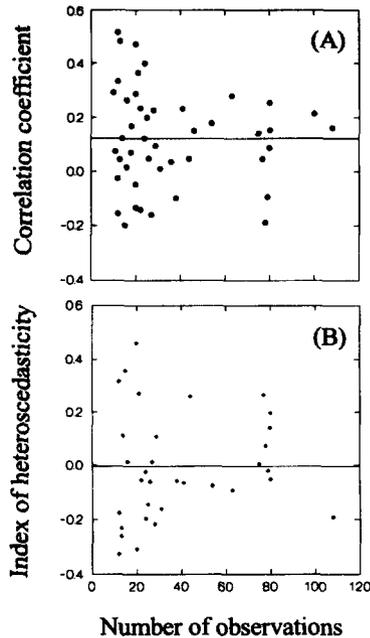


Figure 3. Plots of sample size versus effect size (i.e. funnel plots; Cooper and Hedges, 1994) for (a) the estimate of assortative mating (Pearson correlation coefficients,  $n = 45$ ) and (b) the index of heteroscedasticity (Spearman rank correlation coefficients,  $n = 33$ ). Solid lines represent unweighted means. Note that effect sizes tend to converge around the means with growing sample size.

Appendix) (95% C.I.:  $-0.044 \leq 0.011 \leq 0.066$ ). Again, the magnitude of the index of heteroscedasticity tended to converge on the mean value with increasing sample size (see Fig. 3b: Spearman rank correlation between  $n$  and  $|(r_s + 0.004)|$ ;  $r_s = -0.402$ ,  $n = 33$ ,  $p < 0.05$ ). Mean species values of heteroscedasticity ranged from  $-0.191$  to  $0.048$ , but there were no indications of differences in the index of heteroscedasticity between species either in the weighted test of homogeneity ( $\chi^2 = 34.89$ ,  $df. = 32$ ,  $p > 0.1$ ) or in the unweighted one-way analysis of variance ( $F = 0.743$ ,  $df. = 4$ ,  $p > 0.5$ ; Fig. 4b). The distribution of Fisher's  $Z_r$  transformed indices of heteroscedasticity did not differ from a normal distribution (Kolmogorov–Smirnov test,  $n = 33$ ,  $p = 0.118$ ) (Fig. 2b).

All of these analyses were also performed on data pooled within the population/site (see Methods). However, pooling data within subgroups did not alter any of the above results and conclusions, in terms of our ability or inability to reject null hypotheses at  $\alpha = 0.05$ .

The degree of assortment did not correlate with any other species or sample metric (Table 3). Thus, the degree of assortative mating in a population did not depend significantly on the sample's magnitude of heteroscedasticity, variation in size of either sex, the size ratio of mating to non-mating individuals of either sex or the magnitude of the species' sexual size dimorphism.

The unweighted mean size ratio of mating to non-mating individuals was 1.003 in males and 1.009 in females. The weighted meta-analysis showed that both size ratios are highly significantly different from  $H_0$ : size ratio = 1 and the weighted analysis confirmed that the effect of size is larger in females than in males (see the Appendix). Thus, mating individuals of both sexes are larger on average than non-mating individuals, but this effect appears to be stronger in females

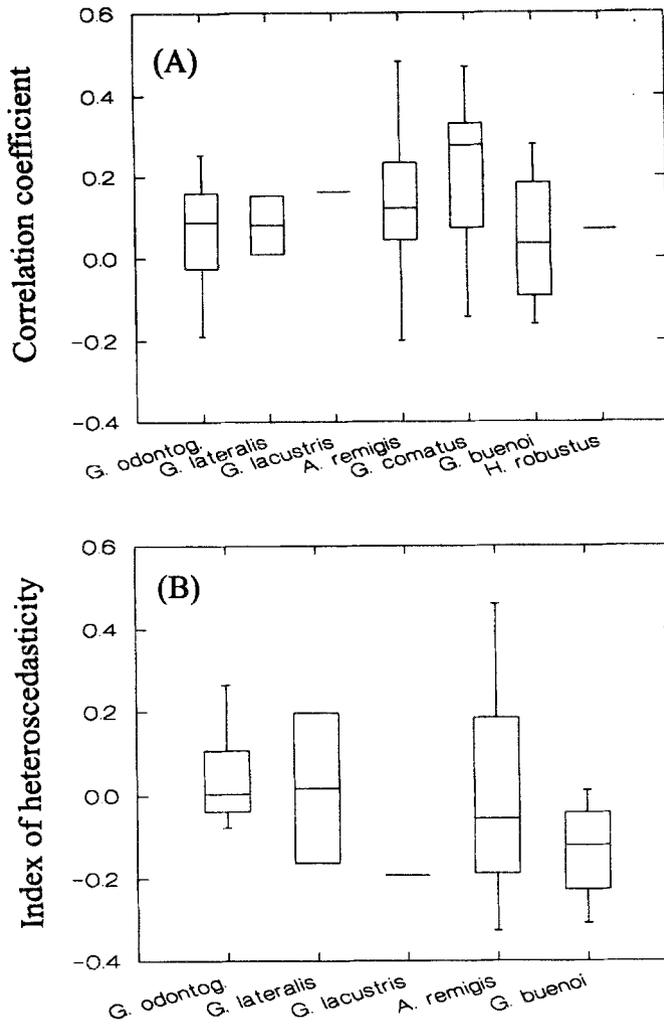


Figure 4. Box-and-whiskers plots showing interspecific variation in (a) assortative mating and (b) the index of heteroscedasticity. Boxes represent the 25th and 75th percentiles and horizontal lines within boxes represent medians.

Table 3. Weighted correlations between the degree of assortative mating and other characteristics of each population

Characteristic	$r$	$n$	$p$
Index of heteroscedasticity ( $r_s$ )	-0.12	33	> 0.5
Male size ratio	-0.16	25	> 0.4
Female size ratio	0.09	25	> 0.5
CV male size	-0.04	44	> 0.5
CV female size	-0.01	44	> 0.5
Sexual size dimorphism	-0.10	45	> 0.5

CV represents coefficient of variation

compared to males. However, a test of differences in the mean size ratio between the sexes only approached significance at the two-tailed  $\alpha = 0.05$  level (conventional paired  $t$ -test,  $t = -1.789$ ,  $df. = 24$ ,  $p = 0.086$ ). The distribution of actual size ratios did not differ significantly from normality in either sex (Kolmogorov–Smirnov test,  $n = 25$ ,  $p > 0.05$  for male size ratio,  $p [\alpha.] 0.5$  for female size ratio). It is worth noting that the mean male size ratio was not significantly different from 1 in an unweighted  $t$ -test, but significantly so in the weighted analysis (see the Appendix). This is due to three observations with size ratios considerably lower than 1, which all had comparatively low sample sizes and were thus given low weight in the meta-analysis.

## Discussion

Our study furthers the study of non-random mating both conceptually and methodologically. We provide a method for assessment of whether assortative mating is of the true or apparent form, a distinction which is of great importance for the evolutionary implications of assortative mating (see below). We also show, by our case study, that meta-analysis at the population level provides a powerful, tractable and coherent tool for detecting overall patterns in non-random mating as well as for assessing the potential sources of variation in these patterns at various levels.

The analyses of our case study revealed four clear patterns of non-random mating by size in this group of insects. First, mating was size assortative. Correlations between male and female size were weak and variable, but overall were highly significant. Second, there was no tendency towards heteroscedasticity in plots of female versus male size. Third, mating individuals were significantly larger than single individuals in both sexes. Fourth, there were no effects of taxonomic affiliation, and mating patterns were consistent among species. This consistency is expected if the major contribution to assortative mating has its origin in the mating system rather than in species-specific factors and if species share a mating system. The species used in our analysis share a similar mating system (type I *sensu* Arnqvist, 1995) and, therefore, we conclude that weak true assortative mating and a relatively large size of mating individuals appear to be general characteristics of water strider species that share this mating system. In the following discussion we put these data to three tasks. First, we use the actual pattern of covariance to distinguish among forms of assortative mating and their causes. Second, we explore the sources of variation among samples in our data set. Finally, we discuss the advantages and disadvantages of our method of analysis of assortative mating.

### *Apparent assortative mating*

Both Rubenstein (1984) and Crespi (1989) have pointed out that assortative mating may result solely from either a large or a small male mating advantage, the strength of which is related to female size. These processes lead to triangular shaped plots (apparent assortative mating) rather than to the linear plots expected from true assortative mating (Fig. 1) (Christy, 1983; Jormalainen *et al.*, 1994; Reid *et al.*, 1994). However, the crucial difference in evolutionary implications of these two forms of assortment has not previously been appreciated, nor have procedures to distinguish between them been suggested. From a population genetic perspective, evaluating the degree of heteroscedasticity is key, since apparent assortment will not be by far as potent as true assortment in promoting the maintenance of genetic variance. Under apparent assortative mating, genetic variance will be diluted by random mating at either large male (Fig. 1b) or small male (Fig. 1c) size extremes and the formal quantitative relationship between the degree of assortative mating and additive genetic variance given by, for example Crow and Felsenstein (1968) and Falconer (1981) will not be applicable. This is most easily illustrated in the case of a single locus with two alleles (cf. Falconer, 1981): in one sex, one of the homozygote genotypes will tend to

mate assortatively while the other will mate at random, while the situation is directly reversed in the other sex (e.g. Fig. 1c). This is equally true for the role of assortative mating in promoting the evolution of co-adapted gene complexes (Williams and Sarkar, 1994). In such situations, alleles in a set of co-adapted alleles will tend to be disassociated at either of the extreme gene complexes under apparent assortment and assortative mating will therefore not necessarily have effects similar to those of genetic linkage (Williams and Sarkar, 1994). Thus, if one wishes to assess the evolutionary implications of assortative mating, a simple correlation coefficient between, for example, the sizes of mates is clearly not sufficient to characterize a population.

Our analyses provide three lines of evidence that assortative mating in water striders is of the true rather than apparent form. First, residuals of regressions for each sample are, on average, symmetrically distributed around the regression axes (Fig. 2b). Second, there was no relationship between the magnitudes of heteroscedasticity and assortative mating. Such a relationship would be expected if apparent assortative mating was contributing significantly to the overall degree of assortment. Finally, the expected patterns in the size ratios of mating to non-mating males and females in apparent assortment were not met. Under simple apparent assortment, and in contrast with our results, we expect size ratios for males and females to differ from one another in deviation from 1 (Table 1), since the relative role of size in one sex is reversed in the other sex (Fig. 1b and c). Thus, we conclude that true assortative mating is characteristic of the water strider species studied here. As Fairbairn (1988) emphasized, even low degrees of assortative mating can significantly increase the overall degree of additive genetic variance. Estimates of narrow sense heritability of size is available only for one of the species included in the current analysis ( $h^2 = 0.59$  for pronotal length in *Gerris odontogaster*; Arnqvist, 1990). Based on this estimate and the equations given by Crow and Felsenstein (1968), a true assortative mating of  $r_p = 0.12$  would elevate the level of additive genetic variance at equilibrium by approximately 8%.

#### *The causes of true assortative mating*

There are a number of causal pathways through which true assortative mating may come about in the absence of any directional inter- or intrasexual selection for large males. Mating constraints are one such pathway (Part 3 in Table 1). Mating constraints comprise those constraints that narrow the potential for pairing to those that achieve some relative fit. For example, if only like-sized males and females can achieve intromission because of some mechanical barrier to other size combinations, then true assortative mating will result. There are some cases in which such constraints have been demonstrated to contribute to assortative mating (e.g. Brown, 1993). However, this mechanism alone would not produce size-related biases in matings and, thus, it cannot account for the significant size ratios we observed in both sexes (Table 1). In fact, all simple forms of mating constraints predict size ratios close to 1 for both sexes and are thus highly unlikely to be causes of assortative mating in water striders.

True assortative mating may also come about if like-sized males and females co-vary in space or time (Part 2b in Table 1). In water striders there is no temporal variation in body size on the time scale of our collections and assortative mating resulting from either spatial or temporal covariation alone would not result in any difference in size between mating and non-mating individuals. Thus, the effect we have observed on male and female size ratios is incompatible with either the spatial or temporal covariation hypothesis acting alone. A second line of evidence against this hypothesis comes from the experiments of Rowe and Arnqvist (1995) on a subset of the species studied here. In laboratory pools where all size classes co-occurred, assortative mating was observed in all three species studied (*Gerris buenoi*, *G. lacustris* and *G. lateralis*).

The remaining pathways through which true assortative mating may come about include some combination of general large male mating advantage in intrasexual competition, male or female choice for large size of mates or large female availability (Table 1). All of these pathways are expected to lead to size ratios larger than 1 in both sexes. The relatively weak male size ratio we observed may offer one explanation for the equally weak assortative mating documented here. This is supported by observations of similarly weak male size ratios compared to female size ratios in a subset of these species in the laboratory (Rowe and Arnqvist, 1995). We suggest that the causes of assortative mating in this group must explain both a strong female size ratio and a weak male size ratio. The in-depth study by Rowe and Arnqvist (1995) suggests that both male and female choice (either active or passive forms) of large mates and male exploitation competition for mates act in concert to produce weak assortative mating in water strider populations.

#### *Sources of interpopulation variance and bias*

Whatever the causes may be, assortative mating in a population reflects the combined effects of the mating behaviours of individuals in an ecological setting. If behaviours depend on that ecological setting, then so will assortative mating. Population attributes such as sex ratio, density, food availability and predator presence are known to have effects on the mating behaviour and non-random mating success of water striders (Arnqvist, 1992a,b,c, 1995; Rowe, 1992; Sih and Krupa, 1992, 1995; Krupa and Sih, 1993; Rowe *et al.*, 1994; Spence and Andersen, 1994). Thus, the degree of assortative mating in a population is likely to be partly related to the ecological setting within which the population occurs. We have documented large variation in the estimates of assortative mating among natural populations of water striders. Our analysis did not reveal any differences among species within the clade or any effects of the population attributes we measured on the degree of assortative mating. Thus, we cannot at this stage reject the hypothesis that interpopulational variance in the estimation of assortative mating is due solely to sampling error. Future investigations should seek relationships between the strength of the non-random mating patterns documented here and factors such as population density, sex ratio, predator presence and food availability in each of the populations included in the analysis.

Under some circumstances, strong interpopulation variation may introduce a bias toward weak assortative mating at the group level. First, combining taxa that are characterized by non-assortative mating with those characterized by strong assortative mating may erroneously lead to the conclusion that weak assortative mating is characteristic of the group, especially if taxa are unequally represented in the material. Second, combining samples of various size, if there is a positive covariance between sample size and the degree of assortative mating, may erroneously lead to the conclusion that species are generally characterized by weak assortative mating. Nonetheless, the weak assortative mating that we observed in the group did not result from either of these effects. Taxonomic affiliation within the clade did not account for any variance in mating patterns, the meta-sample was statistically homogeneous in weighted analyses and the species-level mating pattern did not vary between species in direct tests. There was also no effect of sample size on the magnitude of estimates of assortative mating within samples. Therefore, our conclusion that this group of water striders is characterized by weak assortative mating appears robust.

#### *Levels of analysis*

There has been considerable discussion concerning the appropriate level for analysing assortative mating. This debate results from the realization that attributes of the population (both biotic and abiotic), the species and the mating system may contribute to both the degree of assortative

mating and to its detectability (e.g. Ridley, 1983; Crespi, 1989). On the one hand, processes occurring at the population level may be so strong and specific that assortative mating should be viewed solely as an attribute of the population. On the other hand, restricting one's thinking to single populations alone is clearly unsatisfying. For example, Crespi (1989) criticized Fairbairn (1988) for combining more than one population sample in her attempt to generalize to the species level. Yet, Crespi (1989) clearly recognizes the value of generalization, given his attempt to analyse the underlying processes of assortative mating beyond the population and species, to the phyletic level (Arthropoda). Thus, controversy in levels of analysis are focused on the method of generalizing above population levels, rather than on the desirability of this goal. We have taken a new approach to this problem. Comparative analyses revealed no role of taxonomic affiliation within our data set. We therefore employed statistical methods designed for combining and comparing multiple studies, in an attempt to characterize the mating patterns within the clade. Our approach fully recognizes that assortative mating is a population characteristic, yet still allows analyses at higher levels.

Our method removes some and allows us to test for other potential pitfalls in generalizing patterns of assortative mating at the population level to higher levels. Most importantly, the method recognizes and accounts for intersample differences in reliability, by weighting observations by their sample size. However, it is possible that there are positive covariances between population conditions (e.g. density), the degree of assortative mating and sample sizes (see above). This possibility introduces three potentially serious problems. First, species could be erroneously categorized as mating assortatively or randomly, not because of any difference in assortative mating between species, but only because of differences in sample size. Second, if samples (populations) are combined for analysis (even with ANCOVA, as in Fairbairn, (1988)) then large samples will dominate the estimated species value of assortative mating. Although we have focused on positive covariance between the degree of assortative mating and sample size that is routed through density effects, such covariance (positive or negative) generated for any reason will bias results. Third, whether such covariances exist or not, estimates from large sample sizes when combined with estimates from small sample sizes will dominate the result.

Our method of analysis allows us to test for covariances between the degree of assortative mating and population properties (e.g. sample size). Moreover, the possibility of a biased analysis due to covariance between sample size and the degree of assortment can be rejected for two reasons. First, the magnitude of correlation coefficients did not depend on the sample size (Fig. 3). Second, an unweighted analysis still showed a significant positive assortment (see the Appendix). This test is based on raw correlation coefficients estimated from population samples as observations rather than mating pairs and it thus removes any potential dominance by large samples.

Finally, if one wishes to categorize populations, species or higher groups as non-random or random maters or as exhibiting different levels of non-random mating, then statistical tests are required. Meta-analysis provides several powerful tests for such differences in mating patterns (Hedges and Olkin, 1985; Hunter and Schmidt, 1990; Rosenthal, 1991). Traditionally, such categorizations has typically been carried out by simply noting the significance or lack of significance of correlation coefficients in single samples. If one group (e.g. species) is found to have a significant correlation coefficient and the other is not, then sources for this variation are sought in details of the mating system of each group (e.g. Snead and Alcock, 1985; Fairbairn, 1988). Such comparisons are clearly not satisfactory, since they do not account for variance (e.g. sampling error) within groups (Cohen, 1988). A more powerful test is to compare correlation coefficients statistically in a joint analysis. This is the approach we have taken. Our analysis revealed no differences among species within the clade in either assortative mating or other

patterns of non-random mating. In contrast, Fairbairn (1988) concluded, without a specific statistical test, that *A. remigis* mated assortatively while *G. buenoi* and *G. comatus* did not. However, a meta-analytical reanalysis of her data showed overall significant positive assortative mating (weighted mean  $r_p = 0.158$ , 95% CI:  $0.027 \leq 0.158 \leq 0.289$ , two-tailed weighted Stouffer's  $p = 0.008$ ), but revealed no evidence of a difference between species or samples in assortative mating either in a weighted test of homogeneity ( $\chi^2 = 6.80$ , df. = 10,  $p > 0.5$ ) or in pairwise Z-tests (two-tailed  $p > 0.2$  in all cases). Similarly, Snead and Alcock (1985) found that significant single-sample assortative mating occurred in only one of two meloid beetles and thus concluded that one species (*Lytta magister*) mated assortatively and the other (*Tegrodera aloga*) did not. Again, a meta-analytical reanalysis of an available subset of the data for *T. aloga* (Snead and Alcock, 1985, p. 1129) shows that this species may actually also exhibit positive assortative mating, given a larger metasample, contrary to the authors' conclusion ( $n = 9$ ; weighted mean  $r_p = 0.107$ , one-tailed weighted Stouffer's  $p = 0.102$ ; unweighted mean  $r_p = 0.128$ ,  $t = 0.231$ , one-tailed  $p = 0.026$ ). These examples illustrate the importance of testing hypotheses about interspecific variation in mating patterns by comparing population estimates statistically.

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Appendix A: A summary of the data on mating patterns in water striders

Species	Population/Site	Number of mating pairs	Estimate of assortative mating ( $r_p$ )	Index of heteroscedasticity ( $r_s$ )	Male size ratio	Female size ratio	Source
<i>G. odontogaster</i>	Långskär 1992	80	0.254	0.141	-	-	New data set
<i>G. odontogaster</i>	Lillvitkskär 1992	75	0.141	0.005	-	-	New data set
<i>G. odontogaster</i>	Trehörningsmyran 1992	80	0.088	-0.053	-	-	New data set
<i>G. odontogaster</i>	Trehörningsmyran 1990	77	0.047	0.265	1.003	1.010	New data set
<i>G. odontogaster</i>	Gimonäsdammen 1990	78	-0.189	0.074	1.004	1.011	New data set
<i>G. odontogaster</i>	Kattögeljärn 1990	79	-0.095	-0.021	1.002	1.004	New data set
<i>G. odontogaster</i>	Gimonäsdammen 1988	54	0.178	-0.076	1.003	1.008	New data set
<i>G. lateralis</i>	Tavleån 1985	31	0.010	-0.161	-	-	New data set
<i>G. lateralis</i>	Tavleån 1992	80	0.153	0.197	-	-	New data set
<i>G. lacustris</i>	Nydalasljön 1993	108	0.162	-0.191	0.999	1.008	New data set
<i>G. comatus</i>	Boucherville	16	0.262	-	1.010	0.989	Fairbairn (1988)
<i>G. comatus</i>	Nun's Island	22	-0.142	-	1.002	0.980	Fairbairn (1988)
<i>G. comatus</i>	Nun's Island	10	0.291	-	0.984	1.006	Fairbairn (1988)
<i>G. comatus</i>	Nun's Island	12	0.332	-	0.976	1.003	Fairbairn (1988)
<i>G. comatus</i>	Cap St Jacques	11	0.074	-	0.995	0.997	Fairbairn (1988)
<i>G. comatus</i>	Cap St Jacques	20	0.470	-	0.999	0.992	Fairbairn (1988)
<i>G. buenoi</i>	Nun's Island	20	-0.134	-	0.965	1.001	Fairbairn (1988)
<i>G. buenoi</i>	Nun's Island	18	0.168	-	1.018	1.008	Fairbairn (1988)
<i>G. buenoi</i>	Nun's Island	36	0.035	-	1.011	1.015	Fairbairn (1988)
<i>G. buenoi</i>	University of BC Botanical Gardens 1	27	-0.160	0.012	1.037	1.021	New data set
<i>G. buenoi</i>	University of BC Botanical Gardens 2	25	0.199	-0.145	1.012	1.021	New data set
<i>G. buenoi</i>	University of BC Botanical Gardens 3	20	-0.049	-0.308	1.006	1.016	New data set
<i>G. buenoi</i>	University of BC Botanical Gardens 4	63	0.279	-0.093	1.011	1.007	New data set
<i>A. remigis</i>	Mount St Hilaire	100	0.214	-	0.998	1.024	Fairbairn (1988)
<i>A. remigis</i>	St Saveur	46	0.150	-	1.014	1.051	Fairbairn (1988)
<i>A. remigis</i>	Marble Creek 1 1993	28	0.226	-0.216	-	-	New data set
<i>A. remigis</i>	Marble Creek 2 1993	13	0.045	-0.261	-	-	New data set
<i>A. remigis</i>	Marble Creek 3 1993	12	0.516	-0.326	-	-	New data set
<i>A. remigis</i>	Raven Run 1993	24	0.398	-0.025	-	-	New data set

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Species	Population/Site	Number of mating pairs	Estimate of assortative mating ( $r_p$ )	Index of hetero scedasticity ( $r_s$ )	Male size ratio	Female size ratio	Source
<i>A. remigis</i>	Marble Creek 4 1993	24	0.122	-0.196	-	-	New data set
<i>A. remigis</i>	Raven Run 1989	12	-0.026	0.316	0.999	0.995	New data set
<i>A. remigis</i>	Raven Run 1989	41	0.231	-0.066	0.984	1.017	New data set
<i>A. remigis</i>	Raven Run 1989	22	0.233	-0.055	-	-	New data set
<i>A. remigis</i>	Raven Run 1989	13	0.482	-0.231	-	-	New data set
<i>A. remigis</i>	Raven Run 1992	12	-0.156	-0.176	-	-	New data set
<i>A. remigis</i>	Raven Run 1992	21	0.364	0.271	-	-	New data set
<i>A. remigis</i>	Raven Run 1992	20	0.287	0.460	-	-	New data set
<i>A. remigis</i>	Raven Run 1992	44	0.047	0.259	-	-	New data set
<i>A. remigis</i>	Raven Run 1992	29	0.095	0.108	-	-	New data set
<i>A. remigis</i>	Raven Run 1992	16	0.015	0.013	-	-	New data set
<i>A. remigis</i>	Raven Run 1992	15	-0.200	0.357	-	-	New data set
<i>A. remigis</i>	Raven Run 1991	14	0.122	0.112	1.012	0.998	New data set
<i>A. remigis</i>	Raven Run 1991	26	0.048	-0.061	1.028	1.029	New data set
<i>A. remigis</i>	Raven Run 1993	38	-0.100	-0.059	1.008	1.020	New data set
<i>Halobates robustus</i>	Cartago Bay	18	0.070	-	-	-	Foster and Treherne (1982)

	$n$	45	45	33	25	25
Weighted analysis						
Weighted mean effect size ( $r$ )		0.115		0.011	0.072	0.133
Weighted Stouffer's $p$ (two-tailed)		< 0.001		0.658	0.013	< 0.001
Unweighted analysis						
Arithmetic mean	36	0.123		-0.004	1.003	1.009
SD	27	0.182		0.201	0.015	0.015
$t$ -value		4.56		0.11	1.0	3.0
$p$ (two-tailed)		< 0.001		< 0.5	0.328	0.006