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E-Article

Assortative Mating in Animals

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abstract: Assortative mating occurs when there is a correlation (positive or negative) between male and female phenotypes or genotypes across mated pairs. To determine the typical strength and direction of assortative mating in animals, we carried out a meta-analysis of published measures of assortative mating for a variety of phenotypic and genotypic traits in a diverse set of animal taxa. We focused on the strength of assortment within populations, excluding reproductively isolated populations and species. We collected 1,116 published correlations between mated pairs from 254 species (360 unique species-trait combinations) in five phyla. The mean correlation between mates was 0.28, showing an overall tendency toward positive assortative mating within populations. Although 19% of the correlations were negative, simulations suggest that these could represent type I error and that negative assortative mating may be rare. We also find significant differences in the strength of assortment among major taxonomic groups and among trait categories. We discuss various possible reasons for the evolution of assortative mating and its implications for speciation.

Keywords: disassortative mating, distribution of assortment strength, mate choice, meta-analysis, nonrandom mating, sexual selection, sympatric speciation.

Introduction

Assortative mating is used to describe a variety of patterns of nonrandom mating. In the speciation literature, assortative mating is treated as a mechanism of premating reproductive isolation between distinct species or divergent populations (Johannesson et al. 1995; Seehausen et al. 1997; Coyne and Orr 2004). In the behavioral 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 (Crespi 1989; Harari et al. 1999; Shine et al. 2001). More generally, assortative mating can be defined as a pattern of nonrandom mating, without making specific assumptions regarding its behavioral mechanism or evolutionary role (Lewontin et al. 1968; Kondrashov and Shpak 1998). 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 (Wright 1921; Lipsey and Wilson 2001; Redden and Allison 2006). Assortative mating may be either positive, implying a tendency to mate with phenotypically similar individuals, or negative (also called disassortative), implying the converse (Partridge 1983; Hooper and Miller 2008). There are many empirical examples of both positive and negative assortative mating (Johnston and Johnson 1989; Follett et al. 2007; Pryke and Griffth 2007; Lu et al. 2009), but it remains unclear what the distribution of the strength of assortative mating is in nature, especially whether there is a systematic tendency toward assortment, random mating, or disassortment.

Assortative mating has several important evolutionary consequences. Positive assortment increases homozygosity within loci, promotes linkage disequilibrium between loci, and consequently inflates the variance of quantitative traits (Lynch and Walsh 1998). The resulting deviations from Hardy-Weinberg equilibrium can cause statistical biases in association mapping studies (Redden and Allison 2006) and estimates of quantitative genetic parameters (Gimelfarb 1986). Assortative mating also plays a key role in speciation, contributing to premating isolation between phenotypically divergent populations (Felsenstein 1981; Kondrashov and Shpak 1998; Coyne and Orr 2004; Bolnick and Kirkpatrick 2012). In models of adaptive speciation, reproductive isolation via positive assortative mating evolves in response to disruptive selection (Kirkpatrick 2000; Dieckmann et al. 2004; Gavrilets 2004; Bank et al. 2011). Assortment is hypothesized to reduce the production of less fit phenotypically intermediate offspring. Conversely, stabilizing selection favors the evolution of disassortative mating, which reduces the production of less fit phenotypic extremes (Kondrashov and Shpak 1998; Kirkpatrick and Ravigné 2002). Disassortative mating also increases heterozygosity, decreases inbreeding depression

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(Waser 1993; Pusey and Wolf 1996), and can facilitate the maintenance of sexually antagonistic variation (Arnqvist 2011). Given these multifarious evolutionary effects of assortative mating, it would be valuable to know the distribution of its strength in natural populations, as well as its evolutionary origins.

Two general hypotheses could explain the occurrence of assortative mating. The first asserts that the strength of assortative mating evolves adaptively in response to direct or indirect selection on mating preferences. Selection can act directly on mate choice if fitness depends on the similarity of mated pairs. For example, conjugation in the marine nudibranch *Chromodoris zebra* is facilitated when the partners are of similar size (Crozier 1917, 1918). Alternatively, assortative mating can affect the fitness of a pair's offspring, resulting in indirect selection on the parents' mating behavior. For example, *Heliconius* butterflies that mate assortatively on the basis of mimetic color patterns avoid producing offspring with maladaptive patterns (Chamberlain et al. 2009). More generally, disruptive selection will indirectly favor the evolution of positive assortative mating to avoid producing less fit offspring; conversely, stabilizing selection will favor negative assortment (Dieckmann and Doebeli 1999; Kirkpatrick and Ravigné 2002; Gavrilets 2004; De Cara et al. 2008; Otto et al. 2008). For similar reasons, assortative mating can evolve in response to inbreeding or outbreeding depression (Epinat and Lenormand 2009). Regardless of the type of selection involved, assortment can result from mutual mate choice or by the behavior of only males or females (McNamara and Collins 1990).

Under the second general hypothesis, assortative mating is an incidental consequence of temporal, mechanical, and physiological constraints. In this case, assortment may be neutral, selectively favored, or even deleterious. Several kinds of mechanisms may contribute to these constraints, such as temporal segregation, spatial segregation, intrasexual competition, and intersexual conflict (for details, see "Discussion"; Crespi 1989; Arnqvist et al. 1996; Cézilly 2004). Quantifying the direction and strength of assortative mating may shed light on the prevalence of adaptive and incidental assortative mating, a point to which we return in "Discussion."

Knowledge about patterns of assortment in nature could also be useful in developing more realistic models of speciation. Models have shown how assortative mating can lead to sympatric speciation (Udovic 1980; Felsenstein 1981; Doebeli 1996) and influence the outcome of secondary contact (Kondrashov and Shpak 1998; Kirkpatrick 2000; Bolnick and Kirkpatrick 2012). Unfortunately, such models have generally not been parameterized with empirical data, with a few exceptions (Gavrilets and Vose 2007; Gavrilets et al. 2007; Duenez-Guzman et al. 2009; Sadedin et al. 2009). The typical assumption is that populations initially exhibit random mating, but this may not be empirically justified. Meta-analysis can determine the distribution of assortment within populations, which can be treated as a range of biologically realistic initial conditions in future models.

Despite these needs for an overview of the strength and direction of assortative mating, no comprehensive review currently exists. Many studies focus on a single species or clade and are typically based on a single phenotypic trait (Olson et al. 1986; Arnqvist et al. 1996; Bernstein and Bernstein 2003; Cézilly 2004; Roulin 2004; Wogel et al. 2005). It is therefore unclear what general patterns might exist regarding the strength of assortative mating in animal populations. Outstanding questions include the following: What is the distribution of the strength of assortative mating? How frequent is negative versus positive assortative mating? Are there differences in the strengths of assortment among taxa and among different kinds of phenotypic traits? Are the data consistent with the hypothesis that assortment evolves adaptively in response to indirect effects of stabilizing and disruptive selection? Here we address these questions using a meta-analysis of the strength of assortative mating across diverse taxa of animals based on a variety of assortment traits.

Methods

We conducted a mixed-model meta-analysis of assortative mating based on phenotypic traits within natural animal populations. As our measure for the strength of assortative mating, we used the correlation coefficient for the values of a homologous trait in mated pairs. This statistic is appropriate for a meta-analysis because it is a natural measure of effect size that quantifies the magnitude and direction of assortative mating, in a manner comparable across diverse published studies (Lipsey and Wilson 2001). For studies that report other effect size metrics (F statistics, χ^2 statistics, t statistics, or appropriate descriptive data), we converted these into correlation coefficients using standard methods (Hedges et al. 1985; Cook 1994).

Literature Search

We searched for publications reporting suitable measures of assortative mating, using keywords searches in multiple databases, including Google Scholar, JSTOR, and Web of Science. We also examined the reference sections of relevant publications to find additional studies. To minimize the risk of bias in effect direction, for each keyword search term we also searched for its antonym when possible, for instance, searching for both "assortative" and "disassortative." Appendix A (available online) gives details of our search methods, including keywords and criteria for including studies in our database. The supplementary material (available in Dryad; http://dx.doi.org/10.5061/dryad.r706v) gives a full list of studies included in our final database.

We excluded studies of assortative mating between incipient species, populations undergoing secondary contact or other forms of hybridization, host races, as well as populations whose conspecific status is ambiguous. Our focus is on the strength of assortment within single populations rather than reproductive isolation between divergent populations or incipient species. By focusing on within-population assortment, we are documenting the strength of a potentially important population genetic process and the range of reasonable initial conditions preceding any steps toward speciation. There is an important pragmatic reason to exclude assortment between highly diverged populations: those situations arguably encompass cases of perfect assortment, which then includes all pairs of species on the planet that do not interbreed. In judging whether to exclude case studies from our data set, we relied on the taxonomic status of taxa described by the publication providing relevant assortment data. In cases where no information was provided, we used a Google Scholar search to check the taxonomic status in recent published descriptions. Plants are not included in our study simply because too few studies reported appropriate effect size statistics. We did not include humans because strong cultural influences and substantial recent admixture make human assortative mating hard to compare with other species (Spuhler 1968; Merikangas 1982; Wolański 1994; Courtiol et al. 2010).

We reviewed more than 13,000 publications. While the search was thorough, it is certain that there are publications that our search did not find. However, an exhaustive search is not necessary for meta-analysis, which is fundamentally a sampling activity intended to retrieve studies that are representative of the question of interest. Thus, a meta-analysis can yield accurate results if it is an unbiased sample from a large and representative literature. Conversely, exhaustive samples of the relevant publications are not guaranteed to be representative as a result of publication or reporting bias (Cooper et al. 2009).

Data Collection

For each study, we recorded the scientific name of the focal species, the trait that is subject to assortative mating, the correlation coefficient or other metric of effect size that could be converted into a correlation coefficient, the statistical significance of the reported metric, and the sample size (number of mated pairs). We divided the species into 11 commonly represented taxonomic groups (amphibians, annelids, birds, chelicerates, crustaceans, fishes, gastropods, insects, mammals, protists, and reptiles) and into five phyla (annelids, arthropods, chordates, ciliophores, and mollusks). Assortment traits were divided into 10 general trait categories (defined in table A2, available online). We also recorded whether the focal trait is reported as a categorical trait or a continuous trait. Note that a trait may be listed as categorical either because it takes discrete values or because the researchers divided a continuous trait into discrete categories (e.g., size or age class). The database used for meta-analysis is available in Dryad (http://dx.doi.org/10.5061/dryad.r706v).

For some combinations of species and trait categories, we found more than one estimate for the correlation of mated pairs, for instance, if the correlation was measured in multiple years or within each of multiple populations. To avoid pseudoreplication, we calculated a weighted mean correlation coefficient for each combination of species and trait category, where the weight is the square root of the sample size. We refer to these values as species-trait means and denote them as $\bar{r}$. The sample size associated with each species-trait mean, which we denote as N, is the sum of sample sizes of the amalgamated studies for a given species-trait combination (Borenstein et al. 2009). (We found that using the average sample size of amalgamated studies produces very similar results.) Note that some pseudoreplication remains because traits within a species are phenotypically correlated, and related species can have similar breeding systems because of shared phylogenetic history. Unfortunately, the data are not adequate to eliminate these associations, and we return to this issue in "Discussion." We did not calculate means using Fisher's z transformation because that can lead to positive bias (Hunter and Schmidt 2004; Cooper et al. 2009). The meta-analysis was performed on the basis of the species-trait means, and so each combination of species and trait category therefore appears only once in our analyses. We did not average the assortment strengths for different trait categories within a given species, because the strength of assortment is likely to vary across trait categories.

Meta-Analysis

To summarize the strengths of assortment across taxa and trait categories, we used the weighted average of the species-trait means, where the weight assigned to each species-trait mean effect is the reciprocal of its sampling variance v (Borenstein et al. 2009; Viechtbauer 2010):

$$v = \frac{(1-\bar{r}^2)^2}{N-1}.$$

We used restricted maximum likelihood with a mixed model (Viechtbauer 2010) to test whether the average of the species-trait means differs from 0 and to test for significant variation among factors (taxon, trait category). Each species-trait mean is modeled as the sum of a fixed factor that represents the effect of a category (e.g., taxon or trait category) and a random effect. We report the statistics Q_M and Q_E (sometimes called Q_{bet} and Q_W, respectively). The Q_M indicates the amount of heterogeneity in $\bar{r}$ that is explained by the model (Cooper et al. 2009). A significant Q_M indicates that the strength of assortment differs significantly between the levels of the factor included in the model (e.g., taxon or trait category). The Q_E indicates the amount of residual error heterogeneity. A significant Q_E indicates heterogeneity among observations within groups (i.e., taxa and trait categories) not explained by the model (Cooper et al. 2009). All analyses were performed in R (R Development Core Team 2009) using the package metafor (Viechtbauer 2010).

There is a possibility that publication bias could lead to the underrepresentation of nonsignificant results in the published literature (Hedges et al. 1985; Cook 1994; Palmer 1999; Lipsey and Wilson 2001). We assessed this possibility using a funnel plot of species-trait means against sample size and evaluated the result by a linear regression test using a mixed-effects model with sample size as a predictor (Egger et al. 1997; Cooper et al. 2009; Viechtbauer 2010). We also calculated the fail-safe number, which indicates the number of missing studies with zero effect needed to reduce the mean strength of assortative mating to a value not significantly different from 0 (Palmer 1999; Cooper et al. 2009; Viechtbauer 2010).

Estimating the Underlying Distribution of the Strength of Assortment

The estimates for the correlations between mated pairs in our data set inevitably include sampling variance and measurement error. These errors will cause the observed distribution of $\bar{r}$ to have a different distribution than the actual underlying distribution of correlations in nature. To illustrate this point, imagine a world without negative assortative mating. Because of sampling error, some studies of species with positive assortative mating will estimate negative values for the correlation between mated pairs, and some of these will even be statistically significant (type I error). The frequency of negative assortative mating thus is inflated. Similarly, if negative assortative mating were the general rule, error would instead inflate the observed frequency of positive assortative mating.

It does not seem possible to correct for this effect precisely. That is because there are unknowable sources of measurement error in meta-analyses of diverse studies and because the data are not independent (as a result of phylogenetic relations between species and phenotypic correlations between different traits in the same species; for details, see "Discussion"). Nevertheless, we used a heuristic approach to estimate the underlying distribution of the strength of assortment while accounting for sampling error.

We began by assuming that the true values of assortment for a given species and trait combination, which we denote by ρ, are drawn from a beta distribution that is modified to range from a lower bound of b to an upper bound of 1 (rather than from 0 to 1). We fixed the upper bound because as populations progress toward speciation, they must inevitably approach very strong assortative mating. We let the lower bound vary because we have no prior notion about what the smallest value of ρ in nature might be. This distribution is very flexible; for example, it can take a form similar to a normal distribution, an exponential distribution, or even a bimodal U-shaped distribution. The modified beta distribution is characterized by three parameters: its lower bound b, its mean m, and its variance s^2. We used simulations to determine what values of these three parameters would yield an observed distribution of species-trait means $\bar{r}$ that most closely matches our data, given the sample sizes and pseudoreplication in our data set. The result is an estimate for the true underlying distribution of assortment in nature.

An outline of the algorithm we used follows (further details are given in app. C, available online). Given values for the three parameters for the modified beta, we randomly sampled 360 values of ρ to represent the species-trait means. Each value of ρ was then paired at random with one of the species-trait combinations in our database. For each of these pairings, we determined the number of studies n for that species-trait combination and the sample size N_i for the ith study in that combination. We then simulated n estimates of the correlation; each estimate was obtained by drawing N_i mated pairs of values from a bivariate normal distribution with the given value of ρ. These simulated correlations (corresponding to the individual studies in the database) were then averaged to give a simulated value for a species-trait mean $\bar{r}$ in the same way that we did for the real data. This process is repeated for each of the 360 values of ρ to give a simulated distribution of observed species trait means, with realistic sampling error. We calculated a measure of how well the simulated distribution matches the observed distribution of $\bar{r}$ (for details, see app. C). This was repeated five times for each combination of the three parameters for the distribution of ρ to identify the combination that gave the best fit to the data.

Results

Our database contains 1,116 measurements of the strength of assortative mating from 254 species in five phyla collected from 269 publications (table 1; supplementary material [available in Dryad; http://dx.doi.org/10.5061/dryad.r706v]). Our final data set consists of 360 species-trait means. Of those values, 89% are positive and 11% negative (80% and 19%, respectively, in the 1,116 raw estimates). Birds, insects, crustaceans, and amphibians are better represented than other taxonomic groups (table 1; supplementary material [available in Dryad; http://dx.doi.org/10.5061/dryad.r706v]). At the level of phylum, arthropods and chordates (46% and 52%, respectively, of the raw estimates) together represent almost all of the data set. These studies measured assortment on a wide variety of traits (102 different traits; table A2). A majority of these fall into three trait categories: size (47% of the raw estimates), structural characters that are not a direct measure of overall body size (30% of the raw estimates), and visual signals that are mostly measures of color, pattern, and sexually selected traits such as crest size (47%, 30%, and 14%, respectively, of raw estimates). The complete list of categories and specific traits is given in table 1. Note that the measures of individual morphological traits frequently covary with body size. Nearly all (95%) of the traits in our databases are continuous.

Table 1: Summary of database by taxon and trait category

Phylum and taxon	*N*	Trait category	*N*
Annelida	1 (1)		
Annelid	1 (1)	Age	35 (25)
Arthropoda	516 (124)		
Crustacean	170 (53)	Behavior	1 (1)
Chelicerate	10 (3)	Chemical	6 (2)
Insect	336 (68)	Condition	49 (24)
Chordata	584 (226)		
Amphibian	151 (44)	Ecotype	5 (4)
Bird	377 (148)	Genotype	10 (4)
Fish	45 (27)	Phenology	1 (1)
Mammal	2 (2)	Size	521 (191)
Reptile	9 (5)	Structural	322 (76)
Ciliophora	5 (1)		
Protist	5 (1)	Visual	156 (32)
Mollusca	10 (8)		
Gastropod	10 (8)		

Note: *N* gives the number of raw values from the original studies and (in parentheses) the number of species-trait means. Detailed definitions of the trait categories are given in table A2 (available online).

Distribution of the Strength of Assortative Mating

The distributions of assortative mating strength based on raw estimates and species-trait means are shown in figure 1. The mean value of $\bar{r}$ is 0.28 with a 95% confidence interval of 0.25–0.31, based on a random effects model with no fixed effects and species-trait means as the unit of replication. The mean correlation between mated pairs in the raw data set is 0.24. The test for heterogeneity is significant ($Q_E = 91{,}275$, df $= 359$, $P < .0001$), rejecting the hypothesis that all species exhibit a single shared strength of assortative mating. Rather, our random effects model estimates that the variance of $\bar{r}$ is 0.0698 (SD $=$ 0.264).

Surprisingly, our simulations of sampling error indicate that the best-fit estimate for the underlying distribution of the strength of assortment has no negative assortative mating (fig. 2). This distribution of ρ has a minimum value and a mode at $b = 0.02$ and a long positive tail. The mean and variance of this distribution ($m = 0.27$, $s^2 = 0.047$) are close to the values estimated from a random effects model (mean $= 0.28$, variance $= 0.0698$). The moderate difference in the variance estimates may be due to different assumptions about the underlying distribution: the random effects model assumes a normal distribution, while our simulations assume the modified beta. Simulated data sets using the best-fit distribution of ρ are not significantly different from the observed distribution of $\bar{r}$ (Kolmogorov-Smirnov test, $P \geq .40$ for all replicate simulations of the optimal parameter combinations).

An important conclusion is that it is plausible that most or all published cases of negative assortment are a result of type I error, suggesting that negative assortment is absent or rare in the species included in our database. Two other observations highlight the remarkable goodness of fit between our optimal parameter values (no negative assortment) and our data. First, given a fixed mean of 0.28, as estimated in a random effects model, the best-fit parameter combination ($b = 0$, $s^2 = 0.05$) generates 19.2% negative estimates, a value that is close to the 19% seen in the observed distribution of $\bar{r}$. Second, if type I error is indeed responsible for negative estimates, then studies reporting negative assortment should tend to have a smaller sample size (and thus larger sampling error) than those reporting positive assortment. This is true in both the observed and the simulated databases. In our database, studies reporting negative assortment averaged a sample size of 40, compared with 107 for studies reporting positive assortment (Wilcoxon rank sum test; $P < .0001$). In simulated data sets using the best-fit distribution of ρ, simulated negative and positive estimates of $\bar{r}$ averaged sample sizes of 49 and 112, respectively ($P < .0001$).

We are not, however, able to reject the hypothesis that the underlying distribution ρ includes negative values. Some distributions of ρ that include substantial frequencies of negative assortment ($b > -0.3$) yield estimate distributions that are not significantly different from the observed distribution (Kolmogorov-Smirnov tests; $P > .05$). However, distributions with negative b do not fit the data

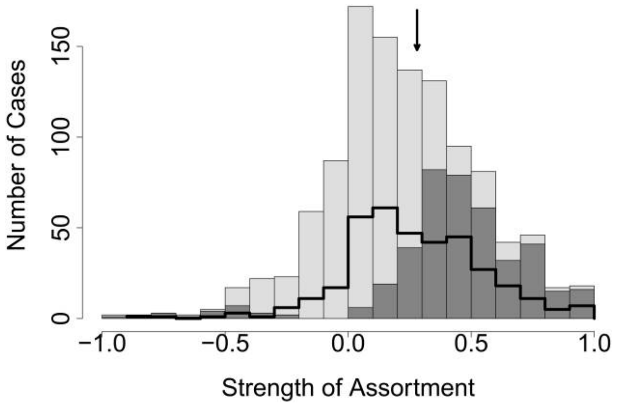

Figure 1: Histogram of the strengths of assortment for 1,116 published empirical estimates. The dark gray and light gray areas indicate the number of significant and nonsignificant values, respectively, based on the raw correlation coefficients collected from the literature. The thick black line shows the distribution of the strengths of assortment based on the species-trait means. The arrow indicates the weighted mean strengths of those values (0.28).

as well as our optimum. As discussed in appendix C, limits to our method prevent us from putting confidence limits on b, and so it is difficult to make a more quantitative conclusion. The best we can say at present is that there is no strong evidence for negative assortment but that it may well occur.

Sources of Heterogeneity in Assortative Mating Strength

The average value for species-trait means based on categorical traits (0.11) is significantly smaller than that based on continuous traits (0.29; table 2). Since categorizing continuous data tends to decrease a correlation (Lipsey and Wilson 2001; Cooper et al. 2009), it is not clear whether there is an intrinsic difference between categorical versus continuous traits or whether this effect size difference is an artifact. To prevent this uncertainty from biasing our results, only continuous traits are included in the following analysis. We also excluded annelids and protists in the following analysis because there is only one example of each.

Mixed-model meta-analyses reveal that the strength of assortative mating differs significantly among phyla and lower taxa (table 2). The difference among taxa remains robust after excluding underrepresented taxa (chelicerates, mammals, and reptiles). We arbitrarily consider an underrepresented group to be any group with six or fewer species-trait means. Increasing the exclusion threshold to eight—and thus excluding gastropods—has minimal impact on our results. The mean value of $\bar{r}$ is largest in fish (0.55), crustaceans (0.46), and chelicerates (0.40) and is smaller in amphibians (0.21) and insects (0.21; table B1, available online). On average, assortative mating is significantly positive within all taxonomic groups ($P < .01$; fig. 3) except reptiles and mammals, which have small sample sizes.

The strength of assortative mating also differs significantly among trait categories. This result remains robust after excluding underrepresented categories, that is, behavior, ecotype, and phenology (table 2). Assortative mating tends to be strongest on phenology and ecotype (mean $\bar{r} = 0.79$ and 0.50, respectively). The species-trait means for visual signals, age, and size (mean $\bar{r} = 0.34$, 0.34, and 0.31, respectively) tend to be larger than those for condition and structural characters (mean $\bar{r} = 0.26$ and 0.21, respectively; table B2, available online). The strength of assortment is significantly positive for all trait categories except behavior, chemical traits, and genotype ($P < .05$; fig. 4).

The tests of between-taxon and between-trait heterogeneity were conducted in separate models. It is possible that biologists are more likely to measure assortment based on certain traits in certain taxa (e.g., chemical cues in insects). Such biases could confound the effects of trait category and taxon. Unfortunately, we are unable to separate the effects for these factors using a single multifactorial model because of the uneven sample size across combinations of taxon and trait category. Only two taxa (birds and insects) contain sufficient (>6) species-trait means within each of two or more trait categories. Only two trait categories (size and structural characters) contain sufficient sample sizes for more than one taxon. Focusing on these subsets of our data, we found no evidence that trait and taxon have confounded effects. We continue to observe significant among-taxon heterogeneity within each of two widely measured traits, size and structural characters (table B3, available online). We also observe heterogeneity among trait categories within each of two taxa (birds, and insects) that have sufficient sample sizes to let us analyze multiple trait categories (table B4, available online).

Tests of Publication Bias

We detected no evidence of publication bias toward either positive or negative assortative mating in the complete set of 1,116 correlation coefficients. The funnel plot is symmetric around mean effect size (linear regression test for asymmetry; $P = .16$, corrected for pseudoreplication), and there is no gap in the mouth of the funnel plot (fig. 5), suggesting that there is no appreciable publication bias against small effect or nonsignificant results. Furthermore, the fail-safe numbers calculated from original data and species-trait means are 15,639,977 and 8,171,541, respec-

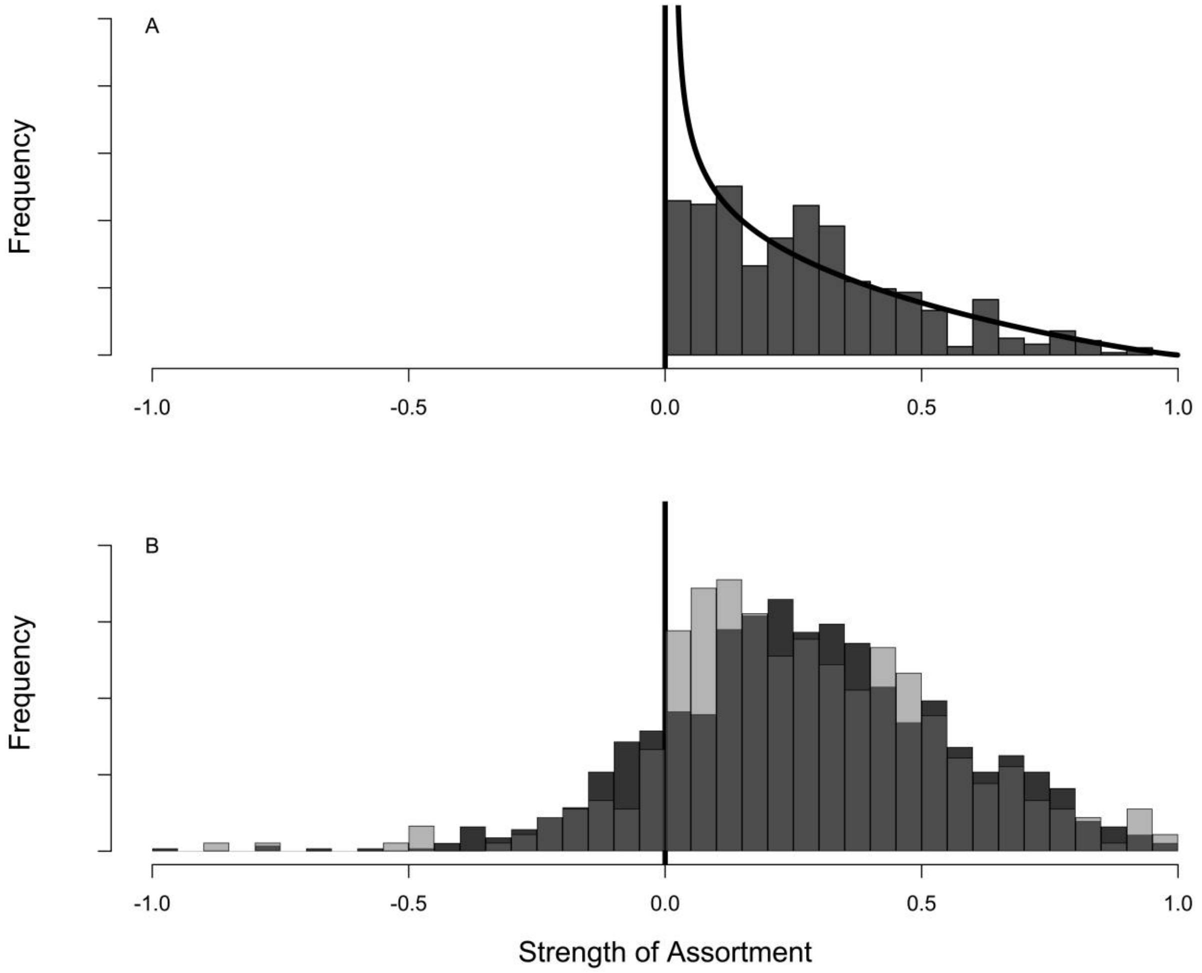

Figure 2: Estimate of the underlying distribution for the true strength of assortment for species-trait combinations. In *A*, the best-fit distribution for ρ is shown by the curve, and a realization of 360 samples from this distribution is shown by the histogram. In *B*, the simulated values for $\bar{r}$ (the species-trait means) that result are dark gray, the observed distribution from our data set are light gray, and overlapping regions are medium gray. In this realization, the difference between the two distributions is not significant (Kolmogorov-Smirnov test; $P = .673$).

tively. Thus, an implausibly large number of missing or unpublished studies with zero effect would be needed to reduce the mean strength of assortative mating to 0. We conclude that our data set, while not necessarily an exhaustive compilation of case studies, is likely to yield an unbiased estimate of the typical strength and direction of assortative mating.

Discussion

Our results provide three core insights. First, weak positive assortative mating is typical in animals; the mean strength of assortment is 0.28. Second, we found that positive assortative mating is observed far more frequently than negative assortative mating. Indeed, the rare cases of negative assortative mating are best explained as type I error arising from small sample size studies of species with random or weakly positive assortative mating. Third, the strength and frequency of assortment differ significantly among combinations of species and traits, among taxonomic groups, and among different categories of traits. These conclusions have implications for adaptation, population genetic structure, and speciation.

Is Negative Assortative Mating Real?

Although assortative mating is predominantly positive, in roughly one-tenth of species-trait combinations, studies estimated negative assortment. Some reports of negative assortative mating are statistically significant. However,

Table 2: Strengths of assortment by different subsets and classifications of the data

Data subset or classification	r	95% CI	Q_M	Q_E
Positive assortment[a]	.33	.31–.36	626	78,047
Negative assortment	−.18	−.26–−.10		
Categorical traits[b]	.11	.03–.21	360	78,650
Continuous traits	.29	.26–.32		
Among-phyla variation[c]			401	31,386
Among-taxa variation[d]			539	29,367
Among-trait category variation[e]			395	36,642

Note: All values for Q_M and Q_E are significant at $P < .0001$. CI, confidence interval.

[a] The Q statistics pertain to the difference between the absolute strength of positive and negative assortment.

[b] The Q statistics pertain to the difference between categorical and continuous traits.

[c] Excluding annelids and protists (because of small numbers of species-trait means).

[d] Excluding annelids, protists, chelicerates, mammals, and reptiles (because of small numbers of species-trait means).

[e] Excluding trait categories with insufficient data: behavior, ecotype, and phenology. Also excluding annelids and protists.

our simulations, which account for the sampling error in the database, suggest that negative assortative mating could be rare or absent. A beta distribution in which the true strength of assortment lies between 0 and 1 produces a distribution of simulated values for $\bar{r}$ that closely matches our data set (fig. 2). Furthermore, the simulations recapitulate, with remarkable quantitative accuracy, the proportion of negative values of $\bar{r}$ and the tendency for those values to come from studies with small sample sizes. Therefore, we conclude that the minority of case studies reporting negative assortative mating may be spurious, resulting from type I error occurring across many studies.

However, we emphasize that the analysis we employed does not prove that there is no negative assortment. Most importantly, distributions of ρ that have lower bounds as small as $b = -0.3$ give reasonable fits to the data, albeit not as good a fit as $b = 0.02$. As we discuss in appendix C, it does not seem possible to obtain confidence intervals to quantify that statement further.

A number of studies have reported negative assortative mating based on the major histocompatibility complex (MHC; Mays and Hill 2004). These are not included in our meta-analysis because the strength of assortment cannot naturally be expressed as a correlation. It seems difficult to draw strong and general conclusions about assortment based on MHC at this time. While many existing studies give persuasive evidence of nonrandom mating, they often do not distinguish between mating based on genetic similarity and that based on heterozygosity. Among the few studies that do distinguish between these two mechanisms, mixed conclusions were drawn (Bonneaud et al. 2006; Beltran et al. 2008). A further limitation to our current understanding of assortment based on MHC is that most studies are of just two species, mice and humans (Roberts and Petrie 2006).

How Does Assortative Mating Evolve?

Theory suggests that the strength of assortative mating can evolve adaptively in response to stabilizing or disruptive selection (Kondrashov and Shpak 1998; Kirkpatrick and Nuismer 2004), though empirical evidence for this claim remains scarce (Rice and Hostert 1993; Coyne and Orr 2004). Stabilizing selection is expected to favor negative assortment, while disruptive selection favors positive assortment. Many evolutionary biologists assume that sta-

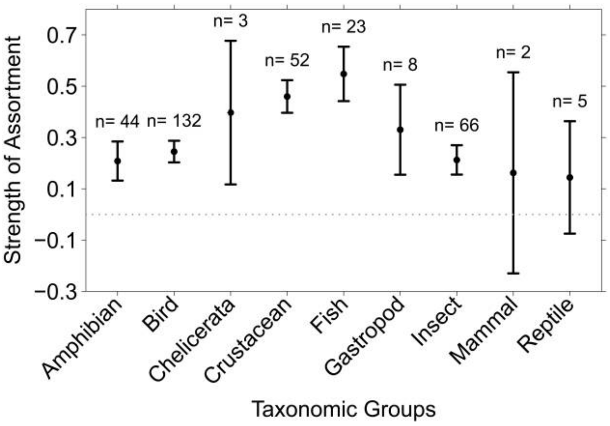

Figure 3: Comparison among taxa of the strengths of assortment, $\bar{r}$. Points show weighted means, and vertical bars show 95% confidence intervals (based on species-trait means). Sample sizes are the number of species-trait means.

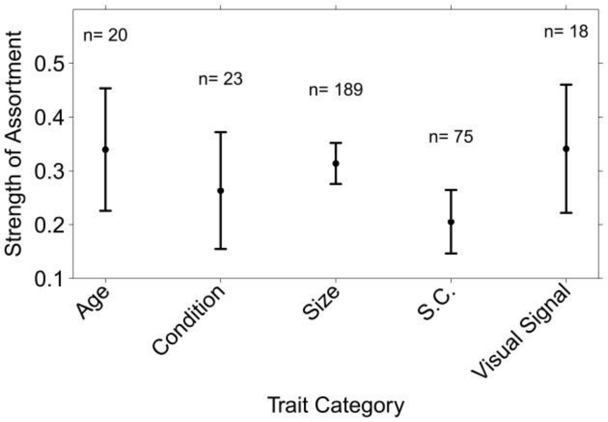

Figure 4: Comparison among trait categories of the strengths of assortment, $\bar{r}$. Points show weighted means, and vertical bars show 95% confidence intervals (based on species-trait means). Sample sizes are the number of species-trait means. S.C., structural characters.

bilizing selection is more frequent than disruptive selection (Endler 1986). If that is true, and if the strength of assortative mating evolves as an adaptation to indirect selection, we would then expect negative assortment to dominate. This expectation is not supported by our results, which suggest that negative assortment is rare or possibly absent. But is the common intuition about the prevalence of stabilizing selection correct? Kingsolver et al. (2001) reviewed more than 2,500 estimates of the strength of phenotypic selection in natural populations and concluded that disruptive selection and stabilizing selection occur at similar frequency and are of similar strength, though both are fairly weak. That result implies that positive and negative assortment should occur at about the same frequency and strength. Our results convincingly reject this expectation as well.

The results therefore suggest that indirect disruptive or stabilizing selection is not the primary force determining the evolution of assortative mating within populations. While indirect selection seems likely to drive the evolution of assortative mating in some cases, our results suggest that it is not a general explanation. An adaptationist explanation of assortative mating would instead have to invoke direct selection favoring trait-matched mate pairs. Examples of such direct selection do exist (Dekkers 1994) but are less widely documented.

An alternative possibility is that assortative mating is typically not adaptive but rather arises as an incidental consequence of other aspects of the mating system. There are at least three proximate mechanisms that could drive the evolution of the strength of assortative mating under the nonadaptive hypothesis (Crespi 1989; Arnqvist et al. 1996; Cézilly 2004). The first mechanism is allochronic isolation (Waser 1993; Helfenstein et al. 2004; Weis 2005; Weis et al. 2005). For example, temporal segregation caused by different arrival dates causes two populations of European blackcap *Sylvia atricapilla* to mate assortatively at a sympatric breeding site (Bearhop et al. 2005). Two analogous processes can also generate assortment. In monogamous species with indeterminate growth, such as seahorses, if young and small individuals form pair bonds and they grow larger together, there will tend to be a correlation in body size between mates (Jones et al. 2003). Similarly, a combination of age-specific access to reproduction and strong mate fidelity can generate age-assortative mating in socially monogamous bird species (but see Cézilly and Johnson 1995).

A second mechanism of incidental assortment arises from spatial segregation, when there is covariance between a phenotype and the habitat in which individuals mate, which increases the probability of encountering phenotypically similar candidate mates (Snowberg and Bolnick 2008). This results when individuals have matching habitat preferences (Edelaar et al. 2008), such as in insect host races that mate on their host plants (Drès and Mallet 2002; Malausa et al. 2005), or when there are phenotypic clines (Edelaar et al. 2008). Roulin (2004) pointed out that birds with similar plumage color tend to occur in the same habitat, and this co-occurrence can cause assortative mating. Similarly, in insects and crustaceans that exhibit spatial variation in body size, assortment can simply arise as a side effect of spatial segregation of individuals with different phenotypes, even when mating within a patch is random (Birkhead and Clarkson 1980; Crespi 1989; Dick and Elwood 1996; Bollache et al. 2000; Bernstein and Bern-

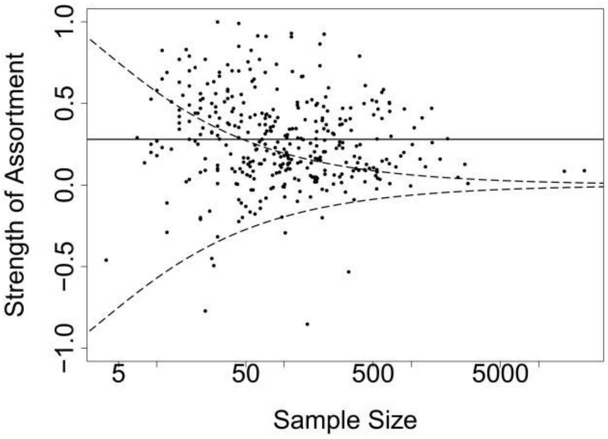

Figure 5: Funnel plot of species-trait mean, $\bar{r}$, versus sample size. The horizontal line indicates the grand mean (0.28). The two dashed lines show critical values for the correlation coefficient needed to achieve significance at $P < .05$ at a given sample size.

stein 2003). Assortative mating arising from these causes, while not an adaptation in and of itself, may still be a key factor facilitating ecological speciation.

Third, assortment can arise as a by-product of intrasexual competition and intersexual conflict (Crespi 1989; Cézilly 2004; Henry 2008). For example, when larger females are more fecund, selection favors male preferences for larger partners (Salthe and Duellman 1973; Kuramoto 1978; Bastos and Haddad 1996). If large males are more successful in courting or defending these females, competitively inferior males end up mating with the remaining less favored females, resulting in positive size assortative mating (Arak 1983; Hume et al. 2002; Wogel et al. 2005). In other cases, large females are more able to resist aggressive male courtship attempts, and only the largest males are able to mate them (Arak 1983), resulting in positive assortment. When one sex exhibits mate choice, as when larger females prefer larger males, a positive correlation between mates can result even if smaller females mate randomly, a phenomenon some call apparent assortative mating (Arnqvist et al. 1996). Assortment resulting from intrasexual selection is commonly documented in anurans (Arak 1983; Wogel et al. 2005) and crustaceans (McLain and Boromisa 1987; Crespi 1989; Bollache and Cézilly 2004). Various intensities of intersexual competition and/or intersexual conflict among populations of the same species or in one population at different times may incidentally lead to substantial variation in the strength of assortment (McLain 1982; McLain and Boromisa 1987; Bernstein and Bernstein 1999; Harari et al. 1999). For example, assortative mating is stronger under high population density in milkweed longhorn beetle *Tetraopes tetraophthalmus* because at high density, large males are more likely to interfere with small males' copulation with large females (McLain and Boromisa 1987).

Clearly, assortative mating evolves adaptively in some cases. Examples include positive assortative mating based on heterozygosity in the lesser kestrel *Falco naumanni*and on MHC diversity in the house sparrow *Passer domesticus* (Bonneaud et al. 2006; Ortego et al. 2009) and disassortative mating in human and mice *Mus musculus*, based on MHC alleles (Yamazaki et al. 1976; Wedekind et al. 1995). We do not suggest that disruptive or stabilizing selection never drives the evolution of assortative mating. Rather, our results suggest that this indirect selection for adaptive assortative mating may be the exception rather than the rule.

Assortative Mating and Speciation

Theory shows that assortative mating could be important to speciation in two contexts. It can cause a single population to split into two, resulting in sympatric speciation (Maynard Smith 1966; Udovic 1980; Felsenstein 1981; Doebeli 1996). Second, assortative mating can contribute to the genetic isolation of two populations that come into secondary contact and so prevent them from merging back into a single population (Kondrashov and Shpak 1998; Bolnick and Kirkpatrick 2012).

How do our results relate to the outcomes for speciation predicted by theory? Unfortunately, it is not easy to make a direct connection. Our data pertain to the strength assortment but give no direct information about parameters that appear in models regarding mate choice behaviors. For example, models of sympatric speciation use mating preference functions that determine the probability a female accepts a potential mate. The width of the preference function is allowed to evolve in response to indirect selection, which then leads to assortative mating. In contrast, the phenotypic correlation between mates (which we analyze here) depends on both mate preferences and the phenotype distribution of the population. The phenotypic variance is itself a dynamic variable, and how it evolves depends on the underlying genetics of the trait. Thus, there is no simple and general set of predictions that can be made about the outcome of speciation based only on the correlation between mated pairs.

It is, however, possible to make inferences in the reverse direction. Given detailed assumptions about genetics and behavior, we can calculate the correlation that is expected from a particular model and then ask where that result falls in the empirical distribution shown in figure 1. Consequently, speciation models making assumptions about mate choice parameters can in the future test whether their assumptions generate empirically reasonable levels of assortative mating (Bolnick and Kirkpatrick 2012). This may be particularly valuable in choosing starting conditions for theoretical models. There is ongoing debate over exactly what initial conditions are required for a given case of divergence to qualify as sympatric speciation (Fitzpatrick et al. 2008). Many sympatric speciation models assume random mating as a starting point. Our results imply that complete panmixia is not necessarily an empirically appropriate initial condition for a speciation model, since many populations exhibit some weak positive assortative mating.

Yet one more factor clouds the relationship between the intermate correlation and the potential for sympatric speciation. If a population currently has a weak correlation, we might be tempted to conclude that there is little opportunity for sympatric speciation. A population subject to disruptive selection, however, may evolve increased choosiness, leading to stronger assortative mating and ultimately speciation (Dieckmann and Doebeli 1999; Gavrilets 2004; Bürger et al. 2006). Consequently, initially weak assortative mating is not necessarily a barrier to future speciation. Furthermore, immediately following sympatric speciation, each nascent daughter species exhibits little within-population phenotypic variance and thus little assortative mating, even though assortment was strong just before the single ancestral population split into two. This returns us to the definitional problem, discussed in "Introduction," of how to delineate populations when estimating the strength of assortment.

Differences between Taxa and Trait Categories

The strength of assortative mating varies among closely related species (Arak 1983; Crespi 1989; Arnqvist et al. 1996; Bernstein and Bernstein 2003). Our analysis reveals heterogeneity at other levels as well: the strength of assortative mating differs significantly among higher taxa and among trait categories. For example, assortative mating is particularly strong in fish (which are well represented among putative cases of sympatric speciation) but weak in birds (which do not appear to undergo sympatric speciation; Coyne and Price 2000). Assortment on phenology is strong, but it is weak for structural characters.

It is not clear why higher taxa and trait categories should on average exhibit stronger or weaker assortative mating. We speculate that this variation may reflect differences in mean levels of allochrony, microhabitat segregation, sensory modality, and sexual selection or in life history or mating system. The intensities of intrasexual competition and intersexual conflict are known to play a role in explaining the different strength of size-assortative mating among some arthropods and anuran amphibians (Arak 1983; Crespi 1989). We endeavored to test whether assortative mating differed by life history or mating system features but were unable to find sufficiently clear-cut categorizations for species in our data set.

A confounding factor in any meta-analysis of assortative mating is nonindependence (or pseudoreplication) in the data. There are several possible sources. The most obvious comes from multiple studies of the same trait in the same species. We controlled for this source of nonindependence by analyzing the mean values across studies for species-trait combinations. A second source of pseudoreplication can arise from using separate estimates of assortment for multiple traits in the same species. These estimates will not be independent when the traits are phenotypically correlated. We were unable to correct for this effect because we lack data on correlations between traits tested for assortment. Further, most studies in our database include results for only a single trait. A third source of pseudoreplication comes from phylogenetic relationships. Clearly, two sibling species that have recently diverged are likely to share similar patterns of assortative mating for purely historical reasons. The same effect occurs to different degrees at all levels of phylogenetic relationship. In principle, it is possible to correct for phylogenetic dependencies using a phylogeny for all species in the database and a plausible null model for how assortative mating evolves (Adams 2008). Since we lack both of those ingredients, we treated species as independent observations. In any event, we know of no reason why these possible causes of nonindependence in our data might bias our general conclusions.

Future Directions

Our results raise many further questions. These include the need to identify the proximate mechanisms that generate assortment, the underlying evolutionary forces that lead to weak positive assortment, its population genetic consequences, and the potential effects of such nonrandom mating on evolutionary and genetic inferences (e.g., Redden and Allison 2006). A key question is, if assortment is adaptive, how often does it result from selection directly favoring trait-matched mate pairs versus selection acting indirectly on the parents' mating behavior in response to the fitness of their offspring? Our results favor direct selection or by-products as explanations for positive assortment, but the mechanisms and frequency of direct selection remain unclear. Alternatively, if assortment is often incidental and nonadaptive, what ecological and evolutionary conditions can explain variation in the strength and direction of the trait correlations? Uncovering the evolutionary cause of positive assortative mating will require a combination of new theory, laboratory evolution experiments, detailed behavioral studies of mate choice and mating competition (Rowe and Arnqvist 1996), and comparative analyses of the strength of assortment across populations subject to different selective pressures or genetic architectures.

The population genetic consequences of assortment in natural populations are not widely considered. To what extent does positive assortative mating inflate the phenotypic variance of quantitative traits, linkage disequilibrium among loci, and drive deviations from Hardy-Weinberg equilibrium? Can assortative mating within populations be extrapolated to explain levels of reproductive isolation among phenotypically divergent populations or closely related species in sympatry (Bernstein and Bernstein 1999; Bolnick and Kirkpatrick 2012)? Answers to such evolutionary questions can be provided by some existing theory but merit more extensive empirical investigation as well. The results in any given case will doubtless depend on the heritability and genetic architecture of the traits subject to assortment. The correlation between mates that we study here is mostly phenotypic and gives minimal direct information about the correlation between the underlying genotypes. Thus, an important early step in future research on this topic is to distinguish between phenotypic and genotypic assortment. If indeed there is a substantial genetic component to this assortative mating, then random mating is not a default feature of animal populations, at least with respect to genes linked to traits subject to assortative mating. Moreover, there is an increasing amount of literature on genotypic assortment that was not included in our database because of the lack of suitable statistical metrics. Future studies on genotypic assortment are highly recommended to provide suitable metrics to facilitate the comparison between genotypic and phenotypic assortment.

In conclusion, we have shown that natural populations vary dramatically in the strength of assortative mating. Positive assortative mating appears to be dominant (and perhaps even exclusive), although the strength of this assortment varies between taxa and among traits for unclear reasons. We believe that these results can be valuable in designing more empirically informed models of adaptive speciation and in explaining standing levels of phenotypic and genetic variation in natural populations.

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