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Rarity of Males in Pea Aphids Results in Mutational Decay

Jennifer A. Brisson (jbrisson2@unl.edu) and Sergey V. Nuzhdin†

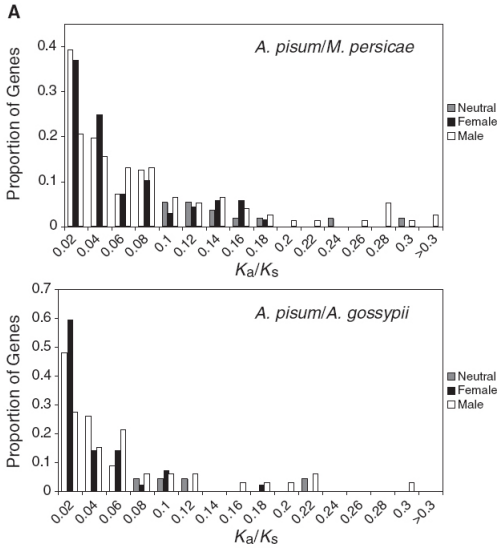
The pea aphid, *Acyrthosiphon pisum*, has a complex life cycle that alternates seasonally between asexual and sexual reproduction (1). During the spring and summer months, *A. pisum* reproduces parthenogenetically, producing clonal daughters for 10 to 20 generations. Fall temperatures and photoperiods induce the production of sexual females and males (2), which mate to produce overwintering eggs that hatch into asexual females [Supporting Online Material (SOM) text].

Asexual females dominate the life cycle because of their short generation time, high fecundity, and longer seasonal presence. We hypothesized that males experience relaxed selection, resulting in accelerated evolution of male-biased genes relative to asexual female-biased genes.

In a previous study, whole-body asexual female and male RNA was hybridized on an *A. pisum* cDNA microarray representing ~10% of the genome (1,734 unique genes) (3). We identified significantly different transcript accumulation between sexes via t test with a false discovery rate (FDR) < 0.05 and at least a twofold change in expression, yielding 107 asexual female-biased, 127 male-biased, and 95 sex-neutral genes (SOM text).

We identified orthologs of *A. pisum* genes in Genbank from the green peach aphid, *Myzus persicae* [in the same tribe as *A. pisum* (Macrosiphini)], and the cotton-melon aphid, *Aphis gossypii* [in the same subfamily but a different tribe (Aphidini)] (4). When comparing *A. pisum* and *M. persicae* orthologs, we found no differences between asexual female-biased and neutral nonsynonymous (K_a) and synonymous (K_s) rates of evolution, nor between their ratios (K_a/K_s). However, both K_a and Ka/K_s were significantly larger (Mann-Whitney U test, P <0.002, all comparisons) in male-biased genes compared with those of asexual female-biased and neutral genes (Figure 1). Male-biased genes also were more divergent, relative to neutral and female-specific genes, in comparisons of *A. pisum* with *A. gossypii* with K_a and K_a/K_s significantly larger (P = 0.016, 0.001 and 0.026, 0.002, respectively). We found no evidence for codon bias (table S1), and it is unknown what proportion of these genes is X-linked versus autosomal. Transcript accumulation level and sex specificity on K_a/K_s values were examined because genes with high levels of transcript accumulation evolve slower than genes with low transcript accumulation (5). Two-way analysis of variance (ANOVA) with expression level and sex bias established significance of both terms (mean square = 0.1365, F = 25.45, P < 0.0001 and mean square = 0.6535, F =121.86, P < 0.0001; respectively). Thus, although weakly expressed genes evolve faster than genes with higher transcript levels, the effect of sex is much stronger.

This accelerated rate of male-biased gene evolution is consistent with both positive and relaxed selection. In some species, accelerated evolution of male-biased genes is influenced by positive selection on reproductive proteins (6). This may be true in *A. pisum*, but it is not likely the case for the genes examined here. Because the microarray was constructed from expressed sequence tags (ESTs) from asexual female cDNA libraries, we did not assay exclusively male-specific transcripts and probably underestimated the overall rate of acceleration of evolution of male-biased genes.



B

Parameter	Male-biased genes	Asexual female-biased genes	Neutral genes
	M. persicae		
N	77	67	56
K_a	0.023	0.015	0.012
K_s	0.262	0.231	0.245
K_a/K_s	0.091	0.047	0.050
	A. gossypii		
N	33	42	23
K_a	0.032	0.010	0.012
K_s	0.416	0.330	0.371
K_a/K_s	0.071	0.029	0.036

Fig. 1. (**A**) Distribution of K_a/K_s values for each class of gene and each species comparison. (**B**) Evolutionary rates for genes with sex-biased or sex-neutral expression in comparisons of *A. pisum* to *M. persicae* and *A. gossypii*.

To distinguish between relaxed and positive selection, we sequenced 14 female- and 13 male-biased genes from 12 geographically disparate *A. pisum* clones and noted nonsynonymous and synonymous changes (table S2, averaging ~10 individuals per locus). Despite low coding region diversity, we found significantly more nonsynonymous changes in male-biased genes (five versus zero; Fisher's exact test, P = 0.05). We also observed an excess of nonsynonymous changes in male-biased genes between *A. pisum* and *M. persicae* homologs (P < 0.001, table S3) consistent with the K_a/K_s comparisons, and the numbers of nonsynonymous changes were consistent between interspecific and intraspecific data sets (P = 0.30 and 0.26 for asexual female-biased and male-biased genes, respectively). The excess of nonsynonymous coding changes and consistency between interspecific and intraspecific patterns support relaxed, rather than positive, selection on male-biased genes in *A. pisum*.

Our data show that the dominance of the life cycle by parthenogenetic females can result in the mutational decay of male-biased genes. Whereas asexual female-biased genes are under constant selection, male-biased genes experience selection at most once per year (SOM text). Sexual selection may further reduce the effective population size of males, resulting in the fixation of weakly deleterious mutations (7). If relaxed selection alone is sufficient to produce accelerated male-biased gene evolution, we predict a similar pattern of decay in sexual female-biased genes. We conclude that the variation in genes related to males and asexual females are different in species combining sexual and asexual reproduction. These findings suggest new prospects for the role of sexual versus asexual reproduction in the adaptability of species to various environmental conditions.

References and Notes

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Supporting Online Material
http://www.sciencemag.org/cgi/content/full/319/5859/58/DC1
Materials and Methods, SOM Text, Tables S1 to S8, References

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