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# Comment on “Transitions to Asexuality Result in Excess Amino Acid Substitutions”

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Paland and Lynch (Reports, 17 February 2006, p. 990) showed that in *Daphnia pulex*, the ratio of amino acid replacement to silent substitution in mitochondrial genes is higher in asexual lineages than in sexual lineages. If this base-composition bias is maintained by selection, it too should alter following transitions in reproductive mode. Analysis reveals no such change in the genomes of *D. pulex*.

Natural selection is expected to operate less effectively in asexual lineages than in sexually reproducing populations because associations between genes can be neither broken down nor built up by recombination. Paland and Lynch (*J*) demonstrated this effect in *Daphnia pulex* by showing that the rates of amino acid replacement substitution are elevated in asexual lineages relative to rates of silent substitution. A class of moderately deleterious amino acid substitutions has a higher probability of spreading to fixation in asexual populations than in sexual populations. The size of this class depends on the effective sizes of the asexual and sexual populations and the distribution of mutational effects on fitness.

Asexual reproduction should have similar effects on other characteristics maintained by a balance between mutation and weak selection in sexual populations. This is expected to include genomic features such as base-composition bias. For the mitochondrial genomes investigated in (*J*), this raises an interesting ques-

tion. Like most animal mitochondrial genomes, *Daphnia* mitochondrial DNA (mtDNA) has a marked excess of A+T nucleotides. This bias may be due to underlying asymmetries in mutation rate, selection, or the balance between these two forces. Although there is extensive evidence for biased substitution rates in animal mtDNA, there is no consensus on whether this is entirely due to the pattern of mutation or is filtered by selection (2, 3). If selection plays a role in maintaining the base composition of *Daphnia* mtDNA in sexual populations, one might expect base composition to deviate from this equilibrium in asexual lineages. The direction of change would depend on whether selection was operating to restrain a bias due to asymmetrical mutation or to create a bias.

In fact, the mean proportion of A and T bases among 13 mtDNA genomes from sexual individuals sequenced by Paland and Lynch (*J*) is  $0.61525 \pm 0.00025$ , whereas the mean for 14 genomes from asexuals is  $0.61526 \pm 0.00021$ . The greatest difference between an asexual genome and its closest sexual relative is 0.0029 (not significant by contingency test). Among 10 independent comparisons, there are five cases where the AT proportion has increased and five

cases where it has decreased in the asexual lineage. The typical pairwise distance between an asexual and its nearest sexual genome is around 1%. If the underlying mutational matrix were symmetrical, such that 50% of bases would be expected to be A or T, this divergence would produce a change of about 0.2% in AT proportion (from 0.615 to 0.613) after removal of selection. A consistent effect of this size would certainly have been detectable, given that Paland and Lynch sequenced all coding regions (>15 kb per strain). Smaller shifts, which would be expected if both selection and mutational pattern contribute to the base-composition bias, would be harder to detect. In older asexual lineages, a change in base composition could be detected with shorter sequences.

This observation suggests that selection is not the major force determining base-composition bias in the mitochondrial genome. However, selection on the mitochondrial genome operates at two levels: among animals and among mitochondrial genomes within animals. Only the among-animal component of selection is modified by asexual reproduction. Therefore, it remains possible that selection among genomes, for example, for rapid replication (4), influences base-composition bias. It will be interesting to measure base composition in asexual lineages of various ages, in coding and noncoding regions, and in taxa with different proportions of AT bases among sexual populations. This will provide a new source of data with which to examine the evolution of mitochondrial genomes.

## References

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