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The Behavior of a *Daphnia pulex* Transposable Element in Cyclically and Obligately Parthenogenetic Populations

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Abstract. Using Southern blot analysis, we have characterized restriction fragment patterns of a transposable element, Pokey, in obligately and cyclically parthenogenetic populations of the cladoceran crustacean *Daphnia pulex*. We show that the element is most likely active in cyclically parthenogenetic populations but is, for the most part, inactive in obligate parthenogens. This result is consistent with theory suggesting that transposable element dynamics are likely to change with a change in reproductive mode. Such changes could have important consequences for the long-term evolutionary potential of obligate parthenogens and may also be informative with regard to the underlying mechanisms that regulate transposable element frequencies in sexual organisms.

Key words: Transposable element — Parthenogenesis — *Daphnia*

Introduction

Parthenogenetic reproduction has arisen on multiple occasions among a diverse array of taxa (reviewed in Suomalainen et al., 1987). Theoretical studies of this process have shown that the shift from sexual reproduction to obligate parthenogenesis should have numerous evolutionary consequences (reviewed in Maynard Smith, 1978 and Michod and Levin, 1988). For example, sexually and parthenogenetically reproducing populations will differ in response to both short- and long-term selection and in their ability to purge deleterious mutations of small effect. Such observations are important in understanding why parthenogenetic lineages typically appear to be short-lived, despite having eliminated numerous costs associated with biparental inheritance and meiosis (Maynard Smith, 1971; Williams, 1971; Bulmer, 1982; Crow, 1988; Joshi and Moody, 1998).

What has not been so readily appreciated in theoretical studies is that change in reproductive mode may also have consequences for some of the underlying genetic mechanisms that are ultimately responsible for the generation of genetic variation. Studies examining the evolutionary potential of sexual and parthenogenetic populations often implicitly assume that, beyond the differences in recombination and inheritance, all other things are equal. Research examining the evolution of ribosomal RNA encoding genes (rDNA) in sexual and parthenogenetic organisms clearly show, however, that certain basic molecular genetic processes are different (Hillis et al., 1991; Crease, 1995). Moreover, there are long-standing reasons for believing that important components of most genomes, transposable elements, should behave much differently in systems of restricted recombination compared to those where it occurs more freely (Hickey, 1982). Given that transposable elements are frequently a significant source of new mutations (Galas and Chandler, 1989; Favor, 1994; Nuzhdin and Mackay, 1995), and that the genome mutation rate is a critical parameter in current theory regarding the maintenance of

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sexual reproduction (Lynch and Gabriel, 1983; Kondrashov, 1988; Howard, 1994), understanding just how transposable element behavior changes with change in reproductive mode is an important issue.

Recently, Sullender (1993) identified a transposable element, referred to as Pokey, in the cladoceran crustacean *Daphnia pulex*. Preliminary sequence analysis showed that Pokey is 7.2 kbp in length, has 16 bp imperfect terminal inverted repeats, and is flanked by 4 bp direct repeats (TTAA). The element was found in approximately 10% of the large subunit ribosomal RNA (LSU rRNA) genes in the same conserved region occupied by other arthropod LSU rRNA insertions (Jakubczak et al., 1991; Burke et al., 1998; Burke et al., 1999). It is also found at numerous other locations in the genome.

Here, we take advantage of the fact that some populations of *D. pulex* have a sexual component to their life cycle (cyclical parthenogenesis), while others do not (obligate parthenogenesis), to explore possible differences in transposable element dynamics under the two modes of reproduction. When environmental conditions are favorable, all female *Daphnia* produce direct-developing eggs via apomictic parthenogenesis (Suomalainen et al., 1987), which results in female offspring that are genetically identical (barring mutation) to their mothers. When crowding occurs or food becomes limiting, cyclically parthenogenetic females produce diploid males (that are also genetically identical to their mothers) and haploid diapausing eggs that require fertilization. While obligately parthenogenetic females may or may not produce males under these same conditions, they always produce diploid diapausing eggs apomictically.

Materials and Methods

Source of Daphnia *and isolation of genomic DNA. Daphnia pulex* used in this study were sampled from both the United States and Canada. Cyclical parthenogens were sampled from Busey Pond (BP) in Champaign County, Illinois (Crease et al., 1990), Portland Arch (PA) in Warren County, Indiana (Crease et al., 1990), Amazon Park (AM) in Lane County, Oregon, and Lava Lake (LL) in Deschutes County, Oregon (Crease et al., 1997). Obligate parthenogens were sampled from populations 21, 35, 36, 41, and 45 (Hebert et al., 1989) in Essex County, Ontario and from Temporary Pond (TP) and Busey Pond (BP), both in Champaign County, Illinois (Crease et al., 1990).

To obtain sufficient tissue for DNA extraction, laboratory cultures were established from individual females and grown under conditions that favor the production of apomictic eggs (Crease, 1986). Genomic DNA was isolated from approximately 100 mg (wet weight) of fresh or frozen tissue by phenol extraction and ethanol precipitation (Crease, 1986).

Southern blot analysis of genomic DNA. To identify individual Pokey insertions, a 4.65 kbp *Sst* I fragment beginning 1.84 kbp upstream of the 3′ end of Pokey was subcloned from a recombinant EMBL3 phage containing a partial element (Sullender, 1993). This subclone, p235, also contains approximately 1.6 kbp of the 3′ end of the LSU rRNA gene and 1.2 kbp of the intergenic spacer. An internal 1.1 kbp *Sst* I-*Hin*dIII Pokey fragment from this subclone, designaed p235RK, was radioactively labeled and hybridized to genomic DNA of *D. pulex* digested with the restriction enzyme, *Eco*R V. This site is just upstream of the *Sac* I site in Pokey. Because there are no other *Eco*R V sites 3′ to this one in Pokey, hybridizing fragments consist of the 3′ end of Pokey and flanking DNA downstream of the element. The size of hybridizing fragments will vary depending on the position of the first *Eco*R V site in the flanking DNA.

Restriction digests were done according to manufacturer's specification. After electrophoresis on 0.8% agarose gels as described in Crease et al. (1989), DNA was transferred to Magnagraph nylon membranes (MSI) in 20 × SSC by capillary action. The p235RK probe fragment was labeled with ^{32}P-αdCTP (Amersham) by random priming (Feinberg and Vogelstein, 1983) and the Southern blots were hybridized to the p235RK using standard methods (Sambrook et al., 1989). Post-hybridization stringent washes were done in 0.1 × SSC, 0.1% SDS at 55°C.

Expected heterozygosity at Pokey loci was estimated for cyclically parthenogenetic populations using the proportion of shared fragments according to Lynch and Milligan (1994). Only fragments above 2 kbp were included in this analysis.

Results

Many fragments ranging in size from 1 kbp to 20 kbp typically hybridized to p235RK. In all cyclically parthenogenetic populations except AM (Fig. 1D), every individual displayed a unique fragment pattern (Figs. 1A, B, C). Moreover, expected heterozygosities within populations were as high as 0.35 ± 0.09 (Table 1). Conversely, obligately parthenogenetic populations displayed no inter-individual variation except for population 21, where individuals displayed one of two very dissimilar fragment patterns. One of the patterns in this population (found in 1/3 of the individuals) is identical to that seen in all individuals from populations 45 (Fig. 2A), as well as all individuals from populations 35, 36, and 41 (data not shown). There are actually two variants of the second pattern, which differ from one another by two fragments (Fig. 2B). In addition, the average number of Pokey fragments above 2 kbp within the four obligately parthenogenetic clones (15.8) was slightly less than the mean of the average number of fragments per individual in the four cyclically parthenogenetic populations (16.6, Table 1).

To further characterize the multiple fragments, the genomic DNA of an individual from population 45 was digested with *Eco*R V and hybridized separately to p235RK and to a LSU rRNA gene probe (Fig. 3). The 4.1 kbp fragment that most strongly hybridizes to p235RK (indicated by # in Fig. 3) appears to correspond to a Pokey-bearing fragment of rDNA, suggesting that it is the most common Pokey insertion site in this isolate. The additional bands that hybridize to p235RK most likely represent Pokey elements that have inserted elsewhere in the genome. If the 4.1–4.5 kbp *Eco*R V fragment observed in other *D. pulex* isolates (Figs. 1 and 2) is the Pokey-rDNA fragment, then not only does Pokey's frequency in rDNA vary among individuals, but it may even have disappeared, or nearly disappeared, from the rDNA of some isolates (e.g., Fig. 1A).

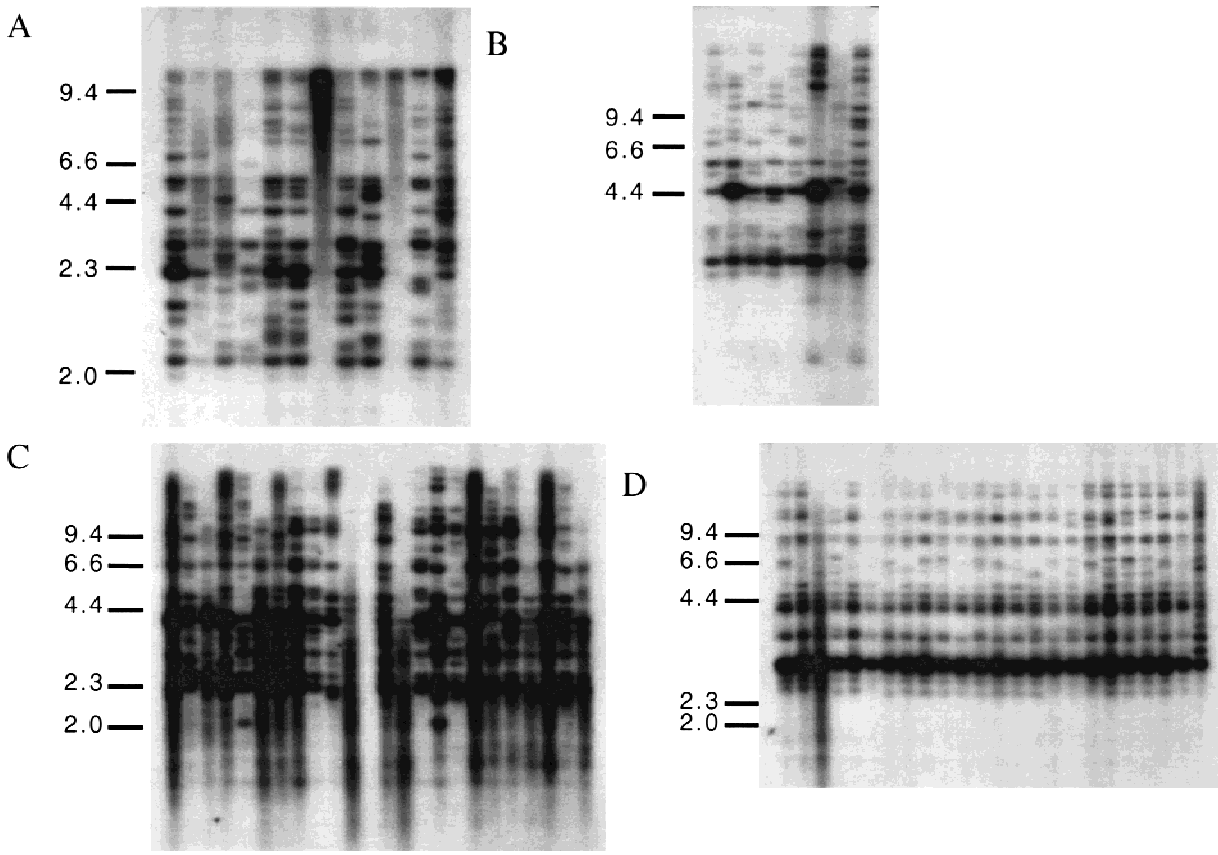

Fig. 1. Hybridization of p235RK to *Eco*R V digests of *Daphnia pulex* genomic DNA from cyclically parthenogenetic populations. Each lane represents a single individual sampled from a natural population. **(A)** Population BP from Illinois. **(B)** Population PA from Illinois. **(C)** Population LL from Oregon. **(D)** Population AM from Oregon. Lambda phage DNA digested with *Hin*dIII was used as a molecular weight marker.

Discussion

Comparison of Pokey fragment patterns in cyclically and obligately parthenogenetic *D. pulex* suggests that Pokey may be behaving differently in the two types of populations. In all cyclically parthenogenetic populations except Amazon, each individual displayed a unique Pokey fragment pattern. Most differences between individuals are likely the result of genetic assortment of the various loci containing Pokey. Nevertheless, the relatively high average expected heterozygosities in some populations (Table 1) and the large number of sites bearing Pokey is consistent with relatively recent Pokey transposition. In the absence of active transposition, average heterozygosities are expected to be relatively low due to the fixation or loss of alleles containing Pokey through genetic drift. Likewise, any deleterious insertions will be eliminated by selection, leading to a net loss in the number of loci containing the element.

The AM population (Fig. 1D) is unusual among the cyclical parthenogenetic populations surveyed because its most intensely hybridizing fragment is only 2.6 kbp in length. This observation, combined with the unusual sequence found in a cloned AM fragment (Sullender,

Table 1. Analysis of Pokey fragments in *Daphnia pulex* reproducing by obligate and cyclic parthenogenesis.

Population	n	No. of fragments per individual[1] (±SE)	Average heterozygosity[1] (±SE)
Cyclical populations			
AM	22	15.96 (0.59)	0.16 (0.04)
BP	7	18.57 (0.57)	0.29 (0.45)
LL	17	15.94 (0.59)	0.35 (0.09)
PA	7	16.00 (1.02)	0.30 (0.01)
Mean		16.62 (0.65)	0.28 (0.04)
Obligate clones			
45[2]	44	19	
21B[3]	24	14 or 16	
BP	4	15	
TP	19	14	
Mean		15.75 (1.11)	

n = the number of individuals included in the analysis.
[1] Only fragments greater than 2 kbp were included in the analysis.
[2] The clone present in populations 35, 36, and 41, and one of two clones found in population 21 all had the same fragment pattern as the clone found in population 45.
[3] Two clones were present in population 21. Clone A had the same pattern as that seen in population 45. There were two variants of clone B, which differed by two fragments.

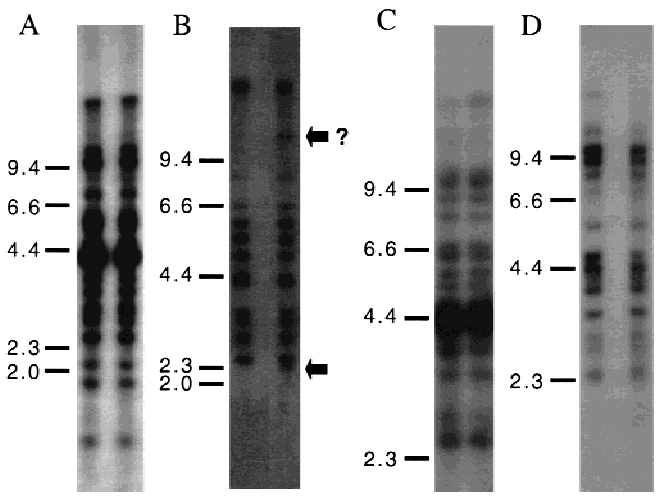

Fig. 2. Hybridization of p235RK to *Eco*R V digests of *Daphnia pulex* genomic DNA from obligately parthenogenetic populations. Each lane represents a single individiual sampled from a natural population. Because individuals in these populations displayed only one or two unique fragment patterns, only two examples of each pattern are shown. The number of individuals sampled in each population is given in brackets. **(A)** Population 45 from Ontario (n = 11) This fragment pattern is also seen in 1/3 of the individuals surveyed in population 21 (n = 12) and all individuals surveyed in populations 35 (n = 6), 36 (n = 5), and 41 (n = 10). **(B)** Population 21 from Ontario (n = 12). Two-thirds of the individuals surveyed display this basic fragment pattern. Half of these individuals displayed two additional fragments (indicated by arrows). **(C)** Population TP from Illinois (n = 19). **(D)** Population BP (A clone) from Illinois (n = 4). Lambda phage DNA digested with *Hin*dIII was used as a molecular weight marker.

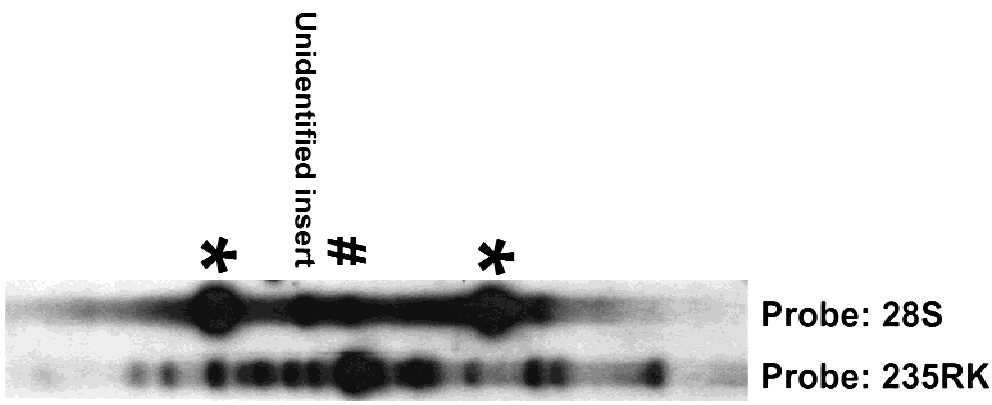

Fig. 3. Comparison of hybridization patterns with p235RK and the LSU rRNA gene. The genomic DNA of a *D. pulex* isolate from Ontario was digested with *Eco*R V and run in two adjacent lanes of an agarose gel. After Southern blotting of the gel, the right lane was hybridized to p235RK and the left lane was hybridized to an internal LSU rRNA gene fragment. The strongly hybridizing bands in the left lane (indicated with an asterisk) correspond to LSU rRNA gene fragments that lack Pokey. The strongly hybridizing band in the right lane corresponds to the rDNA-Pokey fragment (#), which also hybridizes to the LSU rRNA gene as expected.

1993), suggests that Pokey elements in this population may be quite different from those found in other cyclical parthenogens. Moreover, AM individuals differ from other cyclical parthenogens in that there is little interindividual variation in fragment pattern which suggests that many loci are fixed for Pokey insertions in this population.

This result is surprising but could potentially be explained by a model recently developed by Brookfield and Badge (1997). They show that transposable elements can occasionally be fixed at numerous loci if copies with a partner at a homologous site do not recombine ectopically to create deleterious rearrangements, and if such rearrangements play a major role in regulating transposable element number. Since selection only acts against heterozygotes under this model, there will be an unstable equilibrium frequency of 0.5 for the element at each insertion site. Generally, selection will resist increases in transposable element frequency at a particular site. In finite populations, though, genetic drift will occasionally increase the frequency of an element at a particular site to above the unstable equilibrium threshold, where selection will then favor its fixation. As the number of sites with high frequencies of the transposable element increases, transposition from these sites favors fixation at other sites. The process is thus cumulative and is facilitated in its early stages by small population size and weak selection against heterozygotes. It is not presently known whether the AM population differs from other cyclical parthenogenetic populations in ways that would favor this process.

Using allozyme and mtDNA variation, Crease et al. (1989) showed that much of the clonal diversity in the obligate parthenogens examined in this study is derived from multiple, independent transitions to obligate parthenogenesis from a cyclically parthenogenetic ancestor, although mutational divergence within established clones continues to generate some diversity. The results of the present study suggest that each independently derived clonal lineage has a distinct Pokey fragment pattern and that it is very stable over time. Crease et al. (1989) found that populations 36, 41, and 45 all contained the

same clonal lineage and that the clone in population 35 is most likely a mutational derivative of it. All of these populations show the same Pokey pattern. Crease et al. (1989) detected only a single clone in population 21, which differed from the one found in populations 35, 36, 41, and 45. The occurrence of two distinct Pokey fragment patterns in population 21 suggests that it now contains at least two clones, although this has not been confirmed with allozyme and mtDNA data. The Pokey fragment patterns of the obligate parthenogens in the TSP and BP populations are very different from the patterns observed in the Ontario populations, and from one another. Previous allozyme and mtDNA analysis of these populations also showed that they each contain a different clone (Crease et al., 1990).

With one exception (Fig. 2B), no variation was observed within clonal lineages of the obligate parthenogens, despite the occurrence of genetic divergence at other loci. For example, the clone in populations 35, 36, 41, and 45 has persisted long enough to diverge in mitochondrial sequence (Crease et al., 1989), to display considerable IGS length variation (Sullender, 1993), and to show variation in the number of Pokey elements found in rDNA (not shown). Likewise, individuals of the TSP clone show substantial levels of IGS length variation (Crease and Lynch, 1991).

Previous research has suggested that transposable element dynamics will change with the onset of apomixis, but it is not precisely clear how they will change. For example, if ectopic recombination occurs primarily during meiosis, as some evidence seems to indicate (Kupiec and Petes, 1988; Petes and Hill, 1988), and it does play a major role in the control of transposable element number, then transposable elements should increase in frequency with the shift to apomictic reproduction (Sullender, 1993; Charlesworth and Charlesworth, 1995). Even if ectopic exchange does continue to occur in apomicts, its ability to regulate transposable element number will likely be reduced since many chromosomal rearrangements caused by ectopic recombination are only deleterious because they cause chromosomal non-disjunction during meiosis (Sullender, 1993). Because homologous chromosomes do not pair in apomictic organisms, many such rearrangements may not be deleterious (White, 1973) and will therefore not contribute to the control of transposable element copy number. Conversely, an actively transposing element and any loci that modify transposition rate are inextricably associated with the deleterious effects caused by new insertions in an obligately apomictic lineage, so selection favoring both transpositional immunity and repression should be particularly effective (Crow, 1984; Charlesworth and Langley, 1986).

Understanding the precise relationship between these two opposing processes requires further modeling. Nevertheless, any loss of regulation through the elimination or reduced effectiveness of ectopic exchange will be immediate, but any new regulation arising from transpositional immunity and/or repression will take time to evolve. Thus, there should be at least some initial increase in transposable element frequency with the shift in reproductive mode. However, the average number of Pokey fragments (above 2 kb in size) in the four obligately parthenogenetic clones was actually somewhat lower than the average of the mean number of fragments for each of the four cyclically parthenogenetic populations (Table 1).

While the similarity in Pokey fragment number between cyclic and obligate parthenogens could be taken as evidence that ectopic exchange does not play a major role in regulating Pokey frequency in cyclic parthenogens, there is an alternative explanation. Selection against transposition may already have occurred in the apomictic phase of the life cycle in the cyclic parthenogens. For example, interclonal selection could have favored genotypes in which transposition is host-limited by apomixis-specific modifiers of transposition rate, or those in which Pokey elements limit their own transposition. A study by Ribeiro-dos-Santos et al. (1997) suggests that such regulation can evolve in organisms that alternate between sexual and asexual reproduction. Although their experimental design cannot rule out strain-specific effects, they show that Ty3 transposable elements in *Saccharomyces cerevisiae* are 50-fold more active in meiotically dividing cells than they are in asexually reproducing ones. At any rate, if such selection has occurred in *Daphnia* cyclic parthenogens, then mechanisms for regulating transposable element activity during apomixis will be in place before the transition to obligate parthenogenesis. Examining the Pokey fragment pattern of individual *Daphnia* can test this hypothesis. If it is correct, the fragment pattern of the apomictically produced offspring of a single female should vary very little compared to that of sexually produced individuals from the same population.

A somewhat similar experiment has already been performed by Zeyl et al. (1994). Using scanning laser densitometry, they found no significant changes in the abundance of *Gulliver* and *TOC1* transposable elements in sexual and asexual experimental lines of the unicellular, heterothallic chlorophyte alga, *Chlamydomonas reinhardtii.* Activity of the two transposable elements was also examined within two asexual lineages using Southern blot hybridizations. Despite approximately 800 generations separating ancestors and descendants, only one of the 40 descendant fragment patterns examined differed from that of the ancestral pattern (it both lacked a fragment and displayed a new one). The latter result is directly comparable to that seen in obligately parthenogenetic *D. pulex,* and could be explained by the model we propose for *D. pulex* if natural populations of *C. reinhardtii* at least occasionally experience bouts of

asexual reproduction. The *D. pulex* model could also explain the lack of change in abundance if the frequencies of the two transposable elements were already at equilibrium (new insertions being balanced by losses) in the populations from which the strains used in the study were drawn. Our model would predict, however, that if the genomic fragment patterns of individuals from sexual lines of *C. reinhardtii* had been compared, there would have been evidence for transposable element activity.

Understanding how transposable element dynamics differ in sexual species and their parthenogenetic derivatives is important if we are to fully understand the long-term evolutionary potential of obligate parthenogens. Although transposable element insertions constitute only a small proportion of spontaneous mutations in mice (Favor, 1994), they account for between 5 and 40% of all spontaneous mutations in *Escherichia coli* and their phage (reviewed in Galas and Chandler, 1989), and contribute up to half of the spontaneous mutations in *Drosophila melanogaster* (Nuzhdin and Mackay, 1995). When transposable element insertions are an important source of mutation, changes in genomic mutation rate as a result of a change in reproductive mode could affect the expected persistence time of obligately parthenogenetic lineages (Lynch and Gabriel, 1990; Hurst and Peck, 1996) and/or their ability to compete with sexual populations (Lynch and Gabriel, 1983; Kondrashov, 1988; Howard, 1994). Moreover, Butcher (1995) showed that the distribution of mutational effects can also effect the persistence time of an obligate parthenogen. Although data are very limited, there is evidence that the average effect of mutations caused by transposable element insertions differs from that of other types of mutations (Keightley, 1996).

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