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RELATING HYBRID ADVANTAGE AND GENOME REPLACEMENT IN UNISEXUAL SALAMANDERS

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Unisexual vertebrates are model systems for understanding the evolution of sex. Many predominantly clonal lineages allow occasional genetic recombination, which may be sufficient to avoid the accumulation of deleterious mutations and parasites. Introgression of paternal DNA into an all-female lineage represents a one-way flow of genetic material. Over many generations, this could result in complete replacement of the unisexual genomes by those of the donor species. The process of genome replacement may be counteracted by contemporary dispersal or by positive selection on hybrid nuclear genomes in ecotones. I present a conceptual model that relates nuclear genome replacement, positive selection on hybrids and biogeography in unisexual systems. I execute an individual-based simulation of the fate of hybrid genotypes in contact with a single host species. I parameterize these models for unisexual salamanders in the *Ambystoma* genus, for which the frequency of genome replacement has been a source of ongoing debate. I find that, if genome replacement occurs at a rate greater than 1/10,000 in *Ambystoma*, then there must be compensating positive selection in order to maintain observed levels of hybrid nuclei. Future researchers studying unisexual systems may use this framework as a guide to evaluating the hybrid superiority hypothesis.

KEY WORDS: ***Ambystoma*, gynogenesis, hybridogenesis, introgression, selection, vertebrate.**

The study of bizarre biological systems offers both fascination and the hope that we will gain deeper insights into the standard pathways of evolution (Dawley 1989). Of particular interest to biologists are unisexual vertebrates, which have become models for understanding the origins and mechanics of sexual reproduction (Crews 1989; Abt and Reyer 1993; Vrijenhoek 1994; Bogart et al. 2007). To date, approximately 80 fish, reptile, and amphibian taxa have been shown to reproduce through parthenogensis, gynogensis, or hybridogenesis (Vrijenhoek et al. 1989; Avise 2008; Lampert 2009; Neaves and Baumann 2011). As strictly defined, each of these three reproductive modes results in clonal gametic lineages with no lasting inheritance from sexual partners (Schultz 1971; Beukeboom and Vrijenhoek 1998). Because recombination is excluded from such a system, evolutionary theory predicts that parasites and the accumulation of deleterious mutations should cause such lineages to be short lived (Muller 1964; Hamilton 1980; Hurst and Peck 1996; Judson and Normark 1996; Schlupp 2005; Loewe and Lamatsch 2008; Lively 2010).

Increasing evidence suggests that many, if not all, of the gynogenetic and hybridogenetic lineages allow for some degree of introgression of genetic material from outside the lineages (Kallman 1964; Uzzell et al. 1977; Goddard and Dawley 1990; Schartl et al. 1995; Pagano and Schmeller 1998; Beukeboom and Vrijenhoek 1998; Lamatsch et al. 2000; Alves et al. 2004; Nanda et al. 2007; Ramsden 2008; Lamatsch and Stöck 2009). These occasional deviances from pure clonality may be sufficient to reap the benefits of sex while avoiding the cost of producing males, allowing unisexual lineages to persist for very long times

(Maynard Smith 1978, 1992; Green and Noakes 1995; Schartl et al. 1995; Beukenboom and Vrijenhoek 1998; D'Souza and Michels 2010; Lampert and Schartl 2010). Such leakage may occur through occasional incorporation of entire chromosome sets from outside the lineage, incorporation of individual chromosomes, recombination between homeologous genomes, or inclusion of extra-genomic DNA elements (Uzzell et al. 1977; Schartl et al. 1995; Bi et al. 2007; Bi and Bogart 2010b).

The exact cytological mechanisms of reproduction in unisexual vertebrates are still poorly understood, and differ among the taxa. To generate diploid eggs, oocytes of gynogenetic fish *Poecilia formosa* skip meiosis (apomixis; Rasch et al. 1982), whereas the gynogenetic fish *Poeciliopsis 2 monacha-lucida* double oocyte chromosome number prior to meiosis (premeiotic endomitosis; Cimino 1972a). To produce haploid eggs, during premeiotic mitosis in hybridogenetic *Poeciliopsis monacha-lucida*, the *lucida* chromosomes are left to languish in the cytoplasm whereas unipolar spindles attach only to *monacha* chromosomes, which then go through modified meiosis (Cimino 1972b). In diploid water frogs *Rana esculenta*, genome exclusion precedes endomitosis and meiosis to produce haploid gametes (Tunner and Heppich-Tunner 1991).

In an all-female lineage with occasional inclusion of paternal DNA, the flow of genetic material is unidirectional. Donor males cannot receive unisexual DNA, but unisexuals may occasionally receive male DNA. This reasoning assumes that fertile males never arise from the lineage. Consider a primarily gynogenetic system in which females occasionally produce eggs of reduced ploidy that are then elevated in ploidy by inclusion of a sperm nucleus. When ploidy reduction and syngamy in one generation precede gynogenesis in the next, an entire haploid male genome has replaced one haploid set of the unisexual genome. When ploidy reduction and syngamy repeat in each generation, male chromosomes should be replacing unisexual chromosomes little by little if chromosomes assort independently. Over many generations, this would result in replacement of the entire unisexual genome by that of donor males.

Despite the ratcheting influence of paternal introgression, we could explain distinctive genomes maintained in unisexuals by considering three factors: time, dispersal, and selection. If the rate of genome replacement is slow, it may merely be that insufficient time has elapsed for the entire unisexual genome to be lost. Ongoing dispersal may overwhelm the rate of genome replacement in cases where adjacent unisexual populations are breeding with males of different species. One may also posit an adaptive advantage conferred to unisexuals that maintain hybrid nuclei within an ecotone, as most unisexual vertebrates are associated with interspecies hybridization (Wright and Lowe 1968; Schultz 1971; Moore 1977; Hotz et al. 1999; Lampert and Schartl 2008; Neaves and Baumann 2011).

The goal of this study was to provide a formal framework to assess the adaptive advantage of hybridization in relation to the rates of genome replacement and dispersal. First, I performed a stochastic simulation to understand the fate of neutral genomes in a hybrid unisexual lineage that only has contact with one host species. I then combined empirical data with the simulation results in an analytic model that uses the genome replacement rate as a basis to assess whether hybrid nuclei are maintained in situ simply as a relic of the past, by contemporary dispersal, or by positive selection on hybrids.

Methods

STUDY SYSTEM

Unisexual salamanders in the *Ambystoma* genus represent perhaps the clearest case where paternal genomes might be expected to replace unisexual genomes over time. These salamanders have a complex reproductive history that involves recurrent nuclear hybridization between five modern species, yet only one 5-million-year-old monophyletic mitochondrial lineage (Hedges et al. 1992; Robertson et al. 2006; Bi and Bogart 2010a). The literature is replete with research and debate about two aspects of unisexual salamander biology: the geographic distribution of genotypes and the frequency with which nuclear genome replacement occurs (Clanton 1934; Uzzell 1964; Morris and Brandon 1984; Bogart 1989; Lowcock 1989; Elinson et al. 1992; Spolsky et al. 1992; Petranka 1998; Bogart 2003; Lanoo 2005; Bogart et al. 2007; Bi et al. 2008; Bogart and Klemens 2008; Ramsden 2008). Although these two aspects of their biology ought to inform each other, there have been no prior attempts to formally combine inquiries into genome replacement and biogeography into one framework.

Although unisexual salamanders are primarily gynogenetic, there is ample evidence that both reduction of eggs and incorporation of sperm nuclei occasionally occur in unisexual salamanders (Bogart et al. 2007; Bi et al. 2008). In the field, the nuclei of unisexual salamanders usually include a combination of genomes from one or more of: *A. laterale*, *A. jeffersonianum*, *A. tigrinum*, *A. texanum*, and *A. barbouri*. Which species' genomes unisexuals carry is influenced in part by what local host species are present (Bogart et al. 2009). Several different ploidy levels have been observed in adults, in eggs, and even in eggs produced by the same female (Bogart 1989; Bogart et al. 1989; Elinson et al. 1992). Rarely, sterile males occur in the lineage, which suggests that the genome containing the W sex chromosome can be lost during reproduction (Uzzell 1964; Bogart and Klemens 1997; Bogart 2003). In the lab, Bogart et al. (1989) found sperm nuclear incorporation at rates of 27% and 70% in water temperatures of 6°C and 15°C, respectively. Based largely on these observations that suggest high rates of genome replacement, Bogart et al. (2007) concluded that a new term, "kleptogenesis" was warranted to

describe the system. However, there has been extensive debate over the prevalence of genome replacement, and researchers continue to struggle to quantify the rate at which it occurs in nature (Spolsky et al. 1992; Bogart 2003; Ramsden 2008).

In *Ambystoma*, reproduction proceeds through both gynogenetic- and hybridogenetic-like pathways, neither of which are well understood. Unreduced eggs are produced via premeiotic endomitosis (Bogart et al. 1989; Bi and Bogart 2010b). When *Ambystoma* eggs are reduced, unlike in hybridogenesis, paternally derived genomes are apparently neither kept intact nor eliminated prior to meiosis (Bogart et al. 2007). Rare aneuploids with non-integer ploidy levels have been reported. It is possible that many such aneuploid eggs are created but are nonviable, resulting in the observed high rates of embryonic mortality (Bi et al. 2007).

Deviations from pure gynogenesis or hybridogenesis in *Ambystoma* suggest the opportunity for individual paternal chromosomes to take the place of maternal chromosomes during meiosis. *Ambystoma* researchers have typically discussed chromosome sets as cohesive units, describing entire nuclear genomotypes with one letter for each haploid genome set. Thus, an "LJJ salamander" would have one *A. laterale* haploid genome and two *A. jeffersonianum* haploid genomes (Lowcock et al. 1987). However, if L and J chromosomes can be swapped, then these genomes may not be as cohesive as previously thought. Additional evidence has demonstrated the occurrence of recombination between homeologous L and J chromosomes (Bi and Bogart 2006).

All *Ambystoma* eggs need contact with sperm to activate embryo development, and occasionally the sperm nucleus is incorporated into the developing embryo, elevating the offspring ploidy (Bogart and Licht 1986; Bogart 1989). The combination of occasional ploidy reduction of eggs and occasional ploidy elevation by sperm results in the possibility for a single female to produce offspring of multiple ploidy levels. When paternal genomes are inherited by an offspring through syngamy, the paternal genomes must be transmitted to subsequent generations if that offspring reproduces gynogenetically. If offspring never transmit paternally derived genomes, then gynogenesis would be lost from the system through a ratcheting effect that tightens every time a hybridogenetic offspring arises.

One of the striking features of unisexual salamanders is that they can be found deep in the heart of one host species' geographic range carrying nuclear genomes that are derived from distant species (Fig. 1). For instance, unisexuals in northern Wisconsin, northern Maine, and Nova Scotia maintain copies of the *A. jeffersonianum* genome even though they are 400–900 km from the nearest *A. jeffersonianum* populations (Petranka 1998; Bogart and Klemens 2008). Populations of LJJ unisexuals are found in some areas where neither *A. laterale* nor *A. jeffersonianum*, occur, but only *A. texanum* occurs (Morris and Brandon 1984; Lowcock 1989).

One explanation for the success of unisexuals is that, by maintaining hybrid nuclei, they specialize in occupying ecotones where the niches of the two host species overlap (Moore 1977; Kraus 1985). Yet, the distribution of unisexuals is not easily explained by obvious ecotones. Consider the population of isolated LLJ unisexuals sympatric with *A. laterale* in northern Wisconsin (Fig. 1). From North to South, beginning adjacent to this unisexual population, there is a 500 km portion of the *A. laterale* range where no unisexuals occur followed by a 200 km wide area in which both *A. laterale* and LLJ unisexuals occur and then the northwestern edge of the *A. jeffersonianum* range. On purely ecological grounds, it is difficult to explain why LLJ unisexuals are not continuous throughout this range (Uzzell 1964). Lowcock (1989) resolves such disjunct populations as evidence that *A. jeffersonianum* had a more northerly distribution at the height of the climatic warm period that ended approximately 4000 years ago (Viau et al. 2002). If these isolated unisexual populations are relicts from an historic climate, it is not clear whether the J genomes they carry are adaptively advantageous today, or are costly baggage from their past. Costs of carrying foreign nuclei may include environmental maladaptations, sexual selection by the host species, and accumulation of deleterious mutations in the absence of recombination (Muller 1964; Dawley and Dawley 1986; Lowcock et al. 1991).

Our ecological interpretation of unisexual salamanders is colored by what we think the rate of genome replacement is. If genome replacement happens very slowly, then the Wisconsin unisexuals may be on the path to replacing all of their J genomes with L genomes from the local males, but this process simply takes a long time. If genome replacement happens rapidly, however, then we must suspect that positive selection maintains the J genomes.

SIMULATION

I constructed an individual-based simulation of unisexual reproduction to track changes in genotype frequency that would be expected from ploidy reduction and ploidy elevation over many generations. The model can be thought of as representing any discrete genomic unit that is transmitted intact. Thus, an "L" could represent the L-type for a particular locus, or a particular chromosome in the absence of recombination, or an entire genome if genome sets remain cohesive during oogenesis. The simulation output, occurrence of J-haplotypes, should be interpreted at whichever genomic level the model mechanics are thought to operate. Given that the cellular mechanisms of unisexual reproduction are still poorly understood and differ among taxa, the most conservative approach is to view the model as representative of a single locus. This model is only meant to simulate the replacement of haplotypes due to changes in ploidy level, not due to other recombination events.

Figure 1. Ranges of *Ambystoma laterale*, *A. jeffersonianum*, and unisexuals containing hybrid nuclei of the two species. Adapted from Petranka (1998) and Bi et al. (2008).

The model began with a uniform genotype (LJJ or LLJ) for all unisexuals in the population and assumed that population size, N, remained constant. In test simulations, I found that population size had no effect on the mean rate at which J haplotypes were lost from the population. As would be expected, population size did have a strong effect on the variance in simulation outcomes. For these simulations, however, I was interested in how the mean fate of hybrid nuclei is influenced by genome replacement. In simulations, I set N to be approximately the size that a breeding pond could support. This would represent the smallest population unit in the field, and thus model the largest variance. As I scale inference up to the larger region, I would expect the actual trajectory of genotypic change to more closely approach the model mean trajectory.

There were four steps in the model (Fig. 2). In the first step, each salamander produced a set number of eggs with some probability of reduction in ploidy number (p_r). The probability that each egg's genotype was identical to that of the mother was $(1 - p_r)$, whereas the probability that one of the mother's haploid genomes was randomly discarded from the egg was p_r.

In the second step, a male haploid genome was randomly incorporated into each egg with a probability of p_i. Incorporation in this model only counted if the genome could be passed on to subsequent generations. If the male genome would be incorporated only in the adult but selectively excluded (e.g., hybridogenesis) prior to egg formation, this was not included in p_i.

In the third step, fitness coefficients were assigned to the embryos based on their genotypes. For my parameterization, this consisted of setting the fitness to zero for all haploid embryos, all pentaploid embryos, and all embryos where no L occurred (Bogart 2003). All other embryos were assigned a fitness of one. Because I began the bulk of my simulations with LLJ salamanders, the selection against pure J salamanders was equivalent to selection against haploid salamanders.

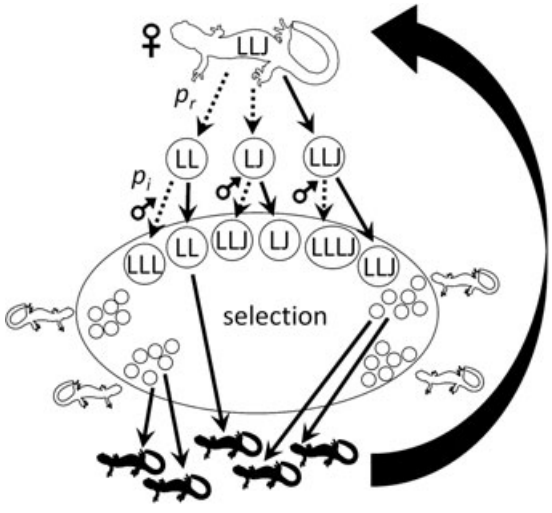

Figure 2. Schematic of individual-based simulation of unisexual reproduction. A unisexual generates eggs, each with a probability (p_r) of ploidy reduction. Male genomes are incorporated to elevate ploidy with a probability, p_i. Relative fitness coefficients are assigned to all embryos from all salamanders in the population. These fitness coefficients are used as weights in a binomial sampling process to select the next generation of adults. White salamanders represent the current generation, whereas black salamanders represent the next generation.

In the final step, all of the embryos from all of the salamanders in the focal generation were pooled, and N of these were selected using a random binomial draw with probability of selection weighted by the fitness coefficients assigned in step three. These selected individuals were then used as the starting adult population for the next generation.

To parameterize the model, I set N at 100 individuals, the number of eggs per individual to 200 (Petranka 1998), and I varied p_r and p_i on a log scale between 1 and 10^{-5} with six steps for each parameter. At every parameterization, I ran 24 simulations for 1000 generations each. I also ran 200 simulations at a parameterization of $p_r = 0.05$, and $p_i = 0.05$. The number of simulation repetitions was limited by available processor time. For each run, I fit an exponential decay curve to the proportion of individuals with J haplotypes remaining as a function of the number of generations elapsed. I then fit a linear model to the logarithm of the mean values of the decay constant as a function of the logarithm of $p_r p_o$ for regions of the parameter space in which the simulation run time was sufficiently long to characterize the decay curves. All simulations were performed in R statistical software 2.10.0 (R Development Core Team 2009).

ANALYTIC MODEL

I constructed an analytic model to relate the rate of genome replacement to the question of whether there is selective pressure maintaining J haplotypes in areas far beyond the range limits of *A. jeffersonianum*. I parameterized this model using the results of my simulation and empirical data from the literature. I also used a basic diffusion model to evaluate the potential for J haplotypes to be maintained in areas far outside of the *A. jeffersonianum* range via ongoing dispersal.

Results

SIMULATION

When I set the probabilities of reduction (p_r) and incorporation (p_i) greater than or equal to 0.001, J haplotypes were seen to decay appreciably out of the population within the 1000 generations included in the simulations. The mean rate of decay fit an exponential curve very well (Fig. 3). Starting with a population of pure LLJ individuals, when both p_r and p_i are set to 0.05, J haplotypes would be expected to occur in half of the individuals after 57 generations. When I started the populations with all LLJ individuals, the mean decay rate was twice that as when I began with a population of LJJ individuals. As the reduction probability and incorporation probability decreased, the length of time that J haplotypes remained in the population increased as a function of their joint probability (Fig. 4). When p_r and p_i were both equal

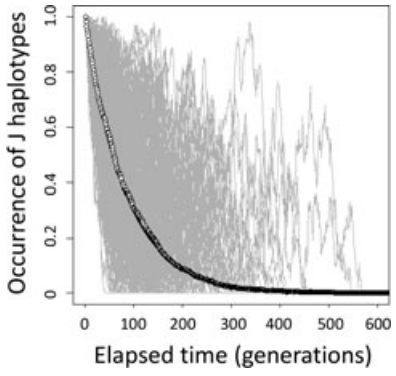

Figure 3. **Occurrence of J haplotypes over time for simulated populations of unisexual salamanders breeding with *A. laterale* males. The probabilities of egg ploidy reduction and sperm incorporation were both set to 0.05. The model ran for 1000 generations in 200 iterations. Each iteration is plotted as a gray line. Points represent the mean occurrence of J haplotypes at each time step. An exponential curve with a characteristic decay time of 82 years is plotted as a dark line beneath and largely obscured by the mean points.**

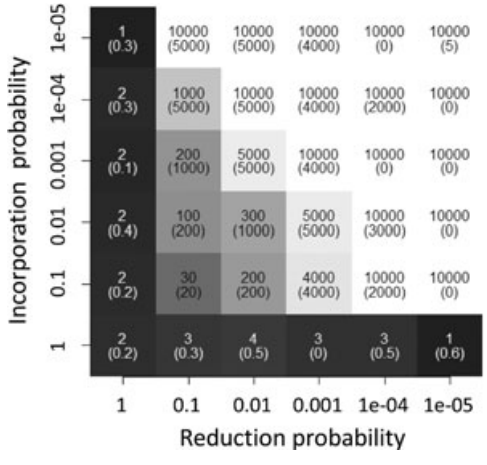

Figure 4. **Half-life for the loss of J haplotypes from a population that began with pure LLJ genomotypes. "Incorporation probability" is the probability that sperm genomes will elevate ploidy, and "reduction probability" is the probability that eggs will have reduced ploidy relative to the mother. Every square represents 24 iterations of 1000-year simulations. Numbers represent median half lives of the best-fit exponential functions, measured in generations, with standard deviations in parentheses.**

and between 1 and 0.001, the mean exponential decay constant, λ, was well described by:

$$\lambda = k\sqrt{p_r p_i}\,, \tag{1}$$

where k is a constant equal to 0.28 for my simulations (Fig. 5). At lower values of p_r and p_i, the decay rate was too low to be characterized within 1000 generations.

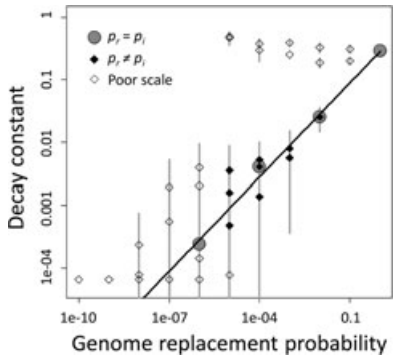

Figure 5. Mean decay constants calculated for the loss of J haplotypes from populations of pure LLJ genomotypes. The probability of genome replacement is calculated as the product of the probabilities of genome reduction (p_r) and sperm genome incorporation (p_i). The trend line was fitted only to the four parameterizations where p_r and p_i are equal and less than 0.0001, shown as gray circles. Empty diamonds represent points where the decay constant was either too large or too small for reliable fitting of the exponential model.

ANALYTIC MODEL

The simulation demonstrated that, if genome replacement occurs, a population of LLJ individuals breeding only with *A. laterale* males would lose all J haplotypes at an average rate described by an exponential decay function. We can greatly simplify the problem by ignoring the particulars of ploidy reduction and elevation and lumping p_r and p_i together into the single phenomenon of genome replacement that occurs with probability, $p_g = p_r p_i$. In reality, the functional relationship between these three probabilities may be more complicated. In particular, we might expect the probability of sperm nuclear incorporation to increase if an egg has lowered ploidy. In the derivation that follows, however, we are concerned with the minimum rate at which J haplotypes would be lost from the population. Relaxing the assumption that p_r and p_i are independent would allow J haplotypes to be lost from the population even more rapidly. It is also reasonable to confine our analyses to the cases where $p_r = p_i$, otherwise we would expect the average ploidy of individuals in the population to be unstable.

Allowing for processes of recombination beyond changes in ploidy would also yield even greater rates of haplotype turnover. This could in principle be incorporated into a single probability of locus replacement instead of the p_g term in the derivations that follow. This would require a modified version of equation (1) to obtain an appropriate decay constant. For this study, however, p_g as defined provides a sufficient minimum for the rate of replacement.

Beginning with a population of LJJ individuals, the expected occurrence of J haplotypes in a population is governed by:

$$J(t) = J_0 e^{-\lambda t/2}, \quad (2)$$

where $J(t)$ is the proportion of individuals containing J haplotypes, J_0 is the initial occurrence of J haplotypes, t is the elapsed time (in generations), and λ is the decay constant. If the initial population consisted of all LLJ individuals, the "½" in the exponent would be removed.

We can apply equation (2) to empirical observations. I will begin by focusing on Massachusetts, because the range limit of *A. Jeffersonianum* bisects the state along a well-defined boundary and Massachusetts unisexuals have been well studied. Populations west of the Connecticut River drainage consist of *A. jeffersonianum* and unisexuals, whereas eastern populations consist of *A. laterale* and unisexuals (Bogart and Klemens 1997, 2008). Let us ignore contemporary dispersal for a moment, and consider the populations in eastern Massachusetts where unisexuals and *A. laterale* are sympatric. Assume that the populations once consisted of LJJ unisexuals hybridizing with *A. jeffersonianum*. At a time τ generations before the present, *A. jeffersonianum* had been completely replaced by *A. laterale*. Note that the math is equivalent if the sexual species have stayed in place but the unisexuals colonized the *A. laterale* ponds carrying LJJ nuclei. Out of 40 polyploid salamanders examined by Bogart and Klemens (1997, 2008) in eastern Massachusetts populations, all individuals contained J haplotypes. From these observations, we can say that at least 97% of the unisexuals in the *A. laterale* region carry J haplotypes.

Estimating τ may be tricky for eastern Massachusetts, but we can place some extreme lower bounds on it. At the very least, the distribution of the species in Massachusetts reported by Uzzell in 1964 matches the current distribution. If we use 2.5 years as the average generation time between *A. laterale* and *A. jeffersonianum*, 1964 was approximately 18 generations ago (Petranka 1998). Using the estimate of 0.28 for k from the simulation, a lower limit of 18 for τ, and a lower limit of 0.97 for $\frac{j(\tau)}{j_0}$, we can combine equations (1) and (2) to find that:

$$p_g < \frac{1}{10{,}000}. \quad (3)$$

This low upper limit for the rate of genome replacement suggests that if genome replacement occurs with any regularity, then there must be some selection to explain the presence of J haplotypes in eastern Massachusetts. The case for positive selection becomes clearer when we expand the scope of inquiry to include the entire unisexual range. In hundreds of polyploid individuals observed across northeastern North America, Bogart and Klemens have yet to find an LLL individual, so our parameterization from Massachusetts is representative of the broader complex. If LLJ populations in Nova Scotia are similar, and if we suspect that these populations have not been in contact with *A. jeffersonianum* populations for at least 1600 years, since the end

of the sub-Atlantic climatic cooling (Viau et al. 2002), then the maximum rate of genome replacement if J genomes are selectively neutral would be approximately 1×10^{-7}.

To incorporate selection into the model, we can transform equation (2) into its analogous form using discrete time steps. We borrow the equation structure from the familiar mutation–selection model in a haploid population with two alleles (Crow and Kimura 1970). Here, we are concerned with the frequencies of two genotypes: those with and those without the J haplotype. The decay rate of J-containing genotypes is analogous to the rate of mutation to the deleterious allele in the classic mutation–selection problem. We then have:

$$J_{t+1} = \frac{e^{-\lambda/2} J_t}{J_t + (1 - J_t)(1 - s)}, \quad (4)$$

where J_t is the occurrence of J haplotypes in generation t, and s is the strength of selection against pure L genomes. Here, J_t is measured in each generation after genome replacement occurs but before selection acts. From equations (1) and (4), we can estimate the strength of selection necessary to maintain the occurrence of J haplotypes at a steady state, when $J_{t+1} = J_t = J$:

$$s = 1 - \frac{e^{-k\sqrt{p_g}/2} - J}{1 - J}. \quad (5)$$

In the classic mutation–selection problem, equation (5) is equivalent to the equilibrium condition that the deleterious allele frequency is the ratio of the rates of mutation and selection. Because s cannot exceed 1, if the occurrence of J haplotypes (J) exceeds the retention rate of J haplotypes ($e^{-k\sqrt{p_g}/2}$), we will be unable to balance equation (5). If $J = 0.97$, then we reach this limit of the equilibrium condition when $p_g = 0.05$. Note that the empirical value for J was measured in the adult population of salamanders, whereas selection may occur early in development. Because equation (4) assumes that J is measured before selection occurs in each generation, higher rates of genome replacement and lower frequencies of J haplotypes in the immature population would be consistent with the derivations, provided that compensating mortality of pure L individuals occurs before reaching the adult stage. Given our initial constraints that $p_g = p_r p_i$, and $p_r = \mathrm{p_i}$, then rates of sperm incorporation and nuclear reduction of 0.01 would require a selection coefficient of 0.05 to maintain J occurrence at 0.97. The rate for nuclear incorporation observed by Bogart et al. (1989) in the lab of $p_i = 0.27$ would imply extreme selection against pure L individuals, including high mortality during the immature stage.

Could the J haplotypes be maintained through dispersal from nearby populations of *A. jeffersonianum*? The distance between the eastern Massachusetts LLJ populations and the *A. jeffersonianum* range is more than 50 km. If we consider the system to be at equilibrium, we could treat the problem as a dispersal-dependent cline following the basic diffusion model (Fisher 1937; Slatkin 1973; Barton and Hewitt 1985). The source of dispersing J haplotypes would be the eastern edge of the range of *A. jeffersonianum* males. Individual unisexuals disperse with a standard deviation, σ, between generations. I treat the tendency of J haplotypes to be replaced by L haplotypes as mathematically equivalent to a form of negative selection acting against J haplotypes in all of the eastern ponds where only *A. laterale* males occur (Robertson 1960). Such a cline would have a characteristic spatial scale of $\sigma/\sqrt{\lambda}$, and a width of the same order (Barton and Hewitt 1985).

To estimate dispersal, we can use data from the closest species that has been sufficiently studied, *A. opacum* (Gamble et al. 2007). Fittingly, the field site for that study was in central Massachusetts near the eastern extent of *A. jeffersonianum*. Setting σ to 0.17 km from the Gamble et al. data, we find that the maximum negative selective pressure for a cline to be maintained over 50 km would be approximately 10^{-5}. Thus, from equation (1), we find that ongoing dispersal could only be important in maintaining J haplotypes in eastern Massachusetts if the rate of genome replacement is less than 10^{-9}.

There are two primary ways in which the equilibrium assumption in the dispersal model could be incorrect, neither of which undermine my argument. If *A. laterale* only arrived in eastern Massachusetts recently, then I have already addressed this problem above in calculating the decay time of J haplotypes. If the system is not in equilibrium because unisexuals only began dispersing recently, then the equilibrium assumption is quite conservative. This second case would yield a steeper cline and it would be even more difficult to explain the presence of J haplotypes in far eastern Massachusetts by dispersal.

Discussion

Here, I have shown that in the absence of selection, occasional genome replacement should lead to the predictable loss of the ancestral haplotypes in a unisexual lineage. Although haplotype turnover would not be expected in perfectly gynogenetic or hybridogenetic lineages, it is clear that most real systems are imperfect. The conditions for the ratchet-like decay of haplotypes described in this study are: (1) a lineage that depends on presence of a sexual host for reproduction (e.g., gynogenesis or hybridogenesis), (2) no mating between any descendents of the lineage (e.g., unisexual), (3) occasional replacement of ancestral genomic elements by genomic elements of the host species, and (4) absence of the ancestral genome within the sexual host (e.g., allopatry or extinction). The ultimate expected outcome under these conditions is that the nuclear genomes in the unisexual population would become indistinguishable from those of the host population.

In any population that meets the above criteria, researchers may use the model predictions as a null hypothesis in testing

for selection. Although my simulation focused on changes in ploidy as the mechanism for haplotype turnover, the subsequent derivations would be equivalent if they began instead with a term describing the probability of recombination at the level of chromosomes or loci. In cases where paternal introgression is limited to inclusion of microchromosomes or ploidy elevation without the loss of maternal chromosomes, as may be the case for *Poecilia*, I would not expect a decay of ancestral haplotypes (Lampert and Schartl 2008). I would also not expect this phenomenon in cases where syngamy results in individuals that do not continue clonal reproduction, as in *Phoxinus* (Goddard and Schultz 1993).

Certain populations of water frogs *R. esculenta* may meet the conditions outlined. Like unisexual salamanders, *R. esculenta* carries genomes far beyond the ancestral species' range boundaries with a leaky form of hybridogenesis (Uzzell et al. 1976, Schmeller 2004; Schmeller et al. 2005). In most parts of its range, the water frog system is complicated by the presence of both sexes within the lineage. However, some populations consist only of male *R. esculenta* (genotypes RL and RRL) breeding with the bisexual *R. ridibunda* (RR) host species (Rybacki and Berger 2001). In these instances, my model would predict the *R. lessonae* haplotype (L) carried only by the hybridogenic males to be decaying from the population in the absence of selection.

In the case of unisexual *Ambystoma*, studies have suggested high rates of genome replacement while describing hybrid nuclei distributed far beyond the bisexual species' contact zones. I have demonstrated that these two ideas cannot be simultaneously true in the absence of strong selection. If genome replacement occurs at any appreciable rate, then positive selection must be acting to maintain hybrid nuclei.

What are the advantages to a hybrid nucleus where the parent species are allopatric? On face value, it would seem that in northern populations where only *A. laterale* persists, L haplotypes would produce the phenotypes best adapted for the environment. Further, if male *A. laterale* preferentially mate with pure *A. laterale* females, either by choice or by phenology, then sexual selection should be against J haplotypes (Dawley and Dawley 1986; Lowcock et al. 1991). Compounding these adaptive disadvantages is the fact that the J portions of the unisexual genomes have no means for recombining with like genomes, and thus should be degrading under the force of Muller's ratchet (Muller 1964). Any repairs made to deleterious mutations must be made by replacement of J portions of the genome with L portions of the genome (Bi and Bogart 2006; Bi et al. 2007).

I can posit some sources of positive selection on the J haplotypes. Perhaps the distributions of unisexual salamanders do reflect intermediate ecotones between *A. laterale* and *A. jeffersonianum* habitat, where they enjoy hybrid superiority (Moore 1977). The peculiar feature of these ecotones is that they would not fully align with the current geographic border of the two species, but would include disjunct portions of the unisexual range far into the range of *A. laterale* (Lannoo 2005; Bi et al. 2008). Another explanation for positive selection on J haplotypes could potentially be found in cytonuclear interactions (Fishman and Willis 2006; Mable 2007). For instance, the unisexual mitochondria in these populations may have coevolved with the J genome to the extent that functionality breaks down if the J genome is replaced by an L genome. This type of effect might explain the puzzling requirement for unisexuals across their entire range to maintain an L genome, with only one reported exception (Bogart and Licht 1986). However, in other parts of their range, unisexuals with no J genomes are commonly encountered (Petranka 1998). If cytonuclear interactions explain the persistence of J genomes in Nova Scotia and northern Wisconsin, then these interactions must have arisen only in those branches of the lineage, and possibly independently. Perhaps, a cytonuclear requirement has developed in which at least one copy of any nuclear genome other than L be present for viability, although it is difficult to speculate on exactly what this mechanism would be. Furthermore, occasional unisexuals with only L genomes have been reported (Lowcock et al. 1991).

Imperfect knowledge of the distribution of unisexuals might also influence my conclusions. If, in fact, vast stretches of the unisexual range remains unstudied and populated largely by LLL individuals, then perhaps the LLJ populations really represent the last remnants of a stochastic decay. Sampling bias in the literature toward studying populations where J genomes persist is plausible (Lowcock et al. 1991). The original identification of unisexuals was based upon observable phenotypic differences due to hybrid nuclear genomes (Clanton 1934). Populations of LLL unisexuals would presumably be phenotypically similar to *A. laterale* populations, except for the prevalence of females. That these populations could go undetected would not seem terribly surprising. Future collection of data in these understudied regions could resolve this question.

Another possibility is that genome replacement truly does not occur very frequently in nature. Colder temperatures in northern climates might cause genome replacement rates to fall toward zero. Perhaps lab-specific conditions other than temperature caused the high genome replacements rate observed by Bogart et al. (1989). If we accept that sperm incorporation does happen 27% of the time in nature, then the model implies strong selection in favor of hybrid nuclei among unisexuals, even though *A. laterale* with pure nuclei must be surviving reasonably well in the same ponds.

My framework provides a formal foundation for exploring the hypothesis of hybrid superiority as it relates to genome replacement rates. This framework offers direction on the future types of data that could be collected to test the model predictions

for unisexual lineages. For *Ambystoma*, field researchers could determine whether unisexuals produce reproductively viable offspring with pure nuclei, the distributions of pure-nuclei unisexuals, the isolation time of unisexual populations from their nuclear parental species, the rates of sperm incorporation in the field, and the rates of egg reduction in the field. Incorporating these data back into the simulation model will allow us to make more specific predictions and better understand one of the most fascinating, yet ecologically vulnerable, vertebrate systems.

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Supporting Information

The following supporting information is available for this article:

Figure S1. Source code for simulated unisexual breeding programmed in R Statistical Software.

Supporting Information may be found in the online version of this article.