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Evolution and ecological correlates of uniparental reproduction in freshwater snails

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Abstract. We review the spatial and temporal correlates of uniparental reproduction in freshwater snails as they pertain to the ecological hypotheses for the maintenance of biparental sex. The biogeographic evidence from two species (*Potamopyrgus antipodarum* and *Bulinus truncatus*) presently supports the Red Queen hypothesis that biparental reproduction is selected as a way to reduce the risk to progeny of parasite attack. Uniparental reproduction in these species is associated with low levels of infection by parasites (castrating digenetic trematodes), suggesting that parthenogenesis or self-fertilization can replace cross-fertilization when the risk of infection is low. In addition, in *B. truncatus*, the opportunity for cross-fertilization coincides with the season in which parasite attack is highest. In a third species (*Campeloma decisum*), parthenogenetic reproduction is correlated with latitude and the presence of a non-castrating trematode that may prevent cross-fertilization; these patterns suggest that parthenogenesis has been selected as a mechanism to assure reproduction. Finally, we discuss the spotty taxonomic distribution of parthenogenetic species.

Key words. Parthenogenesis; self-fertilization; Red Queen hypothesis; reproductive assurance; brooding; selective arenas; selective abortion.

Introduction

The apparent evolutionary stability of biparental sex in many eukaryotes remains a paradox in evolutionary biology[5,59,95]. The paradox arises from the fact that, if sexual and parthenogenetic females have similar fecundities, parthenogenetic females should rapidly replace sexual females. The reason is that sexual females invest in sons which do not directly bear any progeny, while parthenogens invest only in daughters[58,59]. Similarly, an allele for self-fertilization that does not also affect reproductive success through male function should rapidly spread in outcrossing hermaphroditic populations[54,66,95,96]. Offspring produced by selfing, just like offspring produced asexually, receive all their genes from only one parent. This can translate into a 3/2 advantage for a mutation to pure self-fertilization in a non-selfing randomly mating population, assuming no inbreeding depression and no loss of ability to contribute male gametes via outcrossing[14]. Hence, cross-fertilization is subject to invasion and replacement by uniparental forms of reproduction in both dioecious and hermaphroditic populations, and would seem to require a general explanation for its maintenance. Such an explanation should also be consistent with the ecological correlates of uniparental reproduction (review in 5).

In this paper, we first briefly describe the major ecological hypotheses for the maintenance of biparental sex. These ideas are mainly concerned with the adaptive significance of producing variable progeny in variable environments. We then present a review of our studies on three freshwater gastropods, which were designed to discriminate among these alternative hypotheses. These studies involve investigations of the spatial and temporal distribution of uniparental and biparental reproduction within and among populations of a New Zealand prosobranch (*Potamopyrgus antipodarum*), an African pulmonate (*Bulinus truncatus*), and a North American prosobranch (*Campeloma decisum*). Finally, we consider the relationship between brooding and the phylogenetic distribution of parthenogenesis in aquatic invertebrates.

The ecological hypotheses for maintenance of biparental sex

The adaptive variation hypotheses

Three hypotheses for the maintenance of cross-fertilization in natural populations postulate that there is an advantage to producing variable progeny in variable environments. They differ primarily in whether or not the postulated advantage stems from frequency-dependent selection and, if so, whether the frequency dependence comes from intraspecific or interspecific interactions.

Lottery hypothesis. The lottery hypothesis predicts a selective advantage of outcrossing in environments that vary unpredictably over time[21,96]. When offspring experience environments different from their parents, the cost of outcrossing could be offset by the benefit of producing genetically variable offspring, thereby in-

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creasing the likelihood that some survive the new conditions. The advantage to outcrossing under this view is frequency independent, and operates by increasing the expected geometric mean fitness of outcrossing individuals. This view predicts that biparental reproduction will be more common in unstable environments where conditions are likely to vary unpredictably between generations.

The tangled bank hypothesis. The tangled bank hypothesis predicts a selective advantage of outcrossing in heterogeneous environments when there is high intraspecific competition for resources[5,26]. If parents and offspring experience similar environments and resources are limited, offspring which are able to utilize new niches may face less competition. Hence there may be a density-dependent rare advantage that selects for cross-fertilization. The tangled bank hypothesis predicts that biparental reproduction will be more common in stable environments where there is high competition for resources. The biogeographic distribution of uniparental reproduction is consistent with the tangled bank hypothesis in that selfing and parthenogenesis are more common in more homogeneous, less stable habitats at high altitudes or latitudes[5].

Implicit in these predictions is the assumption that biparental reproduction leads to higher levels of genetic variability among offspring[62]. This assumption does not always hold for the case of outcrossing versus selfing[77]. If selfed sibships were more genetically diverse than outcrossed sibships, then patterns opposite to our predictions might be found.

The Red Queen hypothesis. Fluctuations in the biotic environment, in particular some forms of antagonistic coevolution, can also favor outcrossing[5,8,27,32,47,55]. The most common version of this hypothesis, which we call the Red Queen hypothesis after Bell[5], focuses on the interaction between parasites and their hosts. When parasites substantially decrease host fitness, coevolution between parasites and hosts can result in frequency-dependent selection favoring rare host genotypes[27]. A central prediction of the Red Queen hypothesis is that selection for rare genotypes should be stronger in populations where parasites exert a greater selective pressure on their hosts. Uniparental reproduction should be favored in habitats where parasite pressure is weaker. Simultaneous hermaphrodites which outcross will be more successful at generating novel genotypes than those which reproduce by selfing, and this could lead to a stable mixture of outcrossed and selfed progeny within a single parent[53]. Similarly, parasites should select against common clones in gonochoric populations; parasites may eventually eliminate such clones in the presence of either soft-truncation selection resulting from intraspecific competition for resources[28], or if they aid the accumulation of mutations through the action of Muller's ratchet by periodically depressing the numbers of clonal individuals[31,53]. Like the tangled bank model, the biogeographic distribution of uniparental reproduction can be accounted for by the Red Queen hypothesis: marginal, disturbed habitats at high altitude or latitude may have weaker parasite pressure[5].

The reproductive assurance hypothesis

Hypotheses based on reproductive assurance argue that uniparental forms of reproduction will evolve as mechanisms to assure reproductive success in populations where access to mates is severely limited[25,55], or where male gametes are prevented from fertilizing eggs[39]. By themselves, such hypotheses have limited explanatory power, since they do not address why cross-fertilization is advantageous when access to male gametes is not limited. Reproductive assurance is nonetheless likely to explain the occurrence of uniparental populations in some species. In what follows, we review our studies of freshwater snails, which were designed in part to contrast the adaptive variation hypotheses with the reproductive assurance hypothesis. The results show that reproductive assurance is not sufficient to explain the distribution of uniparental reproduction.

Ecological correlates of biparental sex in *Potamopyrgus antipodarum*

Potamopyrgus antipodarum is a small (< 10 mm) hydrobiid snail, native to New Zealand. Some populations consist entirely of parthenogenetic females, while other populations have sexual females and males. Parthenogenesis in this species appears to be apomictic[73], and parthenogenetic individuals have recently been shown to be triploid[92]. Moreover, based on allozyme studies, sexual and parthenogenetic individuals are now known to coexist within the same lake, and the parthenogens are almost certainly derived from the local sexual population[19]. There is therefore no indication that the clones are either migrants or of hybrid origin; thus they are likely to be ecologically similar to the local sexual population from which they are derived. In addition, the diversity of the locally derived clones is very high, with over 30 different clones in some locations[19]. This coexistence of sexual and locally derived parthenogenetic individuals makes *P. antipodarum* ideal for comparative studies contrasting the different ecological theories of sex.

Some simple predictions can be made based on the working hypothesis that streams are more variable in time than lakes; and, as a consequence, competition for resources is more intense in lake populations. New Zealand streams are very prone to rearrangement by flooding, as well as changes in pH[97], so the working assumption has empirical support.

If sex is an adaptation to uncertain physical conditions, as suggested by the lottery models, then males and sexual females would be expected to be more common in the highly unpredictable stream habitats. If, on the other hand, sex is an adaptation to produce variable progeny in highly competitive, but physically stable habitats (the tangled bank hypothesis), then sexual populations should be more commonly found in the large stable lakes. Finally, if sexual reproduction is an adaptive defense against parasites, then sexual females should predominate in populations where there is a high risk of attack by parasites, independent of habitat type. Hence, two of the predictions are habitat specific; the lottery model predicts more sex in streams, while the tangled bank predicts more sex in lakes. The third hypothesis (the Red Queen) makes no specific prediction with respect to habitat, unless it is known in advance that one type of habitat is associated with a higher risk of parasite attack.

Field studies

In order to contrast these hypotheses, lake and stream populations were sampled from glaciated regions of the South Island of New Zealand[48]. It seems reasonable to assume that the snails followed the retreat of the glaciers at the end of the Pleistocene, and colonized the lake and stream habitats that remained. Assuming that there was a fair competition in each location between sexual females and parthenogenetic females, the three ecological hypotheses presented above could be contrasted. However, the competition probably was not completely fair, due to the colonization advantage of parthenogens. Snails were sampled from 21 lakes and 29 streams, and gender and state of infection by digenetic trematodes were determined for 40 to several hundred individuals (usually 100). Sexual females could not be visually discriminated from parthenogens, but males could easily be distinguished from either. Because males are produced only by sexual females, they were used as an indicator of the frequency of sexual reproduction in the population.

In contrast to the prediction of the lottery model, more males were found in lakes than in streams. Thus, if streams are more variable in time than lakes, as assumed, the lottery model can be rejected. The lottery model also fails to explain the primary biogeographic distributions of sexual species[5].

The presence of more males in the lake populations is consistent with the tangled bank model. However, there were also more parasites in lake populations, which is consistent with the Red Queen hypothesis. In order to contrast these two alternatives, a step-wise multiple regression was used to determine whether habitat (lake versus stream) or parasites explained more of the variation in male frequency. Parasites explained more of the variation. The mean frequency of males was indeed greater in lakes, but there was a substantial amount of variation for male frequency in both lakes and streams. In fact, even within lakes, male frequency varied from 0 to 40 percent; and it varied from 0 to 20 percent in streams. Parasites (castrating digenetic trematodes) were correlated with this variation in both habitats. Within lakes, males were positively and significantly correlated with the bird parasite, *Microphallus* sp. Within streams, males were similarly correlated with the eel parasite, *Stegodexamene anguilli.* The sum of these two parasites explained 34% of the variation in both lakes and streams. Hence, the difference between lakes and streams, which originally favored the tangled bank hypothesis, appears to have been driven by parasites. Thus the evidence falls in favor of the Red Queen hypothesis[48]. It is also consistent with the results of Schrag et al.[83] reviewed herein.

This kind of correlative evidence is a very useful way of sorting out alternatives. But it is less than conclusive evidence for any particular hypothesis. The reason is that alternative explanations for the same pattern could also exist. Nonetheless, as far as this study was concerned, any alternative must be regarded as post hoc. One especially appealing, but somewhat complicated, alternative involves reproductive assurance. What if, as discussed in the introduction, cross-fertilization has little to due with either competition or parasitism. Assume, for the sake of argument, that sex is maintained by recombinational repair[6] or by some kind of exogenous repair mechanism (e.g. Muller's ratchet). Then sex should be lost only when populations become so sparse that mates become difficult to find. Moreover, it might be that in such sparse populations, the density of snails is too low to support a stable population of parasites[1,57]. Hence, under this two-part hypothesis, dense populations would be sexual and have parasites, while sparse populations would be expected to be parthenogenetic and have low parasitism, which is exactly what the results of Lively[48] discussed above show.

Fortunately, any hypothesis involving reproductive assurance is testable, and can be falsified by data which show that density is unrelated to reproductive mode. In a survey of 65 lake populations over a five-year period, Lively[50] found no support for the reproductive assurance idea. The results of this more thorough survey, however, were consistent with expectations under the Red Queen hypothesis. Specifically, there were no populations with high male frequency where parasites were rare or absent; but sexual populations were common and correlated with the percent of individuals castrated by digenetic trematodes[50]. Taken together, the results of the field surveys among populations of *P. antipodarum* are inconsistent with the expectations of the lottery model and the reproductive assurance hypothesis. The tangled bank hypothesis cannot be rejected; but, at present, the data provide stronger support of the Red Queen hypothesis.

In a very recent study, the distribution of males was examined within a single lake population (Lake Alexandrina) on the South Island of New Zealand[40]. Surprisingly, the distribution of males was parallel to that observed among populations in that it was correlated with the presence of castrating trematodes. In general, the size-specific prevalence of infection was higher in shallow waters where ducks (one of the final avian hosts) tend to feed; in this area sexual individuals are most common. Hence it would appear the parthenogenetic females have been more successful at replacing sexual individuals in deeper water where the risk of infection is lower. This hypothesis would only make sense if individuals are not moving between shallow and deep areas, which seems to be the case based on the results of a recent electrophoretic survey (J. A. Fox et al., in preparation). In addition, snails in the shallow-water habitats tended to begin reproduction at a smaller size[40], which is consistent with optimization theory for age/size-related mortality[23,46,61] and with the empirical results of Lafferty for marine snails[44].

Reciprocal cross-infection experiments

A direct test of the Red Queen hypothesis requires experimental evidence that parasites can rapidly track genotypes as they become common. Such tracking is essential, otherwise the descendants of clonal mutants would rapidly replace their sexual ancestors. One form of evidence for this kind of tracking is local adaptation. If parasites are locally adapted to their 'home' host population, it is likely that they are tracking genotypes in that population as they become common. One way to test the idea that parasites are locally adapted is to conduct reciprocal cross-infection experiments.

Two reciprocal cross-infection experiments were conducted to determine whether *Microphallus* is locally adapted to its host populations. In the first experiment, involving two lakes on opposite sides of the southern Alps of New Zealand (Lakes Mapourika and Alexandrina), Lake Mapourika parasites were significantly more infective to snails from the same lake. Similarly, Lake Alexandrina parasites were significantly more infective to snails collected from Lake Alexandrina. Similar results were observed in the second experiment, which involved three lakes on the west side of the southern Alps (Mapourika, Wahapo, and Paringa). Parasites from all three lakes were better at infecting snails drawn from their local host populations. Hence, *Microphallus* is adapted to its local host populations[49].

Maintenance of euphally and aphally in *Bulinus truncatus*

Bulinus truncatus (*Audouin*) is a tetraploid snail which lives in a range of freshwater habitats from lakes to temporary pools in northern and western Africa and the Middle East. All *B. truncatus* are self-compatible simultaneous hermaphrodites. Individuals within this species, however, develop into one of two sexual morphs referred to as phally. Euphallics develop an ovotestis and fully functional male and female tracts. Aphallics, in contrast, do not develop the distal portions of the male tract although functional sperm are still produced by the ovotestis[24]. Thus, both euphallics and aphallics can self-fertilize, but aphallics cannot donate sperm. Laboratory studies indicate that there is a cost to the growth and maintenance of a fully developed male tract[34,82]. Nonetheless, the proportion of euphallics in natural populations varies from zero to one[10,45,74,83,84]. If euphallics never donated sperm, selection would be expected to remove euphally because of the growth and maintenance costs associated with developing a full male tract; consequently, when euphally is maintained it must be due to a selective advantage of outcrossing.

Factors maintaining outcrossing have been investigated in a number of theoretical and empirical studies of plant populations[16,17,30,33,62,78,93]. Phally dimorphisms, which have arisen at least 14 independent times in pulmonate snails[85], present a unique opportunity to examine factors maintaining outcrossing within an animal species. *Bulinus truncatus*, one of the few well-studied pulmonates because of its role as an intermediate host for the trematode *Schistosoma haematobium*, is suited to investigations of factors maintaining outcrossing for additional reasons: it has a short generation time of 4 weeks from the egg to egg stage[80]; in lightly pigmented strains phally can be scored without dissection; over small geographic distances (e.g. 10 km along the same road[83,84] the proportion of euphallics has been found to vary by as much as 81%, allowing for direct tests of factors maintaining this variability.

Mechanism of phally determination

Phally in *B. truncatus* develops during the first weeks after oviposition, prior to sexual maturity, and does not change once it develops[45]. Laboratory studies of *B. truncatus* have demonstrated that phally may have a strong heritable component in some populations[45] while in others it is determined by temperatures juveniles experience prior to maturity, with colder temperatures favoring the development of euphally[80,81,84]. There is suggestive evidence that other pulmonate species may also have environmentally-determined phally[69,94]. Field observations of *B. truncatus* in northern Nigeria have demonstrated that colder temperatures during phally development similarly correlate with high levels of euphally in natural populations[84]. A small number of field populations in this region, however, maintained extremely low levels of euphally despite decreasing temperatures, suggesting that populations may have differed in their temperature-sensitivities. Laboratory observations confirmed this between-population variation and further suggested that individuals within some populations varied in their temperature-sensitivities[84].

Adaptive significance of euphally

To test among competing hypotheses for the maintenance of euphally and aphally, a number of ecological variables including water temperature and proportion of euphallics were measured in 49 *B. truncatus* populations in northern Nigeria[83]. Habitats ranged from man-made dams and lakes to small irrigation channels and temporary pools. Proportion of euphallics (based on an average of 50 snails per population) in this region ranged from 0 to 81%, and even sites within close proximity often differed dramatically in levels of euphally.

Across populations there was no association between population density and euphally, inconsistent with standard interpretations of the reproductive-assurance hypothesis for the maintenance of euphally. This result is similar to observations of *P. antipodarum* described above. Furthermore, there was no evidence of a link between euphally and resource availability, contrary to predictions of the tangled-bank hypothesis. Levels of euphally were also not associated with habitat instability (estimated by habitat type, human activity, rate of desiccation, and changes in water chemistry), contrary to predictions of the Lottery hypothesis. This lack of association is also inconsistent with the tangled-bank hypothesis which predicts that more stable habitats will have higher proportions of euphallics.

Conductivity, in contrast, explained a weak but significant percentage of variation in proportion of euphallics, with lower ion concentrations correlated with higher levels of euphally[83]. Conductivity in freshwater is a summary measure reflecting the total concentration of major ions[4]. A similar association between conductivity (in particular, concentrations of Mg^{++}, Ca^{++}, Na^{+} and Cl^{-}) and prevalence of males was found across bisexual and parthenogenetic populations of the freshwater snail, *Melanoides tuberculata*, in Israel[29]. However, the relationships between water chemistry, snail biology and habitat ecology are not well understood[9,42], although calcium is one of the essential elements for snail growth[9]. Middle ranges of conductivity are often optimal for African freshwater snails, while both high and low extremes result in increased hatching time, delayed egg production and decreased fertility[9].

Overall prevalence of trematode infection correlated positively but not significantly with proportion of euphallics, when the effects of time of year (a good indicator of temperature) and mean snail age were controlled for (depending on the length of the pre-patent period, there is a minimum age below which patent infections cannot be scored). However, prevalence of the most abundant trematode taxa, Xiphidiocercariae (which in Nigerian *Bulinus* may consist of 2 trematode species based on morphology[68]), correlated positively and significantly with proportion of euphallics ($r^2 = 10\%$ when the effects of snail size and time of year were statistically removed), in support of the Red Queen hypothesis[83]. Indices of trematode diversity which incorporated both prevalence and richness, also correlated significantly with prevalence of euphally. It may be that parasite diversity per se is an important source of parasite-mediated selection for outcrossing; however, because the diversity indices correlated strongly with prevalence of Xiphidiocercariae infection, this data set did not allow these measures to be distinguished. There was no association between conductivity and trematode prevalence[83].

Of the site-specific variables considered, the two that correlated significantly with proportion of euphallics have been found to correlate similarly in other freshwater snails (trematode prevalence in *P. antipodarum*[48,50] and conductivity in *M. tuberculata*[29]), despite the fact that *B. truncatus* belongs to a different sub-class and has a different breeding system from both *Potamopyrgus* and *Melanoides*. The correlation most easily explained by competing hypotheses for the maintenance of outcrossing suggests that euphally is maintained by parasite-mediated selection for genetically variable offspring.

Why might phally be temperature-sensitive?

Adaptive arguments (based on 15) successfully explain the maintenance of environmental sex determination (ESD) in a wide range of taxa (e.g. refs 18, 67, 89 but see ref. 11 for a counter-example in reptiles). An analogous argument may explain environmental phally determination: temperature-sensitive phally determination will be favored by natural selection when 1) factors determining the relative fitness of selfed and outcrossed offspring vary, 2) these factors are correlated with temperature, and 3) parents cannot predict and offspring cannot control the conditions offspring experience.

Are these three conditions plausible for the case of *B. truncatus*? The across-population correlation between trematode infection and proportion of euphallics described above suggests that the first condition may hold: male outcrossing ability appears to have a selective advantage when parasite pressure is high. In support of the second and third conditions, field observations in natural populations of *Bulinus* snails suggest that water temperature is a good predictor of future levels of parasitism[79,98]. In contrast, parasite prevalence within sites can fluctuate wildly over short periods of time so that current parasite prevalence is a poor predictor of future parasite prevalence[79,98]. Furthermore, low snail mobility suggests that snails themselves cannot choose among habitats.

In northern Nigeria, prevalence of Xiphidiocercariae reaches peak levels in snail populations between March and July[7]. If outcrossed offspring are favored when parasite pressure is high, and this generates a selective advantage to outcrossing and hence euphally, then euphally should be more common among the parents of snails facing this seasonal rise in parasite pressure. Temperature-sensitive phally determination during the juvenile stage would ensure this: juveniles hatching during the months of December and January are more likely to develop into euphallics because this is when temperatures are coldest. These juveniles will reach maturity and start producing offspring just when parasite pressures peak.

Thus, several lines of evidence support the idea that seasonal variation in parasite pressure maintains temperature-sensitive phally determination. A central prediction based on the patterns of variation observed in the field is that populations with low levels of parasitism and/or low levels of fluctuation in parasite pressure should have lower temperature-sensitivities. Long-term field observations of seasonal fluctuations in water temperature, trematode prevalence and proportion of euphallics across and within populations would be necessary to test this prediction.

If temperature is an indirect due for parasite pressure, this might also explain why temperature-sensitivity varies on such a small geographic scale. Thus, while sites in close proximity may not experience large differences in temperature conditions, if levels of parasite pressure differ between sites on a small scale, small scale variation in levels of temperature-sensitive phally determination would be expected. In the Kano City region, only three out of 22 populations where within-site variation in proportion of euphallics was monitored showed little change in proportion of euphallics, suggesting that weak temperature-sensitivity is relatively rare.

Ecological correlates of parthenogenetic and sexual reproduction in *Campeloma decisum*

Campeloma decisum is an ovoviviparous, dioecious prosobranch that is widely distributed and locally common in streams and lakes throughout eastern North America. The biogeographic distribution of parthenogenetic and sexual reproduction in *Campeloma* was considered a classic case of geographical parthenogenesis: parthenogenetic reproduction in northern, glaciated habitats and sexual reproduction in southern, unglaciated habitats[5]. Parthenogenesis could be favored in glaciated regions to assure reproduction where male density is low. Alternatively, the Red Queen hypothesis would predict that parthenogenesis may be favored in these glaciated habitats because parasites are rare in these marginal habitats or, under the tangled bank hypothesis, there is relaxed selection for the production of outcrossed progeny in spatially homogeneous environments in which competition is limited. Given that the original description of the biogeographic distribution of reproductive mode in *Campeloma* is consistent with the reproductive assurance hypothesis and these two adaptive variation hypotheses, Johnson[37–39] explored the biogeographic distribution of reproductive mode in a more thorough fashion, and also examined the correlation between reproductive mode and risk of parasitism. He also explored the possibility that a digenetic trematode may severely limit sperm availability, and that parthenogenesis is favored to assure reproduction. Johnson[39] sampled three geographic regions: northern glaciated regions ranging from Indiana to northern Michigan and Wisconsin; unglaciated habitats in the southeastern United States (Virginia and North Carolina) and unglaciated habitats in the south central United States (Louisiana, Mississippi, Arkansas, and Missouri). Parthenogenetic populations contained no males, while other populations contained >40% males, and were categorized as 'sexual', although some sexual populations may be mixtures of sexual and parthenogenetic females. Thus, the continuous range in functional gender that is seen in *P. antipodarum* or *B. truncatus* is not observed in *Campeloma*. The most common parasite of *C. decisum* is the digenetic trematode, *Leucochloridiomorpha constantiae*. This parasite lives as unencysted metacercaria in the female brood chamber. Prevalence (percentage of snails infected within each population) and intensity of infection (mean number of metacercariae per host) were determined. The consequences of *L. constantiae* infection on female fitness are very weak, although male fitness may be severely limited by the presence of metacercariae (see below; ref. 38). Prevalence of infection by three other trematodes (*Sellacotyle mustelae*, *Cercariae leptacantha*, and *Linstowiella szidati*) was also recorded. These trematodes produce larval stages in the snail reproductive system and cause strong effects on fitness through sterilization[39].

Parasite prevalence was significantly higher in parthenogenetic populations relative to sexual populations[39]. All twenty-six parthenogenetic populations were infected by metacercariae of *L. constantiae* and all fourteen sexual populations were uninfected. Similarly, the prevalence of the three castrating trematodes in parthenogenetic populations was three times higher than the prevalence of these trematodes in sexual populations. Parthenogenesis is not maintained in areas where parasites are absent or rare.

One potentially confounding aspect of these results is that the degree of geographical separation is much greater between sexual and parthenogenetic *Campeloma* populations than that observed in *Potamopyrgus* and *Bulinus*. In addition, sexual and parthenogenetic individuals do not apparently coexist within populations as seen in *Potamopyrgus*. Hence, there is a potential effect of latitude on the correlation between parasite load and reproductive mode, so this study does not represent a very strong test of the Red Queen hypothesis. As outlined below, experimental tests of the Red Queen in this system should alleviate this problem.

Reproductive assurance and parthenogenesis

The biogeographic distribution of sexual and parthenogenetic populations is, for the most part, a typical pattern of parthenogenetic populations in glaciated northern regions and sexual populations in unglaciated southern regions[39]. However, parthenogenesis has arisen in the southeastern United States where there was no Pleistocene glaciation. The presence of parthenogens in North Carolina and Virginia and the coexistence of sexual and parthenogens in the coastal plain of North Carolina suggest that colonization of glaciated regions is not necessary for the establishment of parthenogenesis. However, the predominance of parthenogens in the northern United States suggests that parthenogens may have had an advantage in colonizing northern temperate regions after the Pleistocene glaciers receded.

The absolute congruence of parthenogenetic reproduction in the snail and the presence of the free-living stage (metacercariae) of *Leucochloridiomorpha constantiae* in the brood chamber of female snails led to the hypothesis that this parasite can severely limit sperm availability and that parthenogenesis assures reproduction[38]. The sperm-limitation hypothesis requires that the prevalence and intensity of infection is high and that infections persist throughout an individuals' lifetime. Strong selection against male function is required because sexuals would potentially invade these areas where parasites are common. Infection levels are high and persistent in many parthenogenetic populations[38]. Given the persistent, high level of infection in parthenogenetic populations, what are the mechanisms by which this parasite limited sperm availability when the parasite was introduced historically into a sexual population?

The introduction of *L. constantiae* into sexual populations may have led to elimination of males via sperm ingestion or sperm blockage, thus leading to strong selection for those rare females capable of parthenogenetic reproduction. Sperm are stored in an undifferentiated, open seminal receptacle[91], and metacercariae would have easy access to the stored sperm and would be able to ingest or displace them. Severe sperm limitation in infected populations could result, leading to strong selection for females capable of parthenogenetic reproduction. This hypothesis requires high infectivity of *L. constantiae* when introduced into sexual snail populations and little genetic variation for resistance.

An alternative, perhaps more parsimonious, hypothesis exists to account for the concordance between the presence of *L. constantiae* and the biogeographic distribution of parthenogenesis. There may have been strong selection for females capable of parthenogenetic reproduction to assure reproduction during colonization of marginal habitats, and the high prevalence and intensity of infection by *L. constantiae* may be derived from the ability of parasites to exploit the absence of genetic variation in non-recombining parthenogens. The association between parthenogenesis and parasitism may result from the ability of parasites to rapidly track and infect locally common clonal genotypes. Sexual populations may be exposed to the parasite, but high levels of infection might not occur because there is genetic variation for resistance in sexual host populations. If infection levels remain low, then sexual females could still reproduce and would probably have higher fecundity than parthenogens, because those females capable of parthenogenetic reproduction may have reduced fecundity after switching to ameiotic reproduction[88]. This hypothesis is distinct from the sperm limitation hypothesis in that parthenogenesis is selected to assure reproduction in colonizing females and that high infectivity results from parasite exploitation of common host resistance genotypes. These two hypotheses offer contrary predictions regarding the infectivity of the parasite in sexual and parthenogenetic populations: the sperm limitation hypothesis predicts that sexual and parthenogenetic individuals should experience similar, high levels of infection, while the second hypothesis predicts that there is local parasite adaptation to the host and that parthenogens should be more susceptible to infection by this parasite than sexual individuals. Under the Red Queen hypothesis, there should be greater variability in the prevalence and intensity of infection in sexual individuals. Future experimental work will address these two hypotheses.

Spontaneous and hybrid origins of parthenogenesis

Most parthenogens that originate by hybridization between genetically divergent sexual ancestors have elevated levels of heterozygosity, and the alternate alleles at these heterozygous loci are found in the two putative sexual ancestors. Parthenogens that arise by spontaneous mutation show similar or lower levels of genetic variation relative to their sexual ancestor. There are two classes of parthenogens in *C. decisum*: homozygous parthenogens from North Carolina and Wisconsin and heterozygous parthenogens from Indiana, Michigan and one population from Wisconsin[37]. Parthenogenetic and sexual individuals from North Carolina populations were genetically identical at the nineteen enzyme loci. They were fixed for the same allele at those nine loci that vary across the entire geographic range. The homozygous clones probably reproduce by automictic parthenogenesis. The genetic consequences of automixis over many generation is analogous to complete selfing in that recombination cannot generate rare genotypes, even though there may be multiple clonal lineages derived from a heterozygous founder. Sexual populations from Mississippi, Louisiana, and Arkansas are nearly fixed for an alternative allele at these nine loci. All parthenogens from Indiana and Michigan are heterozygous at six or seven enzyme loci, and share the alleles which are fixed alternately in the North Carolina and south-central sexual populations. These heterozygous clones are probably apomictic parthenogens. The presence of two modes of parthenogenesis potentially offers some insight into the advantages and disadvantages of heterozygous or homozygous parthenogens. From the perspective of the Red Queen hypothesis, the consequences of automictic and apomictic parthenogenesis in the host are similar: neither parthenogen can generate rare resistance genotypes, assuming that automictic parthenogens have undergone many generations of automictic reproduction. Scanty evidence suggests that hybrid mice are more susceptible to parasites[75], but whether hybrid parthenogens are more susceptible to parasitism will depend on the level of recombination and the dysgenic consequences of hybrid genomes. Possibly, the presence of two non-recombining parental genomes in apomictic parthenogens increases the range of resistance genes, thereby increasing the probability of detecting parasite antigens. In this case, hybrids may be less susceptible to parasites. Another interesting pattern is the biogeographic distribution and ploidy levels of these two parthenogens. Heterozygous clones, which are probably polyploid, predominate in the northern region[39], whereas homozygous (diploid?) clones are common in the southeastern region. Whether the selective advantage of polyploidy and heterozygosity in northern temperature regions is due to some general-purpose genotype[56] in these environments deserves careful scrutiny.

Brooding and the phylogenetic distribution of parthenogenesis

Whereas the ecological correlates of cross-fertilization have been addressed by these and other studies, the mechanisms responsible for the spotty taxonomic distribution of parthenogenesis have received little empirical attention. Parthenogenesis is phylogenetically widespread, but many clades contain no known parthenogenetic varieties[5,56]. This pattern may result from two mechanisms. Members of some clades may never be released from the selective forces that act to maintain cross-fertilization (i.e. coevolved biological enemies) or parthenogenesis cannot spread when rare in some groups, because of developmental defects associated with its early evolution[88,90]. These developmental abnormalities are frequent enough during the early evolution of parthenogenesis that the evolution of parthenogenesis may be more paradoxical than the maintenance of outcrossing[90]. If so, brooding lineages in which selective abortion of defective offspring is possible may be expected to be more susceptible to the initial establishment of parthenogenetic mutants[52]. In addition, if zygotes are overproduced, competition among embryos in the confines of the brood chamber may also favor the initial establishment of parthenogens if defective embryos are outcompeted.

Stearns[86] argued that, if zygotes are relatively cheap, overproduction of zygotes would lead to competition within the brood chamber (the 'selective arena' in Stearns' terminology), which would increase the mean fitness of the brood. The model of Lively and Johnson[52] is a special case of this idea: when the early evolution of parthenogenesis is burdened by developmental abnormalities, the selective arenas of brooders could favor the spread of rare parthenogenetic mutants because defective embryos could be culled without much cost to the parent. Zygote overproduction greatly increases the probability that a rare parthenogenetic mutant will spread to fixation compared to non-brooding parthenogens. Brooding may aid in the early evolution of parthenogenesis, but ecological forces, such as escape from parasites, will ultimately determine if parthenogenesis is maintained within a lineage.

An alternative to the selective arena formulation is that inferior offspring are selectively aborted and replaced. In this situation, there would be some cost accrued by a parthenogenetic mutant to replace embryos. A strategy model of selective abortion indicates that the range of values that favors the spread of parthenogenesis increases with the number of times aborted eggs are replaced[52]. Although selective arenas give the greatest advantage to parthenogenesis in these strategy models, selective abortion and replacement of embryos also increase the probability that parthenogenesis will spread. A basic prediction from these strategy models is that parthenogenesis would be more likely to arise in brooding lineages. Because brooding and parthenogenesis are rare traits in most taxa, comparative analyses focused on taxa in which parthenogenesis has arisen independently in various species and for which variation in development exists. There was a strong association between brooding and parthenogenesis in various lineages[52]. In the Cnidaria and Mollusca, parthenogenesis evolved significantly more often in brooding lineages than in non-brooding lineages. Many taxa show consistent relationships between brooding and the evolution of parthenogenesis, although parthenogenesis and brooding are not coupled in sipunculids, gastrotrichs, and tardigrades. All parthenogenetic species in these taxa oviposit uncleaved eggs. It would be valuable to determine whether selective abortion or selective arenas operate in brooding species, particularly in sexual species that are ancestral to brooding parthenogenetic groups.

Developmental defects in parthenogenetic eggs are not strictly required for the hypothesis. Rapid mutation accumulation could also result in a bias towards the evolution of parthenogenesis in brooding species. Suppose, as suggested by Kondrashov[43], that mutations are on the order of at least one per genome per generation, and that all individuals having more than a threshold number of mutations (k) die, but individuals with fewer mutations suffer no loss in fitness (i.e., the fitness function is truncated at k mutations). The equilibrium mean number of mutations in parthenogens after selection is $k - 1$, with very little variance. Then, assuming a Poisson distribution of mutations with a mean of one, approximately 2/3 of the parthenogenetic offspring will have k or more mutations and they will die. But if zygotes are sufficiently overproduced, or there is selective abortion with replacement of offspring, the parthenogenetic female might recover a sufficient number of offspring to have a reproductive advantage over sexual females.

Alternative hypotheses can also predict an association between brooding and uniparental reproduction. The evolution of brooding may be coupled with low offspring dispersal, and there may be subsequent selection against the production of variable progeny in order to preserve locally adapted genotypes[63]. Another hypothesis for the evolution of uniparental reproduction by self-fertilization has been suggested by Strathmann et al.[87] and Eernisse[20]. Their idea is that the limited dispersal of brooded offspring leads to an inbred population structure, which in turn may increase the likelihood that alleles for self-fertilization can spread when rare. These ideas are not mutually exclusive, and further investigations of the association between brooding and uniparental reproduction are warranted.

Finally, if brooding does serve as an exaptation for the evolution of parthenogenesis, then it might also lead to greater extinction rates in certain ecological situations. This increase would be expected if the parthenogens rapidly replace their sexual ancestors, and then later become extinct due to an inability to track climatic changes, or due to the stochastic accumulation of mutations through Muller's ratchet[65]. In such a situation, we would expect species-level selection against the evolution of brooding[72].

Synthesis and conclusions

There are two major hurdles for the successful invasion and spread of uniparental reproduction. The first and foremost of these is overcoming the genetic disadvantages of uniparental reproduction. For selfing the primary problem is inbreeding depression. Reductions in fitness due to inbreeding depression, however, must be severe (greater than 50%) to prevent the spread of selfing within populations[14,60]. Although there are no direct measures of the magnitude of inbreeding depression in populations of *B. truncatus*, theoretical and empirical analyses of population structure[34,70] suggest it is unlikely to be this severe. Furthermore, if a population passes through the initial negative effects of inbreeding, it can evolve into a viable selfing population and is unlikely to revert back to outcrossing[60]. Observations of *B. truncatus* populations which are 100% aphallic in the field and which do not show intra-population variation in proportion of euphallics due to temperature[84] suggest that inbreeding depression is not an insurmountable obstacle to the establishment of 100% selfing populations in *B. truncatus*.

A similar hurdle exists for the evolution of parthenogenesis. The subversion of meiosis can result in developmental defects, which can have similar effects to those resulting from inbreeding depression[88,90]. If these effects are severe enough (i.e., greater than a 50% reduction in fitness), then parthenogenesis cannot spread when rare. Furthermore, lineages may vary in the fitness effects of mutation to parthenogenesis, and this could potentially explain the 'patchy' distribution of parthenogenetic reproduction in eukaryotes[5,56]. However, the patchy distribution of apomictic parthenogenesis might also be explained by differences in life-history strategies among lineages. For example, lineages that brood their offspring could be especially vulnerable to invasion by parthenogenesis, because brooding could allow for the culling of defective embryos through competition among brood mates or through selective abortion[52]; the two parthenogenetic prosobranchs reviewed here are brooders. For similar reasons, selective abortion (or arenas) might allow for the initial spread of selfing even under situations where inbreeding depression is greater than 50%.

If these initial genetic hurdles are overcome, then uniparental reproduction would be expected to spread when rare. The question then becomes whether it would become fixed within populations. Uniparental reproduction may fix if advantages of reproductive assurance outweigh the advantages to cross-fertilization, as appears to be the case for *Campeloma decisum*. In this unique system, sperm limitation by a digenetic trematode may favor females capable of parthenogenetic reproduction and select against sexual females in some populations, even though there would be selection for recombinant progeny. Over time, parasites should disproportionally infect these common, invariant host genotypes. Hence, there is support for the exploitation of the common host genotypes as predicted by the Red Queen hypothesis. Future effort should be directed towards testing the mechanisms by which sexual reproduction is maintained in southern populations.

However, if access to mates is not limited, then uniparental reproduction might not be expected to fix in local populations. The results of field studies of *Potamopyrgus antipodarum* and *Bulinus truncatus* are both consistent with the idea that parasites select for at least partial cross-fertilization. In *Potamopyrgus*, sexual populations are associated with higher parasite loads, which suggests that parthenogens have been able to replace sexual individuals only where parasites are rare or absent[48,50]. There was no indication that parthenogenetic reproduction is associated with populations of low density[50], which would have been consistent with the reproductive assurance hypothesis.

Similarly, across *Bulinus* populations, higher levels of euphally were associated with higher prevalence of trematode infection. Furthermore, seasonal increases in euphally, due to colder temperatures during juvenile development, coincide with increases in parasite pressure. To further test whether the Red Queen hypothesis can explain the distribution of aphallics and euphallics, it will be important to determine whether key assumptions of this hypothesis hold for the case of *B. truncatus*. Fitness consequences of Xiphidocercariae infection (the most common trematode observed in the field remains undescribed and cannot yet be propagated in the laboratory) on host snails are not known although laboratory infections of *B. truncatus* with other trematode species have shown significant fitness reductions including parasitic castration in some cases[2,22,82]. Furthermore, estimates of genetic variability and outcrossing rate within populations will be important to assess directly the relationship between levels of euphally and outcrossing rates, and the potential for outcrossing to generate genetic variability. Electrophoretic analyses of *B. truncatus* population structure have been of limited utility due to high levels of fixed (non-segregating) heterozygote patterns typical of tetraploids[36,71,99] although available evidence points to high levels of selfing in natural populations[70,71]. Nonetheless, observations of genetic variability in temperature-sensitivity within and between populations[84] suggest that genetic variation is present within populations. Advances in methods of genetic analysis (refs 35, 70, 71 for the case of *Bulinus*; ref. 41) may soon make it possible to determine whether individuals are the product of selfing or outcrossing, facilitating tests of both the Red Queen hypothesis and the role of inbreeding depression in maintaining euphally and aphally.

Studies of *Potamopyrgus* and *Bulinus* provide some of the strongest evidence for the maintenance of sex by parasites. Additional correlational support for the Red Queen hypothesis comes from a number of studies (comparative evidence: refs 5, 12; field evidence: refs 3, 13, 51, 64, 76). A powerful adjunct to these correlational studies will be experimental manipulations of parasite pressure in mixed populations of outcrossing and selfing/parthenogenetic individuals. These studies should answer the fundamental question of whether parasites are the major selective mechanism by which rare genotypes generated by sex are favored over uniparental progeny. Clearly, the Red Queen hypothesis offers many testable predictions that can be addressed in a variety of host-parasite interactions.

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