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Theoretically exploring the likelihood for sympatric speciation: interactions between snail shell-coil direction and anti-predation morphology

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ABSTRACT

Background: A single locus in snail genomes encodes alternative shell-coil-direction phenotypes (left or right), termed 'chirality'. Opposite-coil morphs that attempt mating encounter difficulties aligning their genitals and thus experience partial to complete reproductive failure. Individuals with the rarer coil morph in a population thereby incur fitness disadvantages. Gittenberger (1988) suggests, and Ueshima and Asami (2003) document, that snail shell chirality produces sympatric speciation based on a single locus. Predation may also play a role: snakes possess asymmetric jaws, which allow them to prey more effectively on snails with right-coil shells (Hoso *et al.*, 2007).

Hypothesis: In a population containing mostly individuals with right-coil shells, the rarer left-coil morph gains a fitness advantage because it more effectively resists predation from snakes that prey preferentially on right-coil morphs.

Question: Can anti-predation advantages in snail shell morphology compensate for – or overwhelm – any reproductive disadvantages of a particular shell morphology so as to prevent or promote the fixation of shell-coil-direction morphs?

Methods: Computer simulations of a computational model.

Results: Low predation rates in small demes can fix the left-coil morph, which in turn increases the proportion of left-coil morphs in the general population. Intermediate predation rates in larger demes can maximize the chance of fixation of the left-coil morph. But high predation rates reduce the chance of their fixation.

Conclusions: Differences in resistance to predation might explain the shell-coil dimorphisms observed naturally.

Keywords: chirality, computer simulation, evolution, speciation.

INTRODUCTION

Land snail populations constitute plausible model systems for single-gene speciation. Some terrestrial snail populations are characterized by shells that differ among individuals in size, shape, and even chirality (i.e. coil direction).

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Snail shell coil direction is encoded at a single locus (Sturtevant, 1923; Boycott *et al.*, 1930; Freeman and Lundelius, 1982; Hierck *et al.*, 2005; Kuroda *et al.*, 2009; Davison *et al.*, 2016). When snails with opposite-coil direction attempt to mate, their shells can prevent them from aligning their genitals (Asami *et al.*, 1998). Misalignment during mating is also partially determined by shell size and shape (Asami *et al.*, 1998). Snails in wide, globular shells experience great difficulty mating with snails in similar, wide, globular shells but with the opposite coil direction. Snails in narrow, elongate shells mate readily, sometimes even with individuals of opposite-shell-coil direction. Thus snail groups with opposite-coil-direction shells can be isolated reproductively and perhaps form new species. In fact, because shell coil direction is determined at a single locus, reproductive isolation owing to chiral differences should be able to initiate sympatric, single-gene speciation. Indeed, dimorphic shell-coil-direction populations do exist (Schilthuizen *et al.*, 2005).

Snails are characterized by three additional attributes that suggest the possibility of sympatric, single-gene speciation:

1. Coil-direction phenotype is determined by a maternal effect (Sturtevant, 1923; Diver *et al.*, 1925; Boycott *et al.*, 1930; Diver and Andersson-Kottö, 1938; Murray and Clarke, 1966; Freeman and Lundelius, 1982).
2. Populations can be made up of small, isolated groups (i.e. demes) that frequently face extinction and are involved in colonization (Gittenberger, 1988; Orr, 1991).
3. Some snail species are hermaphroditic, so individuals can reproduce by selfing.

The maternal effect is transgenerational: the genotype in the egg-producing individual determines the phenotype of its offspring by encoding a gene product that is incorporated into ova (Freeman and Lundelius, 1982). A mother can produce offspring with a mutant genotype but wild-type phenotype; her daughters will produce mutant grandchildren. The mutant allele thereby can increase cryptically in frequency over generations within populations, carriers avoiding the effects of positive, frequency-dependent selection. The mutant phenotype will be expressed once the frequency of its allele rises to a threshold proportion in the gene pool. Indeed, field malacologists in the early twentieth century reported true-breeding right-coil shell populations suddenly switching to left-coil shell phenotypes (Boycott and Diver, 1923; Sturtevant, 1923; Diver *et al.*, 1925; Diver and Andersson-Kottö, 1938).

Because the demes (i.e. breeding groups) of snail populations contain few individuals, genetic drift may produce fixation. Such small demes are also more vulnerable to extinction, which opens their areas to colonization by other snails searching for new territories. Small, new demes should be more prone to the founder effect (Templeton, 1980; Provine, 2004).

Some snail species are hermaphroditic, thus individuals can self-fertilize. Despite the obvious advantages associated with selfing, individuals in most hermaphroditic snail species outcross (Tsitrone *et al.*, 2003) and, in computer simulations, selfing appears to have minimal impact on single-gene speciation scenarios (Orr, 1991). One explanation for the scarcity of selfing in nature involves inbreeding depression and the low fitness associated with inbred offspring (e.g. Wethington and Dillon, 1997). In this case, left-coil snails should have evolved to attempt outcrossing, even if this would entail reproducing with snails characterized by the right shell-coil phenotype rather than their own.

Although the characteristics of snails – small deme size and maternal effects – potentially promote shell-coil-direction dimorphisms, they are observed infrequently in real populations. That suggests that at least one other factor operates to maintain homochirality. Johnson (1982) suggests that positive frequency-dependent selection is plausible. Snails apparently fail to recognize shell-coil direction when initiating mating and, if they make a mistake, they will invest a long time in continual, unsuccessful attempts at mating (Meisenheimer, 1912; Hesse, 1914; Janssen,

1966; Asami *et al.*, 1998; reviewed in Gittenberger, 1988 and Schilthuizen and Davison, 2005). This will be more of a problem for snails of the less common phenotype because they are more likely to encounter incompatible rather than compatible mates. Consequently, snails of the more prevalent phenotype should expend less energy with incompatible mates, thereby achieving greater reproductive success per courtship. It would seem that individuals with the more common phenotype have an extra reproductive advantage (in addition to the more obvious advantage of being able to find mates more frequently and thereby reproduce more efficiently). Because of these advantages, shell-coil dimorphism ought to be rare.

Indeed, shell-coil dimorphism is generally rare. But one does observe it commonly in some regions (reviewed in Schilthuizen and Davison, 2005). Southeast Asian (Indonesia, Malaysia, Singapore, and Thailand) populations of the land snail genus *Amphidromus* do exhibit shell-coil dimorphism. There the two morphs occur in approximately equal proportions (Schilthuizen and Davison, 2005; Schilthuizen *et al.*, 2005).

Tropical Japanese populations of the land snail *Satsuma caliginosa* exhibit shell-coil dimorphism at unexpectedly high frequencies (Hoso *et al.*, 2010), again suggesting that at least one other factor is important in determining shell-coil dimorphism. However, in the Japanese case, the other factor leads to the maintenance of both chiral forms. Hoso *et al.* (2010) suggest that predation is that factor.

Satsuma caligninosa and its predator, the snake *Pareas iwasakii*, are engaged in an evolutionary 'arms race' (Hoso *et al.*, 2007): *S. caliginosa* evolved a right-coil shell phenotype that helped individual snails to avoid predation by *P. iwasakii. Pareas iwasakii* evolved asymmetric jaws, with more teeth on the right side, increasing their proficiency at preying on snails in right-coil shells. This provides individual snails in left-coil shells with a substantial advantage where dimorphic snail populations are subject to predation. In other regions in Japan and with other snail species, water nymphs have evolved adaptations that facilitate predation on right-coil shells (Inoda *et al.*, 2003). Snails in left-coil shells thus may benefit compared with their right-coil neighbours. The advantages of reduced predation may counteract effects from positive frequency-dependent selection, explaining shell-coil dimorphism in these regions.

We hypothesized that the advantages gained through decreased susceptibility to predation can counteract the reproductive disadvantages imposed by positive frequency-dependent selection. We predicted that the chance of shell-coil dimorphism would correlate with the degree to which predators are adapted to prey on the more common (right-coil) phenotype. We tested this hypothesis via computer simulation, and identified conditions in which shell-coil dimorphism might be most likely to evolve.

METHODS

Using the program of Stone and Björklund (2002) set in a *Mathematica* (Wolfram Research, Inc., 2008) environment, we simulated evolution to study the effects of shell morphology and snail migration on shell-coil dimorphism. We used parameter values and variables appropriate for our study. The computer program emulates five snail demes in two dimensions. Each deme begins with a particular shell type or shell-type distribution: stout; mixed (i.e. stout and narrow in equal proportion); pseudorandom (i.e. shell-type proportions among individuals were determined pseudorandomly); intermediate (i.e. all shell forms midway between stout and narrow); and narrow. Demes were distributed pseudorandomly across the two dimensions, with inter-deme distances varying from simulation to simulation. Demes interacted (i.e. gene flow occurred) only when migration rates exceeded zero, whereupon individuals migrated in a distance-dependent manner.

Each individual had a genome comprising 12 bi-allelic loci: one that encoded sex; one that encoded shell-coil direction; and ten that encoded shell morphology (Fig. 1). Sex was set as if the simulation was a heterogametic system with female and male alleles determining female (00) and male (01) phenotypes. The shell-coil direction, determined by the maternally provided protein, was dextral if mothers had genotypes 00, 01, or 10, and sinistral if mothers had the homozygous recessive genotype 11 (in other words, the left-coil condition was recessive). Shell morphology was determined according to an additive genetic model: allele values were summed over the 10 loci. Alleles with value 1 contributed to a narrow shell phenotype; alleles with value 0 contributed to a stout shell phenotype. Phenotypic values thus ranged between 0 (the stoutest shell phenotype) and 20 (the narrowest shell phenotype). Values between 0 and 20 signalled intermediate phenotypes (lower values associated with stouter shells and higher values associated with narrower shells).

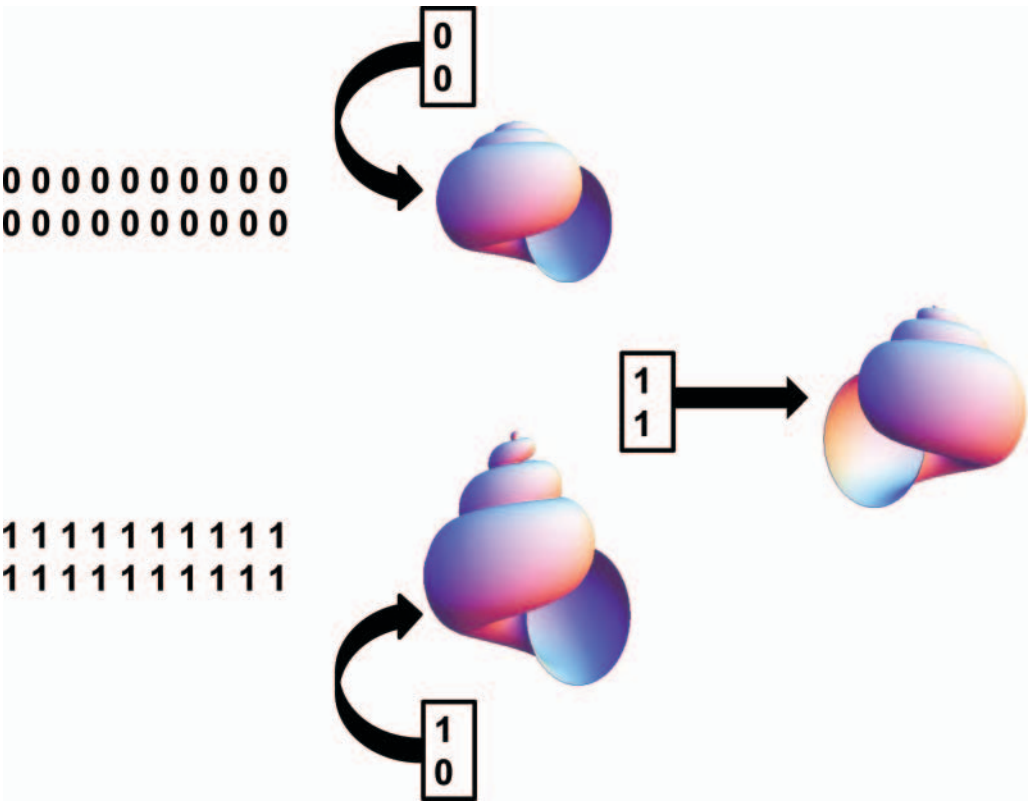

Fig. 1. Shell genotypes and phenotypes. Shell chirality locus genotype in maternal, egg-producing individuals (shown inside rectangles) encodes a protein that is incorporated into ova (indicated by arrows) and determines coil direction phenotype in offspring (presented shell forms). The 00 and 10 genotypes encode right-coil phenotypes, whereas the 11 genotype encodes left-coiled phenotypes. Shell form (i.e. size and shape) is determined in an additive manner over loci, with smaller values encoding stout forms (extreme value 0 shown at the top) and larger values encoding slender forms (extreme value 20 shown at the bottom). Shell-coil direction and form evolved in computer simulations, producing left-coil forms like the one in the middle (at the right) under different conditions.

We used a virtual area of 20 × 20 units for all simulations, with demes, each occupying one square unit, situated pseudorandomly within that area. Initially, each deme contained females and males in equal numbers, with each individual provisioned with one left-coil allele at the chirality locus. For Experiment 1, we used eight snails as both initial deme size (N) and carrying capacity (K) (Stone and Björklund, 2002). Natural demes have been observed to contain as few as 10 snails (Spight, 1974). For Experiment 2, to reduce extinction frequency, we set N and K to 16.

Individuals were paired pseudorandomly each generation, and females and males attempted copulation. Unpaired individuals contributed no alleles to the next generation. Each copulation attempt was associated with a function that determined reproductive success on the basis of shell morphology. Mating likelihood was determined by the formula $e^{(-c(1 - <g>))}$, where c is the 'coition coefficient' (range 1–5) and g is the normalized mean genotypic value over parental shell-shape loci (Stone and Björklund, 2002). Reproductive success peaked when snails with same-coil, narrow shells mated. Reproductive rate r was set to 2, so that each successful mating produced two offspring. As N and K were set to equal values and $r = 2$, simulations involved non-overlapping generations. Parents were replaced by their offspring except if predation had eliminated some individuals; in those circumstances, individuals were retained up to K. Selfing was prohibited because its effects on single-gene speciation have been claimed to be negligible (Orr, 1991) and snails tend to avoid selfing when possible (Asami *et al.*, 1998; Tsitrone *et al.*, 2003). Alleles at non-sex loci were subject to a mutation rate $\mu = 10^{-6}$ per locus per generation (which effectively was equivalent to 0 for so few loci).

Predation rates were set to fixed, different values for snails with different coil-direction shells. As a control condition, predation was set to 0 for snails in right- and left-coiled shells. Treatment conditions added predation for right-coil phenotypes. Each simulation ran for $t = 100$ generations, which was sufficient to achieve sinistral chirality allele fixation as well as reduce processing time and limit extinction events.

In Experiment 1, we ran ten 100-replicate sets for six separate parameter and variable value combinations (i.e. 1000 replicates for each simulated condition). Migration rate m (the probability for an individual to migrate each generation) was set to $m = 0$ for three conditions and $m = 0.01$ for the other three conditions. Each migration rate was associated with three predation rates on snails in right-coil shells; predation rate β (the percentage chance for an individual in a dextral shell to be lost each generation due to predation) was set to $\beta = 0$, 0.01, or 0.001 (Fig. 2).

We tabulated the frequency of sinistral phenotype fixation among demes. We analysed the data with repeated-measures analysis of variance (ANOVA). Subsequently, we explored significant differences using pairwise t-tests and a Bonferroni correction (with significance set conservatively on the basis of the number of possible pairwise comparisons; i.e. $\alpha/10 = 0.005$ for 5 groups).

In Experiment 2, we ran ten 100-replicate sets for five conditions. These simulations differed from the simulations in Experiment 1, in that larger N and K entailed larger deme sizes. Each condition involved a different dextral predation rate: $\beta = 0$, 0.001, 0.01, 0.05, and 0.1 (Fig. 3). We analysed the results with ANOVA. We explored significant differences as we did for Experiment 1.

RESULTS

In both experiments, regardless of the parameter settings, sinistral demes did evolve in some of the simulations (roughly 7 to 21%). Moreover, the parameter settings had an effect on the

proportion of simulations that resulted in the evolution of sinistral demes. We now set out those differences.

In Experiment 1, we rejected the null hypothesis 'no difference among groups' (repeated-measures ANOVA) subjected to different predation rates ($F_2 = 38.6$, $P = 3.90 \times 10^{-11}$) or different migration rates ($F_1 = 6.91$, $P = 0.0111$) (Fig. 2A). Contrary to expectations, sinistral demes were less likely to evolve as dextral predation increased. We rejected the null hypothesis 'no difference between shell-type groups' for comparisons involving wide forms (Fig. 2B). Sinistral fixation occurred least frequently in demes characterized by stout shell forms:

stout vs. mixed:	$t_{118} = 3.66$, $P = 3.77 \times 10^{-4}$
stout vs. pseudorandom:	$t_{118} = 4.60$, $P = 1.06 \times 10^{-5}$
stout vs. intermediate:	$t_{118} = 6.28$, $P = 5.95 \times 10^{-9}$
stout vs. narrow:	$t_{118} = 6.25$, $P = 6.77 \times 10^{-9}$

Demes characterized by narrower shell forms achieved sinistral fixation more frequently, although we were unable to reject the null hypothesis 'no differences between groups' for those comparisons:

mixed vs. pseudorandom:	$t_{118} = 0.290$, $P = 0.773$
mixed vs. intermediate:	$t_{118} = 2.61$, $P = 0.0102$
mixed vs. narrow:	$t_{118} = 2.57$, $P = 0.0115$
pseudorandom vs. intermediate:	$t_{118} = 2.67$, $P = 0.00869$
pseudorandom vs. narrow:	$t_{118} = 2.62$, $P = 0.00989$
intermediate vs. narrow:	$t_{118} = 0.0519$, $P = 0.959$

In Experiment 2 (Fig. 3), we rejected the null hypothesis 'no difference among groups' subjected to different predation rates (repeated-measures ANOVA; $F_4 = 38.48$, $P = 7.79 \times 10^{-14}$). Sinistral fixation frequency peaked at $\beta = 0.01$, an intermediate predation rate. All pairwise comparisons of results from $\beta = 0.01$ with results from other β-values establish $\beta = 0.01$ as the peak. We rejected the null hypothesis 'no difference between predation rate groups' for each pair of β-values as follows:

$\beta = 0.01$ vs. $\beta = 0$:	$t_{18} = 4.33$, $P = 4.02 \times 10^{-4}$
$\beta = 0.01$ vs. $\beta = 0.001$:	$t_{18} = 3.46$, $P = 2.78 \times 10^{-3}$
$\beta = 0.01$ vs. $\beta = 0.05$:	$t_{17} = 6.53$, $P = 5.17 \times 10^{-6}$
$\beta = 0.01$ vs. $\beta = 0.1$:	$t_{18} = 11.56$, $P = 9.18 \times 10^{-10}$

We also could not reject the null hypothesis 'no differences between groups' for three other pairs of β-values:

$\beta = 0$ vs. $\beta = 0.001$:	$t_{18} = 1.00$, $P = 0.330$
$\beta = 0$ vs. $\beta = 0.05$:	$t_{17} = 1.96$, $P = 0.0665$
$\beta = 0.001$ vs. $\beta = 0.05$:	$t_{17} = 3.14$, $P = 0.00602$

DISCUSSION

Dextral-specific predation can enhance sinistral fixation when dextral predation rates are moderate (e.g. $\beta = 0$ vs. $\beta = 0.001$; $\beta = 0$ vs. $\beta = 0.01$; Fig. 3). This finding supports the hypothesis that shell-coil dimorphism can result from chiral-specific predators. But differential predation, alone, is insufficient. Significant results were obtained only with larger deme sizes – when we increased initial deme size and carrying capacity from 8 to 16 individuals (Fig. 3).

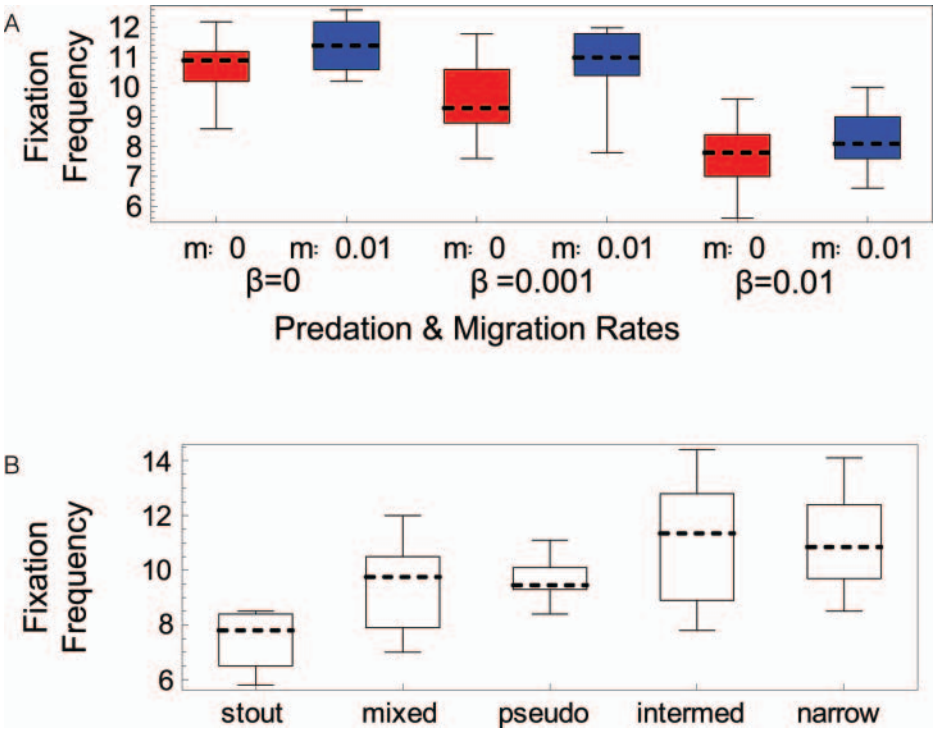

Fig. 2. Experiment 1: Sinistral shell-coil evolution (fixation events per 100 simulations) vs. dextral shell-coil predation (β) and migration rates (m). All demes in this experiment were small ($N = 8$, $K = 8$). There were two migration rates and three predation rates ($m = 0, 0.01$; $\beta = 0, 0.001, 0.01$; panel A). Fixation frequencies were averaged over shell types (A) and across migration and predation rates (B). Sinistral fixation decreased as predation rate increased. It also increased as migration rate increased (A). Sinistral fixation was least likely in demes characterized initially by stout shells relative to demes characterized initially by shell forms that were stout and narrow in equal proportions ('mixed') or narrow (B).

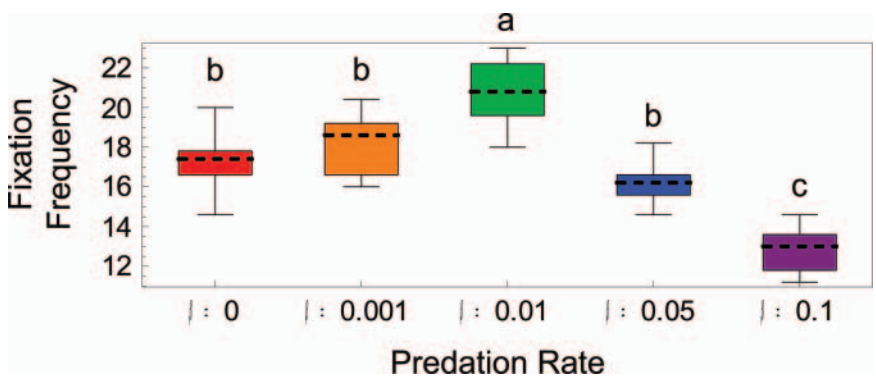

Fig. 3. Experiment 2: Sinistral shell-coil evolution (fixation events per 100 simulations) and dextral shell-coil predation rates (β) in larger demes ($N = 16$, $K = 16$). There was one migration rate and five predation rates ($m = 0.01$; $\beta = 0, 0.001, 0.01, 0.05, 0.1$). Fixation frequencies were averaged over shell types. *Note*: Differences between bars assigned different letters are significant.

With deme size set at 8, attempts to establish sinistral fixation by increasing dextral predation failed (Fig. 2). In fact, increasing dextral predation at this deme size inhibited sinistral fixation. We speculate that this pattern emerged from two related factors. First, small demes are vulnerable to extinction; even without predation, small demes (i.e. $N = 8$) were unlikely to persist for 100 generations (because one sex often was lost by chance). Second, increasing predation ensured that most individuals within demes died; if right-coil individuals carrying left-coil alleles were lost, then left-coil allele frequencies would be determined by mutation rates (which were low in the simulations).

These observations reveal that, despite mating difficulties, interactions between snails in oppositely coiled shells can produce significant effects in evolutionary scenarios. Given that success does occur occasionally, snails in sinistrally coiled shells that attempt to mate with snails in dextrally coiled shells are characterized by greater fitness than are snails that never attempt to mate. At smaller deme sizes, high predation rates on dextral snails can enable increased sinistral fixation frequencies, but such predation rates also can eliminate potential mates. Conversely, low predation rates in larger demes can enable increased sinistral fixation frequencies while maintaining potential mates.

Each simulation started by provisioning each virtual snail with one mutant allele, encoding the sinistral coiling direction, at the chirality locus. For fixation to have occurred in any replicate, the frequency of this allele would have had to increase over multiple generations, initially involving exclusively dextral breeding. During these initial generations, sinistral alleles were carried by snails characterized by dextral coil phenotypes; increasing dextral predation rate consequently indirectly jeopardized sinistral allele transmission. Increasing deme sizes ameliorated this effect by reducing the probability that dextral predation eliminated all snails that possessed sinistral alleles.

Predation rates were most effective at facilitating sinistral fixation when they were set at moderate levels. Setting predation rates too high, even with larger deme sizes, resulted in decreased sinistral fixation (Fig. 3), either by increasing extinction likelihood or by removing mutant-allele-carrying right-coil shell individuals, preventing mating opportunities for them. Conversely, setting predation rates too low resulted in low sinistral fixation frequencies. Predation increased sinistral fixation only when it was strong enough to counteract positive frequency-dependent selection but weak enough to avoid eliminating mutant-allele-carrying right-coil shell individuals while maintaining mating opportunities involving them.

Our results differ from some previous findings (Stone and Björklund, 2002) wherein smaller deme sizes only reduced the time for sinistral fixation. This discrepancy may be explained by examining differences in evolutionary modes. In the previous research, sinistral fixation was achieved through genetic drift (Stone and Björklund, 2002). Fixation through genetic drift is more likely with smaller demes because the likelihood for chance events correlates inversely with group size. We achieved sinistral fixation by balancing genetic drift (i.e. the aforementioned effects from deme size on allele and mating frequencies) and natural selection (i.e. through frequency-dependent effects and differential predation).

However, our results do corroborate other previous findings (Stone and Björklund, 2002). Shell shape significantly affected sinistral fixation (Fig. 2). Shell shapes that allowed interchiral breeding (narrow) facilitated sinistral fixation, whereas shell shapes that inhibited interchiral breeding (stout) were ineffective in producing sinistral fixation. This suggests that sinistral–dextral interactions indeed factor into sinistral fixation likelihoods. We also found that migration enhances the probability for sinistral fixation.

PROSPECTS

We identify three prospects for future research. First, research should focus on emulating the conditions observed on the Ryukyu islands, Japan. Tweaking parameters so that they match deme sizes, migration rates, and differences in predation rates will provide stronger evidence that dextral-specific predation by *P. iwasakii* explains chirality dimorphism in *S. caliginosa*. This will necessitate field studies to determine these characteristics.

Second, the relationship between deme size and the predation rate that maximizes the chance that sinistral demes evolve should be investigated. An increase in deme size should reduce selection resulting from predation on snails in dextral shells but carrying sinistral alleles. This suggests that, with respect to sinistral fixation, the optimal dextral predation rate would increase with larger deme size.

Third, simulations should include selfing. A previous simulation study, involving genetic drift, showed that selfing imparted negligible effects on sinistral speciation (Orr, 1991). However, because speciation modes also can involve natural selection, as in the present study, reassessing effects from selfing is warranted. In particular, if increased dextral predation can prevent sinistral speciation by eliminating mating opportunities involving sinistral alleles in snails characterized by dextrally coiled shells, then introducing selfing should reinstitute sinistral speciation. Furthermore, if selfing can allow dextral predation to facilitate speciation at smaller deme sizes, then we will have identified the mechanism by which increasing dextral predation decreases sinistral speciation.

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