Stable long-period cycling and complex dynamics in a single-locus fertility model with genomic imprinting

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Abstract Although long-period population size cycles and chaotic fluctuations in abundance are common in ecological models, such dynamics are uncommon in simple population-genetic models where convergence to a fixed equilibrium is most typical. When genotype-frequency cycling does occur, it is most often due to frequency-dependent selection that results from individual or species interactions. In this paper, we demonstrate that fertility selection and genomic imprinting are sufficient to generate a Hopf bifurcation and complex genotype-frequency cycling in a single-locus population-genetic model. Previous studies have shown that on its own, fertility selection can yield stable two-cycles but not long-period cycling characteristic of a Hopf bifurcation. Genomic imprinting, a molecular mechanism by which the expression of an allele depends on the sex of the donating parent, allows fitness matrices to be nonsymmetric, and this additional flexibility is crucial to the complex dynamics we observe in this fertility selection model. Additionally, we find under certain conditions that stable oscillations and a stable equilibrium point can coexist. These dynamics are characteristic of a Chenciner (generalized Hopf) bifurcation. We believe this model to be the simplest population-genetic model with such dynamics.

Keywords Population genetics · Fertility selection · Generalized Hopf bifurcation · Gene frequency cycling · Frequency dependence

Mathematics Subject Classification (2000) 92D10 · 92D15

Dedicated to the memory of Samuel Karlin.

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1 Introduction

Even the simplest ecological models can exhibit behavior that includes cycling and chaotic dynamics [32,33]. On the other hand, stable cycling of allele or genotype frequencies is rare in simple population-genetic models. Typically, genotype frequencies converge to locally stable equilibrium values from any initial frequency. In the classical diploid one-locus n-allele model with viability selection, allele frequencies converge for reasonable fitness matrices to an equilibrium at which the population mean fitness is locally maximized [26,40]. In a two-sex model with viability differences, mean fitness is not maximized but convergence to an equilibrium can still be guaranteed when all equilibria are hyperbolic [25,42].

The absence of cycling in these simple models has justified in part the focus on polymorphic equilibria as explanations of persistent genetic variation. Genotype-frequency cycling also can maintain genetic variation, but such cycling is more likely to occur in complex one- or two-locus models. One-locus models that include either frequency-dependent [2,9,16] or density-dependent [5,6] selection can exhibit cycling and chaos in both discrete and continuous time [41]. Two-locus viability models with recombination have also been shown to exhibit cyclic behavior; Hastings [21] showed numerically that stable cycling may occur in the discrete model, and this result was proved by Hofbauer and Iooss [22]. In the continuous model, Akin [1] proved cycling can result from a Hopf bifurcation, which occurs when modulating the value of a single parameter causes a stable equilibrium to give rise to a stable cycle [18]. More complex models that include host–parasite interactions [3,34], sexual selection [23], or behavioral interactions [35] easily elicit stable cycling.

Some of the simplest one-locus two-allele population-genetic models that exhibit stable cycling are models of fertility selection [11,20,24,27,38]. In sexually reproducing diploids, fertility selection is characterized by differential reproduction among mating pairs of different genotypes [7,14,37]. If the ith allele at the locus under consideration is denoted by $A_i$, fertilities for each mating pair can be given as $f_{ijkl}$, which represents the number of offspring produced by the mating of an $A_iA_j$ female with an $A_kA_l$ male. While there are nine different mating pairs, the symmetry of the model allows reciprocal mating pairs, i.e., $f_{ijkl}$ and $f_{klij}$, to be assigned the same fertility [14,20]; this implies that the matrix containing mating pair fertilities is symmetric and that the model requires only six parameters. Hadeler and Liberman [20] studied the discrete-time fertility model under the additional symmetry assumptions $f_{1111} = f_{2222}$ and $f_{1112} = f_{1222}$ and found regions of parameter space in which no equilibria are stable. Josić [24] and Doebeli and de Jong [11] proved that these regions contain stable two-cycles that are generated via a period-doubling bifurcation. Although a succession of period-doubling bifurcations can lead to aperiodic or chaotic behavior, only one of these bifurcations occurs in this symmetric fertility model. In the continuous-time fertility model, Hadeler and Glas [19] proved that every solution tends to an equilibrium point. Koth and Kemler [27] studied the continuous-time model and showed that convergence was no longer guaranteed when both fertilities and viabilities (or mortalities) differ among genotypes. Also, they presented a set of numerical parameter values for which the model admits a Hopf bifurcation.