LETTER

Evolutionarily stable strategies are well studied in periodically fluctuating populations

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Grunert et al. (1) examine evolutionarily stable strategies (ESSs) of a predator–prey system where the population dynamics either tend to an equilibrium or fluctuate periodically. The authors claim to have "extended the ESS concept to be applicable for periodically fluctuating ecological systems." However, the ESS concept is already well-established in periodically fluctuating populations, and, more generally, in variable (nonequilibrium) environments.

The groundwork for considering evolution in variable environments was laid by Metz et al. (2), who noted that the fitness of a mutant in a variable environment is given by its dominant Lyapunov exponent. Metz et al. (2) recognized that, unlike the relatively simple case of a population at equilibrium (where invasion fitness is equal to the dominant eigenvalue associated with the rare mutant dynamics, and often simply its exponential growth rate), in nonequilibrium scenarios, one must consider the dominant Lyapunov exponent to account for variation in growth rate over time. This can be achieved by calculating the Floquet exponents (either analytically or numerically) or through numerically simulating early time invasion dynamics. An ESS in a fluctuating population is therefore defined as one where, if adopted, all nearby strategies have negative dominant Lyapunov exponents. This early work was expanded on by Ferriere and Gatto (3), among others. In particular, Rand et al. (4) showed the conditions for an ESS to exist when a system has a general attractor, regardless of whether it is stationary, periodic, quasi-periodic, or chaotic.

ESSs, and, more generally, evolutionary dynamics, in nonequilibrium environments have since been studied extensively across a wide range of topics. Among the many relevant studies in this area are works on predator–prey systems (5, 6), host–parasite relationships (7, 8), resource competition (9), and reproduction–survival trade-offs (10), as well as several others. Of particular relevance to Grunert et al.'s (1) study, Kisdi and Liu (5) and Geritz et al. (6) examined evolution in predator–prey systems with periodically fluctuating populations, showing that an attracting ESS exists for predator handling time (5), and that stable coexistence of two predators at an ESS is possible (6).

We note that Grunert et al.'s (1) study is one of the few to derive fully analytic conditions for an ESS in a periodically fluctuating environment, which is a welcome contribution to the extensive literature on evolution in nonequilibrium populations. Alongside the previous studies summarized here, there is a strong foundation for future work in this area.

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