



The influence of demographic stochasticity on evolutionary dynamics and stability



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ABSTRACT

We derive the frequency-dependent selection coefficient caused by “demographic” stochasticity resulting from the random sampling of opponents an individual faces during behavioral “contests” with other individuals. The mean, variance, and higher moments of fitness all influence the direction and strength of selection. A frequency-dependent trait can be stable when an individual's fitness depends upon an infinite number of contests with other individuals and unstable when it depends upon a finite number of contests. Conversely, unstable equilibria for an infinite number of contests can be stable when there is a finite number of contests. At stable equilibria for a finite number of contests, higher moments of fitness can outweigh the joint influence of the first two moments so that natural selection favors “within-generation” or developmental-trait variation (also known as phenotypic plasticity) contrary to the claim that natural selection always acts against such variation. We use second-moment estimates of the fitness functions in a diffusion approximation to compute fixation probabilities of competing strategies. These estimates are shown to be qualitatively consistent with those derived from simulations when population sizes are sufficiently large to ignore the contribution of higher-moment terms. We also show that explicit solutions to the diffusion approximation only exist for pair-wise interactions that lead to positive frequency-dependent selection.

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1. Introduction

Competition for mates (Maynard Smith and Price, 1973; Parker, 1978), intersexual conflict (Petrie and Lipsitch, 1994; Mokkonek et al., 2011), parent–offspring conflict (Trivers, 1974; Haig, 1992), and competition for resources (Hammerstein, 1981; Riechert and Hammerstein, 1983; Milinski, 1984) occur in many species. In such competitive “games”, the fitness of a strategy is often influenced by the frequency of other strategies in the population, instead of being constant. This is an instance of phenotype plasticity since the phenotype of an individual is environment-specific rather than constant (see also Smead and Zollman, 2009).

Theoretical analyses of competitive games include the Hawk–Dove game, which describes competition between aggressive and passive behavioral strategies (Maynard Smith and Price, 1973; Maynard Smith, 1982), and the Prisoner's Dilemma game

(Axelrod and Hamilton, 1980), which describes competition between altruistic and selfish strategies. For two strategies, A and B , the pay-offs from pair-wise contests are

$$G = \begin{bmatrix} G_{AA} & G_{AB} \\ G_{BA} & G_{BB} \end{bmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix}, \quad (1)$$

where G_{ij} is the pay-off to an individual of strategy i in a contest with an individual of strategy j . For example, in the Hawk–Dove game if we denote Hawk as type A and Dove as type B , the pay-off to a Hawk in an encounter with a Dove (b) is greater than that in an encounter with another Hawk (a), and a Dove does better in an encounter with another Dove (d) than with a Hawk (c). The same inequalities apply for selfish and altruistic individuals in the Prisoner's Dilemma game.

Most analyses of evolutionary games have identified stable equilibria using the concept of the evolutionarily stable strategy (ESS sensu Maynard Smith and Price, 1973; Taylor and Jonker, 1978; Maynard Smith, 1982; Hines, 1987). An ESS is a “resident” strategy that resists invasion by a rare mutation (see extensions of evolutionary stability by Hofbauer and Sigmund, 1998; Metz et al., 1996). Most of this work has the assumption that the population

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size and the number of contests each individual has with other individuals are infinite. When the number of contests is finite, variance of viability or reproduction at any given time can arise as a consequence of the random sampling of opponents. The influence of such “demographic” stochasticity (Shaffer, 1981, p. 131) on population and evolutionary dynamics has been long studied (e.g., Kendall, 1949; Bartlett, 1960; MacArthur and Wilson, 1967; Levins, 1969; Richter-Dyn and Goel, 1972; May, 1973; Shaffer, 1981; Lande, 1993; Lande et al., 2003).

Demographic stochasticity differs from genetic drift as described by the Fisher–Wright model (Gillespie, 1974, 1975, 1977) in that the former involves a finite gene pool to which contributions of each genotype differ because of variation in survival and reproduction among individuals, while the latter involves finite, non-proportional sampling of alleles from an infinite gene pool. Demographic stochasticity occurs when the fitnesses (net offspring number) of individuals of the same genotype differ at any given time, while genetic drift occurs as a result of stochastic sampling from a pool of gametes or offspring when the fitnesses of individuals of the same genotype are equal at any given time.

Our understanding of the role of demographic stochasticity in evolution remains incomplete in large part because its influence on frequency-dependent selection is not completely understood. This context is arguably the most important one in which to understand the influence of demographic stochasticity because such selection is a typical feature of behavioral contests, which are ubiquitous in nature (see above). Only a handful of studies (e.g. Proulx, 2000; Calsbeek et al., 2001; Orzack and Hines, 2005; King and Masel, 2007) have explicitly considered the evolutionary consequences of demographic stochasticity arising from the formation of contests, and their analyses are only partial. (Other researchers have analyzed the influence of genetic drift arising from the random sampling of offspring resulting from contests, without considering the effects of demographic stochasticity induced by finite contests; e.g., see Nowak and Sigmund, 1990; Fogel et al., 1997; Bergstrom and Godfrey-Smith, 1998; Ficici and Pollack, 2000; Nowak et al., 2004; Wild and Taylor, 2004; Lessard, 2005; Altrock and Traulsen, 2009; Hashimoto and Aihara, 2009; Zhou et al., 2010.)

Here, we further analyze the consequences of this form of demographic stochasticity on the evolutionary dynamics and statics of frequency-dependent natural selection.

1.1. Overview

We analyze the variance in fitness (defined as net offspring production) caused by random sampling of opponent pairs in evolutionary games. In Section 2, we derive the stochastic fitness of a strategy given pairwise contests, both as an exact function of the sampling probabilities and in large populations via a sampling with replacement approximation. In Section 3 we apply these results to compute the exact fitness differences between two evolutionary strategies and illustrate numerically how deterministic equilibria predicted by evolutionary game theory are not necessarily stable in finite populations. We also show that in sufficiently small populations, first- and second-moment approximations to the fitness function need not correctly predict the direction of selection, and that strategies with higher demographic stochasticity can be favored by selection. In Section 4 we analyze the fixation probabilities (global dynamics) for evolutionary games in finite populations using a diffusion approximation to the expected change and variance in fitness under the assumptions of weak selection and large population size. In Section 5, we compare these estimates to those derived from individual-based simulations.

2. Demographic stochasticity in frequency-dependent contests

Consider a population of haploid asexual organisms in which the frequency of a genotype with strategy A is p and the frequency

of a genotype with strategy B is $1 - p$. The pay-offs from individual contests are given by Eq. (1). Henceforth, we use the term “strategy” when referring to a genotype. Assuming infinite contests, the average fitness for each strategy is

$$E[W_A] = ap + b(1 - p), \quad (2a)$$

$$E[W_B] = cp + d(1 - p). \quad (2b)$$

In an infinite population with infinite contests, the dynamics and statics of strategy frequency are determined entirely by $E[W_A]$ and $E[W_B]$.

With pairwise evolutionary contests, the “realized” fitness of a particular individual is a random variable. In the case of an individual of type A , $W_A = a$ with probability p , b with probability $1 - p$ (whereas for B , $W_B = c$ with probability p , d with probability $1 - p$). If both the population size and number of contests are infinite, then the realized average fitness \bar{W}_A , \bar{W}_B of strategies A , B are equal to the values given by Eqs. (2a) and (2b), otherwise, we must distinguish between the realized average fitness of a strategy and its expected fitness.

Consider a finite population of N individuals that meet once in the contest phase of a life cycle; x are of type A . The realized average fitnesses \bar{W}_A , \bar{W}_B of individuals of type A , B are now random variables and depend on the number of contests. For example, if k is the number of A/A contests, there will be $x - 2k$ A/B contests and $(N - 2x + 2k)$ B/B contests. Since k is itself a random variable, the realized average fitness for the two strategies are

$$\bar{W}_A = a \frac{2k}{x} + b \frac{x - 2k}{x}, \quad (3a)$$

$$\bar{W}_B = c \frac{x - 2k}{N - x} + d \frac{N - 2x + 2k}{N - x}. \quad (3b)$$

It follows that the realized average population fitness is

$$\bar{W} = p \bar{W}_A + (1 - p) \bar{W}_B. \quad (3c)$$

To find the expected average fitnesses (and higher moments) for the two strategies, we must derive a pairing distribution $P(k)$. We assume that N is even so that every individual is paired (if there is an odd number of individuals, one can account for the remaining individual, either by, say, having it not contribute to the gene pool or by allowing for a double pairing). The probability of having exactly k A/A pairs given x strategy A individuals and $N - x$ strategy B individuals is

$$P(k) = \frac{\binom{N/2}{k} \binom{N/2 - k}{x - 2k}}{\binom{N}{x}} 2^{x-2k}, \quad (4)$$

for $\max(0, N - x/2) \leq k \leq x/2$, with $P(k) = 0$ otherwise.

To derive Eq. (4), consider a random sequence of x individuals of type A and $N - x$ individuals of type B . There are a total of $\binom{N}{x}$ ways to order the A 's and B 's in this sequence. Assume that contest pairs are the $N/2$ adjacent, non-overlapping pairs of individuals in this sequence, of which k are A/A . We have $\binom{N/2}{k}$ possible positions for A/A pairs, which leaves $N/2 - k$ pairs that are either A/B or B/B . The number of A/B pairs is $x - 2k$, so there are $\binom{N/2 - k}{x - 2k}$ possible orderings of A/B 's. Finally, any pairing A/B is equivalent to B/A , giving us $2^{(x-2k)}$ possible orderings of individuals of type A and B among the $x - 2k$ A/B pairs. Analogous pairing problems arise in estimating the distributions of homozygous and heterozygous genotypes in finite diploid populations, contributing to deviations from the Hardy–Weinberg equilibrium, e.g. Schraiber et al. (2012).

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