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Thomas F. Hansen



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ACCEPTED MANUSCRIPT

ON THE DEFINITION AND MEASUREMENT OF FITNESS IN FINITE

POPULATIONS

Thomas F. Hansen¹

University of Oslo, Department of Biology, CEES & Evogene, PB 1066 Blindern, 0316 Oslo, Norway thomas.hansen@bio.uio.no

Abstract

I argue that some standard accounts of fitness in finite populations are both inaccurate and conceptually misleading. I show that the usual population-genetics conceptualization of fitness as the ratio between amounts of a type after selection and before selection works just as well in finite as in infinite populations. Fitness then becomes a random variable, and selection can be conceptualized as any difference in the distribution of this variable while genetic drift can be conceptualized through realized variation in the variable. I derive exact equations for and novel approximations to the mean and variance of relative fitness, approximations for selection gradients in finite populations, and an expression for the variance effective population size in the presence of selection.

Keywords: Natural selection, Selection gradient, Genetic drift, Effective population size, Propensity interpretation, Bet hedging.

1. Introduction

Gillespie (1974, 1975, 1977) showed that increasing the variance in the number of offspring reduces the relative fitness of an allele in a finite population. He argued that one could use the mean fitness of the allele minus the variance of its offspring distribution divided by population size as a criterion for determining whether the allele would increase in the population. This criterion has motivated further theoretical work (e.g. Proulx 2000; Frank 2011), and become established as a measure of fitness in finite populations (e.g. Hopper et al. 2003; Schreiber 2015). It has also been important as a premise for analyses of the fitness concept in the philosophy of biology literature (e.g. Brandon 1990). For example, Sober (2001) used the

¹ Phone: 4722854521.

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