The generalized multiplicative model for viability selection at multiple loci*

F. B. Christiansen
Department of Ecology and Genetics, University of Aarhus, Ny Munkegade, DK-8000 Aarhus, Denmark

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Abstract. Selection due to differential viability is studied in an n-locus two-allele model using a set indexation that allows the simplicity of the one-locus two-allele model to be carried to multi-locus models. The existence condition is analyzed for polymorphic equilibria with linkage equilibrium: Robbins’ equilibria. The local stability condition is given for the Robbins’ equilibria on the boundaries in the generalized non-epistatic selection regimes of Karlin and Liberman (1979). These generalized non-epistatic regimes include the additive selection model, the multiplicative selection model and the multiplicative interaction model, and their symmetric versions cover all the symmetric viability models.

Key words: Multiple locus selection – Multiple locus polymorphism – Additive selection model – Multiplicative selection model

1. Introduction

The simultaneous evolution at two or more loci under the influence of selection has been studied analytically in various simplified models of the action of natural selection. These simplified models fall into two basic types, namely the symmetric models and models with an additive or a multiplicative structure in fitness. The symmetric models were originally suggested as a two-locus model for viability selection by Lewontin and Kojima (1960) and generalized to a three-locus model by Feldman et al. (1974). The extension to multiple loci was made by Karlin (1977) and Karlin and Avni (1981). The multiplicative model for viability selection (Bodmer and Felsenstein 1967; Moran 1968) has been analyzed as a multi-locus model by Roux (1974) and its combination with the additive viability model (Bodmer and Felsenstein 1967; Karlin and Feldman 1970a; Karlin and Liberman 1978b) leads to selection models with a general

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combination of additive and multiplicative structures (Karlin and Liberman 1979a,d). These models of Karlin and Liberman (1979a,d) will be referred to as the generalized multiplicative models for viability selection at multiple loci.

The most important simplification in these models is that they are made to possess special polymorphic equilibria, the Robbins' equilibria, where the alleles at the various loci occur independently in the gametes of the population, i.e., where linkage equilibrium prevails. In general, the existence of a totally polymorphic Robbins' equilibrium places strict requirements on the fitness matrix (Bodmer and Felsenstein 1967) because it must be an equilibrium of the corresponding multiple allele model obtained for absolute linkage among the loci. However, many aspects of the Robbins' equilibrium point may be viewed as representing aspects of a totally polymorphic equilibrium descending from a totally polymorphic equilibrium for absolute linkage as long as the property of linkage equilibrium is not emphasized.

The analysis of generalized multiplicative viability models has so far concentrated on exploring the conditions for local stability of the Robbins' equilibrium where all loci are segregating, i.e., the totally polymorphic Robbins' equilibrium. However, the interpretation of these conditions as conditions for stability of polymorphic multi-locus equilibria is made difficult because of the arbitrary number of loci chosen for a particular model. For an n-locus model with n large a locally stable Robbins' equilibrium segregating n – 1 or fewer loci is as interesting as the totally polymorphic equilibrium (Christiansen 1988). The analysis of the generalized multiplicative model will be extended to comprise the conditions for stability of these Robbins' equilibria on the boundaries of the gamete frequency domain. Thus, the conditions for stability of the totally polymorphic Robbins' equilibrium given by Karlin and Liberman (1979a,d) will be extended to comprise stability towards the introduction of gametes not present in the equilibrium population.

The analytic method used by Roux (1974), Karlin (1977), Karlin and Liberman (1979a–d), and Karlin and Avni (1981) allows for multiple alleles at the loci considered, and no appreciable simplification is reached by restricting attention to the situation of two alleles per locus. Theoretical considerations of viability selection at a single locus are greatly simplified by the assumption of two alleles, and the present analysis of the generalized multiplicative viability models tries to capture this simplification in multi-locus models. The simplification achieved is considerable in that the complexity of the formulation and of the recurrence equations does not increase with the number of loci.

The description of genotypes and gamete types in the multi-locus model uses a set indexation (Christiansen 1987, 1989a). This indexation is a development of Geiringer's (1944) and Schnell's (1961) description of recombination events in terms of subsets of the set of loci considered: the recombination event that produced a gamete is characterized by the set of loci in which the gamete received a copy of the paternal allele, say, and the rest of the loci, the complementary set, received the maternal allele. The set indexation corresponds to a designation of an allele of interest at each locus in much the same way as in the analysis of classical one-locus models. Then the set describing a gamete simply describes the loci that carry the allele of interest with the remaining loci carrying the alternative allele.