

# The enigma of frequency-dependent selection

Mikko Heino

Johan A.J. Metz

Veijo Kaitala

**Frequency-dependent selection is so fundamental to modern evolutionary thinking that everyone 'knows' the concept. Yet the term is used to refer to different types of selection. The concept is well defined in the original context of population genetics theory, which focuses on short-term evolutionary change.**

**The original concept becomes ambiguous, however, when used in the context of long-term evolution, where density dependence becomes essential.**

**Weak and strong frequency dependence, as distinguished in this article, refer to two very different forms of selection.**

Mikko Heino is at the Division of Population Biology, University of Helsinki, PO Box 17, FIN-00014 Helsinki, Finland (mikko.heino@helsinki.fi);

Hans Metz is at the Section of Theoretical Evolutionary Biology, Institute of Evolutionary and Ecological Sciences, PO Box 9516, NL-2300 RA Leiden, The Netherlands (metz@rulsfb.leidenuniv.nl);

Veijo Kaitala is at the Dept of Biological and Environmental Science, University of Jyväskylä, PO Box 35, FIN-40351 Jyväskylä, Finland (vkaitala@cs.jyu.fi).

Evolutionary change can be studied at different timescales<sup>1</sup>. Over the short-term, the emphasis is on understanding genotypic change – traditionally the realm of population genetics. Over longer timescales, the main interest lies in long-term phenotypic change, in particular in the potential resting points of phenotypic evolution, such as evolutionarily stable strategies (ESS).

Another major distinction between short- and long-term evolution lies in the importance of environmental feedback. Feedback occurs because fitness depends on the genetic or phenotypic composition of the population and on density-dependent population regulation. Ultimately, environmental feedback is essential to understand evolutionary change. However, for short periods, it is often feasible to ignore it, at least partially. Initially, at the outset of population genetics theory, the assumption of no feedback went as far as to assign constant fitness values to different genotypes<sup>2</sup>. Consequently, selection was both density- and frequency-independent. Wallace<sup>3</sup> coined the term 'hard selection' for this type of selection. However hard selection is a rather contrived concept, even in the context of short-term evolution. Fisher<sup>4</sup> pointed out the possibility that the fitness of a certain genotype might depend on the frequencies of other genotypes in the population. This led to the mathematical formalization of frequency-dependent selection, initiated by Haldane<sup>5</sup>, Li<sup>6</sup>, Lewontin<sup>7</sup> and

Wright<sup>8</sup>. There are many definitions of frequency dependent selection (Box 1). These range from the broad classical statement of 'the (relative) fitness of a type varies with the relative frequency of other types in the population' to more narrow definitions, which require frequency dependent selection to result in the stable coexistence between two types (where the fitness of one type increases with a decrease in its relative frequency in the population).

Within the field of population genetics (which ignores density dependence), frequency-dependent selection is a well defined concept. However, outside the realm in which the classical definition applies, it becomes ambiguous because, in literal terms, when density dependence is accounted for, all selection becomes frequency-dependent. Therefore, it is no longer clear what frequency-dependent selection means and consequently there is a need to refine the concept. This should carry the 'spirit' of the classical concept to ecologically more realistic scenarios.

## The classical population genetics concept

Classical population genetics focuses on the changes of genotype frequencies but ignores change in their absolute numbers. The original concept of frequency-dependent selection arose from two lines of thinking. First, it was recognized that fitness values are not usually constant – the relative fitness of a genotype depends on the relative frequencies of other genotypes in the population. Second, frequency dependence could explain stable polymorphisms<sup>2</sup>. To emphasize the argument, we restrict the following discussion to those models assuming clonal inheritance and nonoverlapping generations with only two types (1 and 2). The densities of the newborns we call  $n_1$  and  $n_2$ , and their relative frequencies  $p_i = n_i / (n_1 + n_2)$ , where  $i$  is type 1 or 2. The product of the survival probability to the next breeding season and the number of offspring is called 'fitness', and denoted as  $V_i$ . If a prime indicates the next generation:

$$n'_i = V_i n_i \quad (1)$$

### Box 1. Different definitions of frequency-dependent selection

The usual definitions of frequency-dependent selection are broad and include such statements as the following:

- The selective value of a genotype is frequency dependent when its contribution to the following generation relative to alternative genotypes varies with the frequency of the genotype in the population<sup>2</sup>.
- ...fitnesses are not fixed, but variable, and the values they take on vary as functions of the frequencies of the diploid genotypes they characterize<sup>26</sup>.
- ...a genotype may have different fitnesses depending on ...the relative frequency of other genotypes<sup>27</sup>.
- Frequency-dependent selection occurs when the fitness of genotypes vary as a function of the genotypic composition of the population<sup>28</sup>.
- ...the fitness of a strategy may depend on its frequency relative to that of other strategies even though total population size remains fixed<sup>22</sup>.

In populations subjected to density-dependent population regulation, these definitions become ambiguous: taken literally, all selection is frequency-dependent in the long run (although only in a rudimentary sense).

Sometimes, frequency-dependent selection is defined in a narrower sense as that leading to stable polymorphisms:

- ...fitness values vary so as to favour rare types, and become approximately equal as an intermediate frequency is approached<sup>26</sup>.
- If two types exist in a population, and if the fitness of each is greater when it is rare, then stable coexistence will result<sup>12</sup>.

In practice, this is the meaning of frequency dependence used in fields such as behavioural ecology and life history theory.

The classical assumption is that the fitnesses are constant, which allows the derivation of the autonomous recurrence equation as:

$$p_1' = \frac{sp_1}{sp_1 + p_2}, s = \frac{V_1}{V_2} \quad (2)$$

Population geneticists habitually concentrate on the long-term behaviour of solutions of Eqn 2. They consider that frequency dependence is reached when the ratio  $s$  is not constant but varies with  $p_1$ , and with nothing else. We believe that the operational definition of the strict absence of frequency dependence should be to hold  $s$  constant. This definition is used as a starting point to identify the counterpart of the classical concept in a density-dependent world.

The extension of frequency dependence to diploid models is not straightforward, even in the case of viability selection

(Box 2). The case of fertility selection requires even further adaptation because fertility differences can confound the experimental detection of frequency dependence<sup>9,10</sup> (Box 3).

The ecological scenarios where frequency dependence is typically invoked include rare-type advantage in acquiring matings, mimicry, host–parasite coevolution, predators using search images and kin selection<sup>2,11–14</sup>. These interactions can result in the evolution of polymorphisms, such as the colour morphs of snails and flowers, immunocompetence against parasites and diseases, and alternative mating strategies. From a theoretical perspective, frequency dependence simply means that the conspecifics become part of the environment that an individual experiences, and the influence from the environment plays a role in the selection process. However, the classical population genetics framework permits only partial inclusion

of this environmental feedback because density-dependent components are not accounted for.

**Frequency dependence and long-term evolution**

Evolutionary theory that ignores density dependence does not make ecological sense. However, extending the concept of frequency dependence to account for density dependence is less than straightforward. To achieve a proper understanding of different forms of frequency-dependent selection operating in populations with density-dependent regulation, we need first to review the fitness scenarios applicable to density-dependent evolution.

*Density-dependent fitness*

Fitness is a property of a type of an individual relative to the environment in which it lives. When density dependence is taken into account, describing the environment becomes paramount, in particular that part of the abiotic (e.g. nutrients and light) and biotic (e.g. density of predators and competing conspecifics) environment that is influenced by the presence and actions of individuals of the focal population. This is referred to as the ‘feedback environment’ – it is this environment that is reflected in equations of the population dynamics (Box 4). The dimensions of the feedback environment is the minimal number of variables needed to describe it.

Measuring fitness under density dependence is based on the ability of mutant types to invade a resident population or, more precisely, the environment prescribed by the resident population. The fittest type is the one able to resist invasions by all the other types. This is the ESS idea, on which classical evolutionary game theory is based<sup>15</sup>. In the context of population dynamics, this has led to the invasion fitness concept – a powerful notion that is central to the emerging field of adaptive dynamics<sup>16</sup>. The operational fitness measure is the invasion exponent,  $\rho(\sigma', E)$ , which is the long-term average growth rate of a mutant ‘playing’ strategy  $\sigma'$  in a feedback environment  $E$  set by the resident strategy<sup>17–19</sup>. This feedback environment is constrained by population regulation: at equilibrium the feedback environment  $E_\sigma$  created by the resident strategy,  $\sigma$ , has to satisfy  $\rho(\sigma, E_\sigma) = 0$ ; that is, the resident population is neither growing nor decreasing in numbers in the long run.

*Selection in one-dimensional feedback environments*

The feedback environment is often introduced, perhaps unconsciously, in such a way that it can be characterized by

**Box 2. An ecological perspective on the population genetics concept of frequency dependence: viability selection in diploid populations**

Classical population genetics focuses on randomly mating diploid populations (whose densities are high enough to ensure that every female is mated) with noninteracting generations and a fixed sex ratio<sup>27,29,30</sup>. Environmental changes, including density dependence, are implicitly assumed to affect only those life stages that are different from those affected by genetic changes.

In viability selection, genotypic differences are assumed to affect only survival. This genetic component of survival we denote with  $v_{yz}$ , where  $yz$  is the genotype and is one of the allele combinations  $aa$ ,  $aA$  or  $AA$ . Basic book keeping of newborn density,  $n_{yz}$ , gives, with a prime indicating the next generation:

$$n_{yz}' = C_{yz} f(E) \frac{(v_{yy} n_{yy} + \frac{1}{2} v_{yz} n_{yz}) (\frac{1}{2} v_{yz} n_{yz} + v_{zz} n_{zz})}{v_{yy} n_{yy} + v_{yz} n_{yz} + v_{zz} n_{zz}} \quad (5)$$

where  $c_{yz} = 1$  if  $y = z$  and 2 if  $y \neq z$  and  $f$  is the product of the *per capita* fertility and the survival over the life stages affected by the nonconstant environmental factors. From Eqn 5 we can derive a recurrence equation for the genotype frequencies as  $p_{yz} = n_{yz}/N$ , where  $N = n_{aa} + n_{aA} + n_{AA}$  and is the total population size. However, after one generation the genotype frequencies are confined to the Hardy–Weinberg parabola  $p_{yz} = c_{yz} p_y p_z$  with  $p_a = p_{aa} + \frac{1}{2} p_{aA}$ ,  $p_A = 1 - p_a$ . This permits the recurrence equation to collapse to:

$$p_a' = \frac{(v_{aa} p_a + v_{aA} p_A) p_a}{v_{aa} p_a^2 + 2v_{aA} p_a p_A + v_{AA} p_A^2} \quad (6)$$

Equation 6 further reduces to Eqn 2 (in the main text) when, and only when,  $v_{yz}$  can be written as a product  $v_y v_z$ . Comparing Eqn 6 with Eqn 2 we might say that, from the perspective of the alleles, pairing into individuals leads to frequency dependence, with allele  $a$  having relative fitness  $v_{aa} p_a + v_{aA} p_A$ , thus allowing for cases where  $a$  and  $A$  can stably coexist (the case of heterozygote superiority). However, population geneticists take an individual-centred viewpoint, and speak of frequency dependence if the ratios  $v_{yz}/v_{aA}$  depend on  $p_a$  but are otherwise constant.

**Box 3. An ecological perspective on the population genetics concept of frequency-dependence: fertility selection in diploid populations**

Diploid individuals reproduce through pairing, either directly or through the gamete pool. Therefore, we introduce the fertility parameters  $v_{wx,yz}$ , for the fertility of the pair  $wx$  and  $yz$  (where  $wx$  and  $yz$  are the parental genotypes with possible alleles  $a$  and  $A$ ), multiplied by the survival probabilities of  $wx$  and  $yz$  over the life stages that stay unaffected by the variable environmental factors. The recurrence equations for the genotype frequencies ( $p_{yz}$ ) are similar to those derived from Eqn 5 (Box 2), except that the genetic component of survival ( $v_{yz}$ ) is replaced by linear expressions of  $p_{wx}$ . Population geneticists refer to this effect as ‘apparent’ frequency dependence, implying that in ‘real’ frequency dependence  $v_{wx,yz}$  depends on the genotype frequencies. This apparent frequency dependence precludes the existence of a relationship among the genotype frequencies comparable to that of the Hardy–Weinberg equilibrium, so that no further collapse is possible except when mating occurs via a well-mixed gamete pool so that  $v_{wx,yz} = v_{wx} v_{yz}$ . In the latter case, Hardy–Weinberg equilibrium can be reached, the recurrence equation collapses to Eqn 6 (Box 2), and frequency dependence is taken to mean that  $v_{yz}$  depends on  $p_a$ .

**Box 4. The feedback environment and its dimension**

The feedback environment refers to the full description of the environment as it occurs in the feedback loop in the population dynamics, usually simply some function of the population state. For example, in the Ricker map  $n(t+1) = n(t)\exp(r - \alpha n(t))$  (where  $n$  is the population density,  $r$  is the intrinsic growth rate and  $\alpha$  is a scaling parameter related to the carrying capacity), the condition of the feedback environment at time  $t$  is  $n(t)$ , and the feedback environment is the time-series  $n(t)$ ,  $t = 0, 1, \dots$ . If the dynamics reach a stable equilibrium point, the feedback environment becomes one-dimensional: the condition of the feedback environment is the equilibrium population size. In general, for population dynamics on stable point attractors, the dimension of the feedback environment is the minimal number of variables needed to describe the environment in the equations of the population dynamics. The concept of the feedback environment (and in particular its dimension) belongs only to the world of models, although its formulation should be based on biological reasoning.

The following example on the evolution of maturation in a model with two age-classes (simplified from Ref. 31) illustrates a two-dimensional feedback environment ( $e_1, e_2$ ) and the possibility of a stable phenotypic polymorphism in the age at maturity:

$$n_1(t+1) = \frac{s_0[f_1\gamma n_1(t) + f_2 n_2(t)]}{1 + a_1 e_1(t)}$$

$$n_2(t+1) = \frac{s_1(1 - \gamma)n_1(t)}{1 + a_2 e_2(t)}$$
(7)

where  $n_i$  is the density of the age-class  $i$ ;  $s_i$  and  $f_i$  are the age-specific survival and fecundity, respectively;  $a_i$  is a scaling parameter; and  $\gamma$  is the fraction of individuals maturing at age one. If the population dynamics reach equilibrium, the feedback environment is two-dimensional, given by  $(e_1, e_2) = [f_1\gamma n_1 + f_2 n_2, (1 - \gamma)n_1]$ , – that is, by the densities of newborns and nonreproducing adults. This is because of different resource utilization and/or predation between age-classes. The evolutionarily stable fraction of females maturing at age one is

$$\gamma^* = \begin{cases} 1 & \text{if } s_1 f_2 - f_1 \leq 0 \\ 0 < 1 - \frac{a_1(s_1 f_2 - f_1)}{a_2(s_0 f_1 - 1)} < 1 & \text{if } 0 < s_1 f_2 - f_1 < (s_0 f_1 - 1) \frac{a_2}{a_1} \\ 0 & \text{if } s_1 f_2 - f_1 \geq (s_0 f_1 - 1) \frac{a_2}{a_1} \end{cases}$$
(8)

a single number – it is one-dimensional. Although information about the relative frequencies of different types then disappears, some form of frequency dependence can still occur.

If the broad definitions from Box 1 are taken literally, selection is always frequency-dependent under density dependence (although in a very contrived sense). For invasion fitness, it matters which environment is being invaded – that is, which of the potential residents are present and in what frequencies, hence the frequency dependence. This can be seen in the following example. We extend Eqns 1 and 2 to include density dependence, such that the influence from the environment is introduced as a single multiplicative factor  $f(E)$ . The dynamics are now:

$$n'_i = v_i f(E) n_i \tag{3}$$

where  $v_i$  is a constant demographic parameter and  $E$  represents the environment, including both abiotic and biotic factors that impinge on the fate of the individuals. Assume that only type 1 is present and the population has reached equilibrium, yielding the environmental condition  $\hat{E}_1$ . At the steady-state, the newborn density of type 1 is  $\hat{n}_1 = \hat{n}_1 v_1 f(\hat{E}_1)$ . Therefore, the influence from the environment is  $f(\hat{E}_1) = 1/v_1$ . This is the environment that type-2 invaders experience when they are rare. The initial

growth ratio of an invader is then  $v_2 f(\hat{E}_1) = v_2/v_1$ . The invasion fitness of type-2 individuals invading a type-1 population ( $p_2 = 0$ ) becomes  $\rho(2, \hat{E}_1) = \log(v_2/v_1)$ , but  $\rho(2, \hat{E}_2) = 0$  after fixation ( $p_2 = 1$ ). Adherence to the literal interpretation of the classical concept of frequency dependence would let us classify the fitnesses as frequency-dependent. However, a collapse to recurrence Eqn 2 is possible. To deal with density dependence and long-term evolution it is necessary to shift slightly away from the fitness concept of formal

population genetics, in the direction of the intuitive original meaning of fitness.

Even if we stick to the population genetics definition of fitness, which is only possible in a limited number of ecological scenarios, selection without frequency dependence is rarely encountered in regulated populations, despite the fact that many simple models described in the literature belong to this special case. If we make only a minor change to our model – making the influence of the environment additive instead of multiplicative – frequency dependence emerges. With an additive model, the population dynamics are given by  $n'_i = v_i n_i - f(E) n_i$ . If there are only two types, 1 and 2, the frequency of type 1 in the population follows the equation:

$$p'_1 = [(v_1 - f(E))p_1] / [v_1 p_1 + v_2 p_2 - f(E)] \tag{4}$$

The appearance of  $f(E)$  in the equation means frequency dependence occurs according to our operational definition – the collapse to recurrence Eqn 2 is impossible when  $s$  is held constant.

In general, a frequency-dependent component of selection is absent in regulated populations only when all the demographic parameters, except for an environmental influence, which appears as a single multiplicative factor, are constant. However, although in one-dimensional feedback environments this frequency dependence is technically subsumed under the strict interpretation of the classical concept, it never results in stable phenotypic polymorphisms. Therefore, we refer to frequency-dependent selection occurring in one-dimensional feedback environments as ‘trivial’ frequency dependence (Table 1).

*Multidimensional feedback environments: weak and strong frequency dependence*

A multidimensional feedback-environment requires that there is some ‘structure’ to the population, otherwise a collapse to a one-dimensional feedback environment

**Table 1. Types of frequency dependence in feedback environments of one and two (or higher) dimensions, when it is either possible or impossible to extract autonomous equations for the gene frequencies<sup>a</sup>**

Feedback environment	Possible to extract an autonomous equation for the gene frequencies?	
	Yes: classical population genetics framework of density dependence	No: all other sorts of density dependence
One dimension	No frequency dependence (s in Eqn 2 held constant <sup>a</sup> )	Trivial frequency dependence
Two or more dimensions <i>Weak frequency dependence</i>	Classical frequency dependence (s in Eqn 2 depends only on the gene frequencies <sup>a</sup> )	Strong frequency dependence <sup>b</sup> (stable polymorphisms)

<sup>a</sup>Compare with Eqn 2 in the text.

<sup>b</sup>Strong frequency dependence is a special case of weak frequency dependence and is identified when selection leads to a stable phenotypic polymorphism.

would be possible. Population structure can be genetic, temporal (resulting from environmental fluctuations), physiological (age- or stage-related) or spatial. Population structure enables different individuals to have a different influence on the environment and, moreover, a different perception of environment. Whether the structure creates a multidimensional feedback environment or not depends on how influence and perception are accounted for in the population dynamics model.

If frequency dependence is defined in the narrow sense as that which induces stable polymorphisms, then it can only occur in feedback environments with two or more dimensions. Likewise, if the broad classical definition is upheld (that  $s$  in Eqn 2 is dependent on  $p$ ) then, if the population dynamics underlying Eqn 2 are to be realistic, the presence of a higher dimensional feedback environment is also required. However, a strict absence of frequency dependence (where  $s$  in Eqn 2 is held constant) implies a feedback environment with only one-dimension. We shall equate the presence of a higher-dimensional feedback environment with 'weak' frequency dependence (Table 1).

Intuitively, stable phenotypic polymorphisms can only occur in feedback environments with more than one dimension because, under density dependence, fitness depends on the population density, which requires one environmental variable. The addition of another environmental variable makes it possible for fitness to depend on the relative frequencies in the population. The environmental variables need not include phenotype frequencies explicitly – if different strategies contribute differently to environmental variables then the same outcome will be obtained.

A two-dimensional feedback environment is a necessary condition (although not a sufficient one) for the evolution of stable phenotypic polymorphisms. This follows from Levin's competitive exclusion principle<sup>20</sup>: at most,  $n$  species can stably coexist on  $n$  resources. From the ecological point of view, phenotypes are analogous to species. Different environmental variables can describe different resources, although they are open to a wider interpretation (e.g. different predators or parasites). Thus, an evolutionary analogy to the competitive exclusion principle is that, at most,  $n$ -morphisms can stably occur in a feedback environment with  $n$ -dimensions<sup>21</sup>.

Selection resulting in stable polymorphisms is an important case of weak frequency-dependent selection. Consequently, we refer to this as 'strong' frequency dependence (Table 1). It requires that two conditions are fulfilled. First, the coexisting types increase in relative

frequency when rare enough (negative frequency dependence). Second, the co-existing types are equally fit, with the invasion exponent ( $\rho$ ) equal to zero at some relative frequency. Examples show that these conditions can be satisfied in a variety of models<sup>22–25</sup> (Box 4).

### Concluding remarks

One of the major directions for future research is to extend the theory and ideas reviewed here to temporally variable environments. This is particularly true for the notions of the feedback environment and its dimensions, which are so essential in understanding frequency dependence in a density-dependent world<sup>21</sup>.

The ambiguity in the term 'frequency-dependent selection' was perhaps first noted by Gromko<sup>26</sup>, who distinguished between the classical population genetics concept and the special case leading to stable polymorphisms. Unfortunately, acknowledging density dependence as an essential part of any ecologically realistic model has only increased this ambiguity in recent years. Outside the realm of classical population genetics, in which the concept was originally defined, several interpretations have become possible. Some researchers have accepted the literal interpretation of the classical concept of frequency dependence<sup>11</sup>. However, in other fields, such as behavioural ecology and life history theory, it is customary only to refer to selection leading to stable polymorphisms as frequency-dependent. This confusion and the fact that the concept of frequency dependence rises little above the purely descriptive provide two good reasons to continue to seek its refinement.

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