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The enigma of frequency-dependent selection

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IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 16

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The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

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Contents

Abstract

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 genetical theory focusing 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 paper, refer to two very different forms of selection under density dependence.

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The enigma of frequency-dependent selection

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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 genetical theory focusing 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 paper, refer to two very different forms of selection under density dependence.

Evolutionary change can be studied on different time scales[1]: On the time scale of short-term evolution, the emphasis is on understanding *genotypic* evolutionary change. Traditionally, this is the realm of population genetics. On the time scale of long-term evolution, the main interest lies in long-term *phenotypic* change, and more 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, that is, the dependence of fitness on the genetic or phenotypic composition of the population, and density-dependent population regulation. In the long run, environmental feedback is essential in understanding evolutionary change. However, on the timescale of short-term evolution, it is often feasible partially to ignore environmental feedback. In the early theory of population genetics, this assumption went as far as to assign constant fitness values to different genotypes[2]. Thus, the selection is both density- and frequency-independent. Wallace[3] coined the term 'hard selection' for this type of selection. Hard selection is a rather contrived possibility, even in the context of short-term evolution. Fisher[4] pointed at the possibility that the fitness of a certain genotype might depend on the frequencies of other genotypes in the population. The mathematical treatment of frequency-dependent selection was started by Haldane[5], Li[6], Lewontin[7] and Wright (see Wright[8] for an overview). The definition of frequency-dependent selection, in its classical guise, has been something like 'the (relative) fitness of a type varies with the relative frequency of other types in the population' (Box 1). The importance of frequency-dependent selection is that it allows stable coexistence of different types, if their fitnesses increase with a decrease in their relative frequencies — sometimes this is even given as the (narrow) definition of frequency-dependent selection.

Box 1. Different definitions of frequency-dependent selection

The usual definitions of frequency-dependent selection are broad:

> ‘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’[2].
>
> ‘. . . fitnesses are not fixed, but variable, and the values they take on vary as functions of the frequencies of the diploid genotypes they characterize’[26].
>
> ‘. . . a genotype may have different fitnesses depending on . . . the relative frequency of other genotypes’[27]
>
> ‘Frequency-dependent selection occurs when the fitness of genotypes vary as a function of the genotypic composition of the population’[28].
>
> ‘. . . the fitness of a strategy may depend on its frequency relative to that of other strategies even though total population size remains fixed’[22]

In populations subjected to density-dependent population regulation, these definitions become ambiguous: taken literally, all selection is frequency-dependent in the long run, but only in a rudimentary sense.
Sometimes, frequency-dependent selection is defined in a narrower fashion as selection leading to stable polymorphisms:

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

In practice, this is the meaning of frequency dependence, for instance, in behavioural ecology and life history theory.

Within the realm of population genetics, which ignores density dependence, frequency-dependent selection is a fairly well-defined concept, both from the broad and the narrow point of view. However, outside the realm to which the classical definition is applicable, the definition becomes ambiguous: according to a literal interpretation, when density dependence is accounted for all selection becomes frequency-dependent. Therefore, it is no longer clear what is meant by frequency-dependent selection. Hence, there is a need for refined concepts of frequency dependence. These refined concepts should carry the ‘spirit’ of the classical concept to ecologically more realistic scenarios. To provide some focus, we start by reviewing the classical population genetical concept of frequency-dependent selection. We then discuss refined concepts of frequency dependence when density dependence is accounted for, with the emphasis on phenotypic long-term evolution.

The classical population genetical concept

Classical population genetics focuses on the changes of genotype frequencies, but ignores the changes in their absolute numbers. The original concept of frequency-dependent selection arose within this framework from two lines of thinking: First, it was recognized that fitness values are usually not constant, that is, the relative fitness of a genotype depends on the relative frequencies of other genotypes in the population. Second, frequency dependence could explain stable polymorphisms[2]. To make the argument more transparent, we restrict the discussion to population genetical models assuming clonal inheritance and non-overlapping generations with only two types (say, 1 and 2). The densities of the newborns we call n_1 and n_2, and their relative frequencies $p_i = n_i/(n_1+n_2)$. 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,

$$n_i' = V_i n_i. \tag{1}$$

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

$$p_1' = \frac{sp_1}{sp_1 + p_2}, \; s = V_1/V_2. \tag{2}$$

Population geneticists habitually concentrate on the long-term behaviour of the solutions of (2). In their parlance, frequency dependence obtains when the ratio s is not constant but varies with p_1, *and with nothing else.* We take the possibility of extracting (2) from the population dynamics with s a constant, as the operational definition of the strict absence of frequency dependence. This definition is used as a first reference point when trying to identify the counterpart of the classical concept in a density-dependent world.

The extension of the concept of frequency dependence to models with diploid genetics is not altogether straightforward even in the case of viability selection (Box 2). The case of fertility selection requires even further adaptation, to the extent that fertility differences can confound the experimental detection of frequency dependence[9,10] (Box 3).

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

Classical population genetics focuses on randomly mating diploid populations, at densities sufficiently high that every female gets mated, with non-interacting generations and a fixed sex ratio[27,28,30]. Environmental changes, including density dependence, are implicitly assumed to affect only life stages different from the ones affected by the genetic differences.

If the genotypic differences are assumed to affect only survival, basic accounting gives, when n_{yz} $(y, z \in \{a, A\})$ denotes the density of newborns,

$$\begin{aligned} n'_{yz} = \quad & c_{yz} f(E) \frac{(v_{yy}n_{yy}+\frac{1}{2}v_{yz}n_{yz})(\frac{1}{2}v_{yz}n_{yz}+v_{zz}n_{zz})}{v_{yy}n_{yy}+v_{yz}n_{yz}+v_{zz}n_{zz}}, \\ & \text{with } c_{yz} = \begin{cases} 1 & \text{if } y = z, \\ 2 & \text{if } y \neq z. \end{cases} \end{aligned} \tag{3}$$

where f is the product of the per capita fertility and the survival over the life stages affected by the non-constant environmental factors. From (3) we can derive a recurrence for the genotype frequencies $p_{yz} = n_{yz}/N$, $N := n_{aa} + n_{aA} + n_{AA}$. 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 allows collapsing the recurrence to

$$p'_a = \frac{(v_{aa}p_a + v_{aA}p_A)p_a}{v_{aa}p_a^2 + 2v_{aA}p_a p_A + v_{AA}p_A^2}. \tag{4}$$

(4) further reduces to equation (2) when, and only when, v_{yz} can be written as a product $v_y v_z$. Comparing (4) with (2) we might say that from the perspective of the alleles their 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_{yy}/v_{aA} depend on p_a but are otherwise constant.

The ecological scenarios typically mentioned as conducive to frequency dependence are rare-type advantage in acquiring matings, mimicry, host-parasite coevolution, predators using search images, kin selection, etc.[2,11–14]. These interactions may result in the evolution of polymorphisms: e.g., 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 genetical framework permits only partial inclusion of this environmental feedback, since it cannot account for density-dependent components.

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

Diploid individuals reproduce through pairing, either direct, or through a gamete pool. Therefore we introduce the parameters $v_{wx,yz}$, $w, x, y, z \in \{a, A\}$, for the fertility of the pair (wx, yz) multiplied with the survival probabilities of wx and yz over the life stages that stay unaffected by the variable environmental factors. Basic accounting gives recurrences for the genotype frequencies p_{yz}, which are similar to those derived from (3), except that the v_{yz} are replaced by linear expressions in the p_{wx}. Population geneticists refer to this effect as 'apparent' frequency dependence, implying that in 'real' frequency dependence the $v_{wx,yz}$ depend on the genotype frequencies. This 'apparent' frequency dependence generically precludes the existence of a relation among the genotype frequencies comparable to the Hardy-Weinberg one, 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 obtains, the recurrence collapse to (4), and frequency dependence is taken to mean that the v_{yz} depend on p_a.

Frequency dependence and long-term evolution

Evolutionary theory ignoring density dependence does not make ecological sense. However, extending the concept of frequency dependence to account for density dependence is less than straightforward. Strict adherence to the definitions in Box 1 would let us conclude that density dependence induces a formal form of frequency dependence which does not at all agree with the spirit of the concept. In particular, it is a different kind of frequency dependence from that alluded to in the examples. To achieve a proper understanding of different forms of frequency-dependent selection operating in populations with density-dependent regulation, we first review the fitness concepts applicable to density-dependent evolution.

Density-dependent fitness

Fitness is both a property of a type of individual and of the environment it lives in. When density dependence is accounted for, the dependence of fitness on the environment becomes essential. This applies in particular to that part of the physical and biological environment that both feeds through into the calculated fitness, and that is influenced by the presence and actions of individuals of the focal population. The abstraction of this part of the 'real' environment is referred to as the 'feedback environment' — the environment as it is seen in the population dynamical equations (Box 4). The dimension of the feedback environment is the minimal number of variables needed to describe this feedback.

Measuring fitness under density dependence is based on the idea of invasibility by mutant types of a resident population, or more precisely, of the environment as set by the resident population. The fittest type is the one able to resist invasions of all the other types. This is the idea of evolutionarily stable strategies, on which classical evolutionary game theory is based[15]. When the idea is applied in a population dynamical context, we arrive at the invasion fitness concept. This powerful notion lies at the heart of the emerging field of adaptive dynamics[16]. The operational fitness measure is the invasion exponent $\rho(\sigma, \mathbf{E})$, which is the long-term average growth rate of a mutant 'playing' strategy σ in a feedback environment $\mathbf{E}$ set by the resident strategy[17–19]. This feedback environment is constrained by population regulation: at the steady state the feedback environment $\mathbf{E}_\sigma$ created by the resident strategy σ, has to satisfy $\rho(\sigma, \mathbf{E}_\sigma) = 0$; the resident population is neither growing nor decreasing in numbers in the long run.

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 $n(t+1) = n(t)\exp(r - \alpha n(t))$, the condition of the feedback environment at time t is $n(t)$, and the feedback environment is the time-series $n(t)$, $t = 0, 1, \ldots$. If the dynamics reach a stable point equilibrium, 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 condition of the environment in the population dynamical equations. The concept of 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 evolution of maturation in a model with two age-classes (simplified from Ref. 30) illustrates a two-dimensional feedback environment and the possibility of a stable phenotypic polymorphism in age-at-maturity:

$$\begin{aligned} N_1(t+1) &= \frac{s_0[f_1\gamma N_1(t) + f_2 N_2(t)]}{1 + a_1 e_1(t)} \\ N_2(t+1) &= \frac{s_1(1-\gamma)N_1(t)}{1 + a_2 e_2(t)}, \end{aligned}$$

where s_i and f_i are the age-specific survival and fecundity, respectively, a_i is a scaling parameter and γ is the fraction of individuals maturing at age one. If the population dynamics reaches a point equilibrium, the feedback environment is two-dimensional, for example given by $(e_1, e_2) = (f_1\gamma N_1 + f_2 N_2,\ (1-\gamma)N_1)$, i.e., by the densities of newborns and non-reproducing adults. The rationale for this is different resource utilization and/or predation between age-classes. The evolutionarily stable fraction of females maturing at age one is

$$\gamma^* = \begin{cases} 1 & \text{if } \ s_1 f_2 - f_1 \le 0, \\ 0 < 1 - \frac{a_1(s_1 f_2 - f_1)}{a_2(s_0 f_1 - 1)} < 1 & \text{if } \ 0 < s_1 f_2 - f_1 < (s_0 f_1 - 1)\frac{a_2}{a_1}, \\ 0 & \text{if } \ s_1 f_2 - f_1 \ge (s_0 f_1 - 1)\frac{a_2}{a_1}. \end{cases}$$

Selection in one-dimensional feedback environments

Often the feedback environment is introduced, perhaps unconsciously, in such a way that its dimension is one, that is, such that it can be characterized by a single number. Although all 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, though in a very contrived sense: For the invasion fitness it matters which environment is being invaded, that is, which of the potential residents are present and in which frequencies — hence the frequency dependence. This is seen in the following example. We extend the model (1)–(2) to include density dependence, such that the influence from the environment is introduced as a single multiplicative factor $f(\mathbf{E})$. The dynamics is now

$$n_i' = v_i f(\mathbf{E}) n_i, \tag{5}$$

where v_i is a constant demographic parameter and $\mathbf{E}$ stands for environment, including both abiotic (nutrients, light, etc.) and biotic factors (density of predators, competing conspecifics, etc.), that impinge on the fate of the individuals. Assume that only type 1 is present and the population has reached a point equilibrium, yielding the environmental condition $\hat{\mathbf{E}}_1$. At the steady-state $\hat{n}_1 = \hat{n}_1 v_1 f(\hat{\mathbf{E}}_1)$. Thus the influence from the environment is $f(\hat{\mathbf{E}}_1) = 1/v_1$. This is the environment type-2 invaders experience when rare. The initial growth ratio of an invader is then $v_2 f(\hat{\mathbf{E}}_1) = v_2/v_1$. The invasion fitness of type 2 into a type-1 population ($p_2 = 0$) becomes $\rho(2, \hat{E}_1) = \log(v_2/v_1)$, while $\rho(2, \hat{\mathbf{E}}_2) = 0$ 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. Yet a collapse to recurrence (2) is possible. What happened is that we changed horses in midride. To deal with density dependence and long-term evolution it is necessary to shift away slightly from the fitness concept of formal population genetics, in the direction of the intuitive original meaning of fitness. But the classical idea of frequency dependence was based on that formal fitness concept.

Even if we stick to the population genetical 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 in the literature belong to this special case. If we make only a minor change to our model — additive instead of multiplicative influence from the environment — frequency dependence pops out. In this case, the population dynamics are given by $n_i' = v_i n_i - f(\mathbf{E}) n_i$. If there are only two types, 1 and 2, the frequency of type 1 in the population follows the equation

$$p_1' = [(v_1 - f(\mathbf{E}))p_1]/[v_1 p_1 + v_2 p_2 - f(\mathbf{E})]. \tag{6}$$

The appearance of $f(\mathbf{E})$ in the equation means that there is frequency dependence according to our operational definition, that is, the collapse to the recurrence (2) with constant s is impossible.

In general, a frequency-dependent component of selection is absent in regulated populations only when the demographic parameters are constant but for an influence from the environment which appears as a single multiplicative factor. However, although this frequency dependence in one-dimensional feedback environments technically is subsumed under the strict interpretation of the classical population genetical concept, it never results in stable phenotypic polymorphisms. Therefore, we shall refer to frequency-dependent selection occuring in one-dimensional feedback environments as *trivial frequency dependence* (Fig. 1).

Multi-dimensional feedback environments

Multi-dimensionality of the feedback environment requires that there is some population 'structure' — otherwise a collapse to a one-dimensional feedback environment would be possible. Population structure may be genetical, temporal (resulting from environmental fluctuations), physiological (age- or stage-structure) or spatial. Population structure enables different individuals to have a different influence on the environment, and further, a different perception of environment. Whether a given population structure gives rise to a multi-dimensional feedback environment or not depends on how these two factors are accounted for in the population dynamical model.

A counterpart of the classical concept of frequency dependence, in the narrow sense, that is, inducing stable polymorphisms, can occur only in feedback environments with dimension two or higher. Secondly, the presence of broad sense classical frequency dependence, that is, (2) holding good with s dependent on p, implies presence of a higher dimensional feedback environment in any realistic population dynamics underlying (2). Finally, a strict absence of frequency dependence, that is, (2) holding good with constant s, generically implies one-dimensional feedback environment. Therefore we shall equate the presence of a higher dimensional feedback environment with *weak frequency dependence*.

Intuitively, stable phenotypic polymorphisms can occur only in a higher dimensional feedback environments because under density dependence, fitness depends on the population density, which requires one environmental variable. Another environmental variable makes a dependence of fitness on the relative frequencies possible. The environmental variables need not include phenotype frequencies explicitly — the frequency interpretation also obtains if different strategies contribute differently to environmental variables.

A two-dimensional feedback environment is a necessary condition (but not a sufficient one!) for the evolution of stable phenotypic polymorphism. This follows from Levin's competitive exclusion principle[20]: 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 *in an $n-$dimensional feedback environment, at most $n-$morphism can stably occur*[21].

Within weak frequency-dependent selection, an important special case is selection resulting in stable polymorphisms. We call this *strong frequency dependence* (Fig. 1). This requires that two conditions are fulfilled. First, the coexisting types can increase in relative frequency when rare enough (negative frequency dependence). Second, the coexisting types are equally fit with $\rho = 0$ at some relative

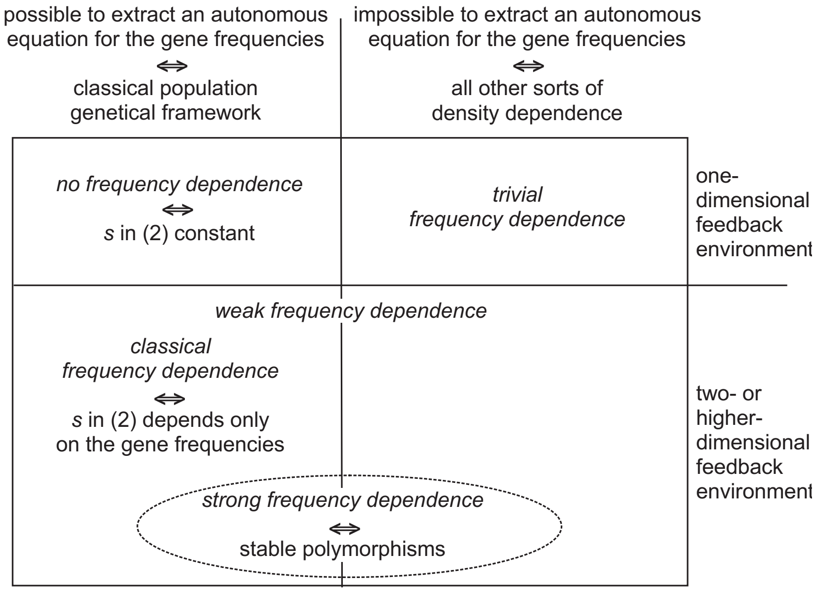

Figure 1: Types of frequency dependence.

frequency. Examples show that these conditions can be satisfied in a variety of models (refs. 22-25, Box 4).

Concluding remarks

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

The ambiguity in the term 'frequency-dependent selection' was perhaps first noted by Gromko[26], who distinguished between the classical population genetical 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 the ambiguity over the recent years. Outside the realm of classical population genetics in which the concept was originally defined, several interpretations become possible. Different interpretations coexist in everyday usage as well. Remarks such as 'it is likely that there is a frequency-dependent component in virtually all selection that operates in natural populations, for interactions among members of a population affect the selective advantage of almost all traits, and such interaction usually give rise to frequency-dependent effects'[11] indicate that some people have accepted the literal interpretation of the classical concept. In some fields such as behavioural ecology and life history theory it is customary to refer only to selection leading to stable polymorphisms as frequency-dependent. Not only is there confusion, presently the concept of frequency dependence rises little above the purely descriptive; two reasons to keep seeking for refinements.

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