NATURAL SELECTION

or the non-survival of the non-fit

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ABSTRACT

The effects of natural selection as a process in natural populations differs from 'survival of the fittest' as it was formulated by Darwin in his 'Origin of Species'. The environment of a population exists of continuous changing conditions, which are heterogeneous in space. During its life each individual successively meets with differing conditions. During these confrontations the individual may appear to be 'unfit' or 'unlucky' and may die. If it survives it will meet the following conditions to which it is 'tested' anew, a.s.o. Hence, many individuals being less fit under certain conditions will survive and reproduce, because they did not meet a deadly moment. Therefore, being 'fit' only refers to special prevalent conditions. In each generation the individuals thus being 'unfit' will be eliminated together with the 'unlucky' ones. All other individuals will survive and reproduce, notwithstanding their properties.

Hence, natural selection results in the **'non-survival of the non-fit'** rather than in 'survival of the fittest', because being 'fit' simply means 'having survived and reproduced', whereas being 'unfit' can be connected with many kinds of properties and environmental conditions, e.g. being killed by a predator. Only after many generations (hundreds or even thousands) the effect of eventually dominating properties of the survivors may result in a set of properties suggesting an overall 'survival of the fittest'. This was what Darwin wanted to explain as he was mainly interested in evolutionary processes.

As natural selection, as an ecological process, cannot be considered in each generation to be 'survival of the fittest', many ecological concepts supposed to be connected with selection resulting in 'survival of the fittest' within a few generations, such as the dominant role of competition, the critical level of the costs of reproduction, the need of optimization and of optimal life-history traits have to be reconsidered more critically in a less deterministic context. Moreover, these aspects of natural selection, which usually lead to impoverishment of the genepool, contradict the need of a high level of genetic heterogeneity as a base for an effective natural selection.

The author gives examples of cases to which these concepts do not apply. On the other hand, natural selection resulting in 'non-survival of the non-fit' allows a continuous reshuffling of all kinds of genes and gene combinations over all kinds of genomes, also many genes with temporarily or even permanently unfavourable effects can be kept in the genepool of the population during a long series of generations. Therefore, natural selection resulting in 'non-survival of the non-fit' leads to **spreading of the risk of extinction** of the population over genotypes and to the gradual development and accumulation of highly sophisticated adaptations. Only in an environment that has been stationary or even almost constant and homogeneous for a long time may natural selection ultimately lead to 'survival of the fittest'.

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1. INTRODUCTION

Population biology is considered to be the science that studies those processes in the field that are expected to result in significant changes of the genetic and phenotypic composition of the population, which ultimately will lead to evolutionary processes. Therefore, both population geneticists and population ecologists are convinced that they are studying the results and consequences of selection processes, so that they deal with and have to think about the ideas of Charles Darwin. It was a surprise to discover that other population ecologists apparently did not realize that the concept of 'natural selection' as it was formulated by Darwin (1859) did not directly apply to the ecological processes they study in the field. However, it considers the expected result of these processes after many generations of selection. Darwin was interested in giving a scientific explanation for the development of differences between species and eventually for the process of evolution, and not in the ecological processes within a single or a few generations in field populations. In my opinion this difference in point of view has led to a number of misunderstandings among both ecologists and evolutionary biologists, e.g. about processes of competition and optimization. To help clarify these misunderstandings in the following it is explained what the expected results of ecological processes in the short term are and where these may differ from the results in the long term. As Darwin himself reformulated his ideas several times I cite his views from the last (6th) impression (1910) of the 'Origin of Species' (Darwin, 1859).

2. SURVIVAL OF THE FITTEST

Chapter IV of Darwin's 'The Origin of Species" (1859) is entitled: 'Natural selection; or the survival of the fittest'. This metaphor is described as: "This preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest. Variations neither useful nor injurious would not be affected by natural selection, and would be left either a fluctuating element as perhaps we see in certain polymorphic species, or would ultimately become fixed, owing to the nature of the organism, and the nature of the conditions." (p. 58).

This description implies that individual properties are either favourable, or injurious, or neutral under a certain set of conditions. Selection of certain individual properties in the course of time will occur only when (1) conditions remain rather constant, so that properties really may be expected to show such a relationship to the conditions, and (2) the relationship itself between properties and conditions remains unchanged, in spite of being realized in different individuals (the fittest?).

Darwin describes this process more closely on p. 60/61: "It may metaphorically be said that natural selection is daily and hourly scrutinising, throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, **whenever and wherever opportunity offers**, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the lapse of ages, and then so imperfect is our view into long-past geological ages, that we see only that the forms of life are now different from what they formerly were." Or formulated differently: "Owing to this struggle, variations, however slight and from whatever cause proceeding, if they be in any degree profitable to the individuals of a species, in their infinitely complex relations to other organic beings and to their physical conditions of life, will tend to the preservation of such individuals, and will generally be inherited by the offspring. The offspring also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, in order to mark its relation to man's power of selection. But the expression often used by Mr. Herbert Spencer of the Survival of the Fittest is more accurate, and is sometimes equally convenient." (p. 45).

3. DARWIN'S DOUBTS

Darwin was well aware of some problems possibly evoked by his description of natural selection as the survival of the fittest. First, there were difficulties with the term 'selection': "Others have objected that the term selection implies conscious choice in the animals which become modified; and it has even been urged that, as plants have no volition, natural selection is not applicable to them! In the literal sense of the word, no doubt natural selection is a false term; but who ever objected to chemists speaking of the elective affinities of the various elements? -and yet an acid cannot strictly be said to elect the base with which it in preference combines. It has been said that I speak of natural selection as an active power of Deity; but who objects to an author speaking of the attraction of gravity as ruling the movements of the planets? Every one knows what is meant and is implied by such metaphorical expressions; and they are almost necessary for brevity." (p. 58).

Darwin realized very well that 'survival of the fittest' should not be taken too literally: "For instance a vast number of eggs or seeds are annually devoured, and these could be modified through natural selection only if they varied in some manner which protected them from their enemies. Yet many of these eggs or seeds would perhaps, if not destroyed, have yielded individuals better adapted to their conditions of life than any of those which happened to survive. So again a vast number of mature animals and plants, whether or not they be the best adapted to their conditions, must be annually destroyed by accidental causes, which would not be in the least degree mitigated by certain changes of structure or constitution which would in other ways be beneficial to the species." (p. 63).

Although with the last quotation Darwin comes close to a much better description of 'natural selection' than 'survival of the fittest', he continues: "But let the destruction of the adults be ever so heavy, if the number which can exist in any district be not wholly kept down by such causes -or again let the destruction of eggs or seeds be so great that only a hundredth or a thousandth part are developed,- yet of those which do survive, the best adapted individuals, supposing that there is any variability in a favourable direction, will tend to propagate their kind in larger numbers than the less well adapted." (p. 63).

When in each generation so many eggs, seeds, young or adults, which potentially are best adapted, are destroyed by accidental causes, will the survivors then be the 'fittest', or simply the 'lucky ones' independent of their properties? Usually environmental conditions change from moment to moment and also between sites.

Therefore, natural selection can neither be a uniform process in time nor in space. Apparently, Darwin, not being an ecologist, was not aware of this aspect of natural selection in the short term.

4. UNCONSCIOUS SELECTION BY MAN AS A MODEL

As Darwin was unaware of the genetic laws of heredity and of the various ways properties can be genetically connected (e.g. pleiotropy) he could not be aware of the full consequences of the restricting remarks he made at page 63. Moreover, Darwin came to his ideas about natural selection, because of the results of artificial selection by man (his Chapters I and II). He especially considered 'unconscious selection' by man well comparable with 'natural selection': "If there exist savages so barbarous as never to think of the inherited character of the offspring of their domestic animals, yet any one animal particularly useful to them, for any special purpose, would be carefully preserved during famines and other accidents, to which savages are so liable, and such choice animals would thus generally leave more offspring than the inferior ones; so that in this case there would be a kind of unconscious selection going on. We see the value set on animals even by the barbarians of Tierra del Fuega, by their killing and devouring their old women, in times of dearth, as of less value than their dogs" (p. 25). And: "As man can produce a great result with his domestic animals and plants by adding up in any given direction individual differences, so could natural selection, but far more easily from having incomparably longer time for action" (p. 59), or: "As man can produce, and certainly has produced, a great result by his methodical and unconscious means of selection, what may not natural selection effect?" (p.60). Again, Darwin did not realize that usually 'natural selection' will not be a directional process, because the driving forces of selection change from moment to moment and from place to place. Moreover, under natural conditions selection will only exceptionally work in the same direction during many generations. Therefore, comparison with selection by man, whether conscious or unconscious, is inadequate.

5. STRUGGLE FOR EXISTENCE

Darwin was also convinced that natural selection must be connected with 'struggle for existence': "A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometric increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manyfold force to the whole animal and vegetable kingdom; for in this case there can be no artificial increase of food, and no prudential restraint of marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them" (p. 46/47). The connection with natural selection is clear: "Natural selection acts solely through the preservation of variation in some way advantageous, which consequently endure. Owing to the high geometrical rate of increase of all organic beings, each area is already fully stocked with inhabitants; and it follows from this, that as the favoured forms increase in number, so, generally will the less favoured decrease and become rare." (p. 79).

Darwin's conviction (mentioned above) gives direction to natural selection. In fact, he formulates here what is called 'competitive selection' by Nicholson (1960). Den Boer and Reddingius (1996; Section 3.1) explain why natural selection will rarely be 'competitive selection'. Arguments from carabid beetles are discussed later in this paper. See further Den Boer (1980), Jermy (1984) and Walter (1988). Until the present day most ecologists are still convinced that competition is one of the most powerful forces in nature and almost all natural processes studied are thought somehow to be connected, directly or indirectly, with competition. But is it true that an important part of the 'innate rate of natural increase' is actually realized, so that every individual in a population has to compete, i.e. has to struggle for existence? Should not in many generations the majority of the 1000 eggs, that 10 female moths (say) have laid, die, either as eggs or as young larvae without competing, so that in many generations the number of adult moths do not increase but rather decrease? Den Boer and Reddingius (1996; Section 2.3) and Den Boer (1998) explain why there will only exceptionally be a direct connection between egg production and size of progeny.

6. COMPETITION AND NATURAL SELECTION

In my opinion, these and Darwin's related ideas, which still fit surprisingly well in the general way of thinking of present-day ecologists and evolutionists, have prevented us from looking more critically at Darwin's descriptions of 'natural selection'. It must be said however, that Darwin's ideas are very logical and form a solid causal structure for the development of modern biology. We cannot blame Darwin for not having considered the ecological aspects and consequences of the process of natural selection, for ecology as a biological discipline had still to be born. Darwin was mainly interested in an explanation of the relationships between properties of organic beings and conditions in the environment and considered the effects of these relations in the first place at a geological time scale. Much as we admire the efficient brainwork of this brilliant naturalist, it is to be regretted that population ecologists did not try to develop better defined ideas about natural selection, instead of becoming firmly fixed in paradigms that directly match Darwin's ideas.

Most ecologists still endorse Darwin's words where he said: "But the struggle will almost invariably be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers." (p. 54).

As far as there is a severe struggle, i.e. severe competition, Darwin is right, of course, but will there always be so much struggle in an animal population? And, if there is competition, will it not be highly variable, i.e. vary from very weak (or non-existing) to strong interactions between individuals with equally variable effects? In fact, the more deterministic view of Darwin led to competition being considered the driving force of both regulation of animal numbers and natural selection (Nicholson 1933, 1960) and of many other ecological processes. Also the connected 'exclusion principle' (Gause 1934) was already formulated by Darwin: "As the species of the same genus usually have, but no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera." (p. 55).

7. OBJECTIONS AGAINST THE DOMINANT ROLE OF COMPETITION

About a century after Darwin published his ideas, the dominant role of competition in ecological and evolutionary processes was questioned by Andrewartha and Birch (1954), presently followed by a number of other ecologists, e.g. Cole (1960), Connell (1971, 1980), Ayala (1979), Jermy (1976, 1984, 1985), White (1978, 1993), Den Boer (1980, 1985, 1986), Chilarov (1984), Andrewartha and Birch (1984), Walter (1988).

Many ecologists are convinced that competition is unavoidable under field conditions, because the amount of energy is limited, thus forcing the individuals to use it 'optimally'. Therefore, it is generally considered useful to calculate the 'costs' of vital processes such as reproduction. It is supposed that energy often is so limited that 'trade-offs', e.g. between reproduction and survival, occur quite often. The incorrectness, or at least incompleteness, of these views is easily shown by counter-examples. For instance, the origin, development and evolution of warm-blooded animals would have been highly improbable, because thermoregulation asks for great amounts of extra energy. And are warm-blooded animals less successful reproducers and survivors than cold-blooded ones? And how should one interpret the enormous 'wastage of energy' by warm-blooded animals, in particular birds, migrating over great distances? Aukema (1991) found that in wing-dimorphic carabid species females spending extra energy in the development of wings and functional wing muscles also produced the highest numbers of eggs. Van Dijk (1979b, 1986, 1994) showed that female carabid beetles producing the highest numbers of eggs also survived best to the next reproduction season, i.e. no 'trade-off' between reproduction and survival, on the contrary! More examples are readily available (see e.g. White 1978, 1993), so that it may be doubted whether competition often plays the supposed dominant role in natural selection, even apart from the legitimate question how often competition actually leads to 'survival of the fittest'. Apart from the above counterexamples, which bear upon general phenomena, the highly variable effects of competition between the individuals of a population does not give much possibility to result in evident population effects very often.

Questioning the dominant role of competition may have consequences for our ideas about the process of natural selection. Together with results of genetic investigations, which were unknown to Darwin, this gives cause to consider the process of natural selection afresh.

8. NATURAL SELECTION RECONSIDERED

In sophisticated experiments Nicholson (1960) tried to show the existence of the 'competitive selection' that is suggested by Darwin's formulations of 'natural selection'. But the experiments of Nicholson were done under constant conditions in closed containers with a permanent shortage of food, so that severe competition was artificially created. In the field however, for most animals the conditions of life vary from place to place and from moment to moment to such an extent that in many cases there is no unidirectional relationship between certain favourable properties and the chance to survive and reproduce. As was already realized by Darwin (p. 63, cited earlier), individuals with highly favourable properties, on average have the same chance to be devoured by a predator as less favoured individuals, unless the favourable properties are somehow connected with a higher chance to escape. Something similar can be said, of course, about the chance to be parasitized or being infected by some pathogen, about the chance of finding or reaching the right kind of food at the right moment, and so on. Favourable properties are only favourable in a special context, i.e. in certain situations and under certain conditions; usually these right conditions do not last for the entire reproductive life of the animal, by which it can always die before having propagated its genes. It is all a question of chances, a 'gambling for existence' (Reddingius 1971), a play of good luck and bad luck at any moment in the life of each organic being. Darwin (p. 60/61, cited earlier) said it very distinctly: "...natural selection is daily and hourly scrutinising, throughout the world, the slightest variations; rejecting those that are bad ....". I want to add: the grounds on which natural selection is scrutinizing variations from moment to moment and from place to place, are the variable conditions, both physico-chemical and biological, to which every individual is exposed at each moment; some individuals will not be able to survive one of these conditions, though they might have been able to survive many others; they were unlucky. This is not 'survival of the fittest', but elimination (non-survival) of the inadequate (non-fit) individuals or elimination by chance (of the unlucky individuals) under special sets of conditions.

9. THE NON-SURVIVAL OF THE NON-FIT

It may be objected: in spite of the relationship between properties and environmental conditions not being as simple and deterministic as often supposed, on average and in the long run favourable properties must have a better chance to dominate the gene pool of a population than less favourable ones. Hence, Darwin was right!

I agree with this, for I am not objecting to natural selection as the driving force of speciation and evolution, but to natural selection being interpreted as an ongoing competitive process of 'survival of the fittest'. If it would be 'survival of the fittest', it would usually be a negative force decreasing genetic diversity. Thus, in spite of all the known kinds of mutation creating new genetic diversity, contradicting the need of a permanently high level of genetic diversity as a base for an effective natural selection. However, because the direction of natural selection changes with changes in environmental conditions, the direct effect of natural selection will usually be 'non-survival (elimination) of the non-fit' and/or unlucky individuals. Survivors may have many different properties, depending on the conditions they have to pass through during their reproductive life. Therefore, even properties that at first sight are unfavourable can be retained in populations for thousands of generations, though in the course of time favourable properties have a better chance to increase in populations than unfavourable ones. At first sight, this characterization of natural selection does not seem to fundamentally deviate from the picture given by modern neo-Darwinism, e.g. by authors like Endler (1986) and Williams (1992). I only want to emphasize the significant influence of environmental variation in space and time, which may cause the effects of natural selection to deviate significantly from the results of tests conducted in experimental situations and mathematical models, at least in the short run.

For ecologists, who usually study population processes for a few generations only, natural selection is non-survival of the non-fit. Only under stationary conditions surviving individuals on average can be expected to be 'fit' for some past conditions, so that after many generations such individuals may approach 'the fittest' more and more. But how often will conditions be stationary for periods of time long enough for significant evolutionary processes to occur? Hence, the effects of the processes studied by ecologists, may fundamentally deviate from those predicted by evolutionary biologists.

10. AN EXAMPLE: EGG PRODUCTION IN CARABID BEETLES

But even in the long run the effects of natural selection in the wild can be unexpected. For instance, beetles producing many eggs are expected to have a better chance of contributing to the genetic properties of future generations than beetles under the same conditions only producing a few eggs of the same size and quality. And in the course of time good reproducers would be expected to increase and bad reproducers to decrease. Therefore, after many generations the range of numbers of eggs laid per female should be narrowed towards the higher ones, and at present, after thousands of generations, the variance is expected to be small.

In Van Dijk's (1979a: Table 5) paper (see also: Den Boer and Van Dijk, 1996: Table 1) we see the result of natural selection: even among the 20 young female beetles (out of 30 that had not reproduced before) surviving two winters and reproducing during three seasons (the fittest) the total number of eggs produced varied between 74 and 674, i.e. egg production per female is extremely variable. Nelemans (1987) found a similar range of egg production (79-891) under constant laboratory conditions in the carabid *Nebria brevicollis*. Can this be the result of 'survival of the fittest' after many generations of natural selection?

These papers of Van Dijk (1979a, b) also show that in the field egg production varies at least as much as under constant laboratory conditions and is greatly affected by temperature and by the quantity and quality of the food, (see Van Dijk 1986). In the field each female during three months produces eggs continuously, so that each female will have its own history of confrontations with environmental conditions, possibly including some interaction with congeners. As carabid beetles rarely are successful hunters many females will not lay the number of eggs they could under optimal conditions according to their genotype and level of metabolism, so that a potentially high egg production may be masked and will not always be favoured by natural selection. In fact, the wide range of individual egg production in Van Dijk's experiment (mentioned above) demonstrates that under field conditions a potentially high egg production will not always increase the chance of belonging to the 'fittest'.

These findings do not fit into the expectations of the recent 'life-history theory' (Stearns 1992; Roff 1992), where 'brood size', 'size of the young', 'time of first reproduction', 'trade-offs between survival and reproduction', and 'semelparity' versus 'iteroparity', are considered to dominate life histories. For deviating life-history patterns see Den Boer and Van Dijk (1996).

It is possible, that the property of producing only a few eggs is connected with some favourable feature. For instance a low level of metabolism (Van Dijk, pers. comm.), by which they better survive periods of food scarcity. However, will carabid beetles, being poikilothermic and highly polyphagous, often be confronted with food scarcity? Sometimes it seems to occur and then the females become 'spent', i.e. they stop egg production (Van Dijk 1972, 1973). But in most cases becoming 'spent' seems to be the result of a decreasing temperature.

It is the more surprising that females producing a low number of eggs, were not selected away a long time ago already, because the eggs of such females suffer a higher mortality than those of well reproducing females (Van Dijk 1982). Van Dijk (1979b, 1994) also showed that poor reproducers do not spread the production of their eggs over years any better than the good reproducers do.

Evidently, bad reproducers are also bad females in other respects. It is only the high variability of conditions of life in the field (both in time and in space) that makes it comprehensible that such females are still present in the population. Each year some of these females are apparently lucky enough to survive and reproduce, and to contribute to the genepool. In other words, there is no optimization of reproduction, as authors such as Pulliam (1974), Charnov (1976), Oaten (1977), and many others, suppose. But see also Gould and Lewontin (1979), Pierce and Ollason (1987), Den Boer and Reddingius (1996: 3.2.8, 3.3.2).

11. GAMBLING FOR EXISTENCE

The above story of the egg production of carabid beetles is not unique. The only selective process continuously operating in populations is the elimination of individuals either being unable to cope with the prevailing conditions, 'non-fit', or were unlucky enough to meet with a lethal moment. An individual that is 'fit' under one set of conditions may be 'unfit' under other sets. Therefore, 'fitness' is not a property of an individual, but the result of meetings of an individual with certain conditions.

It may be objected that this is merely a play upon words, because a long period of 'non-survival of the non-fit' will inevitably lead to 'survival of the fittest', i.e. when all 'non-fit' are eliminated. I do not agree, because in a heterogeneous and unpredictably changing environment at each site natural selection will change direction in time, i.e. the causes of death usually will be very diverse. The survivors are the fittest in a special context of space and time, which is different again for each separate survivor. This is a kind of 'survival of the fittest' that differs remarkably from the process described by Darwin.

In each generation 'non-survival' is only weakly connected with genetic properties, so that all kinds of properties that at any time do not render the individual inadequate in its environment may be retained in the population for a long time. These genes will be taken up in many different genomes and may contribute to genotypes that are more successful under variable and changeable local conditions. This complicated route, along which both a high level of genetic diversity and a certain degree of adaptation to local conditions is obtained, gives ample opportunity to 'try out' all kinds of gene combinations in all kinds of combinations of environmental conditions. In my opinion, individuals end up 'gambling for existence'. This is the most important aspect of natural selection, because it has the significant consequence of 'preparing' the population for future conditions.

12. SELECTION OF PHENOTYPES

A complicating aspect of natural selection is that not separate genes are selected, but entire individuals, phenotypes, the target gene is selected along with a complex of other genes. In the words of Mayr (1963: 295): "The phenotype is the product of the harmonious interaction of all genes. The genotype is a physiological 'team' in which a gene can make a maximum contribution to fitness by elaborating its chemical 'gene product' in the needed quantity and at the time it is needed in development". Because the individual, the phenotype, is the result of a complicated interaction of gene products, natural selection can only indirectly affect gene frequencies, by which natural selection does not necessarily increase the frequency of individuals with favourable properties. Formulated in the words of Williams (1966: 56): "The relationship of genotypes to phenotypes is that different genotypes can produce different phenotypes in the same environment. The genotype is a coded message that is interpreted in some way by the soma. A gene is one of a multitude of meiotically dissociable units that make up the genotype message. No constant phenotypic effect need be associated with a particular gene. The substitution of one allele for another may have one effect in one genotype and an entirely different effect in another, and only the entire message can be said to have a meaning". This relationship between genotype and phenotype is further complicated by crossing-over, inversions, duplications, mutations, pleiotropic effects, and other genetic and physiological processes.

Moreover, the expression of the genotype into the phenotype shows a great plasticity, by which many different genotypes may be hidden under the same phenotype and natural selection hardly has a point of action. Especially genes driving development of the individual are well protected against selection. In the words of Waddington (1960: 393): "It is sometimes useful to discuss development in terms of a diagram in which the course of normal development is represented as the bottom of a valley, the sides of which symbolise the opposition that the system presents to any stresses which attempt to deflect development from the normal course. ..... The surface which in this way symbolises the developmental potentialities of the genotype has been called the 'epigenetic landscape'." See further, for instance, Endler (1986) and Williams (1992).

It might be asked now: when exactly will a certain genotype be 'naturally selected'? At which stage of the life cycle of the resulting phenotype is it 'determined' whether or not its survival and reproduction may contribute to an increase of the relative frequency of certain genes? As the individual will pass through a number of selective events, in each of which it has a chance either to survive or to die such a moment can never be indicated. Often we might be more sure about the phenotypes and their associated genotypes, which do not survive and reproduce and therefore do not contribute to the frequency distribution of genes and genotypes of following generations, i.e. the non-fit.

We should not forget that each individual is a compromise of the effects of many genetic processes, for genes do not operate separately; they have to effectuate their processes in the midst of many other processes running in the body. Nevertheless, the result should be a living individual. To reach that there should be a strict hierarchy in the developmental processes, so that not each gene will have the opportunity to express itself in some recognizable feature.

13. NATURAL SELECTION UNDER FIELD CONDITIONS

It will be evident now that the link between genes for favourable properties and the propagation of these combinations of genes is not a strong one. Most natural environments are so heterogeneous, that the individuals of a population are not distributed homogeneously, but are more or less clustered in groups living in slightly different environments. Such groups ('interaction groups': Den Boer, 1977; neighborhoods': Wright, 1969; or 'local populations': Andrewartha and Birch, 1954), will contain frequencies of phenotypes -and thus genotypes- that differ from those in other such groups. Each group will inevitably pass through a number of selective events. The individuals not selected away by such an event, only survive to meet with another selective event when they are scrutinized again by natural selection. After a number of such events the frequency distribution of phenotypes (and genotypes) in each group will be different and rather unpredictable, and will be further complicated by exchange of individuals between groups. The frequency distribution of genes in the progeny will depend on the frequencies of different kinds of selective events operating during many generations at different sites in the population area. In each selective event the frequency distribution of genotypes will shift in the direction of those individuals that could -for whatever reason- tolerate this event. The survivors and/or their offspring will copulate among each other, and their genes will thus be taken up in a number of different genomes. These genomes are 'tested' again, so to speak, in other selective events, and so on. At each site natural selection thus results in a continuous shifting of gene frequencies and a continuous recombining of genomes. Therefore, at any moment and at any site natural selection as an ecological process is moulding the frequencies of genes and thereby allowing ‘new genomes’ to be put together.

14. SPREADING THE RISK OF EXTINCTION

Critics may object: "Is this anything more than a complicated and difficult description of 'survival of the fittest'?" Yes, it is more, for the resulting genepool will not enable its members 'optimal' survival and reproduction, because they are not 'fit' for all future aspects. The genepool can never be more than an approximated compromise between the mean frequencies of genes and the resulting mean survival values from various sets of environmental conditions in the past. No genome will ever contain the right genes and gene combinations to survive all future selective events, simply because there cannot be unfailing anticipation of future selective events.

Moreover, the presence of certain gene combinations in genomes excludes other gene combinations; only a restricted number of gene combinations can be tolerated in a genome and thus be realized. This means that, if 'optimization' is thought to be an important issue, it should be expressed in terms of tolerable gene combinations, and not in terms of most favourable combinations of properties.

As each genome is the result of a long history of selective events the present gene combinations have proven to be sufficiently tolerable for survival until now, though many other gene combinations can no longer be realized. Therefore, many life histories are far from 'optimal', because in the past special life-history traits have been fixed by natural selection. An example is the seemingly unfavourable life history of the carabid *Nebria brevicollis*. Instead of reproducing in spring or early summer the young adults emerge in May and aestivate, which on average results in 40% extra mortality and reproduce in late autumn. This forces the larvae to grow up in winter, the most unfavourable season concerning temperature and food. This life history has developed in Arctic and Alpine regions where most *Nebria*- species occur and where the short season forces young adults to hibernate before reproduction. Nevertheless, *N.*

brevicollis thrives well in the temperate regions, thus illustrating that also non-optimal life histories can be sufficient to survive and reproduce. See also Den Boer and Van Dijk (1996). Hence, the result of natural selection is not 'survival of the fittest'.

The longer selective processes are allowed to operate, i.e. the longer the population survives, the more the frequency distribution of genomes will match the frequency distribution of selective events that most frequently occurred in the past and have a high probability of occurring in the future. In other words, the statistical outcome of natural selection, operating over many generations in a heterogeneous environment will not be 'survival of the fittest', but will have the consequence of **spreading the risk of extinction over genotypes** (Den Boer 1968).

The latter metaphor means that in the long run the frequency distribution of genotypes in certain respects acquires some correspondence to the frequency distribution of selective events. Special conditions are absorbed, so to speak, by special sets of genotypes, and other conditions by other genotypes. This is spreading of risk over genotypes, an example of which is given by Den Boer *et al.* (1993). Genes that are only favourable under rarely occurring conditions can thus be kept in the population and increase again if and when these conditions occur anew.

This gradual increase of the frequencies of favourable genes will occur most evidently when conditions change in the same direction over large areas and for a long time. The survival value of a long history of risk spreading will particularly appear when, for instance, climate is gradually changing. Because of the great genetic diversity that has been preserved there is a positive chance that genomes are present that anticipate these changes. A recent example is the development of resistance of pathogenes against certain medications. Such processes of 'directed selection' come close to 'survival of the fittest' in the Darwinian sense. But under natural conditions such strongly and continuously directed selection processes will be the exception rather than the rule and selection processes improving spreading of risk ultimately are more important for the survival of species.

In my opinion only the above description of natural selection can make comprehensible that organic beings often show morphological structures, physiological processes, kinds of behaviour and other life-history traits, which are so surprising in their originality, refinement and sophistication that we can hardly imagine how such combinations of features could ever develop. If natural selection can be understood as 'the non-survival of the non-fit', in fact it is not usually a negative process, but a process that preserves genes as long as these do not render their carriers 'non-fit' under all sets of conditions that might occur with a not too low probability. The resulting permanently high genetic diversity allows the creation of less probable gene combinations that sometimes may open entirely new routes of the development of properties.

For many evolutionary biologists it seems difficult to imagine that certain adaptations should have resulted from the accumulation of small selective steps, because most intermediate stages of development cannot have been favourable and should have been selected away or at least not favoured by natural selection. Such an accumulation of small selection steps, each of which need not be favourable, becomes comprehensible if we realize that natural selection is the non-survival of the non-fit: as long as these small selection steps do not render its carriers unfit under the current conditions the results can be kept and accumulated in the genepool.

Hence, in fact natural selection is a conservative process, which gives time for all kinds of combinations of properties to be tried out under all kinds of different conditions. As spreading the risk is always possible, in the long run, life is able to penetrate all kinds of environments and to find 'solutions' for even the most impossible problems, only by making use of time in the most efficient way: only throwing away that which can no longer be used.

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