

Perspective

The objects of selection

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One of the most basic questions of evolutionary biology is what objects are being selected in the process of natural selection? Lloyd (1) found nearly 200 references to books and papers by biologists and philosophers, beginning with Darwin, that treated this question, “and these represent just a fraction of the literature on the topic,” she reports. Indeed in the recent literature the answer to this question has been argued each year by at least a half dozen authors. [This analysis is not a review paper. The listing of the literature is therefore reduced to a minimum. All relevant titles can be found in the works of Lloyd (1) and Brandon (2).] An analysis of this literature has convinced me that some basic conceptual differences, as well as the opponents’ failure to adhere to a rigorous definition of the terms, are the major causes of the confusion. Evidently a new approach that attempts a careful critique of the arguments of the opposing parties is needed. This is what I am attempting here.

The difficulty begins with the exact description of the process of selection. After Darwin had discovered his new principle, he searched for an appropriate terminology and thought he had found it in selection, the term animal breeders used for the choice of their breeding stock (3). However, as first Herbert Spencer and then Alfred Russel Wallace pointed out to him, there is no agent in nature which, like the breeders, “selects the best.” The beneficiaries of selection are the individuals that are left over after all the less fit individuals have been eliminated. Natural selection thus is a process of “nonrandom elimination.” Spencer’s statement, “survival of the fittest,” was quite legitimate, provided the term fittest is properly defined.

There is, however, also a second kind of selection, which Darwin appreciated far better than any of his contemporaries and which he called sexual selection. He indicated how important he considered this process by devoting to it two-thirds of *The Descent of Man* (4). For Darwin sexual selection consisted of the preference of females (female choice) for particular males as well as in polygamous species the battles of males for the greatest possible harem. Since Darwin’s days it has become clear that this kind of selection includes a far wider realm of phenomena, and instead of sexual selection it is better referred to as “selection for reproductive success.” It includes such phenomena as parent–offspring conflict, sib-rivalry, unequal parental investment, unequal rates of division of prokaryotes, and many of the phenomena studied by sociobiology. In all these cases, genuine selection, not elimination, is involved, unlike survival selection. Considering how many new kinds of selection for reproductive success are discovered year after year, I am beginning to wonder whether it is not even more important than survival selection, at least in certain higher organisms.

One additional basic aspect of selection must be mentioned here because it is important for the adoption of an unequivocal

terminology. Darwinian selection, as it is now fully understood by the evolutionists, is a two-step process. The first step is the production of a vast amount of variation that will serve as the material needed for the second step, the actual process of selection or elimination.

History of the Controversy

For Darwin and most evolutionists since 1859 the individual organism was the object of selection. The individual is the entity which survives or not, which reproduces or not, and which reproduces successfully or not. Darwin (4) additionally recognized the social group, particularly with reference to man, as a potential object of selection (see below). In 1962 Wynne-Edwards (5) insisted that certain aspects of behavior, like population movements (dispersion), could be explained only by accepting groups as objects of selection. This proposal of group selection was at once heavily criticized by Lack (6) and Williams (7). Both authors showed that the observations, used by Wynne-Edwards for his interpretation, concern individual organisms and had to be explained by individual selection. The groups involved were not the kinds of cohesive entities that owe their enhanced survival potential to the kind of interactions characteristic of tightly knit social groups. However, I have not carefully analyzed Wynne-Edwards numerous examples to determine whether or not some of them might actually be genuine social groups. The vast majority of them, particularly those relating to dispersion, are clearly not. Lack adopted traditional Darwinian individual selection, but Williams proposed instead to adopt the gene as the target of selection.

Selection of?

Perhaps the two most important questions one can ask about selection are the questions “selection of?” and “selection for?” as Sober (8) perceptively pointed out. The question “selection of?” means what is the particular entity that is selected, in other words, what entity has a superior survival probability or a superior probability to reproduce and to reproduce successfully? I will discuss the possible answers to these questions in the next section. I will attempt to answer the question “selection for?” in another section.

Levels of Selection

Even though most evolutionists agree that the individual organism is the principal object of selection, there is great dissension about also accepting as the object of selection the lower or higher levels in the hierarchies of the living world.

The Gene. The proposal by Williams (7) to adopt the gene as the object of selection not only conformed to the prevailing reductionist spirit of the time but also fitted into the thinking of many geneticists who in the mathematical analyses of population genetics had adopted the gene as the principal entity of evolutionary change. Williams’s proposal was strongly endorsed by Dawkins (9). This idea of the gene as the target

of selection was at first widely accepted, for instance by Lewontin (10). But eventually it was severely criticized (11, 12), and even its original supporters have now moderated their claims. The critics pointed out that “naked genes,” “not being independent objects” (9), are not “visible” to selection and therefore can never serve as the target. Furthermore, the same gene, for instance the human sickle cell gene, may be beneficial in heterozygous condition (in *Plasmodium falciparum* areas) but deleterious and often lethal in the homozygous state. Many genes have different fitness values when placed into different genotypes. Genic selectionism is also invalidated by the pleiotropy of many genes and the interaction of genes controlling polygenic components of the phenotype. On one occasion Dawkins (ref. 13, point 7) himself admits that the gene is not an object of selection: “. . . genetic replicators are selected not directly, but by proxy . . . [by] their phenotypic effects.” Precisely! Nor are combinations of genes, as for instance chromosomes, independent objects of selection; only their carriers are.

The Gamete. Since only a fraction of all eggs are fertilized and only an infinitesimal fraction of male gametes succeed in fertilizing an egg, gametes are obviously a category of entities subjected to intense selection. It is curious that this is virtually never mentioned in the literature dealing with selection, perhaps because we know so little about fitness differences among gametes. For instance, the success in terrestrial vertebrates of a spermatozoon in fertilizing an egg is presumably quite unrelated to the properties of its haploid genome that makes successful adults. Evidently, the ability to swim rapidly, to be able to sense unfertilized eggs, and to be able to penetrate the egg membrane are the properties of the spermatozoon that are most helpful in achieving success. However, these phenotypic properties of the spermatozoa are presumably produced by the paternal testis and are probably part of the extended phenotype of the male parent. They have nothing to do with the haploid genome of the gametes, which, so far as we can tell, has no influence whatsoever on the fertilizing capacity of these gametes. Chance is presumably the most overwhelmingly important factor at this level. But in other organisms gametes (e.g., plant pollen grains and free swimming gametes in aquatic organisms) seem to have gamete-specific properties influencing mating success. They may be genuine selectons.

The Individual Organism. From Darwin to the present day most evolutionists (1) have considered the individual organism to be the principal object of selection. Actually, it is the phenotype which is the part of the individual that is “visible” to selection (14). Every genotype, interacting with the environment, produces a range of phenotypes, called by Woltreck (15) the “norm of reaction.” Therefore, when an evolutionist says that the “genome is a program that directs development,” it would be wrong to think of it in a deterministic way. The development of the phenotype involves many stochastic processes which preclude a one-to-one relation between genotype and phenotype. This is, of course, precisely the reason why we must accept the phenotype as the object of selection rather than the genotype.

Different phenotypic expressions of the same genotype may differ considerably in their fitness value. What is visible to selection is the phenotype which “screens off” the underlying genotype (2). The term phenotype refers not only to structural characteristics but also to behavioral ones and to the products of such behavior such as bird nests and spider webs. Dawkins (13) refers to these as the extended phenotype. However, such species-specific behaviors are programmed in the neural system of these individuals and thus do not differ in principle from the morphological aspects of the phenotype.

In this account, when I refer to the term individual, I always mean what the word individual means in the daily language, that is, the individual organism. Philosophers have also applied

the term to “particulars,” like the species. I have avoided this designation because it is apt to create confusion.

Group Selection. There has been a long and bitter controversy as to whether groups as cohesive wholes can serve as targets of selection. The answer is “it depends.” There are different kinds of assemblages of individuals (“groups”), some of which do and others which do not qualify as targets of selection. At one time I classified groups on the basis of size and geographical relationship (16), but this did not turn out to be a productive approach. However, there is another approach which usually produces clear-cut results. It is obvious that a group, the selective value of which is simply the arithmetic mean of the fitness values of the composing individuals (when in isolation), is not a target of selection. If such a group is particularly successful, it is due to the superior fitness of the composing individuals. This idea has often been included in theories of group selection. However, this false or soft group selection is not group selection at all. In contrast, if, owing to the interaction of the composing individuals or owing to a division of labor and other social actions, the fitness of the group is higher or lower than the arithmetic mean of the fitness values of the composing individuals, then the group as a whole can serve as an object of selection. I call this hard group selection. Interestingly, this was already appreciated by Darwin in a discussion of groups of primitive humans (4). Such hard group selection, a prerequisite for the explanation of human ethics, is still controversial.

It is sometimes difficult to decide whether the success of a particular group is due to soft or hard group selection. However, when a group of ground squirrels is particularly successful, because it has an efficient system of sentinels warning the group of approaching predators, it is clearly hard group selection. This is also the case when a pride of lionesses splits up to block the escape route of an intended victim. The success of surprise attacks by chimpanzees on members of neighboring troupes depends on the well organized strategy of the attackers. In all such cases the successful group acts as a unit and is as a whole the entity favored by selection.

Selection at Higher Levels. There has been much argument about whether there is, or is not, such a phenomenon as species selection. In the early post-Darwinian period when thinking about selection was rather confused, it was often said that such and such a character had evolved because it was “good for the species.” This is quite misleading. The selected character had originated because it benefited certain individuals of a species and had gradually spread to all others. The species as an entity does not answer to selection.

There is, of course, no question that one species can cause the extinction of another species. The introduction of the Nile perch into Lake Victoria in Africa has resulted in the extinction of several hundred endemic species of cichlid fishes. The parasitic cowbird almost exterminated the Kirtland’s warbler in northern Michigan until drastic cowbird eradication procedures in the breeding range of Kirtland’s warbler were adopted. Darwin (3) described in 1859 the extermination of many native New Zealand species of animals and plants by the introduction of competing species from England. The competitors were by no means always close relatives. In spite of all these examples I hesitate to use the term species selection and prefer to call such events species turnover or species replacement because the actual selection takes place at the level of competing individuals of the two species. It is individual selection discriminating against the individuals of the losing species that causes the extinction.

Some authors have also attempted to recognize even higher levels such as family selection or clade selection, but in no case are these entities as such the object of selection. Selection in these cases always takes place at the level of individuals.

Terms for the Object of Selection

A number of terms have been suggested for the entity favored by selection, but all of them, as I will show, are equivocal or saddled with the misleading meaning of their former everyday usage.

Unit of Selection. This term was introduced by Lewontin (10) to designate the object of selection. In science as well as in daily life the term unit usually means some measurable entity. We have units of length, weight, and time, and we have electrical units like volt, watt, ohm, etc. Clearly, unit of selection does not refer to this kind of unit. Occasionally, we also use the word unit for concrete entities, for example, "The president sent several units of marines to the area of the disturbances." The term unit of selection was adopted by many authors, but many others found it so unsuitable that they introduced new terms. Owing to its ambiguity, the term unit has been used less and less frequently in recent years.

Replicator. Dawkins, the author of this term, states, "We may define a replicator as any entity in the universe which interacts with its world, including other replicators in such a way that copies of itself are made" (17). He also states that "a DNA molecule is the obvious replicator." In other words, replicator selection is essentially a new word for gene selection. One of the advantages of his term, says Dawkins, is that it automatically preadapts our language to deal "with non-DNA forms of evolution such as may be encountered on other planets." This strikes me as a rather curious excuse for introducing a new term into science. With the phenotype of the individual rather than the gene being the target of selection, the term replicator becomes irrelevant.

The term is, of course, in complete conflict with the basic Darwinian thought. What is important in selection is the abundant production of new phenotypes to permit the species to keep up with possible changes in the environment. This is made possible by meiosis and sexual reproduction. The replication of DNA has nothing to do with this. To be sure, Mendel's discovery of the constancy of genes, confirmed by all the subsequent work in genetics and molecular biology, is a very efficient way to achieve rapid and unambiguous evolutionary change, and it refuted the inheritance of acquired characters. But such constancy is not a necessity for selection. For Darwin inheritance of acquired characters and a direct effect of the environment were compatible with natural selection. He did not demand complete constancy of the genetic material. Since the gene is not an object of selection (there are no naked genes), any emphasis on precise replication is irrelevant. Evolution is not a change in gene frequencies, as is claimed so often, but the maintenance (or improvement) of adaptedness and the origin of diversity. Changes in gene frequency are a result of such evolution, not its cause. The claim of gene selection is a typical case of reduction beyond the level where analysis is useful.

Vehicle. In due time Dawkins (17) realized that the individual reproducing organism did have a role in the selection process. But being a gene selectionist, he saw this role only as the function to serve as a transport mechanism for the genes. He therefore introduced for individuals the terms "vehicle." Doing so, he missed the decisive point that the phenotype is far more than a vehicle for the genotype. The term vehicle altogether fails to bring out the important role of the phenotype in the process of selection.

Interactor. Hull (18) realized the unsuitability of the term vehicle because he appreciated that the object of selection acts "as a cohesive whole with its environment." To stress this interaction he proposed the term interactor "as an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential." The term interactor has a number of weaknesses. One is the stress on replication while omitting any reference to the production of variation

during meiosis and reproduction. More serious is the fact that interactor is not a specific term for the object of selection. Every cell is an interactor; every organ of an organism interacts with the other organs, species interact, and so do classes of individuals such as the two sexes. Also, interacting is not conspicuous during the process of elimination that results in natural selection. In biology interaction is far more pertinent to functional than to evolutionary biology. When one hears the word interactor, one's first thought would never be natural selection. What is needed is a more specific term.

Target of Selection. For many years I used the term target of selection for the object of selection. The more I realized, however, that natural selection is an elimination process, the more I realized that the eliminated individuals were the real target of the selection process and that it was rather misleading to call the "leftovers" the target of selection.

Meme. Dawkins (19) has introduced the term "meme" for the entities subject to selection in cultural evolution. It seems to me that this word is nothing but an unnecessary synonym of the term "concept." Dawkins apparently liked the word meme owing to its similarity to the word gene. In neither his definition nor the examples illustrating what memes are does Dawkins mention anything that would distinguish memes from concepts. Concepts are not restricted to an individual or to a generation, and they may persist for long periods of time. They are able to evolve.

Selecton. Since all the previously used technical names for the object of selection are unsuitable for one reason or another, I am herewith proposing a new term, "selecton." A selecton is a discrete entity and a cohesive whole, an individual or a social group, the survival and successful reproduction of which is favored by selection owing to its possession of certain properties. The selecton is the answer to Sober's question "selection of?" (see above). This still leaves us with Sober's other question.

Selection for?

The answer to this question is obvious. Any aspect of the phenotype (or the phenotype as a whole) that favors survival or reproductive success will be favored by selection. This may be a structural improvement, a variation of a physiological process, a new or modified behavior, an improved utilization of environmental resources, any improvement of the extended phenotype, or whatever other modification of the phenotype enhances survival and reproductive success.

Since the genotype, interacting with the environment, is the cause of the phenotype, selection is automatically also for any component of the genotype contributing to the favored phenotype. Thus, selection is directly for the phenotype and indirectly for the genotype or parts of it.

The level of organization that benefits ("selection for?") from the selection might be almost any level of biological organization from the base pair to the species and perhaps even to the ecosystem, but only those benefits that explain the process of selection count, as Brandon has correctly reminded me, but not any accidental benefits.

The result of continuously ongoing selection is the adaptation of organisms. I agree with Sober, who concludes that there is no evidence "that selection is insufficient for adaptation" (ref. 8, p. 208).

Exceptions?

The biologist envies the physical scientist, whose universal laws have no exceptions. Alas, most biological regularities ("laws") do have exceptions, and when describing biological processes in terms of regularities, one must be aware of their probabilistic nature. What the biologist describes is what happens "ordinarily." Yes, there will be exceptional cases. This is also true

for natural selection. The description of this process, as presented in the literature, is based almost exclusively on the situation found in multicellular higher animals and plants. These are taken to be "typical." Yet, there are indications that selection processes may be rather different in colonial invertebrates, in any kind of uniparentally reproducing organisms, particularly plants, in protists, and in the prokaryotes. In such forms it is for instance often difficult to determine what an individual is. This problem, owing to the importance of the individual in the Darwinian process, is of considerable importance. It will require far more research on the selection process in the stated kinds of organisms to determine to what extent selection in these groups can be described in the same terms as selection in sexually reproducing multicellular eukaryotes.

It was long believed, and is still largely true, that the first step in selection, involving mutation and recombination, is largely a random process. However, a number of genetic mechanisms that result in biased variation have now been discovered, such as meiotic drive (segregation distorter) and selfish genes. A slightly biased variation can be taken care of at the second step of selection, but drastically biased variation, as in segregation distortion, may override the powers of selection.

Coda

When re-reading my analysis, I was quite surprised how rarely I had to refer to the genetic aspects responsible for the phenotype. Apparently, it does not matter very much how the genes are combined or how much the genotype has to be modified, provided the resulting phenotype is favored by selection. What counts is the adaptedness of the end product.

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