KAM KRÁČÍ MODERNÍ EVOLUČNÍ BIOLOGIE – TEORIE ZAMRZLÉ PLASTICITY A BIOLOGICKÁ PSYCHIATRIE

WHERE IS MODERN EVOLUTIONARY BIOLOGY HEADING – THE THEORY OF FROZEN PLASTICITY AND BIOLOGICAL PSYCHIATRY

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SOUHRN

Mechanizmem přirozeného výběru může docházet k evoluci adaptivních znaků pouze u nepohlavně se rozmnožujících druhů. U druhů rozmnožujících se pohlavně vzniká genotyp jedince v každé generaci náhodným namixováním genů od obou rodičů a biologická zdatnost (fitness) jedince se zde proto nedědí. Pro vysvětlení fungování adaptivní evoluce u pohlavně se rozmnožujících organizmů byla v 70. letech minulého století navržena teorie sobeckého genu. Podle ní v průběhu evoluce nesoupeří jedinci v rámci populace o co největší biologickou zdatnost, ale alely v rámci jednoho lokusu o schopnost předat co nevíce svých kopií do genofondu další generace. Tato teorie ovšem opomíjí skutečnost, že vliv jednotlivých alel na fenotyp i vliv jednotlivých fenotypových znaků na biologickou zdatnost jedince závisí na tom, jaké další alely jsou přítomny v genotypu daného jedince. Teorie evolučně stabilních strategií ukazuje, že za těchto podmínek nemohou vést selekční tlaky k dlouhodobým změnám ve fenotypu organizmů, ale pouze k vychýlení frekvencí jednotlivých alel z rovnováhy. Čím je toto vychýlení větší, tím více genofond těmto tlakům vzdoruje a po přerušení selekčního tlaku se frekvence alel samovolně vrací na původní hodnoty. Teorie zamrzlé plasticity, publikovaná v roce 1998, ukazuje, že pohlavně se rozmnožující druhy mohou evolučně odpovídat na selekční tlaky (jsou evolučně plastické) pouze v době, kdy jsou příslušníci daných druhů geneticky uniformní, tedy například po odštěpení a následném rychlém namnožení malé části populace původního druhu. Po určité době odhadované na základě paleontologických dat na 1-2% doby trvání druhu se v genofondu nahromadí genetický polymorfizmus a nové mutace se tak v každé generaci ocitnou ve společnosti jiných alel - druh se přestane chovat jako evolučně plastický a začne se chovat jako evolučně elastický. V tomto stavu pak existuje až do doby, než se v prostředí nahromadí takové změny, že evolučně zamrzlý druh vymře. Z teorie zamrzlé plasticity vyplývá řada důsledků pro nejrůznější vědní obory, včetně psychiatrie. Vzhledem k tomu, že druh může účelně evolučně odpovídat na vlivy prostředí pouze bezprostředně po svém vzniku, je naprostá většina druhů, se kterými se v přírodě setkáváme, včetně člověka, adaptována nikoli na podmínky, ve kterých momentálně žijí jejich příslušníci, ale na podmínky, které panovaly v době jejich vzniku. Teorie zamrzlé plasticity dále ukazuje, že vznik altruistického chování je mnohem pravděpodobnější, než jak naznačovaly předcházející evoluční teorie.

Klíčová slova: evoluce; speciace, dědivost, altruismus, evoluční zábrany

SUMMARY

The mechanism of natural selection can lead to the evolution of adaptive traits only amongst asexually reproducing organisms. Amongst organisms that reproduce sexually, the genotype of the individual is formed in each generation through the random mixing of the genes of the two parents and thus the biological fitness of individuals is not inherited. The theory of the selfish gene was proposed in the 1970's to explain the functioning of adaptive evolution amongst asexually reproducing organisms. According to this theory, individuals do not compete for the greatest biological fitness in the framework of the population during evolution, but rather the alleles compete in the framework of a single locus for the ability to transfer the greatest number of their copies to the gene pool of the next generation. However, this theory neglects the fact that the effect of the individual alleles on the phenotype and the effect of the individual phenotype traits on the biological fitness of individuals depend on the other alleles that are present in the genotype of the individual. The theory of evolutionarily stable strategies indicates that, under these conditions, selection pressures cannot lead to long-term changes in the phenotypes of organisms, but only to deflection of the frequency of the individual alleles from equilibrium. The greater this deflection, the more the gene pool resists this pressure and, after cessation of the selection pressure, the frequency of the alleles spontaneously returns to the original values. The theory of frozen plasticity, published in 1998, shows that sexually reproducing species can respond evolutionarily to selection pressures (they are evolutionarily plastic) only when the members of the particular species are genetically uniform, i.e. after splitting off and subsequent rapid multiplication of part of the population of the original species. Following a short period of time, estimated on the basis of paleontological data to correspond to 1-2% of the duration of the species, genetic polymorphism accumulates in the gene pool and thus, in each generation, the new mutations are in the presence of different alleles - the species ceases to behave in an evolutionarily plastic manner and begins to be evolutionarily elastic. It then exists in this state until such time as such changes accumulate in the environment that the evolutionarily frozen species becomes extinct. A number of consequences follow from the theory of frozen plasticity for various fields of science, including biological psychiatry. As a species can usefully respond evolutionarily to the effect of the environment only immediately following its formation, the vast majority of the species that we encounter in nature, including human beings, are adapted, not to the conditions in which its members momentarily live, but to the conditions that existed at the time of its formation. The theory of frozen plasticity further indicates that the formation of altruistic behaviour is far more probable than was suggested by the previous theories of evolution.

Key words: evolution, speciation, heritability, altruism, evolutionary constraints

Darwin's classical theory of evolution (Darwin, 1860) assumed that the adaptive traits of modern organisms, i.e. adaptive structures and adaptive patterns of behaviour, were formed during evolution through the action of natural selection. Individuals that bore mutations that allowed them to more effectively utilize the resources in the environment or more effectively defend themselves from natural enemies left more descendants during their lives than individuals without this mutation. These descendants inherit from them not only the advantageous mutation, but also their advantageous phenotype traits. As a consequence, the number of individuals with this mutation gradually increased in the population until it completely predominated – the mutation became fixed. As further and further advantageous mutations became fixed in the population, further and further adaptive traits appeared enabling the members of the individual species to ever better utilize the existing and new resources occurring in their environment.

Approximately until the 1960's, an increasing number of evolutionary biologists began to realize that Darwin's theory of evolution satisfactorily explained adaptive evolution amongst asexually reproducing species, but is much harder to apply to adaptive evolution amongst organisms that reproduce sexually. The biological fitness of an individual is determined by his phenotype, i.e. the sum of his properties, which depend directly or indirectly on his genotype, i.e. on the set of alleles that the given individual has in his cells. While, amongst asexually reproducing organisms, the genotype and thus also the biological fitness are inherited from the parent by the progeny, amongst sexually reproducing organisms the genotype is formed anew in each generation by random mixing of the alleles derived from both the parents. As a consequence, biological fitness is inherited to only a very limited degree, in other words, very fit parents can very easily produce a child with subnormal biological fitness. Darwinistic evolution cannot occur where there is no heritability of biological fitness. Richard Dawkins attempted to resolve this very fundamental problem in the nineteen seventies through his theory of the selfish gene, based on the models of William D. Hamilton (Dawkins, 1976;Hamilton, 1964a;Hamilton, 1964b). According to this theory, amongst sexually reproducing species, individuals in the population (carriers of various mutations) do not compete for the greatest biological fitness (i.e. the greatest number of progeny) but rather the individual alleles (gene variants) compete here in the framework of the same locus to pass the greatest number of their copies down to the gene pool of the next generation. While the genotype of the individual is not inherited, unless the rare phenomenon of mutation occurs, the structures of the alleles are inherited also in sexually reproducing species from one generation to the next in unaltered form. In many cases, the alleles compete together to determine which will increase the biological fitness of "its" individual the most. However, at other times, the alleles increase the number of their copies transferred to the next generation by "programming" their carriers to assist in the reproduction of their relative, who can bear a copy of the same alleles. In some cases, the alleles also achieve "their targets" by simultaneously reducing the biological fitness of their carrier. For example, the t-alleles of mice cause that, in heterozygote males bearing one normal and one t-allele, only the sperm bearing the t-allele are successful, while sperm with the normal allele are unfunctional (Ardlie, 1998). Thus, the male will have lower fertility and leave fewer progeny which will, however, all carry the t-allele.

Although the theory of the selfish gene is probably the most widespread and widely recognized theory amongst evolutionary biologists at the present time, it also exhibits some drawbacks that throw its general validity into doubt (Flegr, 1998). The most important aspect is that it completely ignores the dependence of the biological fitness of carriers of certain traits (certain alleles) on the frequency of the individual traits (or individual alleles) and also that, although the alleles are actually passed on from one generation to the next in unaltered form, their effect on the phenotype of the individual and thus on his biological fitness can change from generation to generation. In addition, the effect of the individual traits is dependent on the context; in the context of a single phenotype, a certain form of a trait may be advantageous, while it may be disadvantageous in the context of some other phenotype. However, under these conditions, not only can Darwinistic evolution based on the competition of individuals in the framework of the population not occur, but Dawkinistic evolution based on competition of alleles in the framework of the individual loci can also not occur. If the population is exposed to selection pressure, it responds to this pressure by a shift in the frequencies of the individual alleles. However, the more the frequencies deviate from the original equilibrium (evolutionarily stable) frequency, the less willingly they respond to the given selection pressure. The frequency of some alleles increases in the population and then, e.g. in the homozygote state or in combination with other, originally rare but now also frequent alleles, they reduce the biological fitness of their carriers. Thus, after a certain period of time, the population completely ceases to react to the given selection pressure and, when selection ceases, the frequencies of the alleles (and thus the phenotype of the individuals in the population) return to the original (evolutionarily stable) values. Consequently, sexually reproducing species act elastically, change through the effect of selection only within certain limits and the acquired changes are usually reversible (Flegr, 1998).

However, according to the theory of frozen plasticity, sexually reproducing species can undergo adaptive evolution in a certain phase of their evolution, i.e. not only Dawkinistic evolution, but also Darwinistic evolution. Species can acquire evolutionary plasticity soon after their formation, but only if they were formed by splitting off of a very small part of the population from the population of the original species, e.g. through peripatric speciation. In this case, the newly formed species loses a large part of its original genetic polymorphism and a further part of the polymorphism disappears subsequently in the small population through genetic drift. If the population again increases in the next phase of the development, ideal conditions are created for the functioning of Darwinistic evolution. As a consequence of genetic homogeneity, in each generation new mutations are present in association with identical or very similar combinations of alleles and their effect on the biological fitness of the individual is identical or similar in each case. Under these conditions, genetic fitness is inherited and Darwinistic evolution can function. However, after a certain time, new genetic variability accumulates in the population, so that the species freezes evolutionarily and again ceases to react to selection pressures or, to be more precise, begins to react like elastic.

In the nineteen sixties, the paleontologists Niles Eldredge and Stephen J. Gould began to notice the long period of evolutionary stasis in the lives of species and introduced their theory of punctuated evolution, also called the theory of punctuated equilibrium, into paleontology (Eldredge and Gould, 1972). On the basis of paleontological data, they estimated that the period of evolutionary plasticity lasts of the order of twenty thousand years, corresponding to 1-2% of the overall period of existence of a species. In their original work, they proposed several possible explanations of the punctuated character of evolution, of which one, genetic revolution in small populations, in principle approached the explanation offered by the theory of frozen plasticity. Gold subsequently rejected this explanation in his last, monumental work (Gould, 2002).

The theory of frozen plasticity has a number of consequences that are important for understanding the natural phenomena studied in various fields of science. Considering only the field of biological psychiatry here, mention can be made, e.g., of the aspect of adaptive behaviour amongst human beings and the aspect of altruistic behaviour.

Evolutionary psychologists generally conclude that inherited patterns of human behaviour are adaptive, i.e. contribute positively to increasing the biological fitness of their carriers. If a certain pattern of behaviour (e.g. homosexuality) currently seems to us to be nonadaptive, not useful, reducing the chance of survival of the individual or the reproduction of its carriers, it is usual to look for the useful function of this pattern of behaviour that we have overlooked. The second possibility that we usually consider is whether the given pattern of behaviour was adaptive in the past and became disadvantageous only recently, under the altered conditions of modern civilization. The theory of frozen plasticity offers a third possibility: the particular pattern of behaviour is disadvantageous, not because our species has not yet managed to adapt to recently altered conditions, but because it did not succeeded to adapt in the short period of time when it was evolutionarily plastic. In the subsequent, probably very long period of frozen plasticity, it could no longer adapt to the conditions, even though these conditions might have remained unchanged for hundreds of thousands of years.

The appearance and maintenance of altruistic behaviour is a mystery for evolutionary psychology and ethology. A population in which altruists are present, i.e. individuals that help other (even non-relative) members of the population, even at the cost of reducing their own biological fitness, can prosper better, on an average, than a population in which altruists are not present. However, of all the members of such a population, selfish individuals still prosper most, i.e. individuals that enjoy the advantages following from the presence of altruists in the population, but do not, themselves, behave altruistically. Here, selfish individuals have the greatest biological fitness and their number in the population should gradually increase until they completely force out the altruists. The theory of frozen plasticity suggests two reasons why altruistic behaviour nonetheless continues to exist in human and animal populations (Flegr, 2006). To begin with, it shows us that the evolution of a phenotype (including patterns of behaviour) has its boundaries in evolutionarily frozen species. Selection pressure preferring selfish individuals can increase the frequency of alleles for selfishness in the population, but can never lead to complete elimination of alleles for altruism in the population. The second reason may be even more important. The inheritability of individual biological fitness and the inheritability of phenotype traits are very low or do not exist at all for frozen species. The alleles that are responsible for altruistic behaviour in the context of a certain genotype can, in the context of a different genotype, cause selfish behaviour, and vice versa. Thus, an altruist can have a selfish (or altruistic) child with the same probability as any other member of the population. Thus, altruism is not inherited in the population, and individuals with altruistic behaviour emerge in the population at random in the families of both altruists and selfish individuals with a probability corresponding to the frequency of the relevant alleles in the population. Thus, a sexually reproducing population does not contain a genealogical line of altruistic individuals that would be predestined to extinction and a genealogical line of selfish individuals that would be predestined for evolutionary victory.

The theory of frozen evolution was published only recently and has certainly not entered the consciousness of the professional public. Thus, the Czech professional public has the opportunity to gain a certain advantage here, as it received the Czech version of the book on Frozen Evolution, where the assumptions and various consequences of this theory are discussed in detail, at an earlier date (Flegr, 2006). Understandably, the validity of the theory and its explanation potential will be verified only with the passage of time.

REFERENCES

Ardlie KG. Trends in Genetics, 1998, v. 14, p. 189-193.

Darwin C. On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life, London, 1860, Murray.

Dawkins R. The selfish gene, Oxford, 1976, Oxford University Press.

Eldredge NS. J Gould, Punctuated equilibria: an alternative to phyletic gradualism, in TJM Schopf (ed), Models in Paleontology: San Francisco, 1972, p. 82-83.

Flegr J. Rivista di Biologia-Biology Forum, 1998, v. 91, p. 291-304.

Flegr J. Zamrzlá evoluce aneb je to jinak, pane Darwin (Frozen Evolution Or, that's not the way it is, Mr. Darwin), Prague, 2006, Academia.

Gould SJ. The structure of evolutionary theory, Camridge, The Belknap Press of Harvard University Press, 2002, p. 1-1433.

Hamilton WD. Journal of Theoretical Biology, 1964a, v. 7, p. 1-16.

Hamilton WD. Journal of Theoretical Biology, 1964b, v. 7, p. 17-52.