The intellectual odyssey of Daniel Frynta: A retrospective on coevolutionary elevator, frozen plasticity, and male homosexuality research

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Abstract. This celebratory article pays homage to the influential contributions of Daniel Frynta, an ethologist and biologist whose work spans multiple disciplines. The author reminisces about their encounters and collaborations with Frynta, highlighting his contributions to several scientific theories and hypotheses, including the coevolutionary elevator theory, the frozen plasticity theory, and the sibling manipulation hypothesis of male homosexuality. Frynta's keen intellect, curiosity, and ability to generate novel insights have left a lasting impact on the fields of ethology, herpetology, mammalogy, and beyond. The extent of his contributions goes beyond what conventional scientometric indices can measure, as his exceptional talent and dedication have profoundly influenced the global scientific community. His work continues to inspire and shape the careers of his peers and students, leaving an indelible mark on the landscape of science.

Our picturesque homeland has given the world numerous luminaries. Some are widely known (Purkyně, Mendel, Heyrovský), while others remain only faintly recognised to the world's shame (Jára Cimrman, Jakub Hron). The truly greatest, such as today's honoree Daniel Frynta, remain virtually unknown (outside a tight circle of specialists: an international community of ethologists, herpetologists, mammalogists, linguists, parasitologists, physiologists, morphologists, reproductive biologists, zoologists, psychologists, psychiatrists, bio-aestheticians, cultural anthropologists, and evolutionary biologists). It is these trailblazers who have shaped, and continue to shape, the landscape of global science, largely through the scholarly works of their peers.

I first met Dan in the depths of the '80s on one of the famed Balkan expeditions. Right away, on our very first encounter, he taught me how to eat black olives and not to sleep in a sleeping bag on mountain trails, especially when there are fresh piles of purple dung on them. At the time, he was primarily focused on herpetology but accurately identified the origin of the dung to be from one of the local omnivorous mammals, specifically a bear. On another expedition, he taught me how not to catch horned vipers (it's not a good idea to grab one in each hand, particularly when your fellow colleagues are too afraid to approach the vipers closer than two meters).

I got to know Dan better after my return from Japan to the faculty in 1991. Once again, he taught me several practical tricks of field zoologists (like how to decapitate a lizard using a herpetological hook). But most importantly, we managed to meet at the faculty a few times and organize

our little private brainstorming sessions. This was back when 90% of a scientist's work wasn't consumed by writing grant proposals and reports or communicating with editors and reviewers of our publications, allowing us to occasionally focus on professional issues.

Coevolutionary elevator theory

It must have been at the very beginning of my tenure at the faculty when Dan came to my lab at the Department of Parasitology with a fascinating idea. Animals are so beautiful, often with colorful and complex ornaments on their body surface, in order for individual alleles to announce their presence and be fixed by sexual selection. According to Dan, the probability that even a relatively useful allele could be fixed by ordinary natural selection without the help of sexual selection in regular populations is minimal. Terrestrial vertebrate populations tend to be too small, so the fate of individual alleles is determined by chance, i.e., genetic drift, rather than selection. Alleles that can inform their surroundings about their presence in an individual's genome, specifically individuals of the opposite sex and even more specifically females, have a much greater chance of spreading and ultimately being fixed. As soon as a pattern or structure on the males' body surface appeals to the females, the corresponding allele practically wins and quickly spreads and often fixes.

I don't remember how far we got in our discussions with this hypothesis, but I guess we ended up with Greenbeards. That is, according to Richard Dawkins, alleles for a conspicuous trait, such as a green beard, that also compel their carriers to help other individuals with a green beard can successfully spread within populations of many species (Dawkins 1976). If a female of a species where many males compete for few females mates with the carrier of a conspicuous trait, it's like helping him. The problem, as Dawkins already pointed out, is that it's difficult for an allele to arise that simultaneously causes the emergence of a green beard in males and a preference for green-bearded males in females. Daniel went on to suggest that the emergence of a new conspicuous trait in males and a preference for this trait in females could lead to a speciation event, with a group of individuals with these two traits forming a separate new species in which both alleles (for the trait and its preference) could be fixed. Thanks to the existence of this speciation mechanism, the number of species and overall biodiversity increases. And due to species selection (competition of evolutionary lineages for the most frequent speciation and rarest extinction), species in which sexual selection operates through female choice accumulate in nature. These are beautiful species, inclined towards self-presentation, which were admired, but not explained, by Austrian naturalist Adolf Portmann (Portmann 1964) and our scholars Zdeněk Neubauer and Stanislav Komárek (Komárek 1997, Neubauer 1985).

The problem of the emergence of alleles for both the trait and the preference for a given trait was solved much later with my coevolutionary elevator theory (Flegr 2005). In short, there is always variability in preferences among females in a population, which manifests itself externally, for example, in the so-called rare-male phenomenon. When a male with a new exotic phenotype appears in the population, most females ignore him, but some strongly prefer him. If there is intense competition among males for females and most of them don't reproduce at all, then males with a rare phenotype can enjoy a significant advantage. Their allele for the rare phenotype, such as a green beard, therefore spreads in the population.

And now, pay attention! Along with it, the allele for the preference for green beards also spreads. If a male has a green beard, his father most likely had one too. And if the father had a green beard, the mother probably had a preference for green beards. So, if an allele programs a female to choose a male with a green beard as a partner, it will pass itself into the next generation in more copies than if the female selected males regardless of beard color. It passes not only the copy of the allele that was in the female but also the copy that was (and did not manifest itself) in the male. The preference allele, therefore, helps to spread not only the allele for green beards (which

it doesn't care about, as each allele only takes care of itself), but also the copy of itself located in the green-bearded males. It somewhat resembles Baron Munchausen, who pulled himself out of the swamp by his hair (along with his horse). Therefore, in 2005, I called this process (with the kind assistance of Stanislav Komárek) coevolutionary elevator (autoelexis).

Frozen plasticity theory

The frozen plasticity theory is yet another area where Daniel made a lasting impact with his important contributions. This theory assumes that most species are evolutionarily frozen because a large portion of their polymorphism is maintained in the population by frequency-dependent selection mechanisms (Flegr 1998, 2008). In such species, selection can only shift the representation of individual alleles in the population's gene pool. However, the greater the shift, the less the frequencies respond to the same selective pressure until, at some point, they stop responding even to very intense selection. When selection ends, the allele frequencies and the species' phenotype return to their original state.

A polymorphic species can only thaw evolutionarily temporarily, immediately after the emergence of a new species through peripatric speciation, i.e., the separation of a small subpopulation from the total population. The subpopulation takes only a small sample of alleles from the original gene pool, majority of these are likely to vanish in the subsequent few generations due to the influence of genetic drift. The population attains genetic homogeneity, and consequently, it can begin to respond to selection favoring new adaptive mutations, exactly as proposed by Darwinian and Hamiltonian-Dawkinsian evolutionary theories. The species thus evolutionarily thaws and can undergo significant changes.

Over time, however, a population gradually accumulates rare mutated alleles with frequency-dependent effects on fitness. The more abundant alleles that have fitness effects that do not depend on frequency either vanish or become entirely fixed, giving the impression of disappearing as well. As a result, the species once again becomes frozen, losing its capacity to adapt to environmental changes, and from that point on, it passively awaits either a rare speciation event to thaw or its eventual extinction due to being outpaced by environmental shifts. As per the frozen plasticity theory, species spend 98–99% of their existence in an evolutionarily frozen state, during which they are incapable of responding plastically to selection and adapting to changes.

When I introduced this theory at the regular seminar series "Biological Thursdays in Viničná" in 1997, our honoree was in the audience, as he frequently attended those events. At that time, I believed that the plasticization of an evolutionarily frozen species occurs when a population becomes genetically uniform, specifically, when it loses all alleles with frequency-dependent effects on fitness. Daniel joined the discussion and quickly corrected my misconception. A small, genetically uniform population cannot respond to selection due to its limited size. The emergence of a new species with a phenotype adapted to current environmental conditions requires more than just plasticization. Another highly improbable event must occur. Natural conditions must temporarily improve so much that the population can grow from a small size, where genetic drift primarily operates, to a large size where selection can begin to function.

Population growth in nature is in principle exponential and therefore can occur within a few generations. Under such circumstances, genetic polymorphism doesn't have sufficient time to re-establish itself, particularly the polymorphism in alleles with frequency-dependent effects on fitness. These initially rare alleles need to accumulate within the population through a relatively slow process of stability-based sorting (Toman & Flegr 2017). Suddenly, we have a large, evolutionarily plastic population that can (temporarily) start responding to selection, and evolve into a new species that is notably adapted to the prevailing environmental conditions. Just as in the case of autoelexis, Daniel's contribution to the frozen plasticity theory was fundamental. Without

the phase of rapid population growth, the frozen plasticity theory would not offer a satisfactory explanation for the shift of a frozen species back to a plastic state.

Sibling manipulation hypothesis of homosexuality
The last scientific merit of the honoree I would like to mention is his contribution to the hypothesis of the origin of homosexuality as a manifestation of sibling manipulation. The occurrence of male homosexuality is an intriguing evolutionary phenomenon, given its substantial impact on reducing an individual's biological fitness (Ciani et al. 2015). There are several theories for its origin. Some involve alleles with antagonistic effects on the fitness of male and female carriers (Ciani et al. 2004), while others assume that homosexuality allows for the acquisition of material and social resources through easier cooperation between homosexual men (Kirkpatrick 2000). Currently, the epigenetic hypothesis is relatively popular, which assumes that male homosexuality results from maternal manipulation of sexual preferences of second- and later-born brothers during embryonic development. A large number of studies show that a man's likelihood of being homosexual dramatically increases with the number of older maternal brothers he has (Slater 1962). The hypothesis assumes that the mother influences the development of later-born male embryos through hormonal or immunological factors. Having the first-born as a heterosexual and, for example, the second-born as a homosexual in a family might lead to a more efficient allocation of resources, thus increasing the mother's inclusive fitness.

The sibling manipulation hypothesis for the origin of male homosexuality offers an alternative to the original hypothesis of the origin of homosexuality through maternal manipulation (Flegr 2022). It assumes that the primary manipulator is not the mother but the older sibling, and that the manipulation is not for the increased overall inclusive fitness of the family members but for the older sibling's direct fitness. If the first-born son manages to influence the mother's organism to reprogram the ontogeny of younger brothers' embryos to be born as homosexuals, he eliminates potential competitors for family resources and potential sexual partners.

When I approached Daniel with my new hypothesis to verify if someone had not maliciously formulated it long before me, he immediately added a highly intriguing insight. In many communities, younger brothers also benefit from this manipulation in terms of biological fitness. In highly socioeconomically stratified societies, not only low-status but also medium-status men have a minimal chance of acquiring a partner and passing their genes to the next generation. If the younger brother becomes homosexual and frees up resources for the first-born, it increases the chances that the first-born will obtain a partner and pass on copies of shared family genes to the next generation. It is, therefore, in the interest of the younger brother not to resist the manipulation and be born as a homosexual. While this may reduce his direct biological fitness, it increases his inclusive fitness – through his older brother, he passes more copies of his genes to the next generation than if he were heterosexual. It is entirely possible that homosexuality does not arise from manipulation by older brothers, but male embryos "voluntarily decide" on this strategy when they find out, perhaps based on the presence of antibodies against male-embryo specific antigens (Bogaert et al. 2018), that they already have older brothers.

Conclusions
I won't delve into more examples, even though there are certainly many to share. It's not that I'm reluctant to do so; my memory simply isn't as reliable as I'd like it to be. Daniel, I express my deepest gratitude for your existence and the countless years of generously sharing your intellectual wisdom with us all. While the inspiration you provide to colleagues and students might not be fully reflected in traditional metrics, it's truly remarkable that, in this fast-paced world, your colleagues have come together to write and publish a celebratory collection in honor of your birthday.

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