# FORUM FORUM FORUM

FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.


# *Can adaptation lead to extinction?*


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**Ever since J.B.S. Haldane proposed the idea, evolutionary biologists are aware that individual level adaptations do not necessarily lead to optimal population performance. A few deeply mathematical models, drawing from a diverse range of systems, even predict that individual selection can lead to the extinction of the whole population, a phenomenon which has become known as evolutionary suicide. Due to the complexity of both following adaptation and determining the exact cause of an extinction, evolutionary suicide has remained untested empirically. However, three recent empirical studies suggest that it may occur, and that suicide should be taken seriously as a potentially important evolutionary phenomenon. Here we ask whether or not evolutionary suicide can occur, briefly reviewing the theoretical and empirical evidence. We further highlight systems which may be used to test whether or not individual level selection can cause extinction.**


J. B. S. Haldane, the pioneer of modern evolutionary biology, suggested that individual adaptation does not necessarily lead to traits which are beneficial to the whole population (Haldane 1932). He suggested that characteristics may evolve that are catastrophically detrimental to the populations in which they are found. It seems counterintuitive that individual adaptations would occur that have such a negative effect on population performance that the population is driven to extinction. While Haldane asserted that this is possible, the phenomenon has been largely dismissed, most likely because his views on the matter have been incorrectly labelled as a "good for the species" argument (Cronin 1993). However, the idea that individual behaviour can harm population performance was rekindled by Garret Hardin, in the form of the tragedy of the commons (Hardin 1968), which stated that, if a common resource is overexploited by individuals acting for their own selfish gain, disaster at the population level can occur. The idea that individual interactions can facilitate extinction should have strong relevance to ecology, but has rarely been observed in natural systems. Here we describe the phenomenon and highlight three examples which allude to extinction due to individual selection. Furthermore, we suggest various systems which may be prone to evolutionary suicide.

## Theoretical background

In recent years, a number of theoretical models have appeared, suggesting that as certain traits evolve they can drive the population in which they are found to extinction (Matsuda and Abrams 1994, Gyllenberg and Parvinen 2001, Dercole et al. 2002, Gyllenberg et al. 2002). These models have focussed on evolution under asymmetric competition (Matsuda and Abrams 1994, Dercole et al. 2002), and the evolution of dispersal (Gyllenberg and Parvinen 2001, Gyllenberg et al. 2002), the latter showing that under certain circumstances the dispersal rate evolves to zero, causing the metapopulation to go extinct. So far, this concept, often referred to as evolutionary suicide, has been largely ignored by empiricists. This is understandable, due to the difficulties in determining the exact cause of a particular extinction, or identifying the behaviour of a species that has gone extinct. However, a few recent studies suggest that evolutionary suicide may be more than a theoretical artefact (Muir and Howard 1999, Fiegna and Velicer 2003, Olsen et al. 2004). To fully understand the role of species selection on the shaping of traits, it is important to understand to what extent adaptive traits can harm a population.

For extinction to occur as a result of adaptation, the fitness of any new invading trait in a population must depend on what other members of the population are doing; selection must be frequency dependent (Matsuda and Abrams 1994, Gyllenberg and Parvinen 2001). In individual-level adaptation, it is the fitness relative to other individuals that is maximised, and the fitness of the individual is independent of absolute, or mean population, fitness (Wright 1969). Population extinction due to the spread of adaptive traits can arise in two ways. First, as a population declines with the invasion of a "selfish" adaptive trait, it may become more vulnerable to extinction due demographic or environmental stochasticity (Dieckmann and Ferrière 2004). Several models have shown that adaptation may drive population to dangerously small numbers, making it vulnerable to stochasticity, either gradually (Matsuda and Abrams 1994) or suddenly (Dercole et al. 2002). It is the lower population size, resulting from the selection on the given trait, which makes the species more prone to extinction. Extinction could also occur as a result of cycling dynamics caused by adaptation (Greenman et al. 2005); if the cycles cause the population to fall below the equilibrium density, stochastic effects may trigger extinction.

Less intuitively, adaptive evolution can lead to the extinction of a population in a purely deterministic way, without the need to invoke stochasticity (Gyllenberg and Parvinen 2001, Gyllenberg et al. 2002). As a trait evolves, the population size decreases; a successful trait leaves more descendents *relative* to other individuals, but this corresponds to fewer *overall* offspring. Mathematically, this can only can happen if the transition to extinction is sudden (Gyllenberg and Parvinen 2001, Gyllenberg et al. 2002); the population evolves itself to death. If population size declines gradually with the magnitude of the evolving trait, other selective forces will have the opportunity to be exerted, rescuing the population (Dieckmann and Ferrière 2004), and suicide can only become possible under stochasticity. Although the distinction between both processes is theoretically clear, the fact that nature is always stochastic makes it impossible to tease them apart empirically. However, the main question, i.e. whether individual adaptation can lead to extinction in real systems, is still open to evaluation.

## Is there evidence for evolutionary suicide?

Linking extinction with a particular adaptation might seem like an impossible task. While a number of studies have demonstrated correlations between adaptive traits and extinction risk, such as sperm competition (Morrow and Pitcher 2003) and selfish genetic elements (Vinogradov 2004), very few studies have shown that the invasion of an individually selected trait can directly lead to extinction. However, three recent empirical studies, drawing on experimentally or anthropogenically manipulated systems, lend support to the notion of adaptation towards extinction, highlighting the need for empiricists to take such phenomena seriously.

The first example is a study on the Japanese medaka fish *Oryzias latipes* (Muir and Howard 1999). Transgenic males which had been modified to include a salmon growth-hormone gene are larger than their wild-type counterparts, although their offspring have a lower fecundity (Muir and Howard 1999). Females prefer to mate with larger males, giving the larger transgenic males a fitness advantage over wild-type males. However, offspring produced with transgenic males have a lower fecundity, and hence average female fecundity will decrease. As long as females preferentially mate with larger males, the population density will decline. Models of this system have predicted that, if the transgenic fish were released into a wild-type population, the transgene would spread due to its mating advantage over wild-type males, and the population would become go extinct (Muir and Howard 1999). A recent extension of the model has shown that alternative mating tactics by wild-type males could reduce the rate of transgene spread, but that this is still not sufficient to prevent population extinction (Howard et al. 2004). Although evolutionary suicide was predicted from extrapolation, rather than observed in nature, this constitutes the first study making such a prediction from empirical data.

In cod, *Gadus morhua*, the commercial fishing of large individuals has resulted in selection towards earlier maturation and smaller body sizes (Conover and Munch 2002). Under exploitation, high mortality decreases the benefits of delayed maturation. As a result of this, smaller adults, which mature faster, have a higher fitness relative to their larger, slow maturing counterparts (Olsen et al. 2004). Despite being more successful relative to slow maturing individuals, the fast-maturing adults produce fewer offspring, on average. This adaptation, driven by the selective pressure imposed by harvesting, seems to have pre-empted a fishery collapse off the Atlantic coast of Canada (Olsen et al. 2004). As the cod evolved to be fast-maturing, population size was gradually reduced until it became inviable and vulnerable to stochastic processes.

The only strictly experimental evidence for evolutionary suicide comes from microbiology. In the social bacterium *Myxococcus xanthus* individuals can develop cooperatively into complex fruiting structures (Fiegna and Velicer 2003). Individuals in the fruiting body are then released as spores to form new colonies. Artificially selected cheater strains produce a higher number of spores than wild types. These cheaters were found to invade wild-type strains, eventually causing extinction of the entire population (Fiegna and Velicer 2003). The cheaters invade the wild-type population because they have a higher relative fitness, but as they spread through the population, they decrease the overall density, thus driving themselves and the population in which they reside, to extinction.

## Future directions

Due to the difficulty of determining the causes of a given extinction, it may seem impossible to find empirical evidence for evolution to extinction. The fact that the three examples here are from widely different systems suggests that it may be possible to find further empirical evidence for individual level selection causing extinction. While these studies only allude to evolutionary suicide, and draw on manipulated systems, there are many other potential cases where evolutionary suicide may be observed.

Extinction is most likely to occur as a result of individual selection in the case where part of the costs involving a trait are borne by other individuals, as opposed to the actor (Kokko and Brooks 2003). In other words, systems where conflicts evolve between individuals are likely to exhibit cases where individual selection can cause extinction. Two well studied areas of focus could potentially be the conflict between social insect workers over reproduction (Hart and Ratnieks 2005) and sexual conflict caused by male harassment (Chapman et al. 2003). In the former, workers are predicted to reproduce under certain conditions, destroying the social order of the hive and leading to catastrophe (Martin et al. 2002, Oldroyd 2002). In the latter, if male harassment is sufficiently strong that females incur a large cost of mating, average population fecundity could be reduced to a dangerously low level (Kokko and Brooks 2003). While we may not find evolutionary suicide in such cases, we must ask what the mechanisms are that prevent it. For example, worker policing (Ratnieks and Wenseleers 2005) and kin relatedness (Wenseleers and Ratnieks 2004) may prevent the collapse of social insect colonies. Likewise, female counter-adaptation to the male trait (Arnqvist and Rowe 2002, Rowe et al. 2005), or reduced benefits of harassment at low density (Kokko and Rankin, in press), could be sufficient to prevent extinction. One also cannot rule out higher levels of selection weeding out populations which are more prone to extinction (Keller 1999), suggesting that evolutionary suicide may yet be revealed to have a strong macro-evolutionary influence.

Due to their short generation time and well studied nature, experiments of this sort could be conducted using insect model systems such as *Drosophila*. For example, a reduction in female fecundity (and population fitness) has been demonstrated in *Drosophila melanogaster* under both sexual conflict (Rice 1996, Holland and Rice 1999) and selection for desiccation tolerance (Hoffmann and Parsons 1989).

Anthropogenic environmental change has the potential to act as a huge selective force (Stockwell et al. 2003). The example of the cod, described above, demonstrates that this selective pressure can result in adaptations which are harmful to the population (Olsen et al. 2004). Human induced rapid evolution could therefore have the effect of causing evolutionary suicide. In addition to the threats imposed on diversity by harvesting and habitat destruction, we must also be aware that our actions may also kick start the evolution of traits potentially harmful to the species as a whole (Ashley et al. 2003, Stockwell et al. 2003).

We know that evolution can be rapid, and the three examples described here show that the mechanisms resulting in evolutionary extinctions can be studied on a realistic time scale. However, there is still a need for further studies to determine how widespread the phenomenon is, and how much of a given extinction can be attributed to stochasticity alone. The examples given here take the idea of evolutionary suicide and bring it out of the theoretical realm, setting the scene for the theory to be tested properly. Designing such empirical tests will be a challenge. The task is now for empiricists to investigate if such extinctions can be seen in nature and if not, to ask why this is not so. Determining whether evolutionary suicide can occur is essential for a better understanding of the patterns of diversity we observe in nature.

*Acknowledgements* – Funding was provided by the Academy of Finland. We thank Hanna Kokko, Katja Bargum, Mike Fowler and Johanna Rönn for stimulating discussions and comments on the manuscript.

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*Subject Editor: Tim Benton*