

## Why are there no ‘Darwinian Demons’?

A ‘Darwinian Demon’ is a hypothetical organism that would start reproduction from birth and continue to breed frequently and with high fecundity throughout its long lifespan. Natural selection would favour this organism due to its maximisation of genetic contribution to the next generation (*Law R, 1979*). The hypothetical nature of this ‘demon’ leads to the question of why such an organism does not exist. Evolutionary biologists have tried to tackle this question with a multitude of different suggestions, none of which are globally held as the one true reason for why such an organism cannot exist and therefore dominate the world’s ecosystems. A widely held view is that some sort of trade-off at an organismal level must exist between reproduction and longevity such that on an evolutionary scale there is a compromise between what selection can achieve and what selection is prevented from achieving with respect to these two aforementioned aspects of life (*Barnes AI & Partridge L, 2003*). In short, this means that within an organism’s life history exists a compromise between how long it lives for and how many offspring it produces in a given time. This is directly related to ‘life history theory’, which is a field that tries to explain how evolution shapes an organism’s life cycle (referring to traits such as average lifespan, age of onset of reproduction and number of offspring produced) such that it confers reproductive success (*Stearns SC, 2000*). However, the mere statement that a compromise exists is too vague an explanation as to why Darwinian demons cannot exist. In order to truly understand why these organisms are not present the specific nature of the constraints that hinder their existence must be identified. The research behind this, and what this essay will mainly focus on, is centred on the costs of sexual reproduction as well as why the process appears to exist in a compromise with longevity.

One theory is that the reproduction appears costly due to the conflicting requirements for resources from different stages in an organism’s life history, coined in Metcalf’s paper as ‘invisible trade-offs’ (*Metcalf CJE, 2016*). Processes in a life cycle such as reproduction, growth and somatic maintenance all require and compete for resources. Therefore, it is impossible to maximise allocation to them all as the resources are shared – for example resources diverted to somatic maintenance cannot also be used in reproduction (*Partridge L, Gems D & Withers DJ, 2005*). All life history stages require at least a minimum threshold of resources in order to permit overall functioning and to ensure reproduction – and so it is the balance of resources allocated to each stage (and therefore the trade-off between reproduction and longevity) that varies between organisms to promote overall fitness with regards to a specific niche. This therefore provides an explanation for the diversity of different life histories observed in animals as well as why all elements of the life cycle cannot be maximised in an organism (to become Darwinian demon).

While this view makes apparent sense for why an organism cannot maximise every aspect of its fitness, it relies on the assumption of the existence of this resource-pool and its allocation within the organism’s life cycle without suggesting any biological mechanisms of how it actually acts. Research has therefore been undertaken on the nematode *Caenorhabditis elegans* to test this view and whether it is a valid suggestion as to why Darwinian demons have not evolved.

In their paper, Barnes and Partridge review the evident cost of reproduction present in *C. elegans* whereby the lifespan of hermaphrodites declines when mating rates increase. They evaluate this with reference to how mutations in genes encoding the insulin/IGF-like signalling (IIS) pathway increase the longevity by causing the developing worms to enter a larval ('dauer') stage for an extended period of time or just by extending the adult lifespan. The mutations also cause a decrease in fecundity to a degree, which correlates with the extent to which lifespan is increased. Barnes and Partridge therefore hypothesise that this phenotype could suggest reallocation of resources from reproduction to somatic maintenance and resource storage. However, this is a contentious theory, as they go on to discuss, because the negative correlation between these two life history processes can be attributed to independent control by a signalling mechanism, as opposed to direct competition for resources (*Barnes AI & Partridge L, 2003*).

Barnes and Partridge go on to assess the reproductive mechanisms in *C. elegans*, stating that the adult gonads derive from two precursor cells that give rise to the somatic gonad and two that form the germ line cells. The ablation of all four of these cells has no effect on lifespan, while ablation of the germ line precursors extend it. It is suggested that this extension relies on normal functioning of genes in the IIS pathway that encode components downstream of *daf-2*, specifically those that encode a transcription factor and a hormone receptor. They suggest that in order for lifespan to extend, germ cell ablation and the insulin receptor must have overlapping mechanisms that require an intact IIS pathway. This result led to the proposal that a signal that down-regulates longevity is passed from the germ line to the soma, and the somatic gonad produces a counter-signal that upregulates lifespan. Therefore in the absence of the entire gonad, lifespan is unaffected. These signals could be fed into the IIS pathway through the action of the genes downstream of *daf-2*. This therefore proposes a mechanism whereby allocation of resources between reproduction and somatic maintenance is regulated (*Barnes AI & Partridge L, 2003*).

Although this is a mechanistic suggestion of the 'invisible trade-off', Barnes and Partridge go on in their paper to highlight three pieces of evidence that support the fact that somatic maintenance and reproduction may in fact not be in a trade-off. They are that ablation of just the gonad does not extend lifespan, germ cell ablation in wild-type *daf-2* mutants does not cause greater lifespan extension and not all long-lived worms have reduced fecundity (*Barnes AI & Partridge L, 2003*). However, these findings do not completely disprove the theory of resource allocation trade-offs, as Barnes and Partridge expand on, only the evidence is not strong enough to attribute the lack of existence of Darwinian demons to this hypothesis alone.

An alternative view, therefore, of why Darwinian demons cannot exist lies in the hypothesis that reproduction and the processes surrounding are costly because they inflict somatic damage and harm to the animal directly, thus decreasing its fitness and longevity (*Partridge L, Gems D & Withers DJ, 2005*). This view is easier to investigate because the proximate mechanisms of how the soma is damaged (or how the organism's lifespan is otherwise negatively effected) can be studied.

In Harshman and Zera's paper, five proximate mechanisms are reviewed that underlie the cost of reproduction and how they reduce the fitness, and ultimately longevity, of the organism at hand. These five components are hormonal regulation,

intermediary metabolism and allocation, immune function, reproductive proteins and defences against stress and toxicity. It is not suggested that any single one of these elements are the primary cause of reduction in fitness, but instead that the whole process of sexual reproduction brings with it an array of problems and mechanisms that in conjugation lead to reduce longevity (*Harshman LG & Zera AJ, 2007*).

An example of one of these components, as stated, includes direct somatic damage and draining of somatic energy reserves, leading to an increase in vulnerability of the organism to environmental stress, toxins and other damaging factors. This was studied in zebra finches, where assays were taken from individuals to test for oxidative stress susceptibility and antioxidant defence following manipulations in brood size. Increased lysis of the red blood cells (and therefore a more compromised antioxidant system) was recorded as a function of reproductive effort in the adults (*Harshman LG & Zera AJ, 2007*). This is just one example of a direct negative effect reproduction can have on other elements of an organisms fitness thus preventing the evolution of a Darwinian demon where all areas of fitness are maximised.

In conclusion, the best support for why Darwinian demons cannot evolve stems from the cost of reproduction for organisms, which lead to a compromise in life history evolution, as fecundity and longevity must exist in a balance whereby, crudely speaking, one will increase as the other decreases.

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‘Darwinian Demons’ fail to evolve and dominate the world’s ecology due to the cost of reproduction with regard to an animal’s lifespan, which must exist in a balance, thereby rendering it impossible for an organism to maximise every element of its fitness within its life history.

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