Population Expansion With (Almost) No Limits

Darwinian Demons

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If evolution of species was not confined by any restrictions, organisms would reproduce right after being born, produce the maximum number of offspring, and live indefinitely. Such hypothetical organisms are dubbed "Darwinian demons." Certain organisms do resemble this "demonic" ideal...

The evolution of organisms is bound by certain restrictions, some of which virtually act like impassible barriers. For instance, it is hard to imagine a species now arising that would violate the basic construction scheme that became fixed in the distant, distant past. Other limitations follow from the "you can't get something for nothing" rule: it is possible for natural selection to improve one trait, yet only at the expense of some other change (usually for the worse). An example? Having higher numbers of offspring usually exposes the parent organism to a higher risk of death.

Hypothetical organisms whose evolutionary path does not abide by such restrictions have been termed "Darwin's demons." Of course, no such demon exists, but nevertheless, biologists do encounter a vast variety of life strategies among the various organisms they study. Perhaps there are certain species whose strategies show characteristics similar to such Darwin's demons?

With sex or without

Let's first take a look at organisms that reproduce by means of gametes. This method of reproduction involves an offspring organism being put together from a unique combination of genes from its parents. Essentially all that is needed to start embryo development is genes and a bit of spare substances. Therefore, such a zygote should be very small at the outset, while a mature organism should be very large in comparison (studies have shown that a larger female usually lays more eggs). This means that a growing sexual organism invests a large portion of its available energy into expanding and developing its own body, rather than into producing offspring. However, this does not mean that sexual organism which requires a long growth period before reaching maturity is evolutionarily "not optimal." The evolution of an organism's life strategy is simply subject to restrictions imposed by its method of reproduction, "chosen" at distant point in the species' evolutionary past. Also consider that the long period of time which passes between egg fertilization and maturity means that the number of offspring from each given specimen in successive generations thus rises at a slow rate.

Next let's consider species that reproduce asexually, for example via division. This method gives rise to a single offspring organ-

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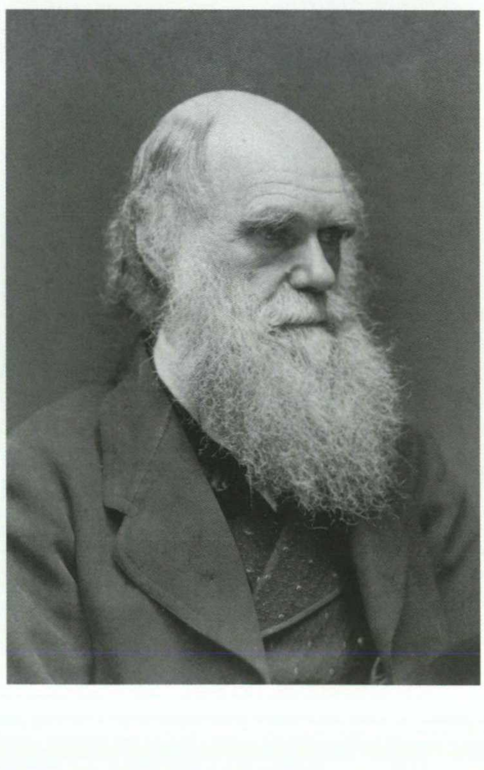


Evolution, whose theoretical underpinnings were described by Charles Darwin, places certain constraints upon organisms. Even so, biologists have discovered certain plants and animals that seem to ignore such barriers

Janusz Uchmański

ism. If the parent organism divides equally in half, the mass of the offspring will already be half that of a mature organism. In such a case subsequent growth does not require an extensive energy investment or a long duration, and so each generation cycle takes less time. Perhaps organisms that multiply via division or budding might be good candidates to be named "Darwinian demons"?

We can take two species being analyzed by our Center for Ecological Research as examples. One is the freshwater oligochaete worm *Stylaria lacustris*, which lives in the coastal zone of lakes and feeds on algae growing on water plants. The other is the common duckweed, *Lemna minor*, a tiny plant freely floating on the surface of water.

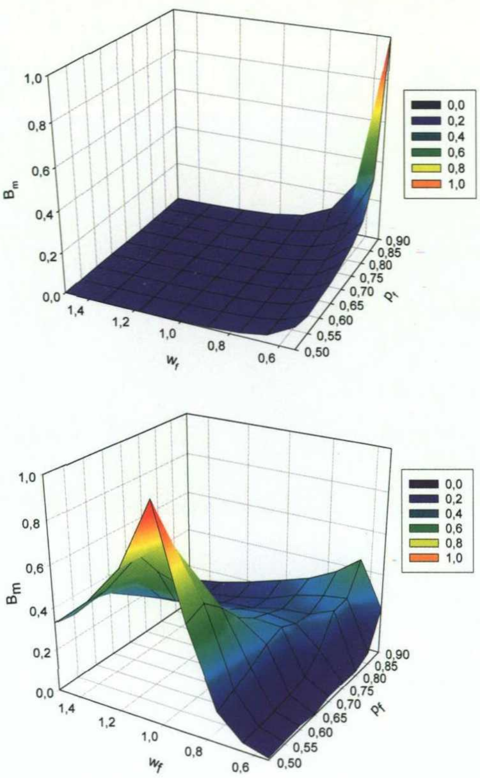
Model goes one way, nature another...

In the period from April to November, *S. lacustris* goes through many generation cycles whereby the specimens in each generation reproduce through division. Only the last, late-autumn generation reproduces sexually, with the eggs so produced surviving through the winter to give rise to the first asexual generation in the spring. Field research has shown that *S. lacustris* divides once it reaches some 15 mm in length and achieves some 1 mg in mass. Division occurs almost at the halfway point along its length – the parent organism thus retains 55% of its length after division. Such reproduction causes the *S. lacustris* population to grow exponentially, and to become highly dense. However, that poses little trouble for this species, as the food resources in its environment are likely to be sufficient and it furthermore falls victim to many predators preying in lake coastal zones (dragonfly larvae being the most threatening).

We might wonder whether this strategy of splitting an approximately 1 mg body nearly in half might be the optimal behavior. Such a notion cannot be tested experimentally: in practice *S. lacustris* simply "resists" division along any other proportions. However, we can build a mathematical model to simulate the division of specimens with various masses and along various proportions, and test the resulting population numbers in the case of

Common duckweed, *Lemna minor*, might be good candidate to be named "Darwinian demon". Millions of these single-leafed plants are capable of entirely covering the surface of small, fertile bodies of water and slow-flowing rivers

The inconspicuous invertebrate *Stylaria lacustris*, whose length is measured in millimeters, is a master of regeneration: specimens grow to a reasonable size before beginning to divide, protecting both the parent and offspring organisms from being wholly consumed by predators



The number of *S. lacustris* specimens belonging to the same clone population capable of reproduction at the end of the season (B_m) depends on the body mass of a specimen at division (Wf) and the proportional ratio along which it divides (P_f). The upper chart shows the output of a model not involving any predator. The optimal strategy is one whereby the organisms remain small and divide asymmetrically. The lower chart, in turn, shows the output of a model simulating a predator that can consume small victims in full, but only damage larger ones. Here, the optimal strategy states that organisms should be of bigger size and divide symmetrically

different strategies. The effectiveness of any given strategy can be evaluated in terms of the numbers of the clone population (all deriving from the same original organism) at the end of the season, when winter eggs are produced by sexual means.

The model we developed showed that under conditions optimal for *S. lacustris* (i.e. a surplus of food and no predators), the best strategy is to divide at the lowest possible body mass, and along very asymmetrical lines. The clone population would be very high at the end of the season if *S. lacustris* divided at a mass of 0.54 mg and along a proportion of 9:1, so that the offspring organism would constitute only 10% of the parent organism's pre-division mass. Yet this is definitely not the way things work in nature, where *S. lacustris* divides at almost twice the mass, and almost exactly in half. Why?

The rationale is to be sought in the presence of predators, which affect *Stylaria* in a very selective way. *S. lacustris* specimens are consumed in full when their mass is less than about 0.54 mg, yet when their bodies are larger predators can only damage them.

If the pressure from prey-consuming predators remains constant throughout the prey organism's life, its best solution is to minimize the time when it is exposed to the threat of such full consumption and mature early (and small). However, the "escaping by growing smaller" method of coping with predators is not optimal for *S. lacustris* because it possesses an amazing ability to regenerate its lost body parts. Instead, *Stylaria* should rather "escape by growing larger," so that predators will be able to merely damage them, not to consume them fully. This means that being large at maturity is not enough; the prey organisms should already be sufficiently large when they are born, so as to avoid being consumed while young. After our mathematical model was modified to introduce a virtual predator, one with traits similar to those of the real predators attacking *S. lacustris* in nature, the results showed that the strategy of dividing into two approximately similar parts, at a body mass of 1.1 mg, indeed yielded the largest clone population at season's end. However, we should note that this population size was smaller than in the predator-free case of virtual *S. lacustris*.

Demonic duckweed

Now let's move on to *Lemna minor*, which can actually be seen to evidence more "Darwinian demon" type behavior than *Stylaria*. Since duckweed is not under any strong pressure from feeders, the size of its body (consisting of a single leaf, called a frond) should be determined by factors other than the aim of avoiding becoming food for another species. What might these factors governing frond size be? Surface-floating leafs belonging to the same clone population should strive to maximize their effective absorption of sunlight falling on the water surface. Geometry would suggest that a given surface area can be best filled with flat objects of small area. And indeed, the Lemnecea family consists of small-sized species.

We might also predict, even though a mathematical model of this process is only now being developed, that the pace of duckweed reproduction is also subject to optimization. *L. minor* multiplies via budding, yet the offspring fronds remain connected to the parent for a long time, exchanging assimilation products and thereby jointly forming a quite broad assimilating surface. This likely increases the pace of frond growth while reducing the energy costs attributable to each unit in the mass of linked leaves. Aside from this, the species exhibits asynchronous separation of offspring leaves. Larger offspring fronds become cut off when another frond appears from the same pocket of the parent organism. The second offspring frond, which continues to be connected to the parent organism, already has a relatively broad surface area, thereby ensuring only small fluctuations in the area occupied by the entire group of linked fronds.

Populations of "Darwinian demons" would be characterized by sudden, exponential population growth. Such behavior can be clearly seen in the case of *L. minor*, which is not restricted by the presence of feeding organisms. The species reaches vast population numbers, forming a dense bed that envelops the surface of water bodies. This greatly changes the physicochemical conditions present in the water, spelling catastrophe for the entire system and requiring the species living there to adopt special adaptation strategies.

True demons

The two above examples alone serve to illustrate that organisms quite similar to the hypothetical "Darwinian demons" really do exist. Rather than multiplying via gametes, they do so through division or budding. They evidence strong natural selection, leading to restrictions on their body size. Because they are small and do not employ gametes, they exhibit fast reproduction rates. When pressured by predators, their body size grows larger, yet they pay for this in terms of slower clone population growth. And if no predator limits their numbers, their populations reach very high densities of devastating impact - exhausting the available resources and completely filling up the occupied space. That is why it is very important for them to adapt to survive such catastrophes - such as having the ability to survive in spore form. Indeed, as would befit true Darwin's demons, both *Stylaria lacustris* and *Lemna minor* have just such an ability. ■

Further reading:

Kaliszewicz A., Johst K., Grimm V., Uchmański J. (2005). Predation effect on the evolution of life-history traits in a clonal oligochaete. *American Naturalist* 166: 409-417.

Stearns S.C., Hoekstra R.F. (2000). *Evolution: an introduction*. Oxford University Press.

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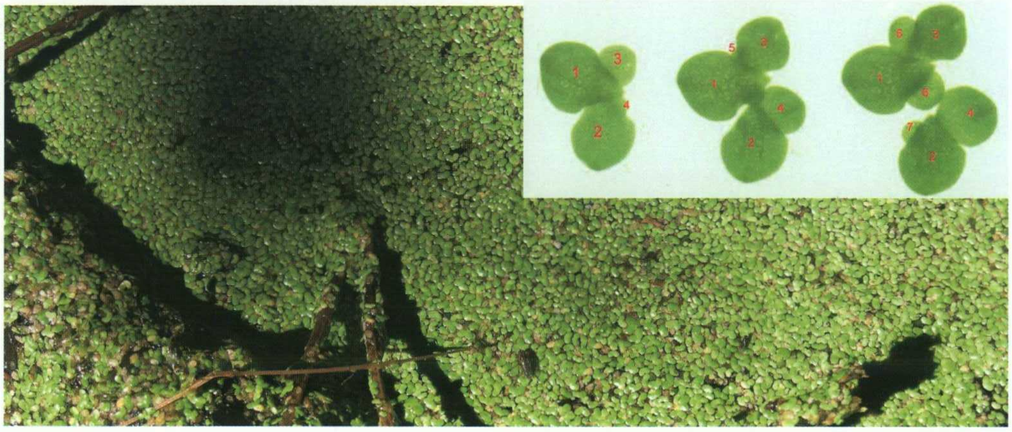

The initial stages of development of a clone line consisting of duckweed (*Lemna minor*) specimens, each of which consists of a single frond. The numbers illustrate the order in which the fronds are generated, number 1 being the founder of the line. The fronds do not develop synchronically, and stay connected for a long time