



Selection in Two-Sex Structured Populations. Promotoren zijn prof. dr. H. Caswell en prof. dr. A.M. de Roos
C. de Vries

Summary

Selection in two-sex stage-structured populations

A hungry caterpillar emerges from an egg. After stuffing itself with leaves, it hangs upside down, dissolves his entire body into a mush, and finally an elegant butterfly emerges from the soup. Helpless, fluffy chicks morph into fierce birds of prey (Figure 2). That is, if the hungry caterpillar and the fluffy chicks do not get eaten by a hungry predator. Helpless, chubby babies turn into hungry PhD students, who morph into full-fledged doctors if fed with enough scientific papers and writing courses. That is, if they survive their defense. These are all examples of life cycles.

Organisms have complex life cycles. Each life cycle represents a different solution to the problem of staying alive. And there are many solutions: the number of species on earth is estimated to be anywhere between 2 million and 10^{12} . Some species survive because individuals of the species live for a very long time, such as corals and sponges, that can live thousands of years. Other species live only very briefly, like mayflies, whose adult lifespan can be as short as 5 minutes for females of the mayfly species *Dolania americana*.

Organisms also have genes, which affect their size, color, and shape, how fast they run, grow, and reproduce, how fast they kill their host, and how fast they kill their parasites. A gene will increase in frequency if the individuals carrying it contribute more offspring to the next generation than individuals without the gene. Individuals procreate and die at rates that are influenced by both their genes and the environment they live in. The environment they live in is shaped by the population they live in. If the population grows very large, there may not be enough food, and individuals may starve. If the population is very sparse, individuals may struggle to find a mate. As a consequence of individuals starving or failing to mate, populations grow or shrink, and gene frequencies increase or decrease.

In summary, genes affect individuals, which affect populations, which affect individuals, which affect how many genes make it into the next generation, etc. For more than a hundred years, biologists have been studying how these two things, genes and complex life cycles, interact. When there are so many interactions and feedbacks, it can be difficult to understand what is happening through verbal reasoning alone. Mathematical models are helpful tools in such a situation. In

this thesis, we combine genetics and complex life cycles into a new mathematical framework to learn more about their interaction.

But so far I have not mentioned any of the words in the title of the thesis yet: “Selection in two-sex stage-structured populations”. What is “selection”, and what are “structured” populations? The term selection refers to the preferential survival and reproduction of individuals with certain genes, or the preferential elimination of individuals with certain genes. That is, when a gene is “selected for”, it means that gene will increase in frequency in the next generation.

A “structured” population refers to a population in which individuals differ due to their age, developmental stage, size, colour, mood, or marital status. You might be thinking, “Surely all populations are structured by that definition?” And I would agree with you. However, including structure into mathematical models of populations makes them a lot more complicated. Biologists therefore often treat all individuals, fluffy or fierce, caterpillar or butterfly, PhD student or professor, as if they are the same in mathematical models.¹

Finally, the thesis title also mentions “two-sex”; so what is that about? We found that the existence of two sexes has a profound impact on the evolution of populations. In sexually reproducing populations, genes live in both males and females², but a gene that is good for males might not be good for females, and vice versa.

To investigate how sex and population structure impact evolution, we calculated under which conditions a gene will be able to invade a resident population of individuals with a different, competing gene at that particular location in the genome (the genetic material of an organism, its DNA). When males and females are identical, we found that new genes can only invade if they lead to individuals that are better somehow, for example by having a higher survival, or reaching maturation faster. When males and females differ, however, genes can invade that benefit males at the expense of females, or vice versa.

Imagine one of our hominoid ancestors, for example. When their brains started getting bigger and babies’ heads grew bigger, it became a huge advantage for females to have wider hips. However, wide hips made males slower runners. So the same gene increased female survival but decreased male survival. Such a gene would have established itself in the population nevertheless, if the positive impact

¹Some argue that this is the fault of physicists and mathematicians, because the people who started modeling populations in this way were mathematicians, chemists, and physicists (e.g. Alfred J. Lotka, Pierre François Verhulst, Vito Volterra). That said, Lotka is also one of the most prominent historical figures in demography.

²Except in some crazy fungi, like *Schizophyllum commune*, which has around 23,000 different sexes or mating types.

of wide hips on female survival was much larger than the negative impact on male survival.

Once the wide-hip gene has spread through the hominoid population, a different gene that can stop the wide-hip gene from being expressed in males would give those small-hipped males an advantage. Males and females would evolve towards having different-sized hips. Differences between the sexes evolve to resolve the conflicting interests of males and females.

Females are usually more important for the survival of a species, because one male can fertilize lots of females, but each female can only produce a limited number of eggs, babies, pups, kittens, or cubs. Therefore if a gene spreads that benefits males over females, the population will grow a little slower, or maybe even shrink. Of course, eventually another mutation might occur that suppresses the expression of the gene in females, or otherwise solve the problem. But if the original male-benefitting gene is sufficiently bad for females, the population can go extinct before the savior gene has managed to save the day.

The fact that sex is dangerous in this way has been known for longer than the author of this thesis has been alive. However, the impact that sexual conflict has on the evolution of life-cycles, referred to as life-history evolution by biologists, has not received much attention.

Demographers and biologists are particularly obsessed with the final stage of every individual's life-cycle: death. Why do some species live thousands of years, like sponges and corals, and others only 24 hours, like the mayflies? Traditionally, demographers have tried to answer these questions using models that only contained females. In general, males are the neglected sex in biology. The results of this thesis suggest that the conflict between males and females might be an important factor in the evolution of such life-history characteristics. By neglecting males, demographers are missing out on the consequences of the ongoing evolutionary tug of war between males and females.

How important the evolutionary tug of war has been in shaping life-history evolution remains an open question. This thesis provides a set of tools (and maybe some motivation) for biologists and evolutionary demographers to answer that question.



Figure 1: Adult Cooper's hawk (*Accipiter cooperii*) feeding his fluffy offspring.
Credits: Tom Muir