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Selection in two-sex structured populations

de Vries, C.

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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

Samenvatting

Hoe werkt de evolutie als individuen van elkaar verschillen in meer dan alleen hun geslacht?

Een hongerige rups kruipt uit z'n eitje. Nadat de rups zich helemaal heeft volgepropt met sappige blaadjes, gaat hij op z'n kop aan een takje hangen en verpopt. Binnenin de pop verandert het lijfje van de rups in een papje van cellen, en van dat papje wordt weer een schitterende vlinder gemaakt die zich ten slotte losworstelt uit de pop en de wereld in vliegt. Maar niet alleen vlinders veranderen enorm gedurende hun leven. Hulpeloze, donzige kuikens worden imponerende roofvogels (Figuur 2). Hulpeloze, mollige baby's worden hongerige promovendi. Tenminste, als de kleine rups en het donzige kuiken niet door een roofdier worden opgesmikkeld, en als de promovenda haar verdediging overleeft. Dit zijn allemaal voorbeelden van levenscycli.

Levende wezens hebben allemaal verschillende, en soms erg ingewikkelde, levenscycli. Elke levenscyclus is een andere manier om te overleven op onze planeet. En er zijn heel veel verschillende manieren om in leven te blijven: het aantal soorten op aarde wordt tussen de 2 miljoen en de 10^{12} geschat (10^{12} is een korte manier om een 1 met 12 nullen op te schrijven). Sommige soorten overleven dankzij de gigantische levensduur van fortuinlijke individuen, zoals koralen en sponzen, die duizenden jaren oud kunnen worden. Individuen van andere soorten leven daarentegen maar hééél even, zoals eendagsvliegen. De volwassen vrouwtjes van sommige soorten eendagsvliegen (*Dolania americana*) leven zelfs maar 5 minuten, maar krijgen het desondanks voor elkaar om zich voort te planten!

Levende wezens hebben ook allemaal verschillende genen. Genen zijn stukjes erfelijk materiaal die onder andere de grootte, kleur, en vorm van de drager van het gen bepalen. Maar genen bepalen, samen met de omgeving van een individu, ook hoe snel de drager van het gen kan rennen, groeien, en zich voortplanten. Als een gen ervoor zorgt dat individuen met dat stukje erfelijk materiaal meer kinderen krijgen dan individuen zonder dat stukje erfelijk materiaal, dan zullen er steeds meer individuen met dat gen in de populatie komen. Het aantal kinderen dat een individu krijgt wordt niet uitsluitend bepaald door zijn of haar genen, maar is ook sterk afhankelijk van de omgeving waarin hij of zij leeft. Een zaadje met fantastische genen zal bijvoorbeeld niet erg oud worden in de schaduw van een grote boom. De omgeving waarin een individu leeft wordt dus sterk bepaald

door de populatie waarin hij of zij geboren is. Als de populatie heel groot is, en er maar beperkt voedsel is, dan zal een nieuwkomer misschien verhongeren. Als de populatie heel klein is, en verspreid over een groot gebied, dan zullen individuen misschien moeite hebben om een maatje te vinden om zich mee voort te planten. Doordat individuen verhongeren, sterven, of zich al dan niet voortplanten, verandert vervolgens de grootte van de populatie en daarmee de frequentie van verschillende genen in de populatie.

Dus genen beïnvloeden het overleven en voortplanten van de individuen die de genen dragen, het overleven en voortplanten van individuen beïnvloedt vervolgens de grootte en samenstelling van de populatie, en dat beïnvloedt dan weer de overlevingskans en het voortplantingssucces van de individuen in de populatie, enzovoort en zo verder. Al ruim honderd jaar proberen biologen deze interactie tussen genen en levenscycli uit te pluizen. Met zoveel interacties en feedback is het vrijwel onmogelijk om te begrijpen wat er aan de hand is door alleen maar hard na te denken over het systeem. Omdat genetica al ingewikkeld genoeg is, wordt er in de meeste wiskundige modellen van de genetica gekozen om de ontwikkeling van een individu door de verschillende stadia in de levenscyclus te negeren. Maar hetzelfde gen heeft vaak een heel ander effect op verschillende levensstadia; in dit proefschrift combineren we daarom een genetisch model met een model van de verschillende levensstadia om de interacties tussen individuele ontwikkeling, de populatie en genen beter te begrijpen.

Tot nu toe heb ik nog geen van de woorden in de titel van mijn proefschrift, *Selection in two-sex stage-structured populations*, gebruikt. Wat is *selection* (selectie), en wat zijn *structured* (gestructureerde) populaties? Selectie slaat op het feit dat individuen met bepaalde genen meer kinderen krijgen dan individuen zonder die genen. We zeggen dan dat zo'n gen "geselecteerd" wordt, omdat dat gen sneller in aantal toeneemt dan de andere genen.

Een *structured population* (gestructureerde populatie) is een populatie waarin individuen van elkaar verschillen, bijvoorbeeld door hun leeftijd, ontwikkeling, lengte, de kleur van hun vacht, hun humeur, of burgerlijke status. Nu denk je misschien terecht, "Ok, maar dan zijn (bijna) alle populaties toch gestructureerd? Zelfs in een klonale populatie is niet iedereen even oud!" En in dat geval heb je helemaal gelijk. Maar een wiskundig model waarin al die verschillen worden meegenomen is best wel ingewikkeld. Biologen maken daarom bij voorkeur modellen waarin alle individuen in een populatie hetzelfde zijn, dus rupsen hetzelfde als vlinders, donzige kuikens hetzelfde als indrukwekkende roofvogels, en gretige promovendi hetzelfde als ervaren hoogleraren.

Ten slotte staat er ook nog iets over twee seksen in de titel van dit proefschrift; wat heeft dat met dit alles te maken? Tijdens mijn onderzoek kwam ik erachter dat

het bestaan van twee verschillende seksen een enorm effect heeft op de interacties tussen de genen, individuen, en populaties die ik hierboven beschreef. Oftewel, het bestaan van twee verschillende seksen heeft een enorm effect op de evolutie. In populaties die aan seksuele voortplanting doen, leven genen in zowel mannen als vrouwen³, maar een gen dat goed is voor mannetjes is misschien helemaal niet zo goed voor vrouwtjes, en andersom.

Om uit te zoeken wat het effect is van seks op de evolutie, hebben we uitgerekend onder welke voorwaarden een mutatie in een stukje erfelijk materiaal (een nieuw gen) zal toenemen in een populatie van individuen die zich seksueel voortplanten. We kwamen erachter dat in soorten waarbij de mannetjes en de vrouwtjes min of meer hetzelfde zijn, een stukje erfelijk materiaal alleen maar kan toenemen in een populatie als dat stukje erfelijk materiaal ook daadwerkelijk het leven van zijn dragers beter maakt, door ze bijvoorbeeld een grotere overlevingskans te geven, of door ze extra sexy te maken voor soortgenoten. Maar als de mannetjes en vrouwtjes van een soort sterk van elkaar verschillen, dan kan een gen verspreiden dat weliswaar het leven van de mannetjes beter maakt, maar dat het leven van de vrouwtjes juist moeilijker maakt, of andersom.

Stel je bijvoorbeeld een van onze eigen verre voorouders voor. Toen onze/hun hersenen steeds groter werden en de hoofdjes van baby's daardoor ook steeds groter werden, hadden vrouwen met bredere heupen een veel betere kans om het baren van een kindje te overleven. Mannen met wijde heupen kunnen daarentegen niet zo snel rennen als mannen met smallere heupen. Dus het "wijde heupen gen" geeft vrouwelijke dragers een veel grotere overlevingskans, maar zorgt er bij de mannen juist voor dat ze langzamer gaan rennen. Omdat de negatieve impact van minder hard rennen op de overleving van mannen waarschijnlijk kleiner is dan de positieve impact op vrouwen, zal een "wijde heupen gen" zich verspreiden door een populatie. Als dat gen eenmaal een groot deel van de populatie heeft overgenomen, dan kan een tweede mutatie dat het gen uitzet in mannetjes, verspreiden in de populatie, omdat het goed is voor de mannetjes en geen effect heeft op vrouwtjes.

Vrouwtjes zijn voor de overleving van de meeste soorten belangrijker dan mannetjes, omdat één mannetje heel veel vrouwen kan bevruchten, maar één vrouwtje maar een beperkt aantal eitjes, baby's, puppy's, of kittens kan produceren. Genen die goed zijn voor de mannetjes maar slecht voor de vrouwtjes, zijn dus eigenlijk ook slecht voor de hele soort. Gelukkig kan de evolutie dit weer oplossen door mutaties die zo'n gen uitzetten in vrouwtjes, maar zo'n reddende mutatie moet dan wel optreden voordat de populatie uitsterft.

³Behalve als je een schimmel bent, sommige schimmels hebben wel 23,000 verschillende geslachten, zoals *Schizophyllum commune*.

Dit soort gevaarlijke neveneffecten van seksuele voortplanting zijn al heel lang bekend. Maar de gevolgen hiervan op de evolutie van levenscycli zijn nog vrijwel onbekend.

Biologen (en levensverzekeringen) zijn vooral erg geïnteresseerd in de laatste fase van elke levenscyclus: de dood. Waarom leven sommige soorten duizenden jaren, en anderen nog geen dag? Waarom leven sommige vrouwen tot ze 116 zijn, ondanks dat ze door de menopauze al decennia geen kinderen meer kunnen krijgen? Traditioneel worden dit soort vragen onderzocht met modellen waarin alleen de vrouwen worden gemodelleerd. Over het algemeen zijn mannen het verwaarloosde geslacht in de biologie. De resultaten van dit proefschrift benadrukken dat zulke modellen een heel belangrijk onderdeel missen, namelijk het feit dat de evolutie telkens het conflict tussen de belangen van mannen en vrouwen moet oplossen. Door de mannen te verwaarlozen, zijn dergelijke modellen blind voor het evolutionaire getouwtrek dat constant plaatsvindt tussen de seksen.

Hoe belangrijk dit getouwtrek tussen de seksen geweest is voor de evolutie van de verschillende levenscycli op onze planeet, en hoe belangrijk dat zal zijn in de wedstrijd van soorten om zich snel genoeg aan te passen aan een veranderend klimaat, blijft een open vraag. De bijdrage van dit proefschrift bestaat vooral uit het benodigde wiskundige gereedschap om die vraag te beantwoorden.



Figuur 2: Een volwassen Coopers sperwer mannetje (*Accipiter cooperii*) geeft zijn donzige nageslacht te eten. Credits: Tom Muir

Author Contributions

2 Selection in one-sex stage-structured populations

Charlotte de Vries and Hal Caswell

HC designed the research, CdV contributed to further development of the idea. CdV analyzed the model and wrote the first version of chapter. HC contributed significantly to later versions of the chapter.

3 Selection in two-sex stage-structured populations

Charlotte de Vries and Hal Caswell

CdV designed the research, analyzed the model, and wrote the first version of chapter. HC contributed significantly to the structure of the chapter and to the writing of later versions of the chapter.

4 Density-dependent selection in one-sex stage-structured populations

Charlotte de Vries, Robert A. Desharnais, Hal Caswell

CdV and HC constructed the model, CdV analyzed the model. RAD designed the experimental part of the paper, and supervised a student (W. Cheung) who performed the research and statistical fitting. CdV analyzed the model and wrote the first version of chapter. RAD, and HC contributed significantly to later versions of chapter.

5 Density-dependent selection in two-sex stage-structured populations

Charlotte de Vries

CdV designed the research and wrote the chapter.

Author Affiliations

Lotte de Vries is at the:

Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam,
P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

Hal Caswell is at the:

Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam,
P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

Robert A. Desharnais is at the:

Department of Biological Sciences, California State University, Los Angeles, USA
Control and Dynamical Systems, California Institute of Technology, Pasadena,
USA