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**Ontogenesis**

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## Summary

### **Ontogenesis: an eco-evolutionary perspective on life history complexity**

In all organisms, ontogenetic development represents an essential life-history process that has major impacts on the interaction between an organism and its ecological environment. Ontogenetic development can be regarded as the collection of changes in the state of an individual that occur during its life, in terms of changes in size, shape, physiology, maturity status, or behavior. Ontogenetic development changes many ecological processes. For example, when organisms grow considerably during life, or undergo metamorphosis, small and large individuals often consume different types of food or live in different habitats. As such, ontogenetic development has consequences for both the type of ecological interactions (e.g. absence or presence of predation or competition) and the strength of ecological interactions (e.g. rates of predation or competitive ability). In turn, changes in ecological interactions during ontogenetic development have major implications for the dynamics of natural populations and communities.

However, there are conditions under which ontogenetic development, through its impact on the ecological interactions of individual organisms, does *not* affect the behavior of populations and communities. These are the conditions of *ontogenetic symmetry*. Ontogenetic symmetry describes how the strength of ecological interactions between an organism and its ecological environment, changes as the ontogenetic development of the organism unfolds. In case of ontogenetic symmetry, the change in ecological interaction strength happens in exact parity with the ontogenetic development of the organism. This creates a type of ecological *symmetry* between individuals that are at different stages of ontogenetic development. In case of a deviation from *ontogenetic symmetry*, the ecological interaction strength changes either faster, or slower, compared to the ontogenetic development of the individual. This is referred to as *ontogenetic asymmetry*. In the event of ontogenetic asymmetry, ontogenetic development will lead to a change in the ecological interaction strength of an organism, in a way that affects population and community dynamics.

The consequences of ontogenetic asymmetry for dynamics of natural populations and communities are well described, both in a theoretical and an empirical context. Furthermore, there are numerous indications that ontogenetic asymmetry pertains to most, if not all populations. However, the evolutionary aspects of ontogenetic asymmetry have not been studied. This thesis takes this step and focuses on the evolutionary origins of ontogenetic asymmetry. For this purpose, mathematical models are used that combine an accurate description of life-history processes (*i.e.* ontogenetic development, reproduction and mortality), with ecological interactions between different populations. The general question of this thesis, is whether and how evolution through natural selection will lead to ontogenetic asymmetry.

Chapter 2 and 3 describe the evolution of ontogenetic asymmetry in a simplified ecological system of a consumer species that lives of a single type of food (*i.e.* resource). Consumer individuals take up and assimilate food to meet the costs of metabolism. On top of that, they can invest energy in growth (both juveniles and adults are assumed to grow) and reproduction (only in case of adults). Because all consumer individuals compete for the single resource, ontogenetic asymmetry leads to a difference in competitive ability between individuals at different stages of ontogenetic development. A good competitor can take up and assimilate resources fast and also requires little energy for maintenance. Therefore, good competitors can spend a lot of energy on growth and reproduction, and this increases their fitness. A poor competitor has a low rate of resource uptake and high maintenance costs. When poor competitors have too little energy for maintenance, their mortality risk increases (starvation) and this leads to low fitness. Through a trade-off it is assumed that a good competitive ability in the juvenile phase, leads to poor competitive ability in the adult phase, and vice versa.

In chapter 2 and 3 it is shown that in this simplified setting, evolution of ontogenetic asymmetry neutralizes strong competitive differences. With the evolved type of ontogenetic asymmetry, individuals at different stages of development (*e.g.* juveniles versus adults), all require the same amount of food to meet their maintenance costs. Consequently, consumer individuals never suffer from starvation. However, differences in competitive ability do arise through differences in growth and reproduction rates. When either the juvenile phase of the life cycle, or juvenile mortality is increased, selection increases juvenile fitness (*i.e.* juvenile growth), at the expense of adult fitness (*i.e.* adult growth and reproduction). Vice versa, an extension of the adult phase of the life cycle, or increased adult mortality, leads to higher adult fitness, and lower juvenile fitness. However, this adaptive response is such that it does not lead to starvation in any part of the life cycle.

The evolved type of ontogenetic asymmetry does not match well with observations from nature. In many natural populations, individuals require different resource levels

to cover their maintenance metabolism. Accordingly, strong competition between individuals in different life stages can induce starvation events. Concluding, the simple ecological setting as studied in chapter 2 and 3 does not explain the type of ontogenetic asymmetry that is observed in nature.

In chapter 4 and 5 it is studied whether the more complex ecological setting of life-history intraguild predation gives rise to the evolution of ontogenetic asymmetry. Intraguild predation describes the mixed predation/competition interaction between a predator and a prey species. Juvenile predators compete with the prey for a shared food source, while adult predators feed on the prey and, in addition, can cannibalize juvenile predators. The shift in diet from resource feeding to predation, implies a change in the type of ecological interaction and this leads to ontogenetic asymmetry. Cannibalism is another source of ontogenetic asymmetry, because it provides a food source for adult predators and leads to higher mortality for juveniles. Taking together the effects of cannibalism and diet shifts can lead to two types of ontogenetic asymmetry in the predator population when it is in equilibrium (*i.e.* population density does not change over time). Either the predator population becomes maturation-regulated, characterized by low juvenile growth rates and high juvenile mortality. Or the population becomes reproduction-regulated, characterized by low adult reproduction and high adult mortality. These two types are separated by ontogenetic symmetry, in which the predator population is neither reproduction, nor maturation regulated.

In chapter 4 it is shown that cannibalism is detrimental for the persistence of the intraguild predator, because it changes the ontogenetic asymmetry from reproduction-regulation into maturation-regulation. In case of maturation-regulation, competition of juvenile predators with consumers becomes too severe for stable predator persistence. Therefore, cannibalism leads to ecological extinction of predators by changing the type of ontogenetic asymmetry.

Chapter 5 describes the evolution of ontogenetic asymmetry in the intraguild predator, dependent on the level of cannibalism. In chapter 5 it is assumed that predators can evolve to increase resource feeding rates of juveniles (which decreases maturation regulation), or increase predation rates of adults (which decreases reproduction regulation). An ontogenetic trade-off between the life stages prevents simultaneous increase in resource feeding and predation rates. In absence of cannibalism, selection on this ontogenetic trade-off leads to an increase in specialization of one life stage, at the expense of feeding performance in the other life stage. Ultimately, increasing one type of specialization causes a shift in the community dynamics to a state in which predators can no longer persist. Consequently, selection on the ontogenetic trade-off in absence of cannibalism leads to evolutionary suicide of the intraguild predator. Cannibalism, however, prevents evolutionary suicide by stabilizing the selection on the ontogenetic trade-off in resource specialization.

In the more complex ecological setting of intraguild predation, ontogenetic asymmetry is also determined by the densities of consumers and resources. Selection on ontogenetic asymmetry leads to an ecological feedback on consumer and resource density. This feedback acts in opposite direction to the forces that drive selection (*i.e.* the amount and direction of ontogenetic asymmetry). Consequently, selection can act to decrease ontogenetic asymmetry, but due to the feedback in the ecological dynamics, selection might not be successful in doing so, or instead, even lead to more ontogenetic asymmetry. Furthermore, cannibalism can induce selection towards ontogenetic asymmetry, because the fitness benefits of cannibalism are greater when the population is in a maturation-regulated state. This is because juvenile density is high in such a state.

Concluding, in intraguild predation systems, the ecological persistence of predators depends crucially on the direction of ontogenetic asymmetry (chapter 4). Furthermore, selection of ontogenetic asymmetry can have unanticipated effects (evolutionary suicide; chapter 5). Increased ecological complexity through cannibalism can stabilize evolutionary dynamics and lead to ontogenetic asymmetry (chapter 5). Comparing these outcomes with the results described in chapter 2 and 3, shows that a certain amount of ecological complexity (as in the number and nature of ecological feedback loops) seems a prerequisite for the evolution of ontogenetic asymmetry.

The evolution of cannibalism can establish a novel ecological interaction and, as such, provides a route to increased ecological complexity in simple communities. Furthermore, cannibalism can inhibit persistence of intraguild predators on ecological timescales (chapter 4), but cannibalism can also stabilize evolutionary dynamics and prevent evolutionary suicide (chapter 5). It is therefore important to understand the conditions that inhibit or promote the evolution of cannibalism. Chapter 6 addresses this topic in the more applied and practical context of fisheries-induced evolution. A model for the population dynamics of cannibalistic Arctic char (*Salvelinus alpinus*), shows that fisheries-induced mortality promotes the evolution of cannibalism. Under low rates of mortality, cannibalism evolution is stabilized by the mortality costs associated with cannibalistic feeding. However, fisheries-induced mortality changes the stabilizing selection into positive directional selection to ever increasing rates of cannibalism. This leads to a double effect of mortality on the population. The fisheries-induced mortality decreases population biomass directly, but also selects for even higher rates of cannibalism, which further reduces population density.

Overall, this thesis combines complex ecological interactions with evolutionary processes that shape individual life histories. This combination has not been used often, but has the potential to provide insights on how complex life forms and ecosystems have coevolved and how they are maintained.

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# Samenvatting

## **Ontogenese: de ecologie en evolutie van complexe levensontwikkeling**

Ontogenetische ontwikkeling is een essentieel proces in het leven van alle organismen en bepaalt in belangrijke mate de interactie tussen organismen en hun ecologische omgeving. Ontogenetische ontwikkeling kan worden beschouwd als de verzameling van veranderingen in afmeting, vorm, fysiologie, levensfase en gedrag, die plaatsvinden gedurende het leven van een organisme. Deze vorm van ontwikkeling is van grote invloed op allerlei ecologische processen. Zo leidt bijvoorbeeld groei in lichaamsgrootte of metamorfose vaak tot veranderingen in het dieet of habitat van het organisme. Op deze manier beïnvloedt ontogenetische ontwikkeling zowel de aard van de ecologische interactie (zoals de aanwezigheid van predatoren of concurrenten), als de sterkte van de ecologische interactie (de predatiedruk of de sterkte van competitie). Veranderingen in ecologische interacties als gevolg van ontogenetische ontwikkeling hebben grote gevolgen voor de dynamiek van natuurlijke populaties en levensgemeenschappen.

Er zijn echter bepaalde omstandigheden waarbij ontogenetische ontwikkeling, ondanks haar invloed op ecologische interacties van individuele organismen, geen effect heeft op de dynamiek van natuurlijke populaties en levensgemeenschappen. Onder zulke omstandigheden verkeert de populatie in een toestand van ontogenetische symmetrie. In het geval van ontogenetische symmetrie is de verandering in de sterkte van de ecologische interactie precies parallel aan de ontogenetische ontwikkeling van het organisme. Op deze manier ontstaat er een ecologische symmetrie tussen individuen die in verschillende stadia van hun ontogenetische ontwikkeling verkeren. Bij een afwijking van ontogenetische symmetrie neemt de sterkte van de ecologische interactie sneller toe of af, vergeleken met de ontogenetische ontwikkeling van het organisme. Dit wordt ook wel ontogenetische asymmetrie genoemd. Bij ontogenetische asymmetrie zorgt de ontogenetische ontwikkeling dus voor een verandering in de sterkte van de ecologische interactie, op een manier die van invloed is op de dynamiek van natuurlijke populaties en levensgemeenschappen.



Er zijn tal van aanwijzingen dat ontogenetische asymmetrie geldt voor de meeste, zo niet alle, populaties, en de gevolgen van ontogenetische asymmetrie op de dynamiek van populaties en ecosystemen worden tegenwoordig goed begrepen. De evolutionaire aspecten van ontogenetische asymmetrie zijn echter minder goed onderzocht. Het onderzoek in dit proefschrift richt zich daarom op de evolutionaire oorsprong en gevolgen van ontogenetische asymmetrie. Hiertoe worden wiskundige modellen gebruikt die een beschrijving van verschillende levensprocessen (bijv. ontogenetische ontwikkeling, reproductie en mortaliteit), combineren met een beschrijving van de ecologische interacties tussen verschillende populaties. De overkoepelende vraag van dit proefschrift is of, en op welke manier, evolutie door middel van natuurlijke selectie leidt tot ontogenetische asymmetrie.

In hoofdstuk 2 en 3 wordt de evolutie van ontogenetische asymmetrie in een gesimplificeerd ecosysteem onderzocht. Dit systeem bestaat uit een heterotrofe consument, die zich voedt met een enkele voedselbron. Consumenten gebruiken de energie van de voedselbron voor hun basale metabolisme. Bovenop de energetische kosten van het metabolisme investeren consumenten energie in lichaamsgroei (zowel juveniele als adulte consumenten kunnen groeien) en reproductie (alleen in het geval van adulten). Omdat alle consumenten afhankelijk zijn van dezelfde voedselbron, leidt ontogenetische asymmetrie tot concurrentieverschillen tussen individuen die in verschillende stadia van hun ontogenetische ontwikkeling verkeren. Een sterke concurrent kan snel voedsel opnemen en is weinig energie kwijt aan het basale metabolisme. Hierdoor kan een sterke concurrent veel energie besteden aan groei en reproductie, hetgeen de biologische fitness verhoogt. Een minder sterke concurrent neemt voedsel langzaam op en besteedt veel energie aan het basale metabolisme. Hierdoor kan een mindere concurrent weinig energie besteden aan groei en reproductie. Tevens kan te weinig energie zorgen voor een verhoogde sterftkans, wanneer er niet aan de kosten van het basale metabolisme wordt voldaan. Op deze manier hebben zwakke concurrenten een lage biologische fitness. Er wordt verder aangenomen dat er een trade-off bestaat tussen de concurrentiekracht in de juveniele fase en die in de adulte fase. Hierdoor leidt een verhoging van de concurrentiekracht in de juveniele fase, tot een verlaging van de concurrentiekracht in de adulte fase, en andersom.

In hoofdstuk 2 en 3 wordt beschreven dat in deze gesimplificeerde ecologische setting de evolutie van ontogenetische asymmetrie de sterke concurrentieverschillen in de populatie neutraliseert. Het type ontogenetische asymmetrie dat hierbij ontstaat zorgt ervoor dat individuen in verschillende fase van ontogenetische ontwikkeling (zoals juvenielen en adulten) dezelfde hoeveelheid voedsel nodig hebben voor hun basale metabolisme. Daardoor treedt er geen verhoogde mortaliteit op als gevolg van voedseltekort. Concurrentieverschillen zullen echter blijven bestaan door verschillen in groei- en reproductiesnelheid. Wanneer ofwel de lengte van de juveniele fase,

ofwel de juveniele mortaliteit verhoogd wordt, verhoogt selectie de juveniele fitness (juveniele groeisnelheid), ten koste van de adulte fitness (adulte groei- en reproductiesnelheid). Andersom zal een verlenging van de adulte fase, of een verhoging van de mortaliteit onder adulten, leiden tot selectie voor verhoogde adulte fitness, ten koste van de juveniele fitness. Deze evolutionaire respons leidt echter in geen enkel deel van de levenscyclus tot extra mortaliteit als gevolg van voedseltekort.

Dit geëvolueerde type van ontogenetische asymmetrie komt echter niet goed overeen met observaties uit de natuur. In veel natuurlijke populaties verschillen individuen uit verschillende levensstadia in de hoeveelheid voedsel die ze nodig hebben voor hun metabolisme. In zulke populaties zorgt competitie tussen individuen uit verschillende levensstadia voor verhoogde mortaliteit. De simpele ecologische setting, zoals beschreven in hoofdstuk 2 en 3, kan dus niet de ontogenetische asymmetrie van natuurlijke populaties goed verklaren.

In hoofdstuk 4 en 5 wordt onderzocht of ontogenetische asymmetrie evolueert in de complexere ecologische setting van leeftijdsafhankelijke omnivorie. Er is sprake van omnivorie wanneer de predator, naast het prederen op de prooi, ook concurreert met de prooi om dezelfde voedselbron. Bij leeftijdsafhankelijke omnivorie beperkt deze competitie zich tot de juveniele levensfase van de predator, terwijl de predatie alleen plaatsvindt in de adulte levensfase van de predator. Daarnaast prederen adulte predatoren ook op hun eigen juvenielen (kannibalisme). De transitie van competitie (als juveniel) naar predatie (als adult) gedurende het leven van de predator, impliceert een verandering in de ecologische interactie en dit leidt tot ontogenetische asymmetrie. Ontogenetische asymmetrie ontstaat ook door kannibalisme van adulte predatoren, omdat het kannibalisme zowel een voedselbron voor adulten vormt als zorgt voor verhoogde mortaliteit onder juvenielen. Wanneer de populatie in evenwicht is (d.w.z. de populatiedichtheid verandert niet door de tijd) kunnen dieetverandering en kannibalisme zorgen voor twee soorten ontogenetische asymmetrie. De predatorpopulatie wordt ofwel gereguleerd door maturatie, met een lage juveniele groeisnelheid en hoge juveniele mortaliteit, ofwel gereguleerd door reproductie, met een lage reproductiesnelheid en hoge adulte mortaliteit. Ontogenetische symmetrie begrenst deze twee manieren van populatieregulatie, waarbij de predatorpopulatie noch door reproductie, noch door maturatie wordt gereguleerd.

In hoofdstuk 4 wordt beschreven dat kannibalisme nadelig is voor het voortbestaan van de predator, omdat het zorgt voor een transitie van reproductie- naar maturatieregulatie. In het geval van maturatieregulatie is de competitie tussen juveniele predatoren en prooien te sterk om het voortbestaan van de populatie veilig te stellen. Kannibalisme leidt dus tot het plaatselijk uitsterven van de predator door een verandering in het type ontogenetische asymmetrie.

In hoofdstuk 5 wordt de evolutie van ontogenetische asymmetrie bij de (omnivore) predator bestudeerd, afhankelijk van het niveau van kannibalisme. In hoofdstuk 5 wordt aangenomen dat evolutie, ofwel de concurrentiekracht van juveniele predatoren verhoogt (dit verlaagt de maturatieregulatie), ofwel de predatiedruk van adulte predatoren verhoogt (dit verlaagt de reproductieregulatie). Een trade-off tussen de verschillende levensfasen verhindert echter dat beide processen gelijktijdig toenemen. Wanneer er geen sprake is van kannibalisme, zal selectie op deze ontogenetische trade-off zorgen voor de specialisatie van een enkel levensstadium (ofwel juvenielen ofwel adulten specialiseren zich op hun voedselbron). Dit gaat ten koste van de mate van specialisatie binnen het andere levensstadium (respectievelijk het adulte of juveniele stadium). Uiteindelijk leidt dit tot een verandering in het ecologische evenwicht en tot het uitsterven van de predator. Selectie op de ontogenetische trade-off zorgt dus voor evolutionaire suïcide van de predator. Kannibalisme kan dit echter voorkomen door de selectie op de ontogenetische trade-off te stabiliseren.

In de complexere ecologische setting van leeftijdsafhankelijke omnivorie wordt de ontogenetische asymmetrie bepaald door de dichtheid van prooien en voedselbron. Selectie op ontogenetische asymmetrie zorgt via een ecologisch terugkoppelingsmechanisme voor veranderingen in de dichtheid aan prooien en voedselbron. De ecologische terugkoppeling werkt echter in tegengestelde richting ten opzichte van de selectiedruk. Hierdoor kan selectie die erop gericht is om de ontogenetische asymmetrie te verminderen, via de ecologische terugkoppeling leiden tot een toename van ontogenetische asymmetrie. Daarnaast kan kannibalisme leiden tot selectie voor ontogenetische asymmetrie, omdat de fitnessopbrengsten van kannibalisme groter zijn in een maturatie-gereguleerde populatie. Dit komt doordat in dit geval de juveniele dichtheid hoog is.

Samengevat, in systemen met leeftijdsafhankelijke omnivorie is het ecologische voortbestaan van predatoren afhankelijk van het type ontogenetische asymmetrie (hoofdstuk 4). Verder leidt selectie op ontogenetische asymmetrie tot onverwachte effecten (evolutionaire suïcide; hoofdstuk 5). Een toename van ecologische complexiteit, door de aanwezigheid van kannibalisme, stabiliseert de evolutionaire dynamiek en leidt tot ontogenetische asymmetrie (hoofdstuk 5). Indien men deze resultaten vergelijkt met de resultaten van hoofdstuk 2 en 3, dan lijkt een bepaalde mate van ecologische complexiteit (d.w.z. het aantal ecologische terugkoppelingen) een voorwaarde voor de evolutie van ontogenetische asymmetrie.

De evolutie van kannibalisme kan leiden tot een nieuwe ecologische interactie, en op deze manier bijdragen aan een toename van complexiteit in simpele ecologische gemeenschappen. Kannibalisme verhindert het voortbestaan van omnivoren op ecologische tijdschaal (hoofdstuk 5), maar stabiliseert ook de evolutionaire dynamiek en het voorkomt evolutionaire suïcide (hoofdstuk 5). Daarom is het belangrijk om

te begrijpen welke omstandigheden de evolutie van kannibalisme remmen of juist bevorderen. Hoofdstuk 6 bestudeert dit onderwerp in de toegepaste context van visserij-geïnduceerde evolutie. Een model voor de populatiedynamiek van kannibalistische trekzalm (*Salvelinus alpinus*) laat zien dat visserij-geïnduceerde mortaliteit de evolutie van kannibalisme bevordert. Bij een lage mortaliteit wordt de evolutie van kannibalisme gestabiliseerd door de negatieve gevolgen van kannibalisme. Echter, bij een verhoging van de visserijdruk verandert deze stabiliserende selectie naar directionele selectie voor toenemende kannibalistische predatiedruk. Dit zorgt voor een tweeledig effect van mortaliteit. De visserij-geïnduceerde mortaliteit verlaagt direct de populatiedichtheid, maar selecteert tevens voor hogere predatiedruk door kannibalisme, wat zorgt voor een verdere afname van de populatiedichtheid.

In dit proefschrift wordt de bestudering van complexe ecologische interacties gecombineerd met de bestudering van evolutionaire processen die de levensontwikkeling van soorten bepalen. Deze benadering wordt nog niet veel gebruikt, maar levert mogelijk belangrijke inzichten op over hoe complexe levensvormen en ecosystemen zijn geëvolueerd en hoe deze blijven voortbestaan.



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# Author Contributions

## 2 **Evolution of Size-Dependent Intraspecific Competition Yields Paradoxical Predictions on the Scaling of Metabolism with Body Size**

*Vincent Hin and André M. de Roos*

VH and AMdR designed the research. VH analyzed the model and wrote first version of manuscript. VH and AMdR contributed to later versions of manuscript.

## 3 **Evolution of Metabolic Scaling**

*Vincent Hin and André M. de Roos*

VH and AMdR designed the research. VH analyzed the model and wrote first version of manuscript. VH and AMdR contributed to later versions of manuscript.

## 4 **Cannibalism and Intraguild Predation Community Dynamics: Coexistence, Competitive Exclusion and the Loss of Alternative Stable States.**

*Benjamin J. Toscano, Vincent Hin and Volker H. W. Rudolf*

BJT and VHWR designed the research. VH and BJT analyzed the model. BJT wrote first version of manuscript. BJT, VH and VHWR contributed to later versions of manuscript

## 5 **Cannibalism Prevents Evolutionary Suicide of Ontogenetic Omnivores in a Life History Intraguild Predation System**

*Vincent Hin and André M. de Roos*

VH designed the research, analyzed the model and wrote first version of manuscript. VH and AMdR contributed to later versions of manuscript.

## 6 **Fisheries-Induced Evolution in Cannibalism Promotes Collapses of Fish Populations**

*Vincent Hin, André M. de Roos and Ulf Dieckmann*

VH and UD designed the research. VH analyzed the model and wrote first version of manuscript. VH and AMdR contributed to later versions of manuscript.



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