Ontogenesis: An Eco-Evolutionary Perspective on Life History Complexity.
V. Hin
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.