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Evolution of Complex Life Cycles

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Frogs are born as tadpoles and butterflies as caterpillars.
These animals have a complex life cycle. Somewhere during their lives, the larval form transforms abruptly into the adult form in a process known as metamorphosis. Not only frogs and butterflies have such complex life cycles, also ladybugs, flatfish, lobsters, salmon, eel, and many other species drastically change their body form during their life. In fact, the majority of animal species have a metamorphosis. Yet, fossil evidence suggests that metamorphosis only evolved a few times in evolutionary history. Why then is metamorphosis so commonly seen in nature? A few species have lost the ability to metamorphose over evolutionary time. One such example is the axolotl *Ambystoma mexicanum*. In contrast to its evolutionary ancestor, this salamander species retains the larval morphology over its lifetime and does not metamorphose. Why did the axolotl and other species lose metamorphosis while others did not?

During metamorphosis the animal body is transformed and rebuilt. This can be advantageous, because it allows species to efficiently exploit different niches during their life. Butterflies, for example, feed on nectar. However, they start their lives as caterpillars, built for nibbling on juicy leaves. To be able to feed on nectar, butterflies need a feeding straw, which caterpillars do not have. Metamorphosis allows the leaf-eating caterpillar to transform into a nectar-consuming butterfly. While metamorphosis can be beneficial for species that change their niche during their development, the process itself is very costly. The energetic costs of rebuilding the body are high and individuals are vulnerable to predation during metamorphosis. Furthermore, individuals that metamorphose are often dependent on two or more habitats for their growth, survival, and reproduction. If the conditions in just one of these habitats deteriorate too much, a metamorphosing species can go extinct.

Not all species that change niches during development have a metamorphosis. Some species, e.g. many fish species, only change their diet during their life, without drastic changes in morphology. It is thought that such ontogenetic niche shifts, have been the first steps in evolutionary history towards complex life cycles where individuals undergo metamorphosis. Consequently, to understand why complex life cycles have evolved and why they are so successful, it is necessary to understand how and why ontogenetic niche shifts have evolved.

The aim of this thesis is to understand under which ecological conditions niche shifts and metamorphosis may have evolved. Niche shifts and metamorphosis are life-history strategies that evolved millions of years ago. Little is however known about the ecological conditions that promoted their evolution. To better understand why metamorphosis and niche shifts are so ubiquitous in the animal kingdom, it is therefore useful to study the evolution of these life-history strategies with an evolutionary model.

Chapter 2 and 3 describe the conditions under which species switch their diet during development, and whether they evolve a morphology specialized in feeding on the food source used early or later in life. Large individuals are assumed to have access to two different types of food, the primary and secondary. Newborn individuals are considered too small to eat the secondary food source and can only feed upon the primary. The two food types are substantially different from each other, such that a morphology that is efficient for feeding on one type of food, is not very useful in exploiting the other food type.

The results in chapter 2 show that, under equilibrium conditions, it is beneficial for individuals to switch diets during their development when this increases their food intake. Even though large individuals then forage mainly on the secondary food source, they cannot evolve a morphology specialized for exploiting this type of food. The mechanisms that prevent specialization on a food source used later in life is studied in detail in chapter 3. Shifting diets increases the food intake of adults, which results in a higher reproduction rate. Because adults produce many offspring, competition for food is very strong among the smallest individuals. It is therefore of crucial importance for small individuals to be very effective at feeding on the scarce, primary food source. Individuals with a morphology that is slightly maladapted in feeding on this food type, are outcompeted by better adapted individuals. As a result, specialization on a secondary food source stands no chance.

Chapter 3 shows that the competition among the smallest individuals is somewhat alleviated when the population exhibits large population fluctuations. When the dominant cohort matures, there is a small timeframe during which less efficient larvae can escape competition and subsequently mature to the larger size class. Since these individuals are more efficient at feeding on the secondary food source as adults, they can produce many offspring. Therefore, specialization on a food source used later in life can evolve in case the population exhibits large population cycles.

Chapter 4 describes under what conditions metamorphosis can evolve as a mechanism to relax the tradeoff between foraging on the primary or secondary food source. Because metamorphosis is costly, it can only evolve when the secondary food source is abundant. Interestingly, as soon as life stages are slightly decoupled by metamorphosis, there is selection to evolve a more pronounced metamorphosis, such that pre- and postmetamorphs become morphologically more distinct from each other. When the conditions change under which metamorphosis initially evolved, metamorphosis often does not disappear. Metamorphosis is therefore not easy to evolve, but, once evolved, it is hard to lose.

Even though metamorphosis is common in the animal kingdom, some species have lost metamorphosis through the evolution of direct development or paedomorphosis. Direct developers are born with the adult morphology. Paedomorphic individuals, in contrast, retain the larval morphology during their whole life. In chapter 5 it is studied under which conditions metamorphosis can disappear. The results in this chapter show that metamorphosis is most of the time an evolutionary dead end. If the availability of one of the two food sources that metamorphosing species uses deteriorates, the species often goes extinct.

When the food source eaten by large individuals becomes scarce, there is an evolutionary response to postpone metamorphosis. This can, under some conditions, lead to the evolution of paedomorphosis, where individuals become mature while having the larval morphology. Vice versa, when the food source eaten by small individuals becomes scarce, it is beneficial to quickly metamorphose such that the secondary food source can be exploited earlier. Larger offspring reach the size at which they can metamorphose earlier, and are therefore selected for when the food source eaten by small individuals becomes scarce. This can sometimes lead to the evolution of direct development, where individuals are born with the adult morphology. The hypothesis that the evolution of direct development was preceded by the evolution of larger eggs was tested among amphibians with the use of a phylogenetic framework. The results of this analysis indeed strongly support the predictions of the evolutionary model.

To summarize, the work in this thesis shows that metamorphosis can be beneficial for species that change niches during their life. Since metamorphosis is costly, it only evolves under very favorable habitat conditions. Once evolved, however, metamorphosis is a robust strategy that does not easily disappear. Metamorphosis allows species to efficiently exploit multiple niches during their lives. While this is beneficial under favorable food conditions, metamorphosing species are vulnerable to habitat degradation since they depend on several food sources for their growth, survival and reproduction. Direct development and paedomorphosis can evolve as a way to deal with deteriorating conditions. The findings in this thesis explain the empirical observation that metamorphosis is ubiquitous in the animal kingdom, despite only a few evolutionary origins.