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Evolution of complex life cycles

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CHAPTER

1

GENERAL INTRODUCTION

Hanna ten Brink

1.1 Background

Voracious caterpillars change into elegant butterflies and swimming tadpoles become hopping frogs. The offspring of asymmetrical flatfish just look like typical, upright swimming, baby fish, and the offspring of most crustaceans (e.g., lobster) bear little resemblance to the adult form. All these species possess a metamorphosis and undergo a radical shift in their morphology, behavior and habitat during their lives. Metamorphosis has not only fascinated biologists but is also a recurrent theme in the classical literature. The famous Roman poet Ovid wrote the narrative poem "The Metamorphoses", consisting of more than 250 myths where humans change to animals, trees or stars, animals into humans, ivory becomes flesh and blood is turned into flowers. In Franz Kafka's *Metamorphosis* (1915), one morning poor Gregor Samsa "found himself transformed in his bed into a monstrous vermin". Each child is familiar with the brothers Grimm fairy tale of the frog that changes into a handsome prince after he is kissed by a princess. Even though these mysterious transformations in the literature are a fascinating topic, this thesis is not about such types of metamorphoses but about the biological process of an animal that undergoes a relatively abrupt life-history transition at a certain point in its life.

There is a continuous gradient from direct developing species that only experience a diet shift during their ontogeny to species that have a complex life cycle with an abrupt ontogenetic change in morphology, behavior, or physiology (Werner 1988; Werner and Gilliam 1984) (see box 1.1 for the definitions of these terms). Among fish for example, size-specific shifts in food type are common without large changes in morphology (Werner and Gilliam 1984). Hemimetabolous insects, such as dragonflies and grasshoppers, undergo some morphological changes during development, but the changes are gradual and not spectacular (Brown 1977). Holometabolous insects, such as bees and butterflies, on the other hand, undergo sharp and abrupt metamorphoses that separate the different life stages. Werner (1988) estimated that approximately 80% of all animal species undergo a metamorphosis during their life cycle. Additionally, a large proportion of species without a metamorphosis have a clear shift in diet during their ontogeny.

Fossil evidence and phylogenetic distributions of complex life cycles indicate that this strategy evolved more than two hundred million years ago in insects (Labandeira and Sepkoski 1993) and amphibians (Wassersug 1975). In marine invertebrates this was already in the Cambrian period (500 Mya) (Strathmann 1993). It has even been suggested that the common ancestor of all animals already had a biphasic life cycle, with a pelagic larva and a benthic adult stage (Jägersten 1972). The ubiquity of complex life cycles is therefore probably not the result of many evolutionary origins but rather of their ecological success. Even though a complex life cycle is apparently a suc-

successful strategy, it also got lost several times in evolutionary history. Via, for example, the evolution of direct development (e.g., in some frog species; Callery et al. 2001) or the evolution of paedomorphosis (e.g., in salamanders; Bonett et al. 2014a). This then raises the question why are complex life cycles so pervasive and under which ecological conditions did they evolve? Why did some species lose a complex life cycle while others did not?

During metamorphosis individuals can rebuild their body plan (e.g., Aguirre et al. 2014). It has therefore been hypothesized that metamorphosis evolved such that individuals can occupy different niches during their life or specialize on different tasks (Moran 1994). Taxa that nowadays exhibit a sharp and abrupt metamorphosis between different life stages have evolved from a situation where the changes from newborn to adult were more continuous. In insects and marine invertebrates it has been shown that the morphological divergence between different life stages has increased during the course of evolution (Brown 1977; Nielsen 1998). Furthermore, the ancestors of frogs looked more like the metamorphosing stage than the larvae or adults of present-day species (Wassersug and Hoff 1982). Gradually the different life stages became morphologically more distinct from each other and ultimately a metamorphosis evolved. Fossils of early amphibians showed that an ontogenetic shift from feeding under water as a larva to feeding on land as an adult was a crucial factor for the evolution of this metamorphosis (Schoch 2009). Based on these observations it is thought that ontogenetic changes in niche were the first steps in evolutionary history towards complex life cycles (Nielsen 1998; Persson 1988; Schoch 2009; Werner 1988). To understand why complex life cycles have evolved and why they are so successful, it is therefore necessary to understand how ontogenetic niche shifts have evolved.

Given the ubiquity of ontogenetic niche shifts and complex life cycles, there is surprisingly little theory on the evolution of these life-history strategies (but see Ebenman 1992; Istock 1967; Werner 1988; Werner and Gilliam 1984). Istock (1967) argued that a metamorphosing population, where larvae and adults can adapt completely independent from each other, is evolutionary unstable. When one of the two life stages is slightly better adapted than the other, selection will favor the reduction and ultimately loss of the other stage (Istock 1967). A metamorphosing population will therefore always evolve to a population without metamorphosis. In contrast to the idea of metamorphosis as being inherently unstable, Ebenman (1992) showed that a metamorphosing population, in which different life stages exploit different food sources, can hardly be invaded by a mutant without a complex life cycle and is therefore evolutionarily very successful. Other studies by Werner and Gilliam (1984) and Werner (1988) mainly focused on the optimal timing of niche shifts and metamorphosis and do not really investigate how complex life cycles arose in the first place. They argue that complex life cycles are selected for in order to maximize growth rates and mini-

Box 1.1: Definitions

Adult: The mature stage of an animal species.

Adaptive dynamics: A mathematical framework to model evolution in an ecological setting.

Complex life cycles (CLC): A life history where individuals abruptly change their morphology, habitat, behavior, physiology, and/or diet at a certain point in their lives.

Direct development: A life history where individuals are born with the adult morphology. The larval stage is completely absent or develops within the parent.

Juvenile: The life stage of a species that mostly resembles the adult but is not yet mature.

Larva: The free-living developmental stage of a species that differs in morphology from the adult stage.

Maturation: The transition from the non-reproducing juvenile to the mature adult stage.

Metamorphosis: A life-history transition from the free-living larval stage to the (non-mature) juvenile stage.

Ontogeny: The development of an individual over its lifetime.

Ontogenetic niche shift: A change in food source and/or habitat use over the course of ontogeny.

Pedomorphosis: A derived life history where individuals never metamorphose and reach maturation with the larval morphology.

Physiologically structured population model (PSPM): A model that characterizes individuals by some state (e.g., size, age, sex or genotype).

mize mortality rates at each size. When the growth rate in one stage is greatly reduced compared to another stage, there would be selection to reduce the time spent in this stage and therefore to change the timing of the niche shift and/or metamorphosis.

What these studies have in common is that they assume fixed growth, mortality, and reproduction rates for a certain strategy. The impact of individuals on their environment is not taken into account. The fitness of an individual depends crucially on growth and reproduction, which are in most species largely determined by food intake (de Roos and Persson 2013). Both metamorphosis and niche shifts during ontogeny will change the food intake of an individual, and result in a change in its fitness. If changing niches during ontogeny increases the fitness of an individual, this trait can in principle spread in the population. However, if individuals start exploiting a different food source, this will affect the densities of the food sources that are used by the population. This will in turn alter the profitability of the niche shift and thereby the fitness of the shifting individual. Hence, this feedback loop between the individuals and the environment should be taken into account when studying the ecological conditions promoting the evolution of complex life cycles.

The aim of this thesis is to provide new insights into the evolutionary gain and loss of ontogenetic niche shifts and complex life cycles, taking into account the feedback loop between individuals and their environment. Ontogenetic niche shifts, metamorphosis, direct development and paedomorphosis (box 1.1) evolved long ago (e.g., Strathmann 1993; Wolfe 2017). The ecological conditions that promoted the evolution of these life-history strategies have probably changed considerably since then. To better understand the ecological conditions that have led to the gain and loss of complex life cycles, it is therefore useful to study an evolutionary model. While there are many ecological factors (e.g., dispersal, predation, or mate finding) that can promote the evolutionary gain or loss of complex life cycles, this thesis focuses on one aspect specifically; the effect of food availability.

1.2 Modeling biological evolution

Concepts such as 'survival of the fittest', 'the struggle for existence' and simple Mendelian inheritance are familiar to first-year biology students and even to laymen, yet evolution is a tremendously complex process. Traits almost never follow simple Mendelian inheritance, where one gene, consisting of two alleles, corresponds to one trait. Instead, traits are often controlled by multiple genes, which furthermore consist of more than two alleles. Additionally, the fitness of an individual depends on many factors, such as the presence of competitors and predators, food availability and environmental conditions. Even though evolution can occur on ecological timescales, it is usually a relatively slow process which makes evolutionary experiments often difficult.

Theoretical models help to better understand evolution and can avoid the difficulty of evolutionary experiments. Models are, however, always simplifications of the real system. The more complex and detailed the model, the harder it becomes to understand the mechanisms leading to a certain result. Therefore, when modeling evolution, simplifications are essential to gain new insights. What to include and exclude in a particular model depends a lot on the question that the modeler tries to answer. Someone interested in the molecular mechanisms underlying metamorphosis needs a different approach than someone that wants to study how a gene that affects the timing of metamorphosis can spread in the population. Every approach that models biological evolution is in a way always a caricature of the system under study since simplifying assumptions have to be made.

One approach, the framework of adaptive dynamics, provides the fundamental tools to study evolution in an ecological context (Geritz et al. 1998). It is, therefore, the appropriate modeling framework for understanding the evolution of complex life cycles. Adaptive dynamics allows for the study of evolution in a detailed ecological setting, often at the cost of ignoring genetic detail. Adaptive dynamics assumes that the

focal population consists only of individuals with one specific, the so-called resident phenotype and evaluates whether or not a mutant with a slightly different phenotype has a positive growth rate and will hence increase in the population. It furthermore assumes that the ecological time scale is much faster than the evolutionary time scale. Therefore, mutant individuals appear infrequently, such that a beneficial mutant becomes fixed in the population and that the ecological dynamics reach a stable attractor before the next mutant arises. The success of a mutant depends not only on its own phenotype but also on the environment it encounters. Since the environment is determined by the strategy of the resident population, the fitness of a mutant depends indirectly also on the phenotype of the resident population (Geritz et al. 1998).

1.3 Size-structured population models

The approach of adaptive dynamics has been applied to many evolutionary problems, such as the evolution of specialization in resource utilization (e.g., Egas et al. 2004 and Nurmi and Parvinen 2013), evolution of habitat choice (e.g., Ravnigné et al. 2009) and evolution of life-history parameters such as survival and reproduction (e.g., White et al. 2006). Most studies of adaptive dynamics use unstructured ecological models, where all individuals within the population are identical (but see Claessen and Dieckmann 2002).

Individuals do, however, grow during their life. After an individual is born it needs to at least double in size before it can reproduce. In many species newborn individuals increase several orders in magnitude in mass before they are mature (Werner and Gilliam 1984). Differently sized individuals differ in rates of food intake, mortality, maintenance, and reproduction (de Roos and Persson 2013). As a result, individuals in different life stages have different effects on the environment and on the population dynamics. Juvenile individuals, for example, do not reproduce and therefore do not contribute to the growth of a population. Adults, on the other hand, do reproduce but do not always eat (e.g., in many Chironomidae). Differently sized individuals can furthermore experience different selection pressures, which can lead to implicit trade-offs between the different life stages.

Ontogenetic niche shifts and metamorphosis are by definition processes that take place during an individual's development, and an individual's ontogeny should therefore be taken into account when modeling complex life cycles. The framework of physiologically structured population models (PSPMs, de Roos and Persson 2001) allows for intraspecific variation among individuals, such as differences in size or age, and can therefore be used to study complex life cycles. In PSPMs, all assumptions pertain to the individual level and the population dynamics than emerge from these individual-level processes. The state of an individual, characterized by variables such as size, age,

or energy reserves, determines an individual's development, mortality, reproduction and its effect on the environment (e.g., food levels or conspecifics). PSPMs are completely deterministic, which implies that all individuals with the same state develop in an identical way.

1.4 Outline of the thesis

This thesis will combine physiologically structured population models and the adaptive dynamics framework to study under which ecological conditions complex life cycles can evolve.

Since it is thought that ontogenetic changes in niche have been the first step in evolutionary history towards life cycles with a metamorphosis, chapters 2 and 3 study how ontogenetic niche shifts can evolve. In both chapters it is assumed that there are two different types of food present. One of these food sources, the primary food source, is available for all consumers. The secondary food source, on the other hand, is only available for large consumers. Small individuals are too small to handle this food source, which is for example the case for many piscivorous fish species that need to reach a certain size before they are large enough to feed upon other fish (Mittelbach and Persson 1998). The two types of food are considerably different from each other, for example plant material and insects, such that an individual specialized in feeding on one food source is not very efficient in feeding on the other.

Chapter 2 studies when consumers switch to the secondary food source and if individuals can specialize in feeding on this new food source. Specialization on the secondary food source comes at a cost since it reduces specialization on the primary food source. This leads to a trade-off between early and late foraging success. A stage-structured consumer-resource model is used to study the evolution of ontogenetic niche shifts.

While in chapter 2 it is assumed that the population is in a stable equilibrium, size-structured populations often exhibit different types of population cycles (de Roos and Persson 2003, 2013; Persson et al. 1998). The evolutionary analysis of non-equilibrium population dynamics is, however, much harder compared to equilibrium conditions, especially for structured populations. Since it has been shown that non-equilibrium dynamics can have a profound effect on the evolutionary behavior of systems (Hoyle et al. 2011; Nurmi and Parvinen 2013; White et al. 2006), chapter 3 investigates how the type of population cycles affect the evolution of ontogenetic niche shifts.

In chapter 4 it is studied under which ecological conditions metamorphosis can evolve in species that change niches over their life cycle. During metamorphosis individuals can rebuild their body plan. This allows individuals to specialize on multiple niches during their lives. However, metamorphosis is an energetically costly process

(e.g., Geffen et al. 2007) and is, furthermore, quite risky (e.g., Wassersug and Sperry 1977). In this chapter it is studied when the benefits of metamorphosis outweigh the costs such that it can evolve.

While metamorphosis is the dominant life-history strategy in the animal kingdom, it disappeared several times during the evolutionary history. Chapter 5 shows under which conditions metamorphosis disappears, either via the evolution of direct development or via the evolution of paedomorphosis. Given that metamorphosing species crucially depend on multiple niches for their survival and growth, I especially focus on the evolutionary loss of metamorphoses under deteriorating food conditions.

In chapter 6 I summarize the results of the thesis and discuss the implications of the results on the understanding of the evolution of complex life cycles.