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Summary
In seasonal environments the timing of various biological processes is crucial for growth, survival and reproductive success of an individual. Nowadays, rapid large-scale climate change is altering species’ seasonal timing (phenology) in many ecosystems. Ecological and evolutionary consequences of warmer temperatures on the timing of seasonal events are well documented in many species. Plants, insects, birds and mammals are shifting their phenology at different rates, leading to phenological mismatches between species at different trophic levels (e.g. herbivore and its host plant or predator and its prey). Organisms are phenotypically plastic in their seasonal timing (i.e. egg laying date in birds) however, this plasticity alone is thought to not be sufficient to keep up with the change in climate leading to directional selection on timing. Since warming trends are projected to intensify, the pivotal question is whether the rate of adaptation will be sufficient to cope with the new conditions and to restore the phenological synchrony between predator and prey or herbivore and host plant.

The aim of this thesis was to explore the mechanisms underlying seasonal timing with the focus on the role of environmental cues such as photoperiod and temperature. Additionally, in order to forecast the rate of micro-evolution to warmer temperatures we investigated the underlying genetic variation. To conduct this work we used the simplified food chain of oak (*Quercus robur*), winter moth (*Operophthera brumata*) and great tit (*Parus major*). At each trophic level, the phenological synchrony with the lower trophic level is crucial for fitness. The winter moth is a herbivorous insect with an annual cycle and the larvae feed in spring on young oak’s leaves. Winter moth adults emerge from pupae in winter (November & December) and after mating, the females lay eggs on the branches of host trees. In spring (April & May) the eggs hatch. The timing of egg-hatching relative to oak bud opening is crucial for the larvae’s survival and growth as the fresh leaves are suitable for feeding only during a short period of time. Timing has also major fitness consequences higher up in the food chain. Later in spring, great tits need to feed their chicks and the caterpillars, rich in proteins, represent a high-quality diet. However, the seasonal caterpillars’ peak in biomass lasts only for a few weeks, thus, great tits have a very restricted period of high food availability.

Temperature plays an important role in this system as oak bud burst, insect development and egg-laying date in the great tit are temperature-dependent. Long-term data show that in the last decades, due to the increased temperatures, phenologies of both oak’s bud burst and winter moth’s egg-hatching have advanced over time. However, timing of egg-hatching in the winter moth has advanced more than the oak bud burst leading to the phenological mismatch and increased selection for later egg-hatching. As a result of the earlier phenology of the insects, at the higher trophic level of the food chain, a phenological mismatch between the great tit offspring’s
food demand and the peak in caterpillars’ biomass has occurred, leading to enhanced selection for earlier egg-laying on the birds.

In this thesis, we first investigated the changes in winter moth egg-hatching date in response to temperature (Chapter 2). Over a period of 10 years (2000-2010) the winter moth has adapted genetically and reduced the phenological mismatch between its egg-hatching date and the oak bud burst date. As a result of the shift, the phenological mismatch between the timing of egg-hatching and bud burst has reduced. Further studies suggest that winter moth’s response to temperature has changed rather than its sensitivity to photoperiod (Chapter 4).

Phenological models are frequently used to describe insects’ responses to temperature and to forecast their phenologies. We explored into detail the role of temperature on winter moth egg development (Chapter 3). Experimental evidence shows that the effect of temperature on egg developmental rate is not linear during development. Based on this finding, we developed a novel phenological model on the basis of an existing model (Sharpe-Schoolfield physiological model) to predict winter moth egg-hatching date. Furthermore, we obtained a preliminary estimation of the additive genetic variance in one of the parameters of the phenological model using a quantitative genetic analysis technique (“animal model”).

Next to temperature, also photoperiod regulates a number of phenological processes, behavioural decisions and physiological changes. In insects, photoperiod regulates diapause (a state of reduced metabolic activity). Part of the work presented in this thesis focused on the effect of photoperiod on the regulation of winter moth development. We clearly showed that photoperiodic cues during the larval stage influence the timing of the following winter moth life-stages (Chapter 5). However, we found that photoperiodic cues during egg development have no effect on the timing of winter moth egg-hatching (Chapter 4).

In addition to the study of the mechanisms underlying seasonal timing in the winter moth, we also explored the mechanisms underlying the timing of reproduction in the great tit. By using an experimental approach on wild birds, we investigated the effect of photoperiod on gonadal growth and timing of egg-laying. Manipulation of the light intensity perceived by the birds through the skull influenced gonadal growth but did not advance laying date (Chapter 6). These results suggested that, in the wild, (i) other environmental factors rather than photoperiod must play a role in fine-tuning timing of egg-laying and (ii) gonadal growth does not necessarily translate in egg-laying decisions.

To conclude, this study contributed to our knowledge on proximate mechanisms underlying phenotypic traits and our understanding of the winter moth’s potential
for adaptation to warmer temperatures. Studies demonstrating genetic adaptation to climate change are still scarce and more studies are needed to further understand the effects and consequences of climate change on species’ phenology. Finally, to forecast future species’ responses under rapidly changing conditions and act accordingly, it is crucial to identify and describe the mechanisms underlying traits under selection and subsequently investigate the genetic variation underlying the mechanisms themselves as this ultimately determines the rate of adaptation, which needs to match the rate of environmental change.
De timing van verschillende biologische processen is cruciaal voor groei, overleving en reproductief succes van een individu dat leeft in gebieden welke gekarakteriseerd worden door sterke seizoensveranderingen. Klimaatverandering zorgt tegenwoordig voor een verandering van seizoensstiming (fenologie) van soorten in vele ecosystemen. Ecologische en evolutionaire gevolgen van warmere temperaturen voor de timing van seizoensgerelateerde gebeurtenissen zijn goed beschreven voor veel soorten. Planten, insecten, vogels en zoogdieren passen hun fenologie aan op verschillende snelheden, wat leidt tot een mismatch in fenologie tussen soorten op verschillende trofische niveau’s (bijvoorbeeld herbivoren en hun waardplanten of predatoren en hun prooidieren). Organismen kunnen hun seizoensstiming aanpassen (zoals vogels hun eilegdatum), echter dit aanpassingsvermogen alleen zal wellicht niet genoeg zijn om de verandering in het klimaat bij te houden, die leidt tot directionele selectie op timing. Omdat voorspelt is dat opwarming van de aarde zal versnellen, is de cruciale vraag of het aanpassingsvermogen groot genoeg zal zijn om om te kunnen gaan met nieuwe condities en de fenologische synchronie tussen predator en prooi of herbivoor en waardplant te herstellen.

Het doel van dit proefschrift is om de mechanismen onderliggend aan seizoensstiming te verkennen, met specifieke aandacht voor de rol van omgevingsfactoren zoals daglengte en temperatuur. Daarnaast hebben we genetische variatie onderzocht om de snelheid van micro-evolutie als gevolg van warmere temperaturen te kunnen voorspellen. Om ons doel te bereiken hebben we de versimpelde voedselketen van de zomereik (Quercus robur), de kleine wintervlinder (Operophtera brumata) en de koolmees (Parus major) als model gebruikt. In deze voedselketen is op elk trofisch niveau de fenologische synchronie met het onderliggende trofische niveau cruciaal voor fitness. De kleine wintervlinder is een plantenetend insect met een jaarlijkse cyclus waarin de rupsen zich in het voorjaar voeden met jonge bladeren van de zomereik. Adulte kleine wintervlinders ontpoppen in de winter (november en december) en na paring leggen de vrouwtjes hun eieren op de takken van de waardplant. De eitjes komen uit in de lente (april en mei). De timing van het uitkomen van de eitjes, relatief ten opzichte van het openen van de bladeren van de eik, is cruciaal voor de groei en overleving van de rups, omdat de verse bladeren slechts gedurende een korte periode geschikt zijn om te eten. Ook hogerop in de voedselketen heeft timing grote consequenties voor fitness. Later in het voorjaar moeten de koolmezen hun jongen voeden; de rupsen, rijk aan proteïnen, vormen een hoge kwaliteit diëet. Echter de jaarlijkse rupsenpiek duurt slechts enkele weken, en dus hebben de koolmezen een zeer beperkte periode van grote voedselbeschikbaarheid voor hun jongen.

Temperatuur speelt een belangrijke rol in dit systeem; het openen van de knoppen van de eik, de ontwikkeling van de wintervlinder en de datum van eileggen van de koolmees zijn allen temperatuursafhankelijk. Data van lange termijn studies laat
zie dat door verhoogde temperaturen in de afgelopen decennia de fenologie van
zowel het openen van de knoppen van de eik als het uitkomen van de eitjes van de
wintervlinder is vervroegd. De wintervlinder is echter meer vervroegd dan de eik,
wat heeft geleid tot een fenologische mismatch en verhoogde selectie voor later uit-
komen van wintervlinder eitjes. Op het hoogste trofische niveau in de voedselketen
is een fenologische mismatch ontstaan tussen de voedselbehoeftie van de koolmees-
jongen en de rupsenpiek, door de vervroegde fenologie van de wintervlinder. Dit
heeft geleid tot versterkte selectie op vroeger leggende koolmezen.

In dit proefschrift hebben we allereerst de veranderingen in het uitkomen van
de eitjes van de wintervlinder als reactie op temperatuur onderzocht (Hoofdstuk
2). Over een periode van 10 jaar (2000-2010) heeft de wintervlinder zich genetisch
aangepast en de fenologische mismatch tussen de datum van het uitkomen van haar
eitjes en de datum van het openen van de knoppen van de eik verkleind. Nader
onderzoek suggereert dat de reactie van de wintervlinder op temperatuur is verand-
erd en niet haar gevoeligheid voor daglengte (Hoofdstuk 4).

Fenologische modellen worden regelmatig gebruikt om de reactie van insecten
op temperatuur te beschrijven en om hun fenologie te voorspellen. Wij zijn tot in
detail nagegaan welke rol temperatuur speelt bij de ontwikkeling van de eieren van
de kleine wintervlinder (Hoofdstuk 3). Experimenteel bewijs laat zien dat het ef-
fekt van temperatuur op ontwikkelingsnuitheid van de eieren niet lineair is. Hierop
voortgeborduurd hebben we een nieuw fenologisch model ontwikkeld, gebaseerd op
een bestaand model (het Sharpe-Schoolfield fysiologisch model), om de datum van
het uitkomen van de eieren van de wintervlinder te kunnen voorspellen. Daarnaast
hebben we een voorlopige schatting van de additieve genetische variantie van één
van de parameters van het fenologische model kunnen maken door een quantitatieve
genetische analyse techniek (“animal model”) te gebruiken.

Naast temperatuur reguleert ook daglengte een aantal fenologische processen,
besluiten over gedrag en fysiologische veranderingen. Bij insecten reguleert dag-
lengte diapause (een staat van gereduceerde metabolische activiteit). Een deel van
het werk gepresenteerd in dit proefschrift richt zich op het effect van daglengte op
de regulatie van de ontwikkeling van de kleine wintervlinder. We hebben laten zien
dat daglengte tijdens het larvale stadium de timing van volgende levensstadia van de
wintervlinder beïnvloedt (Hoofdstuk 5). We vonden echter ook dat daglengte tijdens
de ontwikkeling van de eieren geen effect heeft op de timing van het uitkomen van
deze eieren (Hoofdstuk 4).

In toevoeging op de studie naar de mechanismen achter seizoens timing in de
wintervlinder hebben we ook de mechanismen achter de timing van reproductie van
de koolmees onderzocht. Door gebruik te maken van een experimentele aanpak,
hebben we het effect van daglengte op groei van de gonaden en tijdstip van eileggen bij wilde vogels onderzocht. Manipulatie van de lichtintensiteit die door de vogels door de schedel wordt ontvangen beïnvloedde groei van de gonaden maar vervroegde de eilegdatum niet (Hoofdstuk 6). Deze resultaten suggereren dat, in het wild, (i) andere omgevingsfactoren dan daglengte een rol moeten spelen in het fine-tunen van timen van eileggen en (ii) groei van de gonaden zich niet noodzakelijkerwijs laat vertalen in besluiten over eileggen.

Deze studie heeft bijgedragen aan onze kennis over proximate mechanismen onderliggend aan fenotypische eigenschappen en ons begrip van de mogelijkheden van de kleine wintervlinder om zich aan te passen aan warmere temperaturen. Studies die genetische aanpassing aan klimaatverandering demonstreren zijn nog steeds zeldzaam, en meer studies zijn nodig om de gevolgen van klimaatverandering voor de fenologie van soorten beter te begrijpen. Tot slot, om toekomstige reacties van soorten onder snel veranderende condities te kunnen voorspellen en daarnaar te kunnen handelen is het cruciaal om de mechanismen achter eigenschappen onder selectie te identificeren en te beschrijven, en daaropvolgend de genetische variatie onderliggend aan deze mechanismen zelf te onderzoeken, welke uiteindelijk de aanpassingssnelheid bepaalt die zal moeten matchen met de snelheid van de verandering van onze omgeving.
Nederlandse samenvatting

143
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Acknowledgements
Lucia Salis was born on the 6th of April 1983 in Rome, Italy. She graduated from high school at the Liceo Scientifico Statale A. Righi, Rome. Her fascination for Nature lead her to start her University studies in Biology at the University of Rome La Sapienza, where she obtained a bachelor degree in Ecobiology in 2007 with a thesis on molecular phylogeny of the genus *Lygodactylus* (Squamata, Gekkonidae). Then she continued her studies at the same university, following the master in Evolutionary Biology and she graduated with 110/110 *cum laude* in October 2010. For her master thesis she joined for 10 months the Evolutionary Genetics group at the University of Groningen, the Netherlands, where she studied the genetic basis of diapause in a parasitic wasp, *Nasonia vitripennis* (Hymenoptera, Pteromalidae). As a follow up of her master project, in December 2010 Lucia shortly visited the laboratory of David Doležel at the Institute of Entomology in České Budějovice, Czech Republic, to investigate circadian rhythms in *Nasonia* along a latitudinal cline. After this experience, she went back to the Netherlands and worked for a month as student assistant at the University of Groningen. In April 2011 she started her PhD as part of the project: “Adapting to a warmer world: phenology, physiology and fitness” under the supervision of Marcel Visser and Domien Beersma. This project was carried out at the Netherlands Institute of Ecology (NIOO-KNAW) in the Animal Ecology group. The results of her PhD project are the subject of this thesis.
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**IN PROGRESS:**

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