Seasonal timing in a warming world
Salis, Lucia

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2015

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.


Kinnison, M. & Hendry, A.P. (2001) The pace of modern life II: from rates of contemporary microevolution to pattern and process. Genetica, 112-113,
References


References


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 (Operophtera 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.
NEDERLANDSE SAMENVATTING
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 dieet. 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
zien 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 uitkomen van wintervlinder eitjes. Op het hoogste trofische niveau in de voedselketen is een fenologische mismatch ontstaan tussen de voedselbehoefte 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 verandert 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 effect van temperatuur op ontwikkelingsnelheid 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 daglengte 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 seizoenstiming 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. Studie om genetische aanpassing aan klimaatverandering demonstren 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.
Acknowledgements
Here we are, at the end of this PhD thesis and this beautiful experience which was full of satisfactions, struggles, questions, discoveries, obstacles, challenges, hours of hard work and lots of fun. During this time I often thought about the moment in which I would have written the acknowledgements (which remains, to my opinion, the most read section in any PhD thesis) and several time I feared that, given the tremendous amount of people who helped me counting caterpillars and supported me throughout my entire PhD, I could have forgotten someone in the end! Well, I did my best to try to remember everyone, so I hope that, if you are looking for you name, you will find it in here!

First of all I wish first to thank my daily supervisor, Marcel Visser. Marcel, you provided me the opportunity of being part of an excellent research institute as the NIOO and the dynamic and vibrant Animal Ecology department. I learnt a lot from you. Your ability of managing the department and the different projects, fulfilling all the administrative business and at the same time being an extremely successful scientist is impressing. I am grateful to you for the time and energy you spent to advice, stimulate, encourage and support me at any moment in these past four years. Marcel, I think you have the most essential skill that a boss needs to have: you make people trusting in themselves and believing that they can do it, even when they think they cannot. Our meetings always motivated me to find the answer or to think out a way to run the next experiment. Thanks for leading me to the completion of this PhD thesis.

For my project I spent most of the time in NIOO, but at the same time I had the luck to be advised by two excellent professors at the University of Groningen, Domien Beersma and Roelof Hut. I wish to express my gratitude to both of you for the great interest and the enthusiasm showed about my project. Our stimulating discussions contributed to improve substantially the design of many experiments and the analysis and interpretation of the results.

Domien, thank you very much for proof-reading my manuscripts and the thesis so accurately.
Roelof, thanks for the time you dedicated to my project and in particular to our great tit experiment and for conducting the light transmission measurements.

Next, I would like to express my gratitude to the members of both the assessment and the examining committee to take the time to read my thesis and take part to the defense.

Before coming to the NIOO I had no idea of how fortunate I was. Here I found many people, who not only helped me with practical work and, but guided me through the exciting and complex world of science as whole.
Arie and Kate, many thanks for sharing your vast knowledge with me and, in general, with all the members of the department. Your advices on experimental design and statistical analysis have been very valuable to my work. I extremely appreciated the facility I could approach you, enter your office and discuss about science-related stuff. Your kindness and patience is remarkable.

Marjolein, thanks for introducing me to the unknown universe of modelling. Half-way in the project you got another position, luckily your office was just on the other side of the road. Thanks a lot for coming over all the times for our meetings. Yet another time... thanks a lot!

Samuel, what to say, working with you it was always great. When I think of the cold nights in Oosterhout running the experiment, I smile. Your spirit is contagious and your passion for research is inspiring. I wish to you and your beautiful family all the best in Montepellier.

Bart van Lith, you undoubtedly know better than anyone the amount of work that was done to provide the data for this thesis, and in general to carry out a long-term study. You had to be there, any day of the week, at any time, when it was needed. Thanks for helping all the times!

Louis, I admire your devotion to your work (and all our data)! Thanks to your precision and your patience, all the data collected during these four years are safely stored in our huge and intricate d-base, ready to analyze. Thanks!

During this time I had the opportunity to supervise very good and dedicated students: Lisanne, Joel, Erik, Anouk and Renske. Each of you taught me something and you all did a great job! Most of the work in this booklet is also thanks to you.

At the very start of the project, I had many questions and doubts about winter moths. Margriet, you solved them all! Thanks for being so helpful and kind.

On the other hand, especially during the last stretch, Phillip you have been very important. I “survived” this PhD also thanks to you. Our chats on data-analysis were often enlightening. Many thanks again!

Thinking about data-analysis, Tom, you come to my mind. Thanks for leading my first steps in R and in statistics. Many times your support helped me to gain more enthusiasm to carry with my project. Thank you as well for the very nice social life we shared during the first months in Wageningen together with the rest of the crew: Nerea, Sara, Rosa, Pitu, Almudena, Miguel and Nicolas. It was a lot of fun with you guys! I hope our trails will cross again in the future.

Christa and Agaat, I will keep safe our funny memories of the dissections of the poor green fat caterpillars! And I hope we won’t ever forget the name of our beloved first sequenced winter moth!

Of course I cannot forget to thank all the AnE students who over the years were
“friendly forced” to help me out during the peak of egg-hatching. Thanks also to Anouk, Andrielli, Oscar and Raldi for help during other experiments.

During these years many things have changed and so also my roommates. When I started we were just few PhDs... Luc and Sonja, thanks for introducing me to NIOO and the AnE.

Luc, thanks for teaching me how to ride a Dutch bike while doing fieldwork in the Hoge Veluwe! I hope to come to visit you in Australia soon.

Sonja, I remember that before leaving, you told me that one of the things you loved and you would have missed it was the nice smell of the pine trees near the entrance of the Veluwe, well, I think I will miss it too!

Jacintha, although you were often in Texel or busy with the last bit of the thesis. I really enjoyed our chats in the Vide about work as well as other stuff. I am happy we both attended the R course in Switzerland, it was a good occasion to get to know each other!

By time the group has grown and now we are many more: Barbara, Lysanne, Thomas, Davide, Lies, Irene, Jip & Rasha. I am very happy I got to know you guys. It is quite remarkable to have the luck of working with such nice group of people like you around. I wish you all the best with your projects and I am sure we will meet again in the future.

Els, my Groningense-buddy! I am happy we could share our worries during the last months. Thanks for reassuring me all the times I was super-stressed!

I would like to thank all the members of the Animal Ecology group. Most of you directly or indirectly contributed to my project. I enjoyed very much our science lunches, seminars and journal club meetings and all the everyday chats at the coffee machine. The atmosphere in the department was always friendly and throughout all this time I always felt supported and well-connected with everyone: Kees, Bart N., Andrea, Martijn, Lyanne, Kamiel, Adriaan, Jenny, Callum, Marleen, Gotz, Cynthia, Manon, Peter and Piet, thanks a lot! Erik, thanks for the introduction to InDesign and welcome to the group!

Special thanks go to animal caretakers: Marylou, Coretta and Ruben, thanks not only of taking care of the birds, but also and especially for switching on and off my incubators or check my winter moths during Xmas holidays! Marylou, you are the most positive and strong person I have ever met! I sincerely wish you beterschap!

I also would like to thank the Chronobiology Group in Groningen for fruitful discussion during the seminars and our sporadic visits. Thanks for translating your knowledge to our ecological problems. Among the people from Groningen I also would like to thank my former MSc thesis supervisor: Silvia, thanks for
suggestions, four years ago, to apply for this position! Corine and Maartje, thanks for helping me getting my thesis through the Hora finita system!

No experiment would have been possible without the help of our super-efficient Fytotron manager and technical department! Gregor, thanks for taking such good care of anything in the Fytotron, including our incubators beeping at all times. Gilles, Jeroen and Wim thanks for always finding a solution to my problems... on time! Eke, thanks you for being so kind and optimistic. With your smile, you contribute every day to make this world a better place.

Working at the NIOO was a beautiful and positive experience also thanks to the kind and helpful secretaries: Elly, Gerda, Miriam and Gerrie. Elly, I really would like to express my deep gratitude to you. Hartelijk bedank voor uw steun en de Nederlandse lessen. In addition I would like to thank some colleagues, many of whom by time have become good friends. Thanks Paolo, sei magnifico, grazie di tutto...da paura che sei venuto al NIOO! Luuk, thanks for your help with making the graphs! Bart, Annette, Jan, Michiel, Sven & Mendy, thanks for the Nederlandse lessen. Palomita, time for the nice time spent together inside and outside the NIOO. Any project to do in Wageningen soon? Ruth, Julie, Kadri, Olaf, Kim & Nico thanks for the nice chats and the fun!

While working in the Fytotron I interacted with many interesting people: Arjen Biere, Martine, Olga, Marjolein Kruidhof, Moniek, Minghui, Stijn, Rutger and Jasper. Thanks to you all for all the scientific input, the nice words and the reciprocal support while working. Roel! Thanks for being so nice and kind every day and thanks for explaining your work with the parasitic wasps everytime I brought a new student!

Outside academia many more people helped me, gave me their support and contributed to this work. To Droef 99 and all my lovely housemates: Aart, Dina, Tim, Donna, Johanna & Ko. Thank you guys for all the nice dinners and the time spent together, thanks for helping me rehearsing my presentations and listening to my complains, thanks also for joining in the anti-stress gardening weekends and for the nights at the fireplace. Aart thanks for taking care of my pupae during Xmas! Dina, thank you for being such a nice, sweet and sincere person! Taboza, having you around makes my day!

So many friends made my days during these four years and helped me in the taught moments. Alberto, thanks for the help me in the lab during weekends and thanks for feeding me all the times I came back home late! Toni, thanks for the artwork of the cover, I litterally love it! Roeland...cicio, your help and your company brightened many of my days in the Fytotron. Thanks for all the back
pain relieving massages!

My dear Maaike & vero. Thank you for being my paranymps and sharing with me such a remarkable moment of my life.

Maaike, you are amazing, I do not know anyone else who can combine, as amazingly as you, partying till 4am and giving a superb presentation in the next morning! Thanks for being my companion during this PhD! I truly loved it! I hope our friendship will last longer after my stay at NIOO. Thanks for translating my summary and all the best with completing your thesis!

Vero, I will always remember when you come to pick me up at Ede-Wageningen! I could make a very looong list for what I am thankful to you. In few words: thanks for being my friend and colleague at the NIOO and thanks for our super-nice life together in Droef. Your presence in both places made these last four years even more special. I miss you!

Cari Mamma e Papá, se sono arrivata fin qui, ad ottenere il dottorato, in un altra nazione, in un altra lingua, lo devo soprattutto a voi. Dopo il liceo, per ogni decisione presa, mi avete sostenuto in tutto e per tutto. Ho imparato tanto in questi anni, su animali, piante, evoluzione… quello che vorrei continuare ad imparare ogni giorno di più è la capacità di esprimere la mia gratitudine e il mio amore per voi, per Luca e per Luigi. Anche se siamo lontani, grazie a voi la nostra famiglia rimane unita! Grazie, thanks, gracias!

Ed ora siamo alla fine per davvero… sembra ieri che si parlava al pratino di quanto sarebbe stato difficile andare a fare il dottorato all’estero, eravamo pieni di dubbi e incertezze, con un inglese zoppicante e due lire in tasca. E ora eccoci qua, dopo pochi anni tutti e due con un PhD e tu hai appena iniziato un post-doc… sembrerebbe proprio che ce l’abbiamo fatta! E nel frattempo, tó, ci siamo pure sposati!!! Amore mio grazie per essere stato al mio fianco in tutti questi anni, grazie per aver alimentato il mio interesse per la scienza e grazie per avermi preso con te in questa fantastica avventura che chiamiamo vita. Santos, senza di te sarei come un bruco senza la sua quercia!
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.
AFFILIATIONS OF CO-AUTHORS

Marcel E. Visser
Bart van Lith
Louis Vernooij
Erik van den Hoorn
Department of Animal Ecology,
Netherlands Institute of Ecology (NIOO-KNAW),
Wageningen, The Netherlands

Domien G. M. Beersma
Roelof A. Hut
Chronobiology Unit,
Groningen Institute for Evolutionary Life Sciences,
University of Groningen, Groningen, The Netherlands

Margriet van Asch
IMARES, Wageningen UR
Yerseke, The Netherlands

Samuel P. Caro
Research Group in Behavioural Ecology,
Department of Evolutionary Ecology, CEFE–CNRS (UMR 5175),
Montpellier, France

Marjolein E. Lof
Plant Sciences, Centre for Crop Systems Analysis,
Wageningen University, Wageningen, The Netherlands


**IN PROGRESS:**

Salis, L., Lof, M. van Asch, M. & Visser, M.E. Modeling winter moth egg phenology: nonlinear effects of temperature and developmental stage on developmental rate. *Submitted*

Salis, L., & Visser, M.E. Variation in sensitivity to temperature, but not to photoperiod, underlies genetic variation in timing of egg-hatching in the winter moth. *Submitted*

Salis, L., van den Hoorn E., Beersma, D.G.M., Hut, R.A.& Visser, M.E. Photoperiod at the larval stage sets the timing of entire annual program in the winter moth. *Submitted*


Paolucci, S., Salis, L., Vermeulen, C. J., Beukeboom, L. W., van de Zande L. The genetics of photoperiodic response in *Nasonia vitripennis*: clinal correlation between period alleles and diapause induction. *Submitted*