

EFFECTS OF CLIMATE ON PHENOLOGICAL  
SYNCHRONY BETWEEN BUTTERFLIES AND THEIR  
HOST PLANTS

Diana Posledovich





# Effects of climate on phenological synchrony between butterflies and their host plants

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## List of papers

- I. **Posledovich D, Toftegaard T, Wiklund C, Ehrlén J, Gotthard K.** (2015) Latitudinal variation in diapause duration and post-winter development in two pierid butterflies in relation to phenological specialization. *Oecologia*, 177(1), 181-190.
- II. **Posledovich D, Toftegaard T, Navarro-Cano JA, Wiklund C, Ehrlén J, Gotthard K.** (2014) Latitudinal variation in thermal reaction norms of post-winter pupal development in two butterflies differing in phenological specialization. *Biological Journal of the Linnean Society*, 113(4), 981-991.
- III. **Posledovich D, Toftegaard T, Wiklund C, Ehrlén J, Gotthard K.** Weak effect of spring temperatures on phenological synchrony between herbivore emergence and host plant suitability. Manuscript.
- IV. **Posledovich D, Toftegaard T, Wiklund C, Ehrlén J, Gotthard K.** The developmental race between maturing host plants and their butterfly herbivore – the influence of phenological matching and temperature. Under review, *Journal of Animal Ecology*

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Paper II will also be included into doctoral dissertation of Tenna Toftegaard, 2016

## **Introduction**

### *Phenology and climate change*

Phenology – seasonal timing of life history events – is an essential and at the same time easily observed trait of periodic biological phenomena. An appropriate phenological timetable ensures that life-cycle activities are well-timed to coincide with environmental conditions most suitable for growth, reproduction or dormancy. Moreover, in order to occur, the majority of species interactions require a temporal overlap of organisms in certain developmental stages. For example, larval emergence needs to coincide with leaf unfolding in trees, while hatching of bird nestlings needs to be timed to larval peak abundance. The degree of the temporal overlap determines the strength of a species interaction (Russell & Louda 2004; van Asch & Visser 2007). Interactions that can occur only within a narrow time window are considered to be more sensitive to temporal mismatches between the partner species. Therefore, such relationships are likely to face more severe fitness consequences from phenological asynchrony, caused by shifts in species spring phenologies under climate change.

Changes in species phenologies, associated with climate change, have been well-documented in many systems across the world (Root *et al.* 2003; Parmesan 2007). These results emphasize the need for a better understanding of the mechanisms of phenology regulation and ecological consequences of phenological mismatches between interacting species for food webs and communities. The observed changes in phenologies are mostly associated with spring advancements of different magnitudes (Menzel *et al.* 2006; Parmesan 2007), although delays as well as the absence of response are also observed (Cook, Wolkovich & Parmesan 2012). Negative effects of phenological shifts include species' exposure to unfavourable environmental conditions (e.g. cold spells in early springs) and weakening the strength of species interactions or even their disruptions (e.g. Russell and Louda 2004; Liu *et al.* 2011; Boggs

and Inouye 2012; Høye et al. 2013). A decrease in temporal overlap between the interacting organisms can be a result of phenological shifts in opposite directions between the species or asymmetric changes in a similar direction (Root *et al.* 2003; Parmesan 2006, 2007; Cook *et al.* 2012).

Although the impacts of phenological asynchrony are potentially of great importance for predicting both the persistence of individual species (demographical declines or outbreaks (e.g. Lange et al. 2006; Høye et al. 2013; Kudo and Ida 2013) and functional aspects of natural communities (tropical cascades and range shifts (Buse *et al.* 1999; Harrington, Woiwod & Sparks 1999; Both *et al.* 2009; Thackeray *et al.* 2010; Walther 2010), ecological consequences of phenological mismatches are to a large extent unexplored. Asymmetric phenological shifts between insects and plants can weaken previously existing herbivore – host plant species interactions and lead to a shift in host use (Liu *et al.* 2011). Moreover, phenological mismatches are predicted to reconfigure community interactions even if the degree of asynchrony in species phenologies is relatively moderate (Fabina, Abbott & Gilman 2010). Therefore, revealing the important factors that determine species' spring timing and how their impact may vary at different development stages of a species is an important prerequisite in predicting species phenologies and fitness consequences for the interacting organisms.

In order to estimate fitness consequences of variation in the degree of synchronicity for each of the interacting species, one needs to investigate what factors are likely to affect spring phenologies of the species, how these factors will affect the degree of phenological overlap, and how a change in the overlap may translate into species fitness. Insects, being small ectothermic organisms, are particularly sensitive to environmental temperatures and commonly use them as cues to regulate their life cycle. Spring temperatures, therefore, are the primary cause of yearly variation in spring emergence, as well as phenological shifts due to climate warming. Thermal sensitivity of species to spring temperatures determines their relative developmental rate and thereby the

timing and the degree of overlap between insect herbivores and host plants. The fitness of insect herbivores, however, is determined not only by the ability to synchronize with the period of host plant availability, but also to successfully complete development before the plants become unsuitable for feeding (e.g. Feeny, 1970; Stamp & Deane, 1990; Nava-Camberos *et al.*, 2001). Here, relative larval growth and host plant maturation are strongly affected by thermal conditions during development as well (Stamp & Deane 1990; Hill & Hodkinson 1992). Therefore, studies on plant-insect synchrony are not complete without further investigation of the outcome of the interaction in relation to temperature. Another important aspect is that temperate insects typically spend winter in the state of developmental arrest – diapause. Among other important roles, diapause prevents insects from resuming development during warm periods of weather fluctuation before spring. Insects, therefore, need to terminate diapause before post-winter development can take place. As a result, diapause duration and requirements for its termination contribute to spring phenologies of insect herbivores as well and must be considered when predicting phenological events.

The four papers of this thesis address all these factors determining spring phenology in herbivorous butterflies. They investigate spring phenologies and phenological synchrony between a herbivore and its host plants in the context of climate change and aim to answer the following key *questions*:

- How may the timing of spring emergence in herbivorous butterflies be affected by diapause dynamics and thermal reaction norms of their post-winter development? (**Paper I and II**)

- Do thermal reaction norms of the herbivore and its host plants differ and could the difference lead to shifts in spring synchronicity between the species and, ultimately, alter host use pattern in the butterfly? (**Paper III**)

- Does the degree of synchronicity between the butterfly emergence and host plant reproduction affect fitness of the two interacting species? And does

thermal sensitivity differ between herbivorous larvae and host plants? (**Paper IV**)

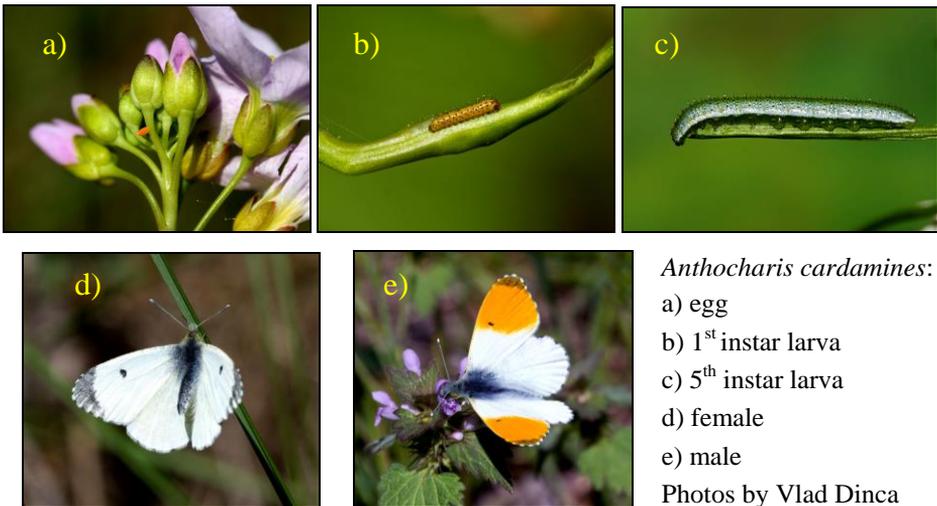
- Is there latitudinal variation in traits that determine spring phenologies and do the answers to the questions above differ depending on latitudinal aspect? (Papers I-IV)?

### **Study system**

Species depending on synchronicity with short periods of resource availability are considered to be more vulnerable to phenological shifts caused by climate change (van Asch & Visser 2007). Such species have a higher risk of mistiming with lower trophic levels if phenological responses are divergent among levels, for instance if phenological changes of insect herbivores and their host plants vary in magnitude (Parmesan 2006; van Asch & Visser 2007). For this reason, generalist species with broader larval diet are expected to experience relatively moderate spring advances due to synchronization with host plants. Even though these species are affected by temperature as well, they have a greater chance that at least some of their host plant species would have spring phenologies similar to them (Dennis and Shreeve 1991; Forrest and Miller-Rushing 2010; but see Diamond et al. 2011). Furthermore, univoltine insects with a fixed overwintering life stage are thought to have a less flexible phenology and therefore suffer the strongest negative impact under climate change (Bale & Hayward 2010).

We used *Anthocharis cardamines* (the orange tip butterfly) and five of its most commonly used Brassicaceae host plant species as a model system for the following reasons. First, adult *A. cardamines* butterflies emerge from pupae in spring and the butterfly larvae feed on the growing reproductive organs of the host plant species. Therefore, both the flight time of adult butterflies and development of larvae depend on a short period of resource availability, implying that the interaction refers to the most vulnerable “time-limited” type. Second, *Anthocharis cardamines* is among the butterfly species

that have most strongly advanced their spring emergence for the last 20-30 years (Diamond *et al.* 2011; Karlsson 2014; Navarro-Cano *et al.* 2015) and therefore, its spring phenology is likely to be particularly sensitive to climate warming. Third, *Anthocharis cardamines* is an obligatory univoltine species, which are considered to have a less flexible phenology and suffer the most pronounced negative impacts from changing climate (Post & Forchhammer 2008; Bale & Hayward 2010). Finally, annual and perennial plant species reveal different magnitude of shifts in spring phenologies (Fitter & Fitter 2002); and host plants of *A. cardamines* include both annual and perennial species.



A part of the studies involved another pierid butterfly – *Pieris napi* (the green-veined white). Larvae of this butterfly feed on green leaves of various Brassicaceae plants and, therefore, are not limited by a short period of plant reproduction, and in the study area have two generations during the growing season. Thus, the two butterfly species are oligophagous and to a large extent share plant species range. However, *A. cardamines* can be referred to as phenological specialist, depending on a particular developmental stage of the host plants. In contrast, *P. napi* can be regarded as phenological generalist,

utilizing plants at any developmental stage as long as they have green leaves. These features make the two species interesting to compare for possible adaptations in life-history traits, associated with the different feeding strategies.

## **Background to the studies**

### *Diapause dynamics and phenology*

In order to emerge in spring at the right time to meet favourable environmental conditions or to match with a certain host plant stage, insect herbivores need to resume development after the winter period of developmental arrest. Usually post-winter development begins in response to the onset of permissive environmental conditions after diapause is terminated (Košťál 2006). Exposure to favourable conditions before this point does not lead to termination of diapause and resumption of development, as many species are not sensitive to environmental cues during the period of endogenous developmental arrest (Tauber & Tauber 1976; Košťál 2006). Therefore, diapause duration and factors influencing it affect life cycle timing of insects in spring. Insects with shorter diapause that are not limited by resource availability are likely to strongly advance their spring activities and demonstrate rapid phenological shifts in response to warmer winters and earlier springs, associated with climate change (Forrest & Miller-Rushing 2010). Conversely, species with long diapause and species with the so-called chilling requirements (i. e. a certain number of “chilling degree-days” below the developmental threshold (Hodek 1996, 2002) are expected to have developmental delays rather than advancements in spring after warmer and/or shorter winters, since the post-winter development can resume only after the chilling thresholds are met (Bale & Hayward 2010; Cook *et al.* 2012; Williams, Henry & Sinclair 2015). Concerning the two butterfly species, used in our study, only *P. napi* is known to vary the timing of adult emergence

depending on duration of cold winter conditions (Forsberg & Wiklund 1988). Whether this variation was due to requirement of a certain diapause length, independent of temperatures, or due to accumulation of cold days, is not clear. As for the other butterfly species – *A. cardamines* – such studies have not been previously done for it.

In **paper I** we investigate latitudinal variation in diapause duration and existence of chilling requirements that influence post-diapause development in two butterfly species *A. cardamines* and *P. napi*.

### *Post-winter thermal reaction norms*

Phenological responses of ectothermic organisms are strongly influenced by ambient temperatures (Parmesan, 2006). Therefore climate change, associated with increase in average temperatures, has entailed shifts in phenologies of many species. All phenotypic trait values (e.g. growth rate, which in its turn determines timing of life-cycle events) that can be expressed by a given genotype under a range of environmental temperatures can be described by thermal reaction norms (Huey & Kingsolver 1989). Many ectotherms, and particularly insects, have evolved genetically based growth capacities increasing with latitude, which are thought to be an adaptation to strong gradients in seasonality (Conover & Schultz 1995). This type of latitudinal pattern is called countergradient variation in growth, and is engendered by the need to maximize reproductive success and survival under decreasing length of the growing season at higher latitudes (Conover & Schultz 1995). The opposite pattern –cogradient variation (Conover & Schultz 1995) – is mainly found in morphological traits, like body shape or body size (Conover, Duffy & Hice 2009). So far, cogradient patterns in growth rate have been described only in relation to the so-called “saw-tooth” phenomenon, when the rate of development sharply decreases at certain latitude due to relaxed time limitation in a population, passing to a lower number of

generations (Roff 1980; Nygren, Bergström & Nylin 2008; Välimäki *et al.* 2013). In this situation when there is just not enough time to produce two generations individuals have relatively more time for development when producing only a single generation. Therefore, selection favors slower development, as maintaining high growth rates can be associated with tradeoffs with other life history traits and with predation risk (Roff 1980; Gotthard 2000). However, high rate of gene flow between populations may counteract any local genetic differentiation. If so, any observed differences in growth rate between populations are caused only by manifestation of one common reaction norm in response to variation in local thermal conditions. Thus, differences in the field can be due to different genotypes or to phenotypic plasticity, and disentangling the basis of population variability is a key step in understanding the nature of variation in phenological responses to the same environmental change (Phillimore *et al.* 2012).

In **paper II** latitudinal variation in thermal reaction norms of pupal growth rate in two butterfly species *A. cardamines* and *P. napi* was explored in order to test if the timing of butterfly emergence in the field is determined by genetic differentiation (local adaptations) or reaction norms (phenotypic plasticity). Here, pupal developmental rate in the post-winter period is an important trait that regulates the timing of the butterflies' emergence, which in its turn determines the degree of temporal overlap with the host plants.

### *Synchrony in the beginning of interaction*

Reproductive success and survival of many herbivorous insects in any given season depend on the degree of phenological synchrony (i.e. simultaneous emergence or development (van Asch & Visser, 2007) with the host plants. If ovipositing female butterflies emerge too early, they can live for some period “waiting” for the host plants to become available during their lifetime, which may last several weeks. However, the longer the “waiting”

period, the higher risk of mortality before the beginning of egg-laying. If butterflies emerge too late, they may not have time to realize their fecundity or may be outcompeted by other females for the available/suitable host plants since each female oviposits a single egg per plant individual (Wiklund & Åhrberg 1978; Dempster 1992). Therefore, a shorter period between butterfly emergence and plant availability is likely to increase female reproductive success.

Since dormant herbivores cannot use the actual abundance of plants as a cue for starting their own development, they need to predict the timing of the relevant phenological events in host plants and develop accordingly in order to emerge at the right time (Visser *et al.* 2010). In this case natural selection would favor developmental plasticity in relation to cues that effect phenology of the host plants, and temperature is one of the most important and universal seasonal cues for different groups of organisms (Dennis & Shreeve, 1991). Direction and the relative magnitude of change in phenologies between the herbivores and host plants in response to new thermal environments, caused by spring warming, determine whether the phenological overlap between them will persist.

In **paper III** we explored how phenological synchrony between the emergence of *A. cardamines* and reproductive stages of its host plants was affected by their relative thermal sensitivity under a range of spring conditions.

#### *Interaction outcome depending on the degree of synchrony in phenology*

Finally, does the degree of phenological synchrony between a plant and a herbivore affect their respective fitness? Several studies have demonstrated negative effects of herbivores emerging too early (due to starvation) and too late (due to accumulation of defensive compounds by host plants) (e.g. Feeny 1970; Stamp and Deane 1990). The consequences of a herbivore's timing for the host plants (represented mainly by tree species) were not estimated within

the framework of those studies. While accumulation of secondary metabolites can also take place in herbaceous host species (e.g. Brown et al. 2003), they pose an additional challenge for less mobile herbivores because of their typically smaller size and rapid development (especially in annuals) in response to increasing temperatures (Atkinson & Porter 1996). As both plant and larval development after the beginning of the interaction (i.e. oviposition) are influenced by thermal environment, depending on the relative thermal sensitivity in their growth rates either a larva of *A. cardamines* may outgrow the plant and consume all its reproductive organs, or a plant may mature and cast the seeds before the larva completes its development. For example, temperature was shown to affect larval survival in *Euphydryas editha bayensis* by influencing the rate of senescence in some of its host plant species (Hellmann 2002).

In **paper IV** the combined effect of the degree of phenological overlap in the beginning of the insect-plant interaction and thermal conditions after egg-laying was investigated for both *A. cardamines*' larvae and different host plant species. Larval performance and risk of being outgrown by the plant were estimated for the butterfly, while the probability of outgrowing a larva and form mature seeds was assessed for each of five host plant species.

## **Results and conclusions**

**Paper I** The two species of the butterflies showed distinct latitudinal patterns both in diapause duration and the existence of chilling requirements. Diapause duration of the phenological generalist *P. napi* showed a latitudinal increase that is likely to be adaptive as winters are longer at higher latitudes. Longer diapause and lower metabolic rates, associated with it, keep insects from resuming development under short-term temperature fluctuations as well as from depleting energy nutrient storage (Denlinger 2002; Hahn & Denlinger 2007; Williams *et al.* 2012, 2015). *Pieris napi* was also found to have chilling

requirement, as diapause duration decreased with pupal exposure to lower temperature during winter. In contrast, the phenological specialist *A. cardamines* exhibited relatively short diapause duration in all sampled populations, independent of latitudinal origin. In addition, no chilling requirement in diapause termination was detected for this species.

We interpret these differences in overwintering strategies between the two butterfly species as the result of selection to synchronize spring emergence with favourable abiotic conditions in *P. napi*, whilst in *A. cardamines* timing to the particular developmental stages of host plants is under stronger selection. As a consequence, warmer and shorter winters may cause developmental delays in northern populations of *P. napi* but have no effect on spring phenology of *A. cardamines*.

**Paper II** Both species of butterflies revealed cogradient latitudinal variation in post-winter developmental time. However, the pattern of variation indicates that these latitudinal clines are due to different reasons in the two species. The cogradient pattern of *A. cardamines* was likely due to selection for phenological synchronicity with its local host plant community, most species of which also demonstrated cogradient variation in the initiation of reproduction (Toftgaard *et al.*, 2015 in review). The latitudinal pattern in *P. napi* was primarily an effect of slow development of only a fraction of pupae from the most northern population, which may be due to the presence of both bivoltine and univoltine strategies in this northern location, i.e. due to the “saw-tooth” effect.

**Paper III** Pupal development in three latitudinally different populations of *A. cardamines* demonstrated temperature-mediated phenological plasticity similar to that of their host plants. This indicates that the butterflies were well-synchronized with the majority of the plant species across the temperature range, which may be the result of the existing preadaptation caused by highly variable environmental conditions between years. However, since some of the

plant species demonstrated higher thermal sensitivity than the butterflies, especially in the northernmost population, we conclude that there is a possibility for host use shifts in *A. cardamines* under spring warming.

**Paper IV** In general, earlier reproductive stages of host plants at the time of oviposition as well as warmer temperatures were overall beneficial for the butterfly larvae, although the effects also were plant species-specific. This implies that the degree of synchrony of the butterflies' emergence with early reproductive period in host plants is likely to be important for butterfly fitness, and even moderate mismatches may have negative consequences. On the other hand, the impact was mediated by host plant species identity and therefore the adverse effects from asynchrony are likely to be buffered by a wide range of plant species, utilized by *A. cardamines*.

Host plant fitness was affected neither by the degree of phenological synchrony nor by the subsequent temperature and was dependent only on the species identity.

The results of these four studies suggest that the plant-herbivore system of *A. cardamines* and its host plants, although being temporally constrained, is unlikely to experience detrimental phenological asynchrony under warmer seasonal conditions. In general, the butterflies and host plants demonstrated a quite high degree of synchronicity under a range of spring temperatures both by the beginning of the interaction (oviposition) and in the relative growth rates during it. However, the comparative experiments on pupal and plant development (Paper III) suggest that warmer springs may induce greater variation in plant phenological stages at the time of butterfly emergence in the northernmost population. This may potentially decrease availability of *C. pratensis* – one of the most reliable and widespread host plant, – as well as *A. glabra*. Thus, changes in host use patterns may be expected in the northern population in response to warmer spring temperatures. That can be reinforced by larval ability to develop quicker under higher temperatures and with a

greater probability complete development before the host plants (Paper IV). Finally, the predicted climate warming during winter would add an extra touch to the picture. *Anthocharis cardamines* appeared to have short diapause duration and no or very low chilling requirements at all the sampled latitudes. This makes the butterfly ready to resume post-diapause development as soon as the conditions become permissive, advancing its emergence with warmer winters and earlier springs. On the other hand, some of its host plants, like *A. thaliana* (Simpson & Dean 2002), *C. bursa-pastoris* (Neuffer & Hurka 1986) and *C. pratensis* (Thurling 1967), are known to have winter chilling requirements, which may cause delays (Cook *et al.* 2012) in their spring phenologies in warmer and shorter winters and make these plants available for oviposition at earlier reproductive stages.

Thus, despite that temporally constrained species interactions are thought to be particularly sensitive to phenological asynchrony and therefore most vulnerable to climate change, they may still demonstrate a high degree of resilience to factors potentially leading to their disruption. Features that are likely to contribute to persistence of such systems are species diversity of the interactions (i.e. generalist strategy, like larval diet breadth) and a high degree of phenotypic plasticity that is similar between the species as a result of coevolution and adaptation to high environmental variability among years.

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## Svensk sammanfattning

Fenologiska förändringar samt förändringar i graden av fenologisk synkronisering mellan interagerande arter har under den senaste tiden fått mycket uppmärksamhet, särskilt i samband med klimatförändringar. Arter som tidigare var synkroniserade, kan, som en följd av dessa fenologiska förändringar, bli skilda från varandra i tid så interaktionen inte längre är möjlig. Denna typ av förändringar kan påverka enskilda arter, t.ex. genom ökad variation i abundans, men kan även påverka hela ekosystem genom att arter på olika trofiska nivåer inte längre är tidsmässigt matchade, eller genom förändringar i samhällsstruktur. Denna avhandling undersöker effekterna av temperatur och fenologisk synkronisering under våren på interaktionen mellan en herbivor insekt, aurorafjärilen *Anthocharis cardamines*, och dess värdväxter ur familjen Brassicaceae.

**Artikel I** visar hur vinterns längd och temperaturförhållanden under fjärlens puppdiaaus påverkar kläckningen av adulter på våren samt att dessa egenskaper kan variera mellan arter som skiljer sig åt i födopreferenser. **Artikel II** visar att de reaktionsnormer som beskriver hur temperaturen under våren påverkar utvecklingshastighet efter övervintring varierar längs latitud, så att populationer längre norrifrån utvecklas långsammare än populationer från mer sydliga områden i hela det undersökta temperaturintervallet.

**Artikel III** visar att temperaturberoende fenologisk plasticitet hos *A. cardamines* och flertalet av dess viktigaste värdväxter är likartade inom populationer från olika latituder. Detta tyder på att fjärlens tajming till värdväxternas utveckling under våren är väl anpassad för att klara av variation i temperaturförhållanden. **Artikel IV** undersöker betydelsen av variation i fenologisk synkronisering mellan fjärlen och dess värdväxter samt temperaturförhållanden under våren då larverna tillväxer på sina värdväxter. Här undersöktes effekterna av detta på viktiga komponenter av både fjärlens och växternas fitness. Graden av den fenologisk synkronisering och

temperaturen efter äggläggningen var båda viktiga faktorer för fjärlens överlevnad och tillväxt. Däremot hade dess faktorer ingen signifikant betydelse för växtens reproduktiva framgång då de attackerades av fjärlslarver.

De fyra artiklarna i avhandlingen visar att de utvecklingsmässiga anpassningar som leder till att insekts herbivorer lyckas matcha sin livscykel till variation i värdväxternas fenologi mellan olika år, leder till att interaktionen också är relativt resilient mot förändrade temperaturförhållanden som kan uppstå p.g.a mer storskaliga klimatförändringar. Resultaten visar också att art interaktioner som är begränsade till ett kort tidsfönster under säsongen inte nödvändigtvis är speciellt känsliga för fenologiska förändringar om de involverar arter som är generalister i andra avseenden av interaktionen.

## Doctoral theses from the Department of Zoology

1906. Nils Holmgren: Studien über südamerikanische Termiten.
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Elin Sigvaldadóttir: Systematics of Spionidae and *Prionospio* (Polychaeta).

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- 1998.** Simon G.M. Ndaro: Ecological aspects of soft bottom meiofauna in Eastern Africa.
- Efthimia Antonopoulou: Feedback control of reproduction in Atlantic salmon, *Salmo salar*, male parr.
- Petra Wallberg: Distribution and fate of polychlorinated biphenyls within the pelagic microbial food web.
- Carl Rolff: Stable isotope studies of contaminant and material transport in Baltic pelagic food-webs.
- Marcus Öhman: Aspects of habitat and disturbance effects on tropical reef-fish communities.
- Cecilia Kullberg: Behaviour under predation risk in birds.
- Thomas Lyrholm: Sperm whales: Social organization and global genetic structure.
- Min-Yung Kim: Neuropeptides related to tachykinins and leucokinins in the developing nervous system of insects.
- Salim M. Mohammed: Nutrient dynamics and exchanges between a mangrove forest and a coastal embayment: Chwaka Bay, Zanzibar.
- Gunilla Ejdung: Predatory processes in Baltic benthos.
- Virpi Sjöberg-Lindfors: Butterfly life history and mating systems.
- 1999.** Karl Gotthard: Life history analysis of growth strategies in temperate butterflies.
- Niklas Janz: Ecology and evolution of butterfly host plant range.
- Staffan Jakobsson: Target organs for androgens in two teleost fishes, Atlantic salmon, *Salmo salar*, and three-spined stickleback, *Gasterosteus aculeatus*.
- Anna Thessing: Genetic and environmental factors influencing growth and survival in willow tits *Parus montanus*.
- Kenneth Ekvall: Alloparental care and social dynamics in the fallow deer (*Dama dama*).
- Gunilla Ericson: <sup>32</sup>P-postlabelling analysis of DNA adducts in fish as a biomarker of genotoxic exposure.
- Karin Maria Björkman: Nutrient dynamics in the North Pacific subtropical gyre: Phosphorus fluxes in the upper oligotrophic ocean.
- 2000.** Olle Israelsson: *Xenoturbella*.

Carl-Adam Wachtmeister: The evolution of courtship rituals.

Cecilia Bornestaf: Mechanisms in the photoperiodic control of reproduction in the three-spined stickleback, *Gasterosteus aculeatus*.

Olle Brick: Risk assesement and contest behaviour in the Cichlid fish, *Nannacara anomala*.

Gabriella Gamberale-Stille: On the evolution and function of aposematic coloration.

Helene Modig: Responses of Baltic soft-bottom invertebrates to settled organic material.

**2001.** Tomislav Vlastic: Gonad and ejaculate allocation in alternative reproductive tactics of Salmon and Trout with reference to sperm competition.

Susanne Stenius: Cooperation and conflict during reproduction in polyterritorial wood warblers (*Phylloscopus sibilatrix*).

Ruben Tastàs-Duque: Studies of Cecidomyiidae (Diptera).

Sven Burreau: On the uptake and biomagnification of PCBs and PBDEs in fish and aquatic food chains.

Åsa Winther: Distribution and actions of insect tachykinin-related peptides.

Fang Fang Kullander: Phylogeny and species diversity of the South and Southeast Asian cyprinid genus *Danio* Hamilton (Teleostei, Cyprinidae).

Magnus G. S. Persson: Distribution and modulatory action of neuropeptides in the insect ventral nerve cord.

Minna Miettinen: Egg carrying in the golden egg bug.

Stefano Gihrlanda: Towards a theory of stimulus control.

Annkristin H. Axén: Behaviour of Lycaenid butterfly larvae in their mutualistic interactions with ants.

**2002.** Patrik Lindenfors: Phylogenetic analyses of sexual size dimorphism.

Patrik Börjesson: Geographical variation and resource use in harbour porpoises.

Michael Norén: Phylogeny and classification of prolecithophoran flatworms.

Johan Liljeblad: Phylogeny and evolution of gall wasps (Hymenoptera: Cynipidae)

Ulf S. Johansson: Clades in the "higher land bird assemblage"

**2003.** Ulf Norberg: Evolution of dispersal and habitat exploration in butterflies.

Johan Lind: Adaptive body regulation in the life history of birds.

Olle Karlsson: Population structure, movements and site fidelity of grey seals in the Baltic Sea.

Helena A D Johard: Neuropeptide signaling in insects: peptide binding sites, tachykinin receptors and SNAP-25

Bodil Elmhagen: Interference competition between arctic and red foxes.

Henrik Lange: Social dominance and agonistic communication in the great tit.

Anna Hellqvist: The brain-pituitary-gonadal axis and gonadotropic hormones in the three-spined stickleback, *Gasterosteus aculeatus*.

Anders Bignert: Biological aspects and statistical methods to improve assessments in environmental monitoring.

Julia Carlström: Bycatch, conservation and echolocation of harbour porpoises.

Kenth Svartberg: Personality in dogs.

Susanna Hall: Moulting strategies in relation to migration in long-distance migrants

Miklós Páll: Role of 11-ketotestosterone and prolactin in the control of reproductive behaviour in the male three-spined stickleback, *Gasterosteus aculeatus*.

Bo Delling: Species diversity and phylogeny of *Salmo* with emphasis on southern trouts (Teleostei, Salmonidae).

Karolina Westlund: On post-conflict affiliation in humans and other primates - methodological considerations.

Malin Ah-King: Phylogenetic analyses of parental care evolution.

**2004.** Jonas Bergström: The evolution of mating rates in *Pieris napi*

Jörgen Ullberg: Dispersal in free-living, marine, benthic nematodes: passive or active processes?

Eva Stensland: Behavioural ecology of Indo-Pacific bottlenose and humpback dolphins.

Helena Strömberg: Benthic cryptofauna and internal bioeroders on coral reefs.

Liselotte Jansson: Evolution of signal form.

Martin Irestedt: Molecular systematics of the antbird-ovenbird complex. (Aves: Furnariidae)

Jesper Nyström: Predator - prey interactions of raptors in an arctic community.

Ola Svensson: Sexual selection in *Pomatoschistus* - nests, sperm competition, and paternal care.

**2005.** Anders Bergström: Oviposition strategies in butterflies and consequences for conservation.

Helena Elofsson: Sperm motility in Gasterosteiform fishes. The role of salinity and ovarian fluid.

Fredrik Stjernholm: Allocation of body resources to reproduction in butterflies.

Fredrik Dalerum: Sociality in a solitary carnivore, the wolverine.

Ana Beramendi: Morphological and functional studies on the *Drosophila* neuromuscular system during postembryonic stages.

Georg H. Nygren: Latitudinal patterns in butterfly life history and host plant choice.

Love Dalén: Distribution and abundance of genetic variation in the arctic fox.

Ulrika Kaby: Attacking predators and fleeing prey: detection, escape and targeting behaviour in birds.

**2006.** Yasutaka Hamasaka: Multiple neurotransmitter inputs modulate circadian clock neurons in *Drosophila*.

Rasmus Hovmöller: Molecular phylogenetics and taxonomic issues in dragonfly systematics (Insecta: Odonata)

Adrian Vallin: On the protective value of conspicuous eyespots in Lepidoptera.

Ryan Tyge Birse: Tachykinin-related peptide signaling and its role in metabolic stress in *Drosophila*.

Lissåker Maria: Paternal care, filial cannibalism and sexual conflict in the sand goby, *Pomatoschistus minutus*.

**2007.** Ulrika Alm Bergvall: Food choice in fallow deer - experimental studies of selectivity.

Petra Souter: Causes and consequences of spatial genetic variation in two species of scleractinian coral in East Africa.

Hanne Løvlie: Pre- and post-copulatory sexual selection in the fowl, *Gallus gallus*.

Kajsa Garpe: Effects of habitat structure on tropical fish assemblages.

Erica Sjölin: Tubificids with trifold chaetae: morphology and phylogeny of *Heterodrilus* (Clitellata, Annelida)

**2008.** Enfjäll Karin: Mobility and emigration in butterflies.

Berger David: Body size evolution in butterflies.

Dehghani Reihaneh: Aspects of carnivoran evolution in Africa.

Ohlson I. Jan: Molecular phylogeny of tyrant flycatchers, cotingas, manakins and their allies (Aves: Tyrannida)

Weingartner Elisabeth: Phylogenetic perspective on host plant use, colonization and speciation in butterflies.

Mehnert Kerstin: Circadian plasticity in the neuromuscular junction of *Drosophila melanogaster*.

Larsson Lena: disentangling small genetic differences in large Atlantic herring populations: comparing genetic markers and statistical power.

**2009.** Pena Carlos: Evolutionary history of the butterfly subfamily Satyrinae (Lepidoptera: Nymphalidae).

Almbro Maria: Escape flight in butterflies.

Hallgren Stefan: Aromatase in the guppy, *Poecilia reticulata* Distribution, control and role in behaviour.

Mwandaya Augustine: Fish community patterns in Tanzanian mangrove creeks.

Envall Ida: Evolutionary Perspectives on Naidinae (Annelida, Clitellata, Naididae): Molecular and Morphological Revelations.

Henshaw Ian: Avian migration: the role of geomagnetic cues.

Balogh Alexandra: Predator psychology and mimicry evolution - a theoretical analysis.

Kodandaramaiah Ullasa: The dispersal-vicariance pendulum and butterfly biogeography.

Dimitrova Marina: Life at stake when playing hide and seek.

Friberg Magne: The evolutionary ecology of niche separation.

Wilhelmsson Dan: Aspects of offshore renewable energy and the alterations of marine habitats.

**2010.** Amir Omar: Biology, ecology and anthropogenic threats of Indo-Pacific bottlenose dolphins in east Africa.

Malm Tobias: Climbing the Trichoptera Tree - Investigations of Branches and Leaves.

Nyström Veronica: Studies of declining populations - temporal genetic analyses of two arctic mammals.

Espeland Marianne: Diversification on an ancient Darwinian island.

Kahsai Tesfai Lily: Distribution and modulatory roles of neuropeptides and neurotransmitters in the *Drosophila* brain.

Palmé Anna: Assessing and monitoring genetic patterns for conservation purposes with special emphasis on Scandinavia.

Liao Te-Yu: A phylogenetic analysis of rasborin fishes (Teleostei, Cyprinidae).

Norén Karin: Genetic structure in the North - population connectivity and social organization in the Arctic fox.

**2011.** Andersson Mathias: Offshore wind farms - ecological effects of noise and habitat alteration on fish.

Bergman Martin: The evolution of territoriality in butterflies.

Enell Lina: Chemical signalling in the *Drosophila* brain.

Aronsson Hanna: On sexual imprinting in humans.

Kolodziejczyk Agata: Chemical circuitry in the visual system of the fruitfly, *Drosophila melanogaster*.

Särnblad Hansson Anna: Ecology and genetic population structure of Indo-Pacific bottlenose dolphins in East Africa.

Yahya Saleh: Habitat structure, degradation and management effects on coral reef fish communities.

Söderberg Jeannette: Neuropeptides and GABA in control of insulin producing cells in *Drosophila*.

Johansen Aleksandra: Seasonal change in defensive coloration in a shieldbug.

Charlier Johan: Monitoring gene level biodiversity - aspects and considerations in the context of conservation.

Tobias Kånneby: Gastrotricha of Sweden - Biodiversity and Phylogeny.

**2012.** Lina Söderlind: Life history consequences of host plant choice in the comma butterfly.

Magnus Geland: Babblers, Biogeography and Bayesian Reasoning.

Jessica Slove Davidson: The plasticity and geography of host use and the diversification of butterflies.

Marianne Aronsson: Colour patterns in warning displays.

Yi Ta Shao: The brain-pituitary-gonadal axis of the three-spined stickleback, *Gasterosteus aculeatus*.

Neval Kapan: Regulation of insulin producing cells, stress responses and metabolism in *Drosophila*.

Helena Larsdotter Mellström: Life history evolution in a bivoltine butterfly.

**2013.** Tomas Meijer: To survive and reproduce in a cyclic environment - demography and conservation of the Arctic fox in Scandinavia.

Martin Olofsson: Antipredator defence in butterflies.

Julia Stigenberg: Hidden Creatures - systematics of the Euphorinae (Hymenoptera).

Emma Lind: Genetic response to pollution in sticklebacks; natural selection in the wild.

Oskar Henriksson: Genetic connectivity of fish in the Western Indian Ocean.

George Sangster: Integrative taxonomy of birds: Studies into the nature, origin and delimitation of species.

Jiangnan Luo: Regulation of insulin signaling and its developmental and functional roles on peptidergic neurons in the *Drosophila* central nervous system.

- 2014.** Mija Jansson: Assessing inbreeding and loss of genetic variation in canids, domestic dog (*Canis familiaris*) and wolf (*Canis lupus*), using pedigree data.

Marianne Pasanen Mortensen: Anthropogenic impact on predator guilds and ecosystem processes - Apex predator extinctions, land use and climate change.

Peter Hellström: Predator responses to non-stationary rodent cycles.

Inger Haugen: The diapause switch - Evolution of alternative developmental pathways in a butterfly.

Inga Meyer-Wachsmuth: Through the magnifying glass - The big small world of marine meiofauna.

Eleftheria Palkopoulou: Genetic structure, demographic change and extinction dynamics in the collared lemming and woolly mammoth.

Jean-Luc Tison: Genetic variation and inference of demographic histories in non-model species.

- 2015.** Karolina Tégélaar: Dynamics of the aphid-ant mutualism.