

HELEN VELLAU

Reaction norms for size and
age at maturity in insects:
rules and exceptions



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Reaction norms for size and
age at maturity in insects:
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Larval growth experiment in progress, focus on instars. *Photo by Siiri-Lii Sandre.*

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by the subsequent Roman numbers:

- I** Teder, T., Vellau, H. & Tammaru, T. Diet-induced reaction norms for development time and body size in insects: a quantitative review and synthesis. *Submitted manuscript*
- II** Tammaru, T., Vellau, H., Esperk, T. & Teder, T. The conservative reaction norm for size and age at metamorphosis: an instar-specific approach in insects. *Submitted manuscript*
- III** Vellau, H. & Tammaru, T. 2012. Larval crowding leads to unusual reaction norms for size and time at maturity in a geometrid moth (Lepidoptera: Geometridae). *European Journal of Entomology*, 109: 181–186.
- IV** Vellau, H., Sandre, S.-L. & Tammaru, T. 2013. Effect of host species on larval growth differs between instars: The case of a geometrid moth (Lepidoptera: Geometridae). *European Journal of Entomology*, 110: 599–604.
- V** Vellau, H., Leppik, E., Frerot, B. & Tammaru, T. 2013. Detecting a difference in reaction norms for size and time at maturation: pheromone strains of the European corn borer (*Ostrinia nubilalis*: Lepidoptera, Crambidae). *Evolutionary Ecology Research*, 15: 589–599.

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Author's contribution to these papers:

	I	II	III	IV	V
Original idea & study design		*			*
Data collection	*	*	*	*	*
Data analysis			*	*	*
Manuscript preparation	*	*	*	*	*

I. INTRODUCTION

One of the primary factors that influences the fitness of an individual is its size. This is particularly true in the case of insects, where the body size has been shown to correlate strongly with reproductive success (Roff 1992, Stearns 1992, Honek 1993). Advantages of large adult size in females are mainly related to increased fecundity (Honek 1993, Tammaru et al. 1996, 2002), egg size (Oberhauser 1997, Garcia-Barros 2000) and better dispersal abilities (Ellers et al. 1998). On the other hand, males benefit from larger size through an increased number of copulations via success in male-male competition (Goldsmith & Alcock 1993), higher mobility (Tammaru et al. 1996) or advantages in sperm competition (Nylin & Gotthard 1998).

It is often fairly easy to assess the benefits of larger body size, but direct evidence of the cost remains unclear (Blanckenhorn 2000). Still, it has been suggested that predation pressure may increase in connection to increasing size, but this effect is highly dependent on predator taxon (Rommel et al. 2011). A clear trade-off between growth rate and predation risk has been shown (Gotthard 2000); however, higher mortality risk on larger larvae may also occur irrespective of growth rate (Berger et al. 2006). Also, larger individuals may suffer more from intrinsic factors such as less efficient energy use, greater heat stress or larger oxidative damage (Blanckenhorn et al. 2011, Dmitriew 2011). Additionally, there could be a trade-off at the level of resource allocation if nutrients are limited: investing in growth may negatively affect other vital functions – e.g. immunity or activity may be inhibited (Zera & Harshman 2001, Dmitriew 2011).

Furthermore, a rather universal cost of larger size is a higher mortality due to longer development time – early maturing organisms may escape unfavourable conditions and have a higher probability of surviving to maturity (Stearns 1992). One of the main costs associated with longer development time is the risk of being preyed upon (Hägglström & Larsson 1995, Abrams & Rowe 1996, Rommel et al. 2011). Empirical examples of costs associated with long development time also include parasitism (Benrey & Denno 1997) or delay of reproduction (leading to lower fitness; Blanckenhorn 2000). Moreover, ephemeral organisms also risk the depletion of temporary habitats (Newman 1992).

In insects, traits related to size and development time have frequently been found to be phenotypically highly plastic (Nylin & Gotthard 1998, Blanckenhorn 1999, Benard 2004). Phenotypic plasticity can be quantitatively described by a reaction norm, which is basically a response of one genotype to different environmental conditions by producing phenotypes of different character (Stearns 1992). Variation in body size and development time can be described by reaction norms, having environmental quality on abscissa. If the plasticity of a trait is high, then the reaction norm can obtain diverse shapes with either a positive or negative slope. Traditionally only one parameter is plotted as the

response variable, but the way to link both body size and development time at maturity is to form a reaction norm for both these two variables (Figure 1): a set-up called the ‘bivariate’ reaction norm (Stearns & Crandall 1984). This layout still enables a visual comparison of growth rates (although not plotted on axis), which are assumed to reflect the environmental quality: growth rates are expected to be higher in favourable conditions (the slope of the growth trajectory is steeper). From now on, a positively sloped bivariate reaction norm will be referred in the text as PRN and a negatively sloped reaction norm NRN.

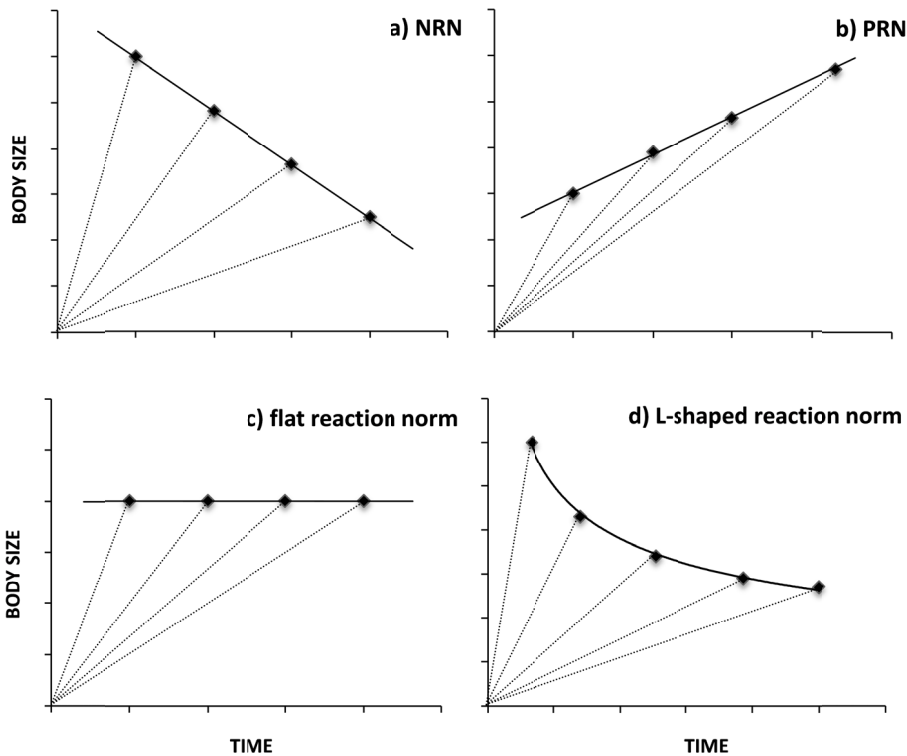


Figure 1. Bivariate reaction norms (solid line) with various shapes. Dashed lines represent growth trajectories in different environments: the steeper line stands for higher growth rate.

To fully understand the adaptivity of a trait value one must consider optimality of phenotypes in several environments or, in other words, the adaptivity of a reaction norm. As an example, differences are predicted to exist in optimal size and age at maturity between males and females. Males are expected to mature earlier when there is selection for protandry (Singer 1982, Nylin & Gotthard 1998). Early maturing males secure the chance to mate by being present when

females mature. Females, on the other hand, have frequently more to gain by having larger body size (but see Leimar et al. 1994). Nevertheless, the shape of a reaction norm is not necessarily a result of adaptation only. The adaptive evolution may be constrained by several types of costs to maintaining plasticity, as well as by limits to the ability of an organism to reach the optimal phenotype (Pigliucci 2005). There is always the possibility of some kind of constraints influencing the evolution of a trait (Smith et al. 1985, Kirkpatrick & Lofsvold 1992, Davidowitz et al. 2003), but very little empirical evidence exists (Tammara 1998, **II**). The scarcity of empirical evidence of constraints may partly be based on conceptual ambiguity: a constraint is defined and measured differently. From now on, I will follow the approach of Schwenk & Wagner (2004): constraints are involved whenever a developmental or physiological selective pressure is in conflict with ecological selective pressures, so evolutionary changes in trait value become slow or lacking.

Optimality models have generally predicted that bivariate reaction norms for size and age at maturity should have a negative slope, i.e. individuals prolonging growth will still remain smaller than their conspecifics growing for a shorter time (Roff 1992, Stearns 1992; Figure 1a). Such predictions stem from optimality models that make predictions about evolutionary equilibrium and are thus nongenetic in their approach (Scheiner 1993). One of the classical models to predict the optimal reaction norm with a negative slope was presented by Stearns & Koella (1986) who assumed that fecundity will increase with size and juvenile mortality rates decrease as age-at-maturity of parents increase. As another example, a simple model by Berrigan & Koella (1994) predicts a negative slope when assumptions (the net reproductive rate is maximized, growth is determinate, mortality does not depend on age and size at maturity) of this model are met.

Empirical examples of NRNs include responses to diet quality and quantity. These kinds of NRNs are not restricted to some specific taxa, but are very common in the animal world (Berrigan & Koella 1994, Day & Rowe 2002, **I**). For insects, individuals will grow longer but still remain smaller when larval diet is lacking some vital component. In other words, the growth rate is low in unfavourable environments. For herbivores, plant phenology may play the crucial role as a determinant of growth rates: several studies show how insect larvae grow larger when feeding on young plant parts (van Asch & Visser 2007; from now on, an herbivore = an insect consuming leaves and stalks of a living plant). Additionally, if the diet contains some deterrent, it may also cause delayed maturation at a smaller size. For example, tannins have been shown to have a negative impact on larval growth (Bourchier & Nealis 1993, **IV**). Perhaps the most studied parameter causing differences between growth rates is the host plant species, as larvae feeding on host plants they are adapted to attain larger size in shorter time compared to larvae on novel hosts (Lepidoptera: Diamond et al. 2010; Coleoptera: Keese 1998, Ueno et al. 2001). Furthermore, diet quantity can also have a direct link with insect growth: lack of food

typically results in delayed maturation and small body size (Tammaru 1998, Blanckenhorn 2006, **II**).

Reaction norms for size and age for maturity have been predicted not only to be negatively sloped but also convex, labelled L-shaped reaction norms (Figure 1d). This shape can arise from the assumption that an individual has to attain a certain size before it can undergo metamorphosis, but there is no general agreement on defining 'L-shapedness'. This was formalised by Day & Rowe (2002) who suggested the existence of a 'developmental threshold' implying that fitness would be zero for any individual below the threshold size. In consequence, individuals smaller than the threshold size (Nijhout 1975) or the critical weight (Davidowitz et al. 2003) will 'try' to prolong their development to become larger at the cost of particularly prolonged development.

There is some empirical evidence about convex reaction norms, however. For example, a study by Plaistow et al. (2004) showed strong prolongation response of a soil mite to food reduction. A recent study by Phelan & Rotiberg (2013) showed that some combinations of factors can cause almost a double delay in maturation in *Anopheles* mosquito. Also, prey density can be responsible for a threefold difference in age at maturation in *Harmonia* ladybird (Agarwala & Bhowmik 2011). However, despite several empirical examples, there is no meta-analysis that has reviewed the diet-related circumstances leading to differently shaped reaction norms.

In contrast to the apparent abundance of NRNs, several theoretical models (Stearns 1992, Abrams & Rowe 1996, Abrams et al. 1996, Marty et al. 2011) have also predicted reaction norms with a positive slope. In other words, in certain environmental conditions, some individuals are predicted to stop growing earlier and at a smaller size, while under other conditions they continue to grow and become larger. The model that applies best in the insect world is from Abrams et al. (1996), who assumed that the growth rate of an individual is subjected to adaptive variation and it can be increased at the expense of higher mortality risk. Additionally, it is beneficial to stop growing at a small size when environmental conditions are expected to change and no longer support growth, i.e. when resources are running out (Fox et al. 1999, Johansson & Rowe 1999). Another cause for an adaptive PRN can be a difference between mortality rates among environments (**III**). A modification of this assumption claims that mortality risk will differ between habitats and depend on individual size. This implies that larger body size will cause higher risk of mortality or, if higher growth rate will negatively affect the probability to survive, then selection will favour maturation at smaller body size (Nylin & Gotthard 1998).

The first situation (deteriorating environment) is widely studied, but only in a limited number of ecological situations. Those include exhaustion of discrete food resources (e.g. seeds, dung, plant stalks; Blanckenhorn 1999, Fox et al. 1999, Bonal & Munoz 2008) or onset of an unfavourable season (Tauber et al. 1986, Johansson and Rowe 1999, Johansson et al. 2001; but see Pöykkö & Hyvärinen 2012, where populations had NRN irrespective of overwintering

decision). The second situation (differing mortality risks between habitats) includes size dependent variation in predation risk (Abrams & Rowe 1996, Berger et al. 2006, Wardhaugh et al. 2013). Another frequently observed mechanism to include such variation in mortality risk is larval crowding (Wall & Begon 1987, Barnard & Geden 1993, Agnew et al. 2002); however, it is a complex case. Crowded larvae can exhaust resources and the probability of getting an infection is higher, therefore it is reasonable to escape that situation by maturing earlier at small size (Bauerfeind & Fischer 2005, **III**). On the other hand, crowding may also lead to NRNs (Tammaru et al. 2000) because crowding as such may result in deterioration of the environment, lower growth rates and delay in maturation thereby.

Perhaps the most studied environmental parameter to cause a PRN in insects is the ambient temperature (Atkinson 1994, Kingsolver & Huey 2008). The response is also known as ‘temperature-size rule’: in cooler environments individuals grow for a longer time and attain larger body size (Berrigan & Charnov 1994, Atkinson 1996; for opposite examples, see Walters & Hassall 2006). Larval size and development time can primarily be influenced by the ambient temperature, as recent work has shown that it may be the strongest constraining factor on insect fitness, followed by host plant availability (Berger et al. 2012). Despite the general acceptance of the temperature-size rule, to date no general explanation to this mechanism has been proposed (Atkinson & Sibly 1997, Angilletta & Dunham 2003; but see Callier & Nijhout 2013). However, the ‘temperature-size rule’ framework is beyond the scope of my thesis.

PRNs are more often documented in organisms other than insects. Due to economic interest, fish – representing a taxon with indeterminate growth – are widely studied. An experiment with Atlantic salmon revealed that manipulating food quality resulted in early maturation at smaller size (Jonsson et al. 2013); peculiarly, a high lipid diet resulted in earlier maturation. An example of multiple factors influencing maturation is provided by the sea trout *Salmo trutta*, where smaller males were forced to migrate (=maturation), because of competition for food and space (Landergren 2004). Similarly, spadefoot toads completed development at earlier age when food was eliminated (Morey & Reznick 2000). Fishing is a widely studied environmental factor selecting for maturation at small size and young age in several fish species, which could also be viewed as predation (Grift et al. 2003, Olsen et al. 2004, Kuparinen & Merilä 2007). However, a PRN in a flounder fish was detected, even though the population was under low fishing pressure (Barot et al. 2005). Additionally, pond drying has been shown to cause maturation at earlier age and smaller size in various amphibian larvae (Doughty & Roberts 2003, Marquez-Garcia et al. 2010, Perotti et al. 2011).

In herbivorous insects, I would consider most of the above scenarios quite improbable. For example, it is not likely that exhaustion of food has an important selective pressure (except for a few outbreaking species), because ‘the world is green’ (Hairston et al. 1960). Due to the typically strong top-down

regulation of insect populations, crowding conditions are not frequent in insects other than in those inhabiting environments with special characteristics, like cow dung or fruits. Empirical examples of PRNs exist (Shen et al. 2006, **I**), but these cases has never been systematically reviewed, nor have the ecological conditions leading to evolution of such reaction norms been thoroughly analyzed.

Besides reaction norms being negatively or positively sloped, there also exists a possibility of a reaction norm with a horizontal slope – a flat reaction norm (Diamond & Kingsolver 2012, Hector & Nakagawa 2012). This is in some contrast with optimality models which predict that phenotypic plasticity is favoured when variation between habitats is high or cost of plasticity is low (Scheiner 1993). Of course, it is statistically impossible to prove that something (the slope, in this case) is exactly zero, but nevertheless this option should not be overlooked. In principle, individuals may develop at different durations, but still reach maturity at the same size. In other words, individuals may have a ‘canalized’ or ‘targeted’ size (Stearns & Kawecki 1994, Teder et al. 2008, Liefting et al. 2009). This situation can also be viewed as a full compensation (Hector & Nakagawa 2012) when it actually pays off to prolong the development to attain the same body size as faster growing individuals. As an example, the comma butterfly *Polygonia c-album* reared on a number of natural host plants kept final size rather constant while development time differed (Nylin 1988). Females of a caddisfly had a rather flat reaction norm in response to a dry supplement diet (Jannot et al. 2008).

One way to view reaction norms is to visualize situations as shifts along two different intersecting axes (Figure 2). Reaction norms with a negative slope correspond to a shift along the axis of growth rate which is the common response to varying environmental quality in insects (**I**). In contrast, PRNs correspond to a shift along the axis of maturation decision. Also, some evolutionary changes in life history parameters can be considered as the shift along the maturation axis and therefore viewed as analogous to PRNs. A clear example of this is provided by sex-related differences in growth parameters in sexually dimorphic insects: females attain their larger size by growing for a longer time (Esperk et al. 2007, Tammaru et al. 2010). Another example will be provided in **V**. However, there is no clear comprehension on the frequency, range or environmental conditions causing the evolutionary shifts along the maturation axis.

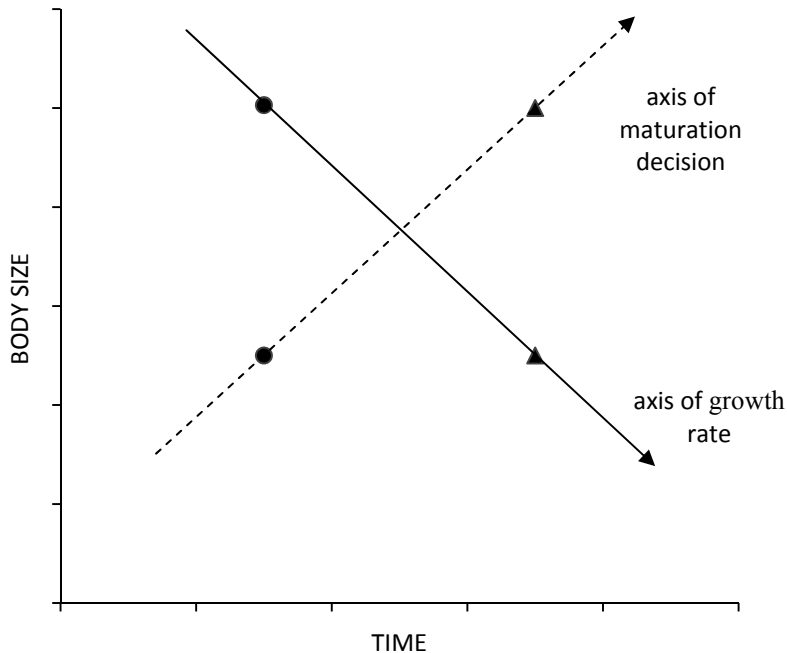


Figure 2. A way to visualize the positive reaction norms as a shift along the axis of maturation decision (modified from Tammaru et al. 2000, 2010). A plastic shift along the axis of growth rate is a common response to varying environmental quality. Each point represents a potential metamorphosis decision, i.e. a size and age at the point when growth stops. Round symbols represent sample environments, triangles represent alternative environment for the same genotype.

The aim of this thesis is to study reaction norms for size and age at maturity in insects. First, I will summarize the reviewed literature to evaluate the relative frequency of negatively and positively sloped bivariate reaction norms and discuss what could be the conditions inflicting those situations. To my knowledge, there is no such meta-analytic overview on reaction norms in different insect taxa. Second, I will present empirical studies showing the case that can be considered the general one – i.e. the L-shaped reaction norm – and some exceptions to the prevailing relationship. A novel aspect of my empirical work is the original methodology of studying larval growth curves (Tammaru et al. 2000, Esperk & Tammaru 2004, Tammaru & Esperk 2007, Tammaru et al. 2010). In particular, paying attention to specific larval instars and recording both development time and final size for separate instar is an approach not often used in case studies on evolutionary ecology of larval growth. Additionally, we rely on interim values of larval growth that allow us to estimate the instantaneous growth rate; a variable less ambiguous in comparison to the more often used integral measures, which are obtained from final weights and total developmental times only.

2. MATERIAL AND METHODS

All data for constructing bivariate reaction norms were obtained from laboratory experiments, except for paper I. To establish laboratory populations that the papers II, III and IV are based on, wild fertilized females were caught near Tartu, Estonia. At least 7 broods per species were used in each of the rearing experiments. In experiments reported in II, III, IV and V, the same traits were recorded: development time and final weight of focal instars. The morphology of the pupa was used to determine the sex of an individual. In papers III and V, ‘growth rate’ was expressed as $((\text{final weight})^{1/3} - (\text{initial weight})^{1/3})/\text{development time}$. Statistical analyses were carried out with SAS 9.2 (SAS Institute Inc., 2009) or Statistica ver 10. Larval growth experiments for papers II, III and IV were conducted at University of Tartu, Estonia. The experiment for paper V was conducted at The French National Institute for Agricultural Research, France.

2.1. The review (Paper I)

The main aim was to conduct a meta-analysis on the shape of diet-induced reaction norms by reviewing relevant literature. Google Scholar, Cambridge Scientific Abstracts and ISI Web of Science were searched for case studies on larval development time and body size (both pupal and adult size were accepted). Only studies including manipulations of food amount and food quality were reviewed; studies where larval development was manipulated by predators, seasonal cues, larval crowding or temperature were not included. Data from multifactor studies were split; otherwise, data from different studies were treated as different datasets. Treatment mean values of development time and body size for about 230 species of insects were gathered, from a total of 426 datasets. Prior to analyses, all measurements of weight were linearized using the cube-root transformation. In order to make different datasets comparable, all treatment-specific values of body size and development time were standardized by dividing each value by the across-treatment average. A Pearson correlation coefficient between body size and development time was calculated for each dataset, with treatment-specific means taken as individual observations. The meta-analysis of coefficients was performed to evaluate the amount of positive/negative correlations in different subsets of the data.

2.2. Starvation treatments (Paper II)

The objective of this study was to quantitatively describe reaction norms for final size and development time of focal larval instars, with a particular aim to search for evolutionarily conservative elements of developmental schedules. Experiments were conducted with the map butterfly *Araschnia levana*

(Lepidoptera: Nymphalidae) and the hebrew character moth *Orthosia gothica* (Lepidoptera: Noctuidae). Larvae were reared individually in vials and were fed with fresh leaves of nettle (*Urtica dioica*) and silver birch (*Betula pendula*), respectively. Both species were reared in growth chambers under 18 °C and constant light. To manipulate growth rates, there were three treatments applied: 1) ‘control’ – larvae were fed continuously; 2) ‘mild starvation’ – larvae were deprived of food for 9 h out of 24 h throughout the focal instar; and 3) ‘severe starvation’ – larvae deprived of food for 15 h daily throughout the focal instar. Starvation treatments were applied to either the penultimate or ultimate instar (last but one and last, respectively), identically for both species. As the absolute values of weight and age differed considerably between the groups (species, instars, and sexes) the values were log-transformed prior to the analysis.

2.3. Larval crowding (Paper III)

The experiment to study reaction norms in response to larval crowding was conducted with the common heath moth *Ematurga atomaria* L. (Lepidoptera: Geometridae). There were three treatments: 1) ‘solitary’ treatment – larvae that were reared singly in a vial throughout the development; 2) ‘group’ treatment – larvae that were reared in groups of 4–6 individuals; and 3) ‘solitary to group’ treatment – larvae that were reared singly up to last instar, then in pairs. All larvae irrespective of treatment were fed with fresh bilberry (*Vaccinium myrtillus*) leaves. Conditions (temperature, light regime) in the growth chamber resembled natural conditions during the larval period.

2.4. Host plant chemistry (Paper IV)

In this experiment we studied host plant-induced differences in growth parameters. The data were obtained from experiments in 2008 and 2009, originally conducted to study larval colouration of the common heath moth *E. atomaria*. Larvae were fed with shoots of either heather (*Calluna vulgaris*) or bilberry (*V. myrtillus*), both common host plants for this moth. Larvae were reared individually in vials at conditions resembling natural conditions during the larval period in Estonia. Phytochemical analyses to determine causes of larval growth differences were conducted on heather and bilberry in 2011 and 2012. Shoots of six plants from both species were dried and individually analyzed for the content of nitrogen, carbon, polyphenols and tannins.

2.5. Host strains (Paper V)

The aim of paper V was to detect evolutionary changes in maturation decisions. The experiment was conducted with the European corn borer moth *Ostrinia nubilalis* (Lepidoptera: Crambidae) representing two strains – E and Z, feeding naturally on mugwort (*Artemisia vulgaris*) and maize (*Zea mays*), respectively – with two populations per strain. Laboratory harbored Z strain populations originated from Central and Western France, with wild-caught individuals added annually; E strain populations originated from Eastern USA and Slovenia, with a few wild-caught individuals added regularly. All larvae were reared on an artificial diet singly in a vial, with conditions resembling natural conditions during the larval period in Central Europe. Up to the last instar all larvae were reared on a wheat diet, which was considered neutral for both strains. In the last instar, half the larvae from both strains were continually reared on neutral diet, and half were changed to a mixture of their respective native diet.

3. RESULTS AND DISCUSSION

3.1. The review

To quantitatively estimate the occurrence of either positive or negative correlations between age and size at maturity (PRN or NRN, respectively), we reviewed published empirical case studies where the slope of a reaction norm could be derived. We focused particularly on responses to diet quality and quantity. In 48 datasets (11%), treatment had no significant effect on either variables, so these datasets were not considered in further analyses. The bivariate reaction norms mostly had a negative slope – 284 of 378 datasets (about 75%). A positive slope was found in 94 datasets (25%). The latter situation was mainly found in parasitoids, particularly idibiont parasitoids (i.e. inhibiting host's further growth). Also, PRNs were only derived from datasets where diet-induced levels of variability in development time and body size were relatively low.

Based on these results, we conclude that variation in diet quality and quantity predominantly causes NRNs across insect taxa with differing ecology. It is in contrast to reaction norms caused by variation in temperature, which are mainly positively sloped (Atkinson 1994). Furthermore, negative correlations also tended to be stronger than the positive ones. Our findings are consistent with the classic life-history theory that predicts negative correlation between development time and body size being the general case.

Nevertheless, PRNs can be observed in nature, but seem to appear only under specific circumstances. As discussed above, one scenario to select for early maturation at small size is exhaustion of food. This is the case in idiobiont parasitoids, which showed highest prevalence of PRNs in our meta-analysis. Larvae of these insects are restricted to the host; as hosts are paralyzed during egg laying, they provide a finite amount of resources for developing parasitoids (Godfray 1994). In herbivorous insects, however, exhaustion of food is not likely to occur frequently.

The second scenario selecting for PRNs is a predictable difference in mortality rates among the environments. Though possible (Rommel et al. 2011), this scenario appears to be uncommon among herbivores. Indeed, negative slopes dominated among herbivorous insects, and the few cases of PRNs were not particularly convincing. This is because just one dataset had a positive correlation consistently across all treatments. Moreover, the PRNs were mainly obtained, when comparing growth patterns of individuals on different artificial diets or artificial diet vs. natural host plant. Additionally, only a few of those studies were performed to investigate the evolutionary ecology of larval growth patterns. Larvae tended to grow for a longer time and become larger on artificial food (Allsopp et al. 1983, Ojala et al. 2005), which is a novel diet for individuals. Presumably they are not adapted to this diet, so the growth decision could be based on something other than a growth rate or body size *per se*.

3.2. Starvation treatments

In search of conservative elements of larval growth trajectories, we conducted an experiment where larval growth rates were manipulated by food availability using refined starvation treatments. Two levels of starvation were imposed on *A. levana* and *O. gothica*, with the two last instars and sexes observed separately. Compared to the control treatment, the larvae of all subsets responded to the mild (9 h daily) starvation treatment by a roughly 10% reduction in their instar-specific final weights and development time prolonged 10 to 20%. The larvae that were severely starved (15 h daily) ended up on average with about 20% lower final weights, whereas the corresponding prolongation of development time was more variable but roughly two-fold. In the third species discussed in Paper II, *E. autumnata* that was studied previously (Tammaru 1998); mild starvation (12 h daily) also resulted in larger size and shorter development time than in severe starvation treatments (15h and 18 h daily). However, prolongation of development time in response to treatments was not so pronounced in *E. autumnata* as for *A. levana* and *O. gothica*.

As was shown in Paper I, the typical response of herbivores to varying diet quality/quantity – delayed maturation at smaller size – was obtained, which is a clear case of a shift along the growth rate axis. However, there is limited empirical evidence that it also applies on instar-level (Klingenberg & Spence 1997; Tammaru 1998; Esperk & Tammaru 2010), where our study contributes to. All 8 subsets (species x instar x sex) clearly differ in their ecology and therefore one would expect different selective pressures on growth strategies also. Surprisingly, reaction norms were quantitatively very similar among different subsets of data and obtained an L-shape, the similarity being formally supported by the weak interactions of treatment with other terms (instar, species) in the analyses. In particular, for the penultimate instars, the responses of both sexes of both species were nearly identical for both time and size. For the final instars, however, the responses appeared to be more variable. The ‘not so prolonged’ development time in third species *E. autumnata* could be explained by a fact that it is a spring feeder (van Asch & Visser 2007). Thus delaying development even for a week may imply a dramatic decrease in the quality of host foliage the larva encounters (Ayres & MacLean 1987).

Our interpretation of these rather conservative growth trajectories is that the physiological mechanisms generating L-shaped reaction norms are particularly well preserved (considerably invariability across species and sexes) in the younger instars but have been modified to some extent in the final instar (see Tammaru 1998, Stillwell et al. 2010, Esperk et al. 2013; for similar results), likely in response to species- and sex-specific selective pressures (e.g. Teder & Tammaru 2005).

Despite some qualitative differences in reaction norms, the growth trajectories are very similar in several aspects in *Orthosia*, *Epirrita* and

Araschnia, although these genera are separated by about 120–150 millions of years of independent evolutionary history (Mutanen et al. 2010, Wheat & Wahlberg 2013). This should indicate that some underlying developmental mechanisms responsible for such a shape of reaction norms are evolutionarily highly conservative and may thus reflect constraints on adaptive evolution of plastic responses in larval development. What exactly they are and how those conservative elements of development act, appear to be unclear. Despite intensive research, the nature of the physiological mechanism triggering moult or pupation still remains insufficiently known (Mirth et al. 2005, Callier & Nijhout 2011, Andersen et al. 2013).

3.3. Larval crowding

A case study with crowding *E. atomaria* revealed a clear positive correlation between final body size and development time. Crowded larvae completed development earlier but remained smaller, providing a clear case of a shift along the maturation axis. The positive relationship was apparent in terms of the treatment means both when recorded at the end of the 4th instar and entire larval period (Figure 3). Also, growth rates of the crowded larvae were higher both during the first four instars and in the final instar. Additionally, we could show that the positive slope of the reaction norm is not induced during a particularly sensitive period of larval development (Lester et al. 2005, Friberg et al. 2011): the response of larvae to crowding occurred both early in their development and during the final instar.

As discussed in the **Introduction**, herbivores typically do not encounter any of the conditions that would result in an evolution of a PRN. In this study, food for the crowding treatment larvae was always available *ad libitum*, also in nature *E. atomaria* is not likely to be food-limited under normal conditions (for opposite examples, see Haukioja et al. 1988, Smits 2002). Moreover, any interaction between crowding and the onset of an unfavourable season can hardly account for early pupation as this univoltine pupal-hibernating species has plenty of time to complete its life cycle (cf. Tammaru et al. 2001). There is also no reason to expect a time stress driven by host plant shortage, as the larvae pupate long before autumn, and, additionally, some host plants of the species (e.g. *Calluna vulgaris*) are evergreen.

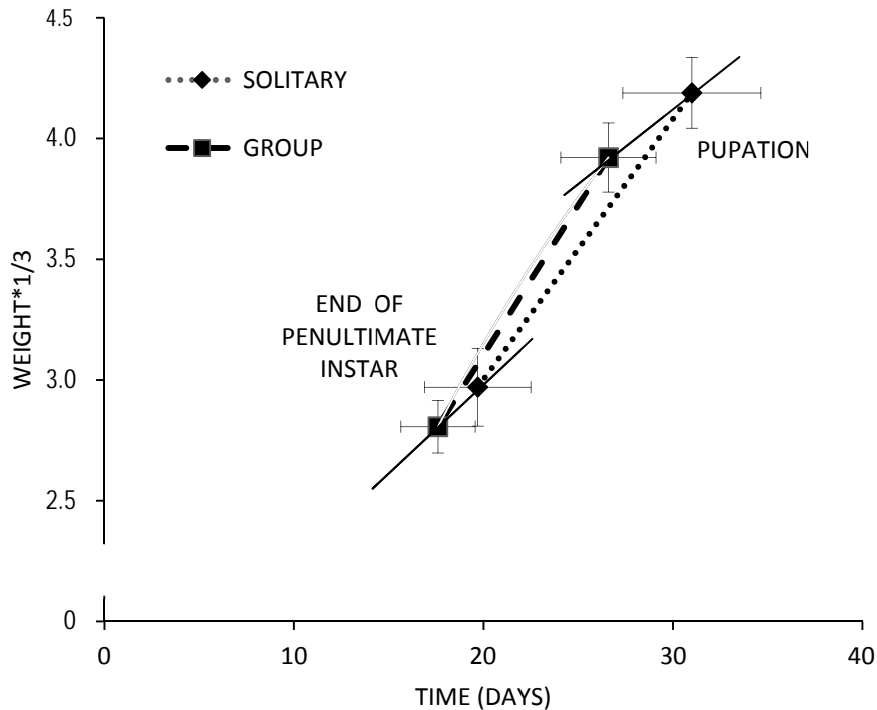


Figure 3. The positive relationship between development time and final body weight (solid lines) of *E. atomaria* reared in the ‘solitary’ and ‘group’ treatments. Values were recorded at the end of the 4th (penultimate) instar and after pupation. Error bars indicate standard deviations. Weight is cubic-root transformed to linearize the growth trajectories of the larvae, making it easier to compare the growth rates (slopes of the dashed and dotted lines). Figure from Paper III.

As we were not able to show the influence of any environmental deterioration on larval growth decisions, we speculate the answer could lie in perception of higher mortality rates of crowded larvae. However, although density-dependent effects typically start to operate at higher densities, which are not typical for this species, we may assume that larvae that perceive the presence of conspecifics or any other animal are selected to escape the associated increase in mortality risk. This may be due to their limited sensory capability not allowing them to distinguish between conspecifics and predators. If this explanation would be true, the specific reaction norms in response to larval crowding (Tammaru et al. 2000) may exemplify the second general scenario leading to PRNs, i.e. the environment-specific differences in predicted mortality rates.

3.4. Host plant chemistry

A rarely recorded exception to overwhelming NRNs was discovered in an experiment with *E. atomaria* feeding on heather and bilberry, where the food plant species caused a PRN in penultimate instar larvae, but not in the final instar larvae (Figure 4). In particular, larvae developed longer on heather up to the end of fourth instar and also in the final instar. For body size, larvae fed with heather were heavier at the end of their fourth instar but not in the final instar. The results were consistent over two years of the study.

To determine the causes for larval growth differences plant chemical composition was analysed in 2011 and 2012; results also being qualitatively consistent. In particular, bilberry had higher nitrogen content (not significant in 2011) and lower carbon content than heather; and the content of tannins was consistently higher in bilberry. The differences in the polyphenol content of the two plants were minor and inconsistent. Temporal trends in chemical composition of the plants were not significant, except for a tannin increase in bilberry in 2012.

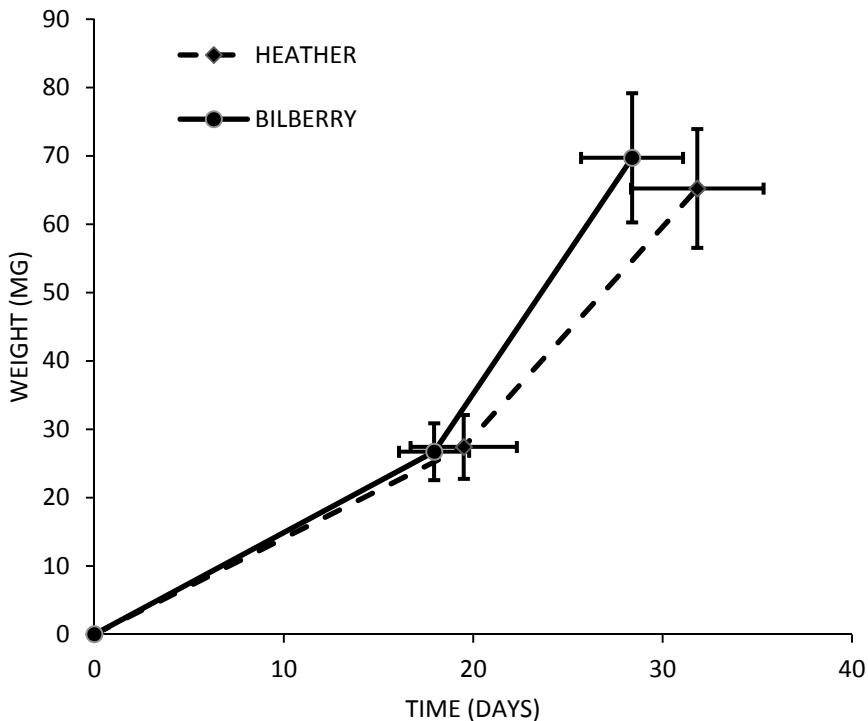


Figure 4. Growth trajectories of larvae fed on heather or bilberry. Development time and body weight (averaged over both years) are recorded at the end of the fourth (penultimate) instar and after pupation. The slopes of the continuous and dashed lines illustrate growth rates. Error bars indicate standard deviation. Figure from Paper IV.

Those results led to the conclusion that bilberry was a superior host for last instar larvae, as inferior host quality typically leads to both lower final weights and prolonged developments. However, as larval performance differed between instars, the superiority of one host plant is disputable. Our finding was the opposite to the ontogenetic hypothesis by Bernays & Chapman (1994) which expects younger larvae to perform better on nitrogen rich plants and older larvae to perform better on more carbon rich plants. Our results are more consistent with the possibility that differently aged larvae vary in tolerance to defensive compounds produced by the plants (Schoonhoven et al. 2007). Tannins have been found to be important feeding deterrents, but evidence is somewhat controversial (Bourchier & Nealis 1993, Barbehenn & Constabel 2011). Indeed, bilberry contained more tannins and polyphenols throughout the season and bilberry was shown to be an inferior host for younger larvae.

We conclude that for *E. atomaria*, the feeding deterrents seem to have obtained higher significance over nutrients, corresponding to the idea of higher susceptibility of the juvenile organism. This suggests that there may be a proximate physiological mechanism behind the appearance of a PRN. Furthermore, our result also contributes to the nutrient-metabolite framework (Bernays & Chapman 1994, Schoonhoven et al. 2007), emphasising the fact that a plant species is not necessarily an equally suitable host throughout larval development.

3.5. Host strains

A positive correlation between size and age at maturation was found in *Ostrinia nubilalis*, where two host strains (sometimes also considered sibling species) differed in maturation decisions under common garden conditions (Figure 5). Insects representing strain Z (from maize) were about 20% heavier in terms of pupal mass and developed longer than larvae of strain E (from mugwort) when diet groups were pooled together. However, growth rate of the last instar did not differ between the populations, but differed between diets – for both strains, the larvae showed higher growth rates on the neutral diet than on diets that included the respective native host plant. The diet did not affect pupal mass, but only the development time in the last instar.

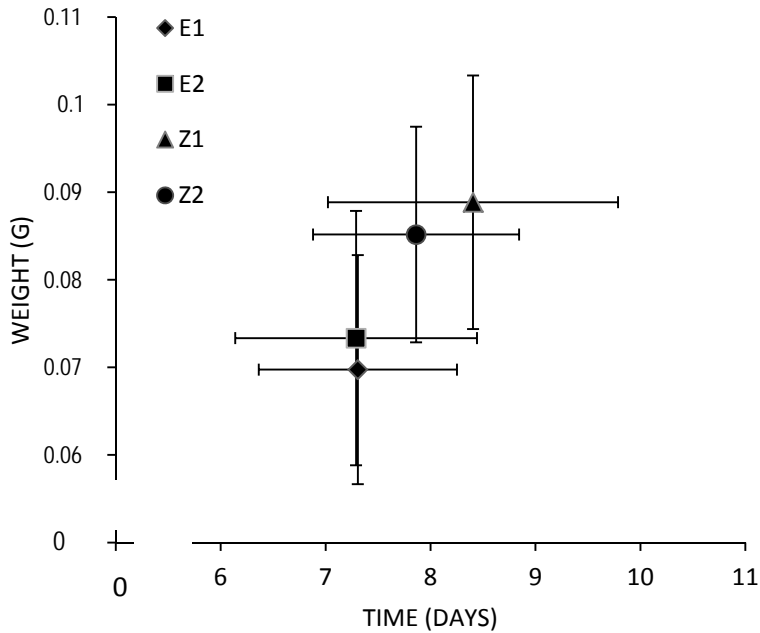


Figure 5. Time and size for maturation in four populations of European corn borer. Average values of a population are used, as there were no significant differences between neutral and native diet groups. Error bars denote standard deviation. Figure from Paper V.

A likely adaptive explanation for the among-strain differences in maturation decisions by the European corn borer moth rests on the difference in the phenology of the two host plants, mugwort and maize. It is possible that the nutritional properties of mugwort decline faster than those of maize, so *O. nubilalis* larvae need to complete their development on mugwort faster. Indeed, Thomas et al. (2003) showed that under both laboratory and field conditions, strain E moths emerged on average 3 days and 10 days earlier, respectively. Furthermore, even more simple explanation may be related to the size of the plants: the amount of food provided by a maize plant is unlikely to be exhausted, whereas that may not be the case for the much smaller mugwort plant. As it was shown by Losey et al. (2002), stem diameter (artificial tubes and several plant species) influences larval survival, with a larger diameter being more favourable.

The case of *O. nubilalis* can be interpreted as an evolutionary change in the reaction norm for size and age at maturation *per se* (Introduction, Figure 2) rather than a shift along an invariable reaction norm, an interpretation that is supported by two lines of evidence: first, there were among-strain differences in developmental traits despite no differences in growth rates. Second, there was a positive correlation for the strain-specific means of size and age at maturation.

Both these patterns are consistent with an evolutionary shift along the axis of maturation decision but inconsistent with a shift along the axis of growth rate.

In conclusion, our extensive literature review showed that the NRN between size and age at maturity appeared to clearly prevail in herbivorous insects. Generally, the response of individuals to suboptimal conditions was qualitatively the same across most taxa and ecological groups considered. This is consistent with the idea that environmental conditions selecting for PRNs are not frequently met among herbivorous insects. Moreover, physiological mechanisms leading to the L-shaped reaction norms appear to be conserved evolutionarily so that only strong selective pressures can be expected to cause substantial modifications. Nevertheless, regardless of their scarcity, examples of PRNs can be found. Our empirical studies illustrate that refined rearing experiments with large sample sizes prove useful to detect more exceptions to the general rules. The novel aspect of my empirical work was the instar-based approach on larval growth experiments. It involved daily inspection of larvae, which enabled me to make more precise calculations of growth parameters and to assess the effect of environment throughout different stages of larval development. Studies focusing on evolutionary ecology of insects have so far primarily used only the data of the entire growth phase, which may have led to false interpretations of evolutionary processes. The clearest example of the benefit of the instar-based approach is perhaps detecting differences in host plant superiority presented in Paper **IV**. Also, by observing the whole growth phase we could make conclusions about the conservatism of growth patterns across different subsets in Paper **II**. In Paper **V**, we could not have drawn the conclusion about the shift along the maturation decision axis, if we had not measured growth rates on the basis of short-term trials and shown these to be equal. In general, drawing conclusions from more data points gives increased statistical power and more reason to argue that results were not obtained by chance. Additionally, at the practical level, as instars are distinct units, it provides a particular time frame for applying different comparable treatments.

4. SUMMARY

The main goal of my thesis was to study reaction norms for size and age at maturity in insects. In particular, I aimed to describe reaction norms with different slopes and discuss environmental conditions that could be responsible for evolution of such differences. I summarized the reviewed literature to evaluate the relative frequency of negatively and positively sloped bivariate reaction norms and discuss the conditions inflicting those situations. Furthermore, I performed several empirical studies describing a case which can be considered the general one as well as demonstrated some exceptions to the prevailing relationship.

Bivariate reaction norms for size and age at maturity have mostly been predicted to have a negative slope. However, several theoretical models have alternatively predicted reaction norms with a positive slope. A meta-analysis on relevant literature showed that indeed, a vast majority of reaction norms have a negative slope (Paper I) when the environmental variation is induced by diet quality or quantity. Our original work with several lepidopteran species showed that reduction in food quantity invariably leads to prolonged development time, but still does not result in larger body size (Paper II). Furthermore, the comparison of NRNs of different species, sexes and instars revealed remarkable similarity, suggesting some conservatism in development mechanisms and proving the existence of some constraints on adaptive evolution of larval growth.

As proposed by several theoretical works, a positive correlation between development time and body size can be selected for by a predictably deteriorating environment, e.g. when discrete food units are exhausted. Another theory states that a predictable difference in mortality rates between environments leads to a PRN. Based on very limited number of reports on PRNs among herbivorous insects, I believe that both these scenarios are rare. However, larval crowding is an often discussed situation which can combine elements of both food exhaustion and predictably increased mortality rates. In Paper III I examined the growth trajectories of crowded *E. atomaria* larvae, that indeed showed shorter development times and smaller sizes compared to their solitary siblings. As the food was available *ad libitum* for all treatments, the food exhaustion could not be the mechanism responsible for a PRN. Therefore I concluded that the reason behind this growth strategy was indeed the contact with con-specifics, likely indicative of high mortality rates.

Interestingly, I also found a PRN in a situation that to my knowledge has been recorded just once before. In Paper IV I could detect a difference in instar-level growth decisions in connection to host plant chemistry. This result is not in accordance with either explanation: there was neither food exhaustion nor size-related difference in mortality. Based on plant chemical analyses, I suggested a pure physiological explanation – *E. atomaria* larval age-specific difference in sensitivity to deterrent compounds.

Additionally, I could find evidence about a clear case of an evolutionary shift along the axis of maturation decision. That was in connection to host plant races, where *O. nubilalis* mugwort strain finished development earlier and at smaller size than maize strain irrespective of larval diet (Paper V). However, there were no differences in growth rates between strains. That left me to conclude, that the differences could be caused by some evolutionary factor, perhaps the adaptation of strains to their host's specific physical parameters.

A novel aspect of my empirical work was the use of rather uncommon methodology, in particular, paying explicit attention to larval instars and recording both development time and final size for separate instars. Furthermore, the extensive literature review now enables us to make generalizations and conclusions about shapes of reaction norms in insects.

5. SUMMARY IN ESTONIAN

Kehasuurst ja kasvamiseks kulunud aega siduvad reaktsiooninormid putukatel: reeglid ja erandid

Käesoleva doktoritöö eesmärgiks oli uurida valmiku kehasuurst ja kasvu lõpetamise aega siduvaid reaktsiooninorme putukatel, pöörates põhilist tähelepanu reaktsiooninormide kujule ja erinevaid reaktsiooninorme põhjustavatele keskkonnatingimustele. Kirjanduse põhjal koostatud ülevaates hinnatakse positiivse ja negatiivse kaldega reaktsiooninormide esinemissagedusest ning analüüsitakse, millised tingimused on viinud vastava kujuga reaktsiooninormide tekkeni. Lisaks esitan nelja empiirilise uurimuse tulemused, millest üks kirjeldab looduses väga levinud negatiivset korrelatsiooni kehasuurst ja vanuse vahel, teised aga erandeid sellele üldisele reeglile.

Kahe muutujaga reaktsiooninormid, mis seovad kehasuurst ja arenguks kulunud aega on eeldatavalt peamiselt negatiivse kaldega; see tähendab, et ebasoodsates tingimustes kasvanud isendil kulub suguküpsuseni jõudmiseks kaua aega, kuid kehamõõtmed jäävad väikeseks. Siiski on mitmed teoreetilised mudelid ennustanud ka positiivse kaldega reaktsiooninormide olemasolu. Tõepoolest, ulatusliku kirjandusülevaate (I artikkel) põhjal võin väita, et kui keskkondadevaheline erinevus seisneb toidu kvaliteedis või hulgas, on valdav enamus reaktsiooninorme negatiivse kaldega. Minu originaalkatsed erinevate liblikaliikidega näitasid, et toidu hulka varieerides on tulemuseks alati negatiivne seos lõpliku kehasuurst ja kasvamiseks kulunud aja vahel (II artikkel), ehk siis vähesel toidul kasvanud isendid jäävad suuruselt liigikaaslastele alla, kuigi kasvamisele kulub aega rohkemgi. Lisaks näitas erinevate liikide, sugude ja kasvujärgkude kasvutulemuste võrdlus, et reaktsiooninormide kujud on väga sarnased, kuigi nende rühmade optimaalsed kasvustrateegiad peaksid olema erinevad. Selline gruppidevaheline sarnasus annab alust oletuseks, et putukate arengumehhanismid on suhteliselt konservatiivsed ning on võimalik, et vastsejärgus kasvamise adaptiivset evolutsiooni mõjutavad piirangud olulisel määral.

Mitmed teoreetilised tööd on eristanud kahte stsenaariumi, kus on optimaalne lõpetada kasvamine varakult ja väiksema kehasuurst juures. Esiteks – positiivse kaldega reaktsiooninorm võib evolutsioneeruda olukorras, kus keskkonnatingimuste halvenemine on ennustatav; näiteks juhul, kui toidu hulk on piiratud ja see hakkab ammenduma. Teiseks – isendid võivad lõpetada kasvamise varem selles keskkonnas, kus on suurem suremusrisk. Põhinedes I artikli tulemustele järeldasin, et mõlemad stsenaariumid esinevad herbivoorsete putukate puhul väga harva. Ometi, üsnagi sagedasti esinev putukate suur asustustihedus on olukord, mis hõlmab endas mõlemat stsenaariumi: mida rohkem on putukavastseid ühe toiduühiku kohta, seda suurem on kisklusrisk ning ka tõenäosus, et toit ammendub. III artiklis olen ma ka empiirilisel näidanud, et kõrgema asustustiheduse korral lõpetasid võsavaksikud (*Ematurga atomaria*) kasvamise varem ja väiksema suuruse juures kui üksikuna elavad liigikaaslased.

Mõlema katserühma röövikutel oli toit saadaval piiramatul hulgal, seega ei olnud toidupuudus määravaks faktoriks positiivse kaldega reaktsiooninormi tekkeks. Sellest tulenevalt ma järeldasin, et kasvustrateegias sai otsustavaks füüsiline kontakt liigikaaslastega, mis võis anda isendile vihje tihedusest sõltuva suremusrisiki kohta.

Oma katsete käigus avastasin positiivse kaldega reaktsiooninormi olukorras, mida minu teada on varem kirjeldatud vaid ühel korral. **IV** artiklis analüüsisin võsavaksiku röövikute kasvatuskatse tulemusi ning leidsin toidutaimest sõltuva positiivse seose kehasuuruse ja kasvuks kulunud aja vahel kasvujärgu tasemel. Selline tulemus ei sobi kummagi eelmainitud stsenaariumiga: keskkonnatingimused ei olnud ennustatavalt halvenemas, samas ei ole põhjust oletada ka kehasuurusest sõltuvat suremusrisiki. Vastsete toidutaimede keemilise koostise analüüsid aga näitasid, et positiivse kaldega reaktsiooninormil võis olla puhtalt füsioloogial põhinev seletus – putuka vanusest sõltuv tundlikkus taimedes leiduvate sekundaarsete metaboliitide suhtes.

V artiklis kirjeldan standardsete kasvutingimuste (*common garden*) katset, milles leidsin tõendeid evolutsioonilistest muutustest kasvustrateegiates. Sõltumata rööviku toidust lõpetas pujult pärinev varreleediku (*Ostrinia nubilalis*) rass kasvamise kiiremini ning väiksema kehasuuruse juures kui looduses maisil kasvav rass. Samal ajal ei leitud erinevust rasside kasvukiiruste vahel, mis oleks olnud tõendiks adaptatsioonist toidutaimespetsiifilistele toitainetele. Kuna kasvukiiruses erinevust ei olnud, siis võib väiksem lõppsuurus olla tingitud mõnest evolutsioonilisest faktorist – näiteks kohastumisest mõnele toidutaimespetsiifilisele füüsikalisele parameetrile.

Minu doktoritöö uudse aspektina tuleb välja tuua meetodilist külge, sest putukate kehasuuruse ja kasvamiseks kulunud aja detailset mõõtmist kasvujärgu tasemel on evolutsioonilise ökoloogia kontekstis väga harva kasutatud. Samuti puudus varem ulatuslik kirjanduse ülevaade reaktsiooninormidest putukatel, erineva kujuga reaktsiooninormide esinemissagedustest ja erinevate kujude evolutsioneerumiseni viivatest keskkonnatingimustest.

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