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LARVAL INSTAR AS A KEY ELEMENT OF INSECT GROWTH SCHEDULES

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LIST OF ORIGINAL PUBLICATIONS

This thesis is a summary of following papers which are referred to in the text by their Roman numerals:

I Tammaru, T., Esperk, T., Castellanos, I. 2002. No evidence for costs of being large in females of *Orgyia* spp. (Lepidoptera, Lymantriidae): larger is always better. *Oecologia* 133: 430–438.

II Esperk, T., Tammaru, T. 2004. Does the 'investment principle' model explain moulting strategies in lepidopteran larvae? *Physiological Entomology* 29: 56–66.

III Tammaru, T., Esperk, T. Growth allometry of Lepidopteran larvae: a life history perspective. Manuscript.

IV Esperk, T., Tammaru, T., Nylin, S. Intraspecific variability in the number of larval instars in insects. Submitted, invited to *Journal of Economic Entomology*.

V Esperk, T., Tammaru, T. Determination of female-biased sexual size dimorphism in moths with variable instar number: the role of additional instars. *European Journal of Entomology* 103: 575–586.

VI Esperk, T., Tammaru, T., Nylin, S., Teder, T. Achieving high sexual size dimorphism in insects: females add instars. Tentatively accepted by *Ecological Entomology*.

VII Tammaru, T., Esperk, T., Ivanov, V., Teder, T. Proximate mechanisms leading to sexual size dimorphism in Lepidoptera: locating constraints on larval growth schedules. Manuscript.

The author was primarily responsible for conducting the experiments in I–VII, surveying and examining literature in IV and VI, analysing data in II, IV, V, VI and writing in II, IV, V, VI. The author substantially contributed to planning the work in I–VII, data analysis in I and VII and writing in I, III and VII.

1. INTRODUCTION

Moulting is a phenomenon shared by larvae of all arthropods. Moulting is not just casting off old skin, moulting process has a much stronger impact on arthropod growth curves than it may seem at first glance. Moulting cycle is a very complicated process which starts long before the abandoning of old cuticle and proceeds even some time after the actual casting event (= ecdysis) (e.g., Sehnal 1985, Nijhout 1994). Larvae stop feeding at certain time point during the moulting cycle and will be able to continue consuming (and growing) only after the cycle has ended, they follow therefore a complex discontinuous growth trajectory. As a consequence, the growth curve of arthropods is divided into discrete growing periods, typically called instars, which are separated by moults. Moreover, intense growth can take place only in the first half of the instar, while, due to initiation of new moulting cycle, it slows down remarkably in the second half of instar and stops entirely before the ecdysis (Sehnal 1985, Ayres & MacLean 1987, II).

While there is little doubt that such a complicated growth curve has a strong effect on the life histories of arthropods, it has received undeservedly little attention in this context. The moulting process, as well as the instar-related complex growth dynamics, is often totally ignored in life history studies of arthropods. This is unfortunate because knowing the proximate nature of growth would certainly help us to understand what is, and what is not possible in growth curve of arthropods. Such an understanding, in turn, is necessary to determine the set of possible reaction norms for age and size at maturity, as well as to reveal the possible constraints on arthropod life histories stemming from peculiarities of their growth schedules.

The aim of the present thesis is to investigate the nature of the growth curve of insects, and to determine the role of instars in their life histories. In particular, the within- (II, V, VII), and among- (III) instar growth dynamics is investigated in lepidopteran larvae. As both the proximate and ultimate causes of moulting are still largely unclear, the hypothesis that growth of rigid body parts is the main cause of moulting is tested (II). Particular attention is given to those aspects of growth which critically influence the final body size attained. Such an emphasis is justified because it is still unclear which costs or constraints are able to balance the obvious benefits of large body size in insects (Blanckenhorn 2000, I). As the number of instars is definitely an important factor in the determination of final body size, a literature-based overview of the intraspecific variability in instar number is given (IV). In most insect species, females are larger than males, the proximate mechanisms leading to size differences between the sexes are, however, still poorly known. The ways how the difference can, or cannot be achieved, may shed light on possible constraints on larval growth. Sex-specific growth curves of several lepidopteran species, exhibiting notable female-biased sexual size dimorphism (SSD), with

(V) or without (VII) sexual difference in the number of larval instars, were therefore investigated (V, VII). In addition, a literature-based study investigating determination of SSD in species with sexual difference in larval instar number, was performed (VI).

2. BODY SIZE AS A LIFE HISTORY TRAIT

2.1. The costs and benefits of being large

Due to its high impact on various physiological processes and fitness characters, body size is definitely one of the central life history traits of any organism (Peters 1983, Calder 1984, Reavey 1993). Accordingly, optimality models for size and age at maturity constitute one of the central issues in the contemporary evolutionary ecology (Rowe & Ludwig 1991, Roff 1992, Stearns 1992, Abrams et al. 1996, Day & Rowe 2002). These models generally assume a trade-off between size at maturity and development time, and a stabilising selection on body size as a result of antagonistic evolutionary forces. The optimum is usually assumed to be at a value intermediate between the physiologically determined minimum and maximum.

There are various advantages of being large. Most probably, one of the main benefits of being a large female is the frequently observed strong positive correlation between female size and fecundity (reviewed by Shine 1988, Blanckenhorn 2000). The intraspecific positive correlation between female body mass, and the number of offspring that a female is able to produce is especially strong among invertebrates (e.g., Gilbert & Williamson 1983, Head 1995) and ectothermic vertebrates (e.g., Woolbright 1983, Shine 1994). The relationship is typically almost linear in insects (Honěk 1993, I). Another possible benefit favouring large size is related to the better quality and higher survival of offspring of large mothers (Ralls 1976).

In males, the advantages of being large are mainly related to sexual selection (Trivers 1972, Blanckenhorn 2000). Accordingly, larger males achieve more matings by either being more successful in male-male competition, or being preferred by females (reviewed by Andersson 1994, Blanckenhorn 2005, Isaac 2005). While the positive effects of large size on male fitness are not rare among insects and other invertebrates (e.g., Blanckenhorn et al. 2003, Uhl et al. 2004, Teder 2005), these relationships are presumably less pronounced than the fecundity advantage of large females (Tammaru et al. 1996).

While there is a vast amount of evidence confirming the advantages of large body size, the evidence for costs of being large (or benefits of being small) is surprisingly scant (Blanckenhorn 2000). Whereas the possibility that some evolution towards larger body size may indeed occur cannot be ruled out (Kingsolver & Pfennig 2004, Hone & Benton 2005), in most organisms it is still perhaps justified to expect forces counterbalancing the benefits of large size which lead to stabilizing selection. The most commonly expected cost of large body size is increased cumulative mortality which is related to the prolonged growing period of large individuals (Roff 1992, Stearns 1992). However, this hypothesis assumes a positive correlation between final body size and growing period while the opposite is often observed (Klingenberg & Spence

1997, Day & Rowe 2002). Moreover, at least in some species of insects, unrealistically high levels of larval mortality have to be assumed to make mortality effect able to balance the strong fecundity advantage of large size (Tammaru 1998).

Another group of potential costs of large body size are related to the disadvantages of *being* a large adult. These disadvantages often operate through the viability cost, as large size, for several reasons, may lower the probability of survival (Blanckenhorn 2000 and references therein). Moreover, it has been proposed that, in insects, higher potential fecundity of larger females may not necessarily translate into higher realized fecundity, as for various reasons, large females may be less efficient in laying their full egg complements (Leather 1988, Klingenberg & Spence 1997).

As an original contribution, we looked for possible costs of being a large adult in two species of lymantriid moths, the Holarctic *Orgyia antiqua* L. and the Nearctic *O. leucostigma* J.E. Smith (I). As females of these insects are wingless and do not move far from their native cocoons, these species provide excellent model objects for studying various components of (female) adult fitness in conditions close to natural. Moreover, as adults of these species do not feed and egg-load is complete already at female's eclosion (characteristic of capital breeders, Tammaru & Haukioja 1996), potential fecundity can easily be measured. A strong positive correlation between both pupal and adult mass and potential fecundity (eggs laid plus those found inside female's abdomen) was found (I). Furthermore, as oviposition success was remarkably high (>90%) in both species, and did not correlate significantly with female body mass, a strong relationship between female size and realized fecundity was observed. The proportion of non-fertilized eggs, on average, was extremely low (<1%) and hatching success was very high (>95%), while neither did correlate with female size (pupal weight). Pupal mortality was also low (<3%) in laboratory trials and did not correlate with pupal mass while adult longevity even tended to show a positive correlation with pupal mass. The only parameters which showed negative correlations with body size, were pupal and adult survival (survival to oviposition) in the field experiments, however, even these relationships remained statistically insignificant in all cases. We therefore did not find any potential costs of being large adult that would qualify as a candidate for balancing fecundity advantage in these species.

Besides the adaptationistic possibilities discussed above (i.e. ecological costs of large size), constraint based explanations should be considered. In particular, evolution toward the larger size may be strictly limited by genetic, phylogenetic, developmental or physiological constraints (Maynard Smith et al. 1985). However, all of these constraints, except physiological ones, more likely constitute temporary limits which could be overcame by time and are therefore not "absolute" (Blanckenhorn 2005). Therefore, while approaches based on such transient effects may be applied to explain specific cases, they probably do not provide candidates for general explanations. Physiological constraints, in turn, definitely set boundaries to minimum and maximum body sizes, which could not be exceeded, however, they are likely not sufficient to explain why smaller scale shifts towards larger body size do not take place.

It may be concluded that there is probably no simple explanation why organisms do not continuously evolve towards larger body sizes, and there is likely no single force that could universally counterbalance the benefits of large size. The eventual cost of large size may result from a combination of several minor costs and/or constraints, and these components may be highly species-specific. Moreover, as most studies have concentrated only on one particular life-stage of an organism (mostly the adult stage), several possible costs and constraints may not yet be revealed. For example, selection may, indeed, favour large body size in adults, but in the same time act against it (i.e. favouring small size) in juveniles (Price & Grant 1984, Schluter & Smith 1986). Therefore, studies covering all developmental stages of an organism are highly recommended. However, this task may be hard to achieve for several reasons, and thus there are only few papers available that meet these criteria (e.g., De Block & Stoks 2005). A promising possibility is then to concentrate on the developmental stages and life history aspects that are understudied in the present, and try to fit these with the better known aspects of this life history puzzle in the future. The possible effects on fitness stemming from the juvenile (larval) stage, and from the peculiarities of growth curve, clearly represent the "fuzzy puzzle pieces" at present. Therefore, they were chosen to constitute the main focus of the present thesis.

2.2. Sexual size dimorphism

Sexual size dimorphism (SSD), defined as the inequality of body sizes of the two sexes, is a widespread phenomenon among different groups of animals (reviewed by Shine 1989, Fairbairn 1997, Badyaev 2002, Blanckenhorn 2005). Females are the larger sex in many invertebrates and poikilothermic vertebrates (e.g., Shine 1979, 1994, Head 1995; Teder & Tammaru 2005) while the male-biased SSD predominates in birds and mammals (e.g., Cabana et al. 1982, Weatherhead & Teather 1994, Isaac 2005). SSD has been typically ascribed to sexual differences in selection pressure on adult body size. Traditionally, fecundity selection is proposed to be the major force driving to the female-biased SSD whereas sexual selection is often related to the male-biased size dimorphism (Darwin 1871, Trivers 1972). However, it has been argued by many authors that these factors alone are not sufficient to explain sexual differences in body size. Instead, only the *net selection*, an outcome of fecundity-, sexual- and viability selection, acting on both sexes and viewed within constraint-based framework may lead to different body sizes of sexes

(Shine 1989, Fairbairn 1997, Karubian & Swaddle 2001, Badyaev 2002, Blanckenhorn 2005, Isaac 2005).

While the ultimate causes of sexual size dimorphism have been extensively studied (reviewed e.g., by Shine 1989, Dunn *et al.* 2001, Karubian & Swaddle 2001, Blanckenhorn, 2005), proximate mechanisms leading to SSD have received considerably less attention. Moreover, most studies focus on sexual size differences in adult stage while aspects of juvenile development are often ignored (Badyaev et al. 2001, Badyaev 2002). However, without knowing the details of juvenile growth schedules, it may not be possible to fully understand the mechanisms underlying the evolution of SSD. This is because the different growth strategies leading to sexual differences in body size, rather than adult body sizes, may constitute the subjects of selection (Arak 1988, Crowley 2000, Badyaev et al. 2001, Badyaev 2002).

3. GROWTH SCHEDULE AS A LIFE HISTORY TRAIT

Individual growth curve is a central feature of juvenile period of every organism and, by virtue of connecting age and size at maturity, it is clearly an important life history trait of its own right. However, until recently, the independent effect of the growing process on fitness and life history of organisms has been largely ignored in life history studies. This is mainly because of the intuitive benefits of fast growth (in terms of rapid maturation and/or large size at maturation), growth rates are often assumed to be invariably close to their physiological maxima for given environmental conditions, and thus not of much interest (e.g., Roff 1992, Stearns 1992). There is a growing body of evidence, however, suggesting that growth rates may vary adaptively and are perhaps only rarely maximised (Case 1978, Abrams et al. 1996, Arendt 1997, Nylin & Gotthard 1998, Gotthard 2001, 2004, Tammaru et al. 2004). The likely reason for submaximal growth rates may lay in various costs, like higher mortality or purely physiological problems for example, which may accompany the fast growth and could be avoided by growing slower than physiologically possible (Abrams et al. 1996, Arendt 1997, Nylin & Gotthard 1998, Gotthard 2001, 2004, Metcalfe & Monaghan 2001, Fischer et al. 2004, Stoks et al. 2006).

There are several further, more specific aspects related to the growing stage which have to be considered when explaining growth rates of particular organisms, living in particular environments. Organisms living in temperate environments for example, have to adjust their life cycle according to the length of favourable season. The large majority of insects are capable of surviving the unfavourable season only in a certain developmental stage (either egg, larva, pupa or adult) (Tauber et al. 1986). As having reached the hibernating stage by the beginning of the unsuitable season is crucial, the seasonality has important consequences to insect life histories. In particular, there cannot be “partial” generations and therefore temperate insects may be facing serious time constraints when the growing season is short, or when the species has several generations within one year (Taylor 1980a, Roff 1983, Reavey & Lawton 1991). On the other hand, univoltine species (one generation per year) may have to “consciously” retard their development (e.g., by slowing down the growth rates) when growing season is relatively long, in order not to surpass the hibernation stage (Taylor 1980a, Reavey & Lawton 1991). As years differ considerably in the quality of the suitable season, capacity of plastic adjustment of development time and/or growth rates according to the cues of seasonal progression is of particular importance for temperate insects (Taylor 1980b, Tauber et al. 1986, Reavey & Lawton 1991, Nylin & Gotthard 1998, Gotthard 2004).

In organisms with complex life cycles and growth schedules like arthropods, several (physiological) aspects of juvenile development and growing process may have a strong impact on their life histories (Higgins & Rankin 1996). Some of respective traits may be plastic (varying in response to environmental changes) while others are canalised (not varying in response to environmental changes) and may therefore represent possible constraints (Maynard Smith et al. 1985). Finding out which elements of the growing process are plastic and which are canalised, is clearly an important task for understanding the role of juvenile development in determining the life histories of insects (Higgins & Rankin 1996).

3.1 Special features of insect growth curve

3.1.1. Why do insect larvae moult?

During the immature development, larvae of insects and other arthropods moult regularly, i.e. replace their exoskeletons. As a result, growth curve of these animals is discontinuous, being divided to discrete growing periods – called instars –, which in turn, are separated by moults. While moulting is a phenomenon common to all arthropods and definitely has a considerable impact on life history evolution in these animals, the definitive proximate and ultimate reasons for moulting, or at least the exact reason for observed moulting frequencies is, quite surprisingly, still unclear. According to a classical view, inextensible mechanical nature of the exoskeleton sets strict limits to the growing capacity and, therefore, growing arthropods must moult regularly to replace the old cuticle with a new, larger one. However, at least in larvae of holometabolous insects, the body is predominantly soft with highly extensible covers, and, therefore, physiological limits to the extensibility of the cuticle are likely not reached (Nijhout 1981, 1994, Sehnal 1985).

While there is thus probably no simple mechanical constraint on within-instar mass increment, one should turn to the optimality approach when explaining the observed moulting frequencies. Alternatively, constraints other than inextensibility of cuticle may occur. There are several potential costs associated with moulting, from which remarkable time loss seems to be one of the most serious ones. Growth slows down remarkably with moult approaching, and ceases completely during the process (e.g., Sehnal 1985, Ayres & MacLean 1987, II). Using the data from two species of lymantriid moths, we were able to show that without slowing down the growth rate prior to moult, larvae might theoretically achieve body masses twice of what was actually observed (II). Other potential costs of moulting include the loss of substances with abandoned exuvia, and higher vulnerability to predators during the moulting process (Sehnal 1985). The former are likely not to play an important role as a cost of moulting, because the amount of substances lost is minor at least in holometabolous insects (Nijhout 1994), while the importance of the latter still remains to be studied.

From the possible benefits of moulting, the opportunity to replace heavily sclerotised body parts sounds most promising (Nijhout 1981). In particular, there are still some body parts, such as mouthparts (jaws) and legs, which, due to their highly sclerotised nature, are inextensible in all insect larvae and grow only in connection to moultings (Nijhout 1981, Sehnal 1985). Following this idea, Hutchinson and co-workers (1997) proposed an optimality model for growing and moulting strategies in insects and other arthropods. As an assumption of their model, the main benefit of moulting is the possibility to enlarge mouthparts which limit the consumption rates and thereby slow down the growth rates of the larvae. Therefore, their model predicts that larvae must moult at the moment when the insect's "feeding potential" exceeds the consumption capacity which, in turn, is limited by the size of its mouthparts. The authors stress, however, that their model is largely theoretical and needs to be tested empirically. We tested the model's central assumption – i.e., that larvae moult primarily to increase their mouthparts – on two species of lymantriid moths, *Lymantria dispar* L. and *Orgyia antiqua* L. (II). If consumption rates are, indeed, determined by the size of mouthparts, the following is expected: constancy of absolute growth rates within an instar, dependence of growth rates on head capsule size within an instar, and higher absolute growth rates in older instars. Results of our experiment, however, did not support these assumptions. In particular, head capsule size had only a weak effect on growth rates in one of the species, and no effect in the other while absolute growth rates tended to increase during the development within an instar. Moreover, higher growth rates of older instar larvae were explainable by an allometric relationship that extrapolates from growth within the preceding instar, indicating that nothing was gained by moulting in terms of growth rates. We therefore concluded that the model of Hutchinson et al. (1997) appears not to be directly usable to explain moulting strategies in the lepidopteran larvae studied (II). However, as the size of the mouth-parts would necessarily start to limit consumption and growth at some point, moulting may be initiated just before that point and therefore enlarging the mouthparts may still be an important reason for moulting.

There are several further hypotheses proposed to explain the moulting strategies of insects. In particular, avoiding pathogens (Zacharuk 1973) or replacing the deformed cuticle (Nolte et al. 1996) have proposed as causes of moults in some cases. However, these are, most likely, highly specific cases and their applicability to the wider range of insect species is questionable. A more promising hypothesis was recently proposed by Greenlee and Harrison (2004, 2005). In their approach, these authors still rely on the idea that some heavily sclerotised body parts grow only during moults, but instead of mouthparts they concentrated on the respiratory system of insects. As the tracheal system also grows only during moults, they were able to demonstrate the reduction of aerobic capacity associated with growing within an instar. Therefore, even if universality of this hypothesis still remains to be tested, the main cause of moulting may indeed be renewing the respiratory system, and reducing oxygen limitation thereby. However, even if this hypothesis turns out to be successful in explaining moulting strategies in most cases, it certainly fails to explain, for example, such special cases when moulting is not related to growth of linear measurements (stationary moults, IV) or growth between moults is negative (regressive moults, IV). It may be concluded that the cause of insect moulting is far from clear at present and while the efforts to find general explanation of this phenomenon are highly appreciated, the existence of one single answer is still not likely.

3.1.2. Growth within instars

The within-instar growth of insects follows a complex trajectory, whereas both absolute and relative growth rates are higher in the first half of the development within an instar, while growth slows down in the second half of an instar, and may be even negative right before and during the moulting process (Sehnal 1985, II). This complexity however, is largely ignored in insect life history studies. For example, one of the indirect methods used for estimation of instantaneous growth rates (mass increments) of insects in a certain instar, is dividing instar's final-initial mass ratio by instar duration (e.g., Gotthard et al. 2000, Telang et al. 2001, Stoks et al. 2006). This method, however, mixes the "true" instantaneous growth rate and "premoult waiting" period, and may therefore give both quantitatively and qualitatively inaccurate results about actual instantaneous growth rates, when duration of the premoult period differs between the groups or individuals being compared. Therefore, only a direct measurement of mass increment during a short, specified time period seems to be a reliable index of instantaneous growth rate in insects. Moreover, as instantaneous growth rates differ remarkably in different phases within an instar (II) and also between instars (III, see below), comparing exactly the same phases of growth curves is of particular importance in order to detain accurate results. Another practical problem lies in the extreme sensitivity of larval growth rates to environmental conditions like temperature (e.g., Ayres and MacLean 1987, Kingsolver et al. 2004) and food quality (e.g., Scriber & Slansky 1981, Awmack & Leather 2002). Heterochronous comparisons of growth rates should be therefore treated with extreme caution.

Within-instar relative mass increments may vary notably both within and between insect species (Nijhout 1981, Sehnal 1985, Elmes et al. 2001, III, V, VII) and therefore severe physiological constraints on this parameter are not likely. However, as final weights of the instar still tend to depend strongly on the instar's initial weights (Nijhout 1975, Tammaru 1998, Tammaru et al.

2004, original unpublished results of the analyses performed with the data set presented in III), the mass increment within one instar is still likely to be limited. The nature of these limitations however, is still unclear (see above). In consistence with the presence of some, though not too severe limitations to the within instar growth, insect larvae seem to be capable of a limited compensatory growth in terms of both higher growth rates and extended instar durations after environmental perturbation (Tammaru et al. 2004).

3.1.3. Growth in different instars

It is often claimed, or at least implicitly assumed that insect larvae grow exponentially i.e. that relative growth rates of larvae are independent of body size (e.g., Nylin 1992, Tammaru 1998, D'Amico et al. 2001). Such an assumption has a strong impact on expected reaction norms for age and size at maturity, as it implies that growing in late larval period must be highly efficient in terms of a high mass increment during a short time period. However, paradoxically, this assumption has hardly ever been properly tested in insect larvae. The notion of exponential growth implies the allometric exponent, which relates growth rates to body mass, to be equal to one. There is a large body of empirical evidence however, which indicate that values of the allometric exponent, relating metabolic activity (and, often also the growth rate) to body mass, are below 1 in most cases and are typically close to 2/3 or 3/4 (West et al. 2001, 2004, Ricklefs 2003, Glazier 2005).

We examined the allometric relationship between growth rates and body mass in larvae of 11 unrelated species of Lepidoptera (III). In particular, when estimating the allometric relationship between instantaneous growth rates and body mass, growth rates of the second day (as a representative of the "free" growing period in the beginning of the instar, see II, III) of the penultimate and ultimate instar larvae were compared. To facilitate a quantitative comparison of growth rates of different instars, the sample of each species was divided into two asynchronously developing "rearing waves", shifted relative to each other in time by temperature manipulations in egg or early larval stage. As a result of the manipulations, all larvae of both waves moulted to either final or penultimate instar at the same time. They were allowed to resume feeding strictly synchronously, so exactly the same growth phases of the different instars were secured to occur simultaneously.

We found that the values of the allometric exponent, relating absolute instantaneous growth rate to body mass, differed significantly from the value 1 in all species, but the one with the lowest sample size (III). Moreover, the observed values were generally, though not always, close to the range of 2/3 to 3/4 (III, Figure 1) which is consistent with the scaling rules of general allometry (Reiss 1989). Accordingly, in all species studied, the values of instantaneous relative growth rates (RGR, calculated as log (final mass/ initial mass)/time) were lower in the ultimate instar, as compared to those of the penultimate instar. Typically, the instantaneous RGR in the final instar constituted only 65% of that in the penultimate one (III, Figure 2). The pattern remained qualitatively unchanged when the growth rates were expressed in terms of entire growing periods within larval instars, i.e. measured from the start of instar to the time point when maximal mass was achieved. In particular, an almost twofold decrease in such instar-specific relative growth rates occurred when penultimate and ultimate instars were compared. Our results thus clearly indicate that growing in the late instars is not even nearly as efficient as it would be predicted under the assumption of exponential growth. The remarkable decrease of relative growth rates in later instars should substantially contribute to the cost associated with adding of additional instars to the growth schedule (see below). However, the exponent relating growth rates to body mass still substantially exceeded zero (characteristic of linear growth) in all species studied, *absolute* growth rates are thus still higher in the later instars. Although instar's maximal/ initial mass ratio showed some tendency to be higher in the penultimate instar when compared to the ultimate one, this pattern was inconsistent between species (III, Table 3). Therefore, a general trend towards the decrease of the growth capacity in later instars is not expected.

3.1.4. Number of instars

The number of larval instars varies widely across insect taxa. There are apparently some exceptional species which go through only 1 larval instar (Jarjees & Merritt 2002), while in others more than 30 instars are recorded (e.g., Clifford et al. 1979). Larvae of most of the insect species however, tend to have 3–8 instars. The number of instars is apparently not related to the adult size characteristic of the species, as for example, some of the world's largest insects, like saturniid moths and goliath beetles, go through only 2–4 larval instars (Nijhout 1981). This may also be seen as indirect evidence of no severe (mechanical) constraints on the within-instar growth (relative mass increment) in larvae of holometabolous insects. However, the rigid exoskeletons may still set strict limits to the within-instar growth in some phylogenetically older orders, like Ephemeroptera, Odonata and Plecoptera, as larvae from these taxa generally have notably higher number of instars (usually more than 10) than those from other taxa.

Instar number is much more canalised within species. While most insects are considered to have constant number of instars, there are numerous species which show variability in this parameter. However, as the data about this phenomenon are extremely scattered and there is no general understanding of several aspects related to the intraspecific variability in instar number in insects, a review about this topic was needed. Based on published case studies, we were able to find data about a variable instar number in 145 insect species, belonging to 12 orders and 49 families (IV, Table I). Typically, the intraspecific range of variability in the number of instars was found to be as low as 1–3, however remarkable exceptions from this trend were met. Temperature, photoperiod, food quality and quantity, humidity, rearing density, physical condition, inheritance and sex were found to be the most common factors influencing intraspecific instar number (IV). Interestingly, in most species exhibiting intraspecific variability in the number of instars, some variation appears to be "inavoidable" as it invariably occurs even in standardized rearing conditions (IV, Table 1). This finding is in opposition to the claim of some authors that, even in species which show intraspecific variability in instar number, number of instars is usually constant in "normal" conditions and varies only when larvae are exposed to adverse conditions (e.g., Nijhout 1994). In contrast, our results, based on the survey of relevant case studies, suggest that if variability has once evolved, instar number tends to remain highly plastic at the intraspecific level.

If the relative within-instar mass increment is limited intraspecifically, as indicated by the high correlation between instar's initial and final mass (see above), an invariable number of instars may form a constraint which prevents attaining large body size, both at the ecological and evolutionary time scales (Tammaru 1998). The species which show variability in instar number, in turn, are likely not affected by this constraint. It is therefore expected that under favourable conditions, larvae of these species should take the advantage of the possibility to attain large size at relatively low cost (in terms of lower cumulative mortality), and go through a higher number of instars (the "opportunistic" scenario). Alternatively, a higher intraspecific instar number may be a compensatory mechanism which enables the larvae to attain certain species-specific threshold size which has necessarily to be achieved in order to initiate metamorphosis (Nijhout 1975). According to this "compensation" scenario, we should expect a higher number of instars in unfavourable conditions. This is because, due to low within-instars increments, the larvae may need to go through additional instars in order to attain the threshold size (Nijhout 1975).

In an attempt to evaluate the two alternative scenarios, we asked if a higher number of instars in insects is more likely to occur in favourable, or adverse environments. We found published data about 25 insect species, in which instar number differed between treatments which could unambiguously be classified as favourable or adverse (IV). In 22 species out of 25, a higher number of instars occurred in adverse conditions (IV, Table 2). This result clearly indicates that, in most cases, the compensation scenario is likely to hold true. Moreover, the validity of the compensation scenario is further strengthened by the general trend that, under standardized conditions, only smaller individuals tend to have additional instars (IV, V, VI). It follows that even if the option of adding instars to growth schedules, and to achieve larger body size thereby, is available for species which show variability in instar number, this possibility is not always used. Therefore, there must exist some costs associated with adding additional instars. It is possible for example that due to a significant decrease of relative growth rates in late instars (III), the expected increase in cumulative mortality could outweigh the benefits of the extra mass increments to be achieved by the additional instars.

Several other explanations of intraspecific variability may be proposed in addition to the two discussed above. For example, the adaptive value of the variability in instar number may lie in reaching or maintaining the developmental stage adapted to hibernation, in the form of omitting or inserting instars according to the progress of favourable season (e.g., Goettel & Philogène 1978, Kfir 1991, Shintani & Ishikawa 1998). Larvae of multivoltine (i.e. several generations within a year) species in turn, may omit an instar and mature earlier when there appears to be sufficient time to have an additional generation (Gomi 1996, Fischer & Fiedler 2001, Gomi et al. 2003). Some species may even have an indeterminate number of regressive moults (i.e. negative growth of linear measurement during moults) when exposed continuously to adverse conditions like starvation or inadequate diet (Titschack 1926, Beck 1971). The adaptive function of negative growth of linear measurements during these moults is proposed to be the increase of surviving probability under the long lasting adverse conditions, by means of reduced requirement of energy and water (Beck 1973, Kfir 1991).

3.1.5. Differences in growth schedules between the sexes

In most insect species, females attain higher final body mass than males i.e. female-biased sexual size dimorphism in adult sizes is observed in most species (e.g., Teder & Tammaru 2005). As insects do not grow after maturity, growth curves of larvae between the sexes should necessarily differ to produce a difference in final sizes. There are three basic mechanisms that can lead to sexual size dimorphism. Individuals of the ultimately larger sex could be larger at hatching/birth, grow faster or grow for a longer time. In the case of insects, the few studies that have focused on the role of the egg/hatchling size have not revealed any effect (Mackey 1978, Ernsting & Isaaks 2002, Yasuda & Dixon 2002). In contrast, both sex-related differences in development time (e.g., Mackey 1978, Brakefield & Mazzotta 1995, Nylin et al. 1993, Mikolajewski et al. 2005) and sex-specific growth rates (e.g., Bradshaw & Holzapfel 1996, Telang et al. 2001, Yasuda & Dixon 2002, Blanckenhorn 2005) have been reported repeatedly in insects.

In most cases however, development time and growth rates have been measured, or calculated, over the entire instar (see above) or, even more typically, over the entire larval period (e.g., Nylin et al. 1993, Bradshaw & Holzapfel 1996, Ernsting & Isaaks 2002). Methods based on instar-specific measurements are not able to distinguish between the “free growth” and "premoult waiting" phases of the particular instar, and may therefore inaccurately estimate true differences in instantaneous growth rates (see above). The methods based on entire larval periods however do not only amplify remarkably the inaccuracies of the former method, but are also prone to additional errors. In particular, if the number of instars differs between the larvae, such methods may underestimate instantaneous growth rates and growing time of larvae that go through higher number of instars. This is because these larvae have extra premoult waiting periods connected to additional moults and therefore use less time for actual growth than those which go through fewer instars. Because of these potential shortcomings of the commonly used methods of estimating growth, it is hard to unequivocally interpret the results of most studies analysing growth curves of insects. Therefore, again, it has to be concluded that the only possibility to adequately measure instantaneous growth rates seems to directly record growth rates in specific growth phases within particular instars.

In an attempt to avoid the methodological problems mentioned above, we studied proximate determinants of sexual size dimorphism (SSD) in six unrelated lepidopteran species, all those showing no intraspecific variations in instar number (VII, Table 1). Instantaneous growth rates were expressed as logarithmical relative mass increments of the second day of an instar. Additionally, the formation of SSD during the ontogeny of the larvae was followed by calculating the female-male mass ratio on the final day of each instar, while the ratio of pupal masses was taken as the index of final SSD. In one species, the saturniid moth *Saturnia pavonia*, individuals were weighed since the egg stage while monitoring of mass increments was initiated later in larval ontogeny in other species. We found that while all species exhibited notable SSD in pupal masses, females were invariably heavier already in early larval instars (VII, Figure 1). Moreover, the relative increase in body mass per larval instar (growth ratio) was, with one exception, always larger in females than in males in both penultimate and ultimate instar (VII, Tables 2, 3). Notably, in all species, the higher relative within-instar mass increments of females were achieved by extended durations of instars in females rather than their higher instantaneous growth rates (VII, Table 2). However, there was no difference between the sexes in the masses of eggs and newly hatched larvae in the species in which these parameters were recorded.

It may therefore be concluded, that in lepidopterans with notable SSD in final size, and no sex-related difference in number of larval instars, size difference between the sexes accumulates during several larval instars, while the starting point of this accumulation is in early larval life. This pattern may be interpreted as another indirect evidence of the constraints on within-instar growth patterns. In particular, it is possible for females to have somewhat higher within-instar mass increments than those in males, however their ability to do so appears to be limited, and high differences in size cannot be achieved during one instar. Interestingly, prolongation of the duration of instars, and not the option of higher instantaneous growth rates, was invariably used by female larvae in order to achieve higher within-instar mass increments as compared to males. This finding suggest that the costs associated with fast growth (e.g., Arendt 1997, Nylin & Gotthard 1998, Gotthard 2001, Metcalfe & Monaghan 2001) may outweigh the likely survival costs of prolonging instar durations and the first option is avoided when possible.

In insects, a higher number of larval instars in females is a specific mechanism which may lead to female-biased SSD. While the phenomenon of females having a higher number of instars has been known in several insect species, and has assumed to be related to the formation of female-biased SSD (e.g., Benson 1950, Sephton & Hynes 1982), empirical support of this notion has largely remained indirect and scattered. To fill this gap, we compiled a review on sexual differences in instar number in insects, giving special attention to the role of additional instars in the determination of SSD (VI). We were able to trace published data on sexual differences in instar number for 56 insect species from 9 orders: in 54 species, the female sex was the one which developed through a higher number of instars (VI, Table 1). In most species however, instar number varied also within sexes, and typically, some overlap occurred between the sexes. Notably, the species in which females had higher average instar number than males, exhibited an unusually high female-biased sexual dimorphism in final weight with females being, as an among-species average, nearly twice the size of the males (VI, Fig. 2A). Even though females are the larger sex in the majority of insects, SSD typically remains much lower, with an estimate of the mean around 1.3 and median around 1.2 over a large set of species (Teder & Tammaru, 2005). Moreover, among the species with sexual differences in instar number, there are species which exhibit some of the highest SSD values among insects (lymantriid moths for example). These results suggest that adding instars to growth schedule may be the only possibility in female insects to achieve *much* larger body sizes than do conspecific males. Importantly, as a general rule, there was no notable SSD in earlier larval life in species with sexual difference in instar number (VI, Fig. 2B), indicating that the considerable size dimorphism in final size was achieved solely due to the additional instars of females. The absence of an early sexual growth divergence may indicate that the higher instar-specific increments in females, potentially leading to SSD, are always avoided when not ‘needed’. In particular, in the likely case when the optima of body sizes do not differ between sexes in the juvenile stage but do differ in adult stage, additional instar may allow larvae to follow the same developmental trajectories until the late juvenile phase and only then switch to achieving different size optima of the adult stage (VI).

In two moth species, *L. dispar* and *O. antiqua*, we investigated the formation of SSD in more detail (V). These species exhibit very high female-biased SSD, and sexual differences in instar number, females typically going through one additional instar compared to males, and forming pupae that are more than twice the weight of the males. Moreover, the fact that in both species instar number differs also within sexes, allowed us compare the determination of SSD in cases when the number of larval instars did not differ between sexes, with those in which it did. Results of this study were generally consistent with the results presented above. In particular, when the females with an additional instar were compared to males, SSD was not present in earlier larval life. These females thus achieved their higher pupal mass solely through the additional instar while their larval period was considerably prolonged when compared to males. The pattern of SSD formation was different however, when the larvae with no sexual differences in instar number were compared. In this case, females were larger already in earlier instars, and had substantially higher instar-specific mass increments than males. In both species, the larger final size of females could largely be ascribed to prolongation of development time while in *L. dispar*, higher instantaneous relative growth rates of females played also an additional role.

Results of this study confirm the occurrence of two different strategies leading to SSD. When instar number does not differ between sexes, SSD accumulates during several instars in a stepwise manner. In the case of additional instars of females however, the formation of size difference is "postponed" to the late juvenile phase. The coexistence of these strategies within the same species, however, indicates that alternative pathways are available for growth and development, while the choice of the pathway may be related to the size (quality) of the larvae. In particular, only the larvae which were initially smaller and had lower within-instar mass increments, tended to go through additional instars in both species studied. This suggests that the insertion of additional instars is avoided by larger (better quality) female larvae, which are capable of achieving the large final size by slightly higher mass increments within each successive instar. It can be concluded then that while additional larval instars in females clearly serve as an important mechanism leading to high female-biased SSD in insects, such option likely entails certain costs (e.g., higher cumulative mortality due to prolonged larval period), and is still avoided when possible.

4. CONCLUSIONS: LINKING BODY SIZE TO GROWTH SCHEDULES IN INSECT LIFE HISTORIES

There are several limitations to (constraints on) the growth and size determination in insects which are related to the specific growth curve, subdivided into discrete instars. Intense growth is possible only in the beginning of each instar, while, in preparation to approaching moult, growth slows down rapidly in the second half of an instar (Ayres & MacLean 1987, II). As a consequence, moulting involves notable costs in terms of time lost, which could be otherwise used for growing (II). The evolutionary determinants of observed moulting frequencies still remain unclear. The once popular hypothesis about the need of resizing mouthparts as the main cause of moulting (Hutchinson et al. 1997) was not supported in two moth species tested (II). While there is evidence against severe constraints on within-instar mass increments in insects (e.g., Nijhout 1981, Elmes et al. 2001), a high correlation between initial and final masses (e.g., Tammaru et al. 2004) of instars still points towards the limitations to relative within-instar mass increments. Moreover, the fact that, in species with high female-biased sexual size dimorphism, size difference between the sexes accumulates during several instars (V, VII), further suggest that within-instar mass increments are limited to a certain extent. In particular, some increase in within-instar increments is possible, but it appears that it is not possible, or at least is substantially disadvantageous, for females to achieve their large adult body size during only one larval instar. Limited within-instar growth ratio in turn, directly sets upper limits to the final size when intraspecific instar number is invariable. As in most insect species instar number is likely to be invariable, there may be a basis for a common constraint which prevents insects to achieve large(r) final sizes, both at the ontogenetic and evolutionary time scales (Tammaru 1998). Adding an instar to growth schedule, in turn, is an obvious way to overcome this constraint. This idea is supported by the fact that in insect species exhibiting very high female-biased size dimorphism, female larvae tend to go through more instars than males (VI). However, within sexes, only smaller larvae or larvae reared under suboptimal conditions, tend to have more larval instars (IV, V, VI). This indicates that within sexes, additional instars are likely used as a compensatory mechanism to achieve certain species-specific threshold weight (Nijhout 1975, 1994), and are avoided when possible. Therefore, inserting an extra instar to growth schedule likely entails costs which must outweigh high benefits that are expected to accompany the large final size to be attained. It may be possible for example, that due to lower relative growth rates in older instars (III), the mass increment in the additional instar would be too low to counterbalance the cost of the (considerably) prolonged larval period. There are several unclear aspects related to growth curves of insects, which need further studies. Among other, there is still not clear why do insect larvae moult or, at least, why do they moult as frequently as they do. However, as growth ratio within instars seems to be limited, the answer, in most general terms, may still be that insects moult in order to grow. Then the question arises what limits the within-instar mass increment, as a classical argument that the within-instar mass increment is strictly restricted by the rigid nature of exoskeleton is not likely valid, at least in the case of holometabolous insects. The limited aerobic capacity caused by the fact that the tracheal system does not grow during instar (Greenlee & Harrison 2004, 2005) provides a promising explanation, however, it still likely fails to explain the observed variability in within-instar mass increments between and within the species. The nature and the magnitude of costs and benefits associated with additional instars make up an other obscure topic. There have to be high costs associated with additional instars that must outweigh the benefits of large final size. On the other hand, as extra instar is important, and possibly, the only mechanism that enables females to achieve considerably larger final sizes compared to males, the benefits of larger size seem to clearly outweigh the costs of additional instars in between-sexes comparisons. The interesting result that sexual size dimorphism in lepidopterans is achieved by prolonging growing period rather than increasing growth rates indicates than fast growth may incur higher costs than prolongation of growing period. Further experiments on other insects are needed to find out if this is a general phenomenon among insects. Importantly, instantaneous growth rates have to be determined on the basis of short-term measurements that explicitly account for the phase of within-instar growth curve.

SUMMARY

During their immature development, larvae of insects and other arthropods moult regularly, i.e. replace their exoskeletons. As larvae do not grow in weight when moulting, growth curves of these animals are discontinuous, being divided into discrete growing periods, called instars. Intense growth takes place only in the first half of each instar, while, due to the initiation of new moulting cycle, growth slows down remarkably in the second half, and stops right before and during the moulting process (II). While such complexity is expected to substantially interfere with life history evolution, it has received undeservedly little attention in this context. However, knowing the proximate nature of growth would necessarily help to determine the set of possible reaction norms for age and size at maturity, and to reveal possible constraints on arthropod life histories thereby.

The aim of the present thesis was to analyse insect growth curve in the life history context, with a focus on determining the role of instars in insect life histories. Particular attention was given to those aspects of growth which critically influence the attained final body size. This is because potential costs or constraints which counterbalance the remarkable benefits of large body size in insects are still poorly known (I). Two of the studies (IV, VI) are literature-based reviews, while others constitute experiments with different lepidopteran species.

While moulting is a phenomenon common to all arthropods, the exact, both proximate and ultimate, reasons for moulting are still unclear. As within-instar relative mass increments may vary notably both within and between insect species (III, V, VII), there are likely no severe constraints on this parameter, and adaptive explanations are to be sought. One of the hypotheses having been proposed – the main benefit of moulting being enlargement of mouthparts – was tested on two species of lymantriid moths (II). If growth rates were determined by the size of mouthparts, one would expect constancy of absolute growth rates within an instar, dependence of growth rates on head capsule size within an instar, and higher absolute growth rates in older instars. Results of the experiment however, did not support these assumptions. In particular, the size of head capsule had no notable effect on growth rates, absolute growth rates tended to increase during the instar and higher growth rates of older instar larvae were explainable by an allometric relationship that extrapolates from growth within the preceding instar. It was therefore concluded that the hypothesis about enlargement of mouthparts being the main cause of moulting, appears not to be directly usable to explain moulting strategies in lepidopteran larvae. However, it is still possible that moulting is initiated exactly before the point when size of the mouth-parts would start to limit consumption rates, and growth rates thereby.

The growth of an insect larva is often assumed to be exponential, implying that relative growth rates do not depend on body size of larvae. While this assumption has a strong impact in expected reaction norms for age and size at maturity, it has hardly been adequately tested in insect larvae. A proper attention to larval instars is needed to solve this problem correctly. The allometric relationship between instantaneous growth rates and body mass was studied in larvae of 11 unrelated lepidopteran larvae, relying on the fast growth phase of penultimate and ultimate instar (III). The observed values of the allometric exponent were close to 2/3, or 3/4, being therefore consistent with the general scaling rules of allometry. The values of instantaneous relative growth rates were almost twice times lower in the ultimate instar, when compared to those of the penultimate instar, indicating that growing in the late instars is not nearly as efficient as predicted by the assumption of exponential growth.

While most insects are considered to have constant number of larval instars, there are numerous species which show variability in this parameter. Based on published case studies, an overview about intraspecific variation in instar number was given (IV). The phenomenon in question was demonstrated to occur in all major insect orders, in both hemimetabolous and holometabolus taxa. Temperature, photoperiod, food quality and quantity, humidity, rearing density, physical condition, inheritance and sex were found to be the most common factors influencing instar number. In most cases, instar number was higher in adverse conditions, suggesting that, within sexes, additional instars are mostly used as a compensatory mechanism to reach the species-specific threshold weight.

Females are larger than males in most insect species. However, the proximate mechanisms leading to female-biased sexual size dimorphism (SSD) are poorly known. Proximate determinants of SSD were investigated in six unrelated lepidopteran species, all those exhibiting notable female-biased SSD, but having an invariable number of larval instars (VII). Females were found to be heavier already in early larval instars, and their instar-specific relative increase in body mass was observed to be larger than in males. In all species, the higher relative within-instar mass increments in females were achieved by extended durations of instars, but not through higher instantaneous growth rates. These results indicate that females' ability to increase the within-instar mass increments is limited and, high female-biased SSD is likely to be reached only by accumulation of the size difference in the course of several instars.

However, in a number of insect species, the sexes tend have a different number of instars as larvae. In far most of species with a sexual difference in instar number, females developed through a higher number of instars than males (VI). Typically, the species in which females had higher average instar number than males, exhibited an unusually high female-biased sexual dimorphism in final size. These results suggest that adding instars to the growth schedule may be the only possibility how female insects can achieve much larger body sizes than do conspecific males. Notably, size difference between the sexes was achieved solely through the additional instar of females, as no sex-related size difference was observed earlier in larval life (V, VI). This scenario differs considerably from the accumulation of size difference, observed in species with no sexual difference in instar number (VII). The absence of early sexual growth divergence may indicate that the higher instar-specific increments in females, potentially leading to SSD, are avoided when not 'needed'. On the other hand, adding an extra instar provides an opportunity for considerable increase in final size – if this option is not used, there should be reasons for it.

It should be concluded that the instar-divided growth curve sets several limits to the pathways of size determination, both at the ontogenetic and evolutionary levels. Most importantly, within-instar size increments of insect larvae appears to be limited for reasons unknown at present. While inserting additional instars to the growth schedules sounds a promising mechanism to achieve large size, it seems to be used only conditionally. Therefore, the nature and the magnitude of costs of additional instars also calls for further studies. The remarkable time loss which accompanies extra moult and lower relative growth rates in older instars, may constitute an important component of this cost. In any case, however, the combination of limited capacity of within-instar growth and the presumably high cost of additional instars, has definitely a potential to preclude the evolution towards large body size in insects.

KOKKUVÕTE

Kasvujärk kui putukate kasvukõvera keskne element

Kõigi lülijalgsete vastsed kestuvad arengu käigus korduvalt, so nad uuendavad regulaarselt välisskeletti. Kuna kestumiste ajal vastse mass ei kasva, on tulemuseks ebapidev kasvukõver, mis on kestumistega jagatud diskreetseteks kasvuperioodideks ehk kasvujärkudeks. Intensiivne kasv toimub ainult kasvujärgu esimeses pooles, samas kui seoses uue kestumistsükli algamisega aeglustub kasv kasvujärgu teisel poolel tunduvalt ning peatub täielikult kestumisprotsessi ajaks ja sellele vahetult eelnevaks ning järgnevaks perioodiks (II). Selline spetsiifiline kasvukõver avaldab kahtlemata olulist mõju lülijalgsete elukäigule, samas on sellele teenimatult vähe tähelepanu pööratud. Kasvukõvera detailne tundmine võimaldab mõista lõpliku kehasuuruse ja kasvuperioodi pikkuse determinatsiooni reaktsiooninorme ning kasvu iseärasustest elukäigule tulenevaid piiranguid.

Käeoleva doktoritöö eesmärgiks on analüüsida putukate kasvukõverat elukäiguteooria kontekstis, keskendudes eelkõige kasvujärgu rollile putukate elukäigus. Leidmaks võimalikku suurte kehamõõtmete saavutamisega kaasnevat hinda, pööratakse erilist tähelepanu kasvu nendele aspektidele, mis mõjutavad oluliselt lõpliku kehasuuruse saavutamist. Seitsmest esitatud originaalpublikatsioonist kaks (IV, VI) on kirjandusel põhinevad ülevaateartiklid, ülejäänud erinevate liblikaliikide vastsetega teostatud empiirilised uuringud.

Kuigi kõigi lülijalgsete vastsed kestuvad arengu käigus, on kestumise põhjused siiani täpselt teadmata. Traditsiooniliselt on kestumise põhjuseks peetud välisskeleti vähest venivust, mis seab piirid kasvujärgusisesele kasvule. Kuna putukatel erineb kasvujärgusisene kasv suuresti nii liikide kui liigikaaslaste vahel (III, V, VII), ei ole selline seletus rahuldav ning tuleb kaaluda adaptiivseid seletusi. Ühe varem esitatud hüpoteesi kohaselt kestuvad vastsed selleks, et suurendada suiseid, mis omakorda võimaldaksid kiirendada konsumeerimist ja seeläbi kasvu. Kõnealust hüpoteesi kontrolliti kahel lainelaste sugukonda kuuluval liblikaliigil (II). Eeldusel, et kasvukiirus on määratud eelkõige suiste mõõtmete poolt, peaks absoluutne kasvukiirus kasvujärgu sees olema konstantne ning sõltuma otseselt peakapsli suurusest, samuti peaks kasvukiirus olema suurem hilisemates kasvujärkudes. Eksperimendi tulemused ei kinnitanud antud eeldusi, kuna peakapsli mõõtmed ei korreleerunud oluliselt kasvukiirusega, kasv kiirenes kasvujärgu siseselt ning suuremad absoluutsed kasvukiirused hilisemates kasvujärkudes olid seletatavad kehakaalu ja kasvukiiruse vaheliste allomeetriliste seostega. Seetõttu jõuti järeldusele, et hüpotees suiste suurenemistest kestumise peapõhjusena ei ole otseselt liblikaröövikutele kohaldatav. Samas jääb võimlus, et kestutakse vahetult enne hetke kui suiste mõõtmed hakkavad piirama toidu manustamise ning seeläbi ka kasvu kiirust.

Tihti on eeldatud, et putukavastsed kasvavad eksponentsiaalselt ehk siis on oletatud, et suhteline kasvukiirus ei sõltu kehamõõtmetest. Kuigi sellisel eeldusel on oluline mõju oodatavatele lõpliku kehasuuruse ja kasvuperioodi pikkuse reaktsiooninormidele, ei ole seda eeldust putukatel korrektselt kontrollitud. Käesolevas töös uuriti allomeetrilist seost kehasuuruse ja kasvukiiruse vahel üheteistkümnel liblikaliigil (III). Leiti, et kõnealust allomeetrilist seost iseloomustav eksponent oli enamasti lähedane väärtustele 2/3 või 3/4, olles nii kooskõlas üldiste füsioloogiliste seaduspärasustega. Suhteline kasv viimases kasvujärgus osutus ligi kaks korda aeglasemaks kui eelviimases järgus, mis näitab, et tegelik kasv hilisemates kasvujärkudes on oluliselt ebaefektiivsem kui eksponentsiaalse kasvu korral võiks oletada.

Kuigi enamusel putukatest arvatakse kasvujärkude arv olevat konstantne, on siiski mitmeid liike, millel järkude arv varieerub. Avaldatud teadustööde põhjal koostati ülevaade kasvujärkude arvu varieeruvusest putukatel (IV). Leiti, et liike millel järkude arv varieerub, esineb kõigis suuremates putukaseltsides nii täismoondega kui vaegmoondega taksonite hulgas. Peamisteks liigisisest järkude arvu mõjutavateks teguriteks osutusid temperatuur, valguspäeva pikkus, toidu kvaliteet ja hulk, niiskus, asustustihedus, isendi konditsioon, pärilikkus ning sugu. Enamasti oli kasvujärkude arv suurem ebasoodsates oludes, kinnitades seega hüpoteesi, et nn lisakasvujärke kasutatakse eelkõige kompensatsioonimehhanismina metamorfoosi alustamiseks vajaliku liigispetsiifilise suuruskünnise saavutamiseks.

Putukatel on emased valmikud enamasti suuremad kui isased, samas on kehasuuruse erinevustele viivad arengulised mehhanismid siiani ebapiisavalt tuntud. Käesolevas töös selgitati sugudevahelise kehasuuruste erinevusi põhjustavaid kasvukõvera iseärasusi kuuel liblikaliigil, millel kõigil on emased valmikuna suuremad kui isased, samas kui liigisisene järkude arv ei varieeru (VII). Leiti, et emased on suuremad juba varastes vastsejärkudes ja emaste suurema järgusisese kasvu tõttu suurenes sugudevaheline kehasuuruse vahe vastseperioodi käigus. Kõigil liikidel saavutasid emased suuremad mõõtmed järgusisese kasvuperioodi pikendamise, mitte aga kasvukiiruse tõstmise teel. Kõnealused tulemused annavad alust arvata, et emastel on võimalik järgusiseselt isastest rohkem kasvada vaid piiratud määral ning suur kehamõõtmete erinevus sugude vahel on võimalik saavutada ainult suuruse erinevuse akumulatsiooni teel mitme kasvujärgu jooksul.

Mitmetel putukatel erineb kasvujärkude arv sooti ning valdaval enamusel sellistest juhtudest läbivad emased rohkem kasvujärke kui isased (VI). Selgus, et taolistel liikidel on sugudevaheline valmikute kehasuuruste erinevus selgelt suurem kui putukatel keskmiselt, mis viitab sellele, et lisajärgu läbimine emaste poolt võib olla ainsaks võimaluseks väga suure sugudevahelise kehasuuruse erinevuse tekkeks putukatel. Tähelepanuväärne on asjaolu, et emaste suurema järkude arvu korral tekkis sugudevaheline kehamõõtmete vahe pelgalt tänu emaste lisakasvujärgule samas kui enne lisajärku kehasuurus sugude vahel ei erinenud (V, VI). Erinevuse puudumine arengu algfaasides annab alust oletamaks, et suuremat kasvu järgu sees võimalusel välditakse. Teisest küljest võimaldaksid lisajärgud saavutada oluliselt suuremaid kehamõõtmeid, kuna aga seda võimalust ei kasutata sugugi alati, peab selleks olema põhjus.

Käesoleva töö tulemusest saab järeldada, et järkudeks jagatud kasvukõver seab mitmed piirangud putukate kehasuuruse determinatsioonile nii ontogeneetilises kui ka evolutsioonilises ajaskaalas. Kõige olulisem näib olevat piirang kasvujärgusisele kasvule, samas selle piirangu olemus on seni teadmata. Lisakasvujärgud võimaldaksid sellele piirangule vaatamata saavutada suuremaid mõõtmeid, samas kasutatakse neid sel otstarbel ainult mõningatel juhtudel. Seetõttu vajab lisajärkudega kaasneva hinna olemus ja suurus täiendavaid uuringuid. Kestumisega kaasnev suur ajakulu ning madalam suhteline kasvukiirus hilisemates kasvujärkudes võivad olla lisajärkude hinna olulisteks komponentideks. Igal juhul võib järgusisene piiratud kasv koos lisajärkude kõrge hinnaga olla oluliseks tõkkeks putukate kehasuuruse evolutsioonilisele suurenemisele.

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PUBLICATIONS

Tammaru, T., Esperk, T., Castellanos, I. 2002. No evidence for costs of being large in females of *Orgyia* spp. (Lepidoptera, Lymantriidae): larger is always better. *Oecologia* 133: 430–438.

Esperk, T., Tammaru, T. 2004. Does the ‘investment principle’ model explain moulting strategies in lepidopteran larvae? *Physiological Entomology* 29: 56–66.

Tammaru, T., Esperk, T. Growth allometry of Lepidopteran larvae: a life history perspective. Manuscript.

Esperk, T., Tammaru, T., Nylin, S. Intraspecific variability in the number of larval instars in insects. Submitted, invited to *Journal of Economic Entomology*.

Esperk, T., Tammaru, T. Determination of female-biased sexual size dimorphism in moths with variable instar number: the role of additional instars. *European Journal of Entomology* 103: 575–586.

Esperk, T., Tammaru, T., Nylin, S., Teder, T. Achieving high sexual size dimorphism in insects: females add instars. Tentatively accepted by *Ecological Entomology*.

Tammaru, T., Esperk, T., Ivanov, V., Teder, T. Proximate mechanisms leading to sexual size dimorphism in Lepidoptera: locating constraints on larval growth schedules. Manuscript.

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II. Research history

1. Research interests

The evolution of body size in insects, the effects of specific, instar-divided growth curve to the life histories of insects

2. Publications

Tammaru, T., Esperk, T., Castellanos, I. 2002. No evidence for costs of being large in females of Orgyia spp. (Lepidoptera, Lymantriidae): larger is always better. Oecologia 133: 430–438.

Esperk, T., Tammaru, T. 2004. Does the 'investment principle' model explain moulting strategies in lepidopteran larvae? Physiological Entomology 29: 56–66.

Esperk, T., Tammaru, T. 2006. Determination of female-biased sexual size dimorphism in moths with a variable instar number: the role of additional instars. European Journal of Entomology 103: 575–586.

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Tartu University research scholarship for doctoral students no. DBGZH 0625: 2003–2004;

Estonian National Scholarship Programme *Kristjan-Jaak* for scientific research in Stockholm University 09-12.2003.

4. Research-administrative experience

Conference theses

Esperk, T., Tammaru T. Does a general model fit to explain moulting strategies in lepidopteran larvae? Ninth Congress of the European Society for Evolutionary Biology. 18–24 August 2003, Leeds, Great-Britain. Symposia of the evolution of sexual size dimorphism. Poster presentation

Tammaru, T., Esperk, T., Castellanos, I. No costs of large boduy size in female Orgyia spp. (Lepidoptera: Lymantriidae): larger is always better. Ninth Congress of the European Society for Evolutionary Biology. 18–24 August 2003, Leeds, Great-Britain. Symposia of the evolution of sexual size dimorphism. Poster presentation

Esperk, T., Tammaru, T., Nylin, S. The role of additional larval instars in determination of female-biased SSD in insects. International workshop of the evolution of sexual size dimorfism. 21–26 August 2005, Locarno, Switzerland. Oral presentation.

Esperk, T. The complex growth curve of insects: what is and what is not possible in life history? Evolutionary conservation biology workshop. 11–14 october 2005, Häädemeeste, Estonia. Oral presentation.

Membership in societies:

Estonian Naturalists' Society;

Estonian Seminatural Community Conservation Association

III. Improvement of skills

Scientific research in Stockholm University 09-12.2003 working with evolutionary ecology research group leaded by professor Sören Nylin.

CURRICULUM VITAE

I. Üldandmed

1. Ees- ja perekonnanimi	Toomas Esperk
2. Sünniaeg ja koht	29.06.1977, Pärnu linn
3. Kodakondsus	Eesti
4. Perekonnaseis	vallaline
5. Aadress	Suur-Posti 19, Pärnu; telefon: + 372 53 302 480; e-post: tome@ut.ee;
6. Praegune töökoht, amet	Tartu Ülikool, Zooloogia ja Hüdrobioloogia instituut, erakorraline teadur
7. Haridus	Pärnu 6. Keskkool (põhiharidus): 1992; Pärnu 2. Keskkool (keskharidus): 1995; Tartu Ülikool, *baccalaureus scientiarum* zooloogia erialal: 2000; Tartu Ülikool, *magister scientiarum* loomaökoloogia erialal: 2002
8. Keelteoskus	eesti, inglise, vene
9. Töökogemus	Eesti Maaülikool, laborant ja vanemlaborant 2000–2006; Tartu Ülikool, erakorraline teadur alates septembrist 2006

II. Teaduslik ja arendustegevus

1. Peamised uurimisvaldkonnad

Kehasuuruse evolutsioon putukatel, putukavastsete kasvuga seotud plastilisus ja piirangud

2. Publikatsioonide loetelu

Tammaru, T., Esperk, T., Castellanos, I. 2002. No evidence for costs of being large in females of Orgyia spp. (Lepidoptera, Lymantriidae): larger is always better. Oecologia 133: 430–438.

Esperk, T., Tammaru, T. 2004. Does the 'investment principle' model explain moulting strategies in lepidopteran larvae? Physiological Entomology 29: 56–66.

Esperk, T., Tammaru, T. 2006. Determination of female-biased sexual size dimorphism in moths with a variable instar number: the role of additional instars. European Journal of Entomology 103: 575–586.

3. Saadud uurimistoetused ja lepingud

Tartu Ülikooli doktorandi teadustöö stipendium DBGZH 0625: 2003–2004

Kristjan-Jaak stipendium (Eesti Haridusministeerium ja S/A Archimedes) teadustööks Stockholmi ülikoolis: 2003

4. Muu teaduslik organisatsiooniline ja erialane tegevus

Konverentside ettekanded:

Esperk, T., Tammaru T. Does a general model fit to explain moulting strategies in lepidopteran larvae? Ninth Congress of the European Society for Evolutionary Biology. 18–24 august 2003, Leeds, Suurbritannia. Sektsioon: The evolution of sexual size dimorphism. Stendiettekanne.

Tammaru, T., Esperk, T., Castellanos, I. No costs of large boduy size in female Orgyia spp. (Lepidoptera: Lymantriidae): larger is always better. Ninth Congress of the European Society for Evolutionary Biology. 18–24 august 2003, Leeds, Suurbritannia. Sektsioon: The evolution of sexual size dimorphism. Stendiettekanne.

Esperk, T., Tammaru, T., Nylin, S. The role of additional larval instars in determination of female-biased SSD in insects. The evolution of sexual size dimorfism, international workshop. 21–26 august 2005, Locarno, Šveits. Suuline ettekanne.

Esperk, T. The complex growth curve of insects: what is and what is not possible in life history? Evolutionary conservation biology workshop. 11–14 oktoober 2005, Häädemeeste, Eesti. Suuline ettekanne.

Erialastesse ühingutesse kuulumine:

Eesti Loodusuurijate Seltsi liige

Pärandkoosluste Kaitse Ühingu liige

III. Erialane enesetäiendus

09-12.2003 teadustöö ja stažeerimine Stockholmi Ülikoolis professor Sören Nylini poolt juhitava evolutsioonilise putukaökoloogia uurimisrühma juures.