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Body size evolution in insects
with different colouration strategies:
the role of predation risk



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LIST OF ORIGINAL PUBLICATIONS

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

- I **Rommel, T.**, Davison, J., Tammaru, T. Predation on Lepidopteran larvae: a life history perspective. *Manuscript*.
- II **Mänd, T.**, Tammaru, T. & Mappes, J. (2007) Size dependent predation risk in cryptic and conspicuous insects. *Evolutionary Ecology*, 21, 485–498.
- III **Rommel, T.**, Tammaru, T. Size dependent predation risk in tree-feeding insects with different colouration strategies: a field experiment. *Journal of Animal Ecology* (conditionally accepted).
- IV Sandre, S.-L., Tammaru, T. & **Mänd, T.** (2007) Size-dependent colouration in larvae of *Orgyia antiqua* (Lepidoptera: Lymantriidae): A trade-off between warning effect and detectability? *European Journal of Entomology*, 104, 745–752.
- V **Rommel, T.**, Tammaru, T. Evidence for a higher importance of signal size over body size in aposematic signaling in insects. *Manuscript*.
- VI **Rommel, T.**, Tammaru, T. & Mägi, M. (2009) Seasonal mortality trends in tree-feeding insects: a field experiment. *Ecological Entomology*, 34, 98–106.

The author contributed to designing the experiments (II, III, V, VI) and analysing the results (I, II, V), and was responsible for data collection (I, II, III, V, VI), analysis (III, VI) and writing the papers (I, II, III, V, VI), with a contribution to writing in IV.

I. INTRODUCTION

Body size has long been a focus of studies on animal life histories, as it is a trait that inevitably interacts with a variety of other fitness-related traits. As a general rule, large body size is thought to have a predominantly positive effect on reproductive success in both males and females: large body size tends to increase fecundity in females and competitive abilities in males. Assuming that body size is evolutionarily stable, these advantages should be counterbalanced with opposing selective factors (Endler 1986, Stearns 1992, Blanckenhorn 2000, Roff 2002). While selection for larger body size is often easy to detect and can be fairly consistent across species, the counterbalancing factors tend to be much less obvious (Blanckenhorn 2000, Tammaru et al. 2002).

The fecundity advantage of large size is clearest in ectothermic animals. Several laboratory studies have demonstrated that female reproductive output in insects increases considerably (sometimes even proportionally) with body size (Honěk 1993, Blanckenhorn 2000, Roff 2002, Tammaru et al. 2002). This poses the question of why insects do not evolve infinitely increasing sizes. In response to this, various costs associated with reaching or maintaining large body size have been suggested. Perhaps the most widely recognized of these is the long development time required to reach large final size and the consequent increase in juvenile predation risk (Roff 2002, Gotthard 2004, Kingsolver et al. 2004). Indeed, numerous authors have argued that high predation pressure in juvenile stages selects for earlier maturation and, consequently, smaller body size (e.g. Stearns 1992, Stoks et al. 1999, 2003, Beketov and Liess 2007).

However, in some cases, an elevated predation risk seems to be insufficient to balance the potential benefits of continued growth. In particular, various insect species exhibit accelerating larval growth trajectories (Leimar 1996, Tammaru 1998, Margraf et al. 2003, Davidowitz and Nijhout 2004, Esperk and Tammaru 2004, Gotthard 2004), and are thereby capable of increasing their potential fecundity considerably by prolonging their growth period just slightly. It is therefore hard to explain the generally observed small sizes and short maturation times of insect larvae on the basis of juvenile mortality risk alone. In some cases, the “paradox of small size” may be solved by reconsidering the assumption of a linear relationship between female size and fecundity. For example, Gotthard et al. (2007) found that time limitation during oviposition results in an asymptotic size-dependent fecundity curve in a Nymphalid butterfly species. However, in species with less time-limited oviposition success, the paradox persists. In particular, Tammaru et al. (2002) showed that, in a species of Lymantriid moth, the fecundity function remained linearly size-dependent both in the laboratory and in the field.

An alternative explanation for the moderate body sizes of most insects is that predation risk is *positively size-dependent* during the juvenile period. This could lead to an increase in mortality as larvae grow and result in far stronger selection against large body sizes than if predation risk were constant with

respect to size (Leimar 1996, Blanckenhorn 2000, 2005). Indeed, there is a fair amount of evidence to suggest that such a relationship exists in insect larvae (Berger et al. 2006, Berger and Gotthard 2008, **I, III**). However, the true importance of size-dependent predation in providing an adaptive explanation for the growth schedules of insect larvae cannot be resolved without case-specific quantitative optimality models. In order to construct such models, it is essential to make realistic, empirically based assumptions about larval predation rates and the patterns of size dependence. Unfortunately, such data are not readily available in the literature (reviewed in **I**).

Bird predation represents a factor that could plausibly drive size-dependence in juvenile survival rates. Birds are typically the predominant cause of larval mortality in herbivorous insects, particularly for the late instars (Dempster 1983, Cornell and Hawkins 1995, Grushecky et al. 1998, **I**). Moreover, birds are visual hunters and are known to discriminate between differently sized prey items (Gamberale and Tullberg 1996b, Grieco 2002, Jones et al. 2005). Various arthropods represent another potentially size-selective guild of predators; however, they are frequently most efficient at killing small larvae (e.g. López and Potter 2000, Roger et al. 2000, but see Berger et al. 2006). This suggests that arthropod predation is unlikely to constitute a strong selective force against large larval size.

Prey size can affect predation risk in two major ways: (1) larger prey animals may be more efficiently *detected* by predators; and (2) predators may preferentially *accept* either smaller or larger prey individuals following their detection. Another component in determining predator success is the ability of prey animals to *resist* attack and survive with minimal damage (Vermeij 1982). Such an ability may substantially contribute a differential mortality risk in insect larvae of different size in the case of arthropod predators (e.g. López and Potter 2000), though its importance in the case of bird predation is probably minimal.

Assessment of size dependence in juvenile predation risk cannot be made without considering the effects of other relevant larval traits. In particular, warning colouration is very likely to alter the way that body size is related to mortality, especially in the case of bird predation. Aposematic animals (or their mimics) typically use conspicuous warning signals to advertise their unpalatability or toxicity to potential predators (Poulton 1890). It is reasonable to assume that birds might respond differently to the body size of cryptic *vs* warningly coloured prey. Indeed, birds have been reported to show stronger aversion towards warningly coloured insects with larger body size (Gamberale and Tullberg 1996b) or group size (Gamberale and Tullberg 1996a, Mappes and Alatalo 1997, Gamberale and Tullberg 1998, Riipi et al. 2001). Additionally, there is some other, less direct evidence for size dependence; for example, warning colouration appears to be more effective when displayed on large areas or when using larger colour signal elements (Forsman and Merilaita 1999, Lindström et al. 1999a). However, since the signal elements of aposematic

animals tend to become larger as animals grow, it is still unclear which of these components – body size or signal element size – is more important in determining predator reactions. This is unfortunate because, in the context of body size evolution, it would be desirable to understand the impact of body size *per se* on predation risk, i.e., independent of other factors.

The aversion of birds to larger aposematic prey could theoretically lead to negatively size-dependent predation risk in conspicuous species. For this reason, it is often assumed that large size should be more profitable to aposematic insects than to cryptic ones (Forsman and Merilaita 1999, Nilsson and Forsman 2003). This is because cryptic insects do not possess the warning signals that might reduce the predation risk associated with large body size. However, this reasoning only takes account of the *acceptability* of different sized prey while ignoring their differential *detectability*, which should, intuitively, be positive for both types of colouration. Moreover, it is likely that the size-dependent slope of detectability is not the same for conspicuously and cryptically coloured larvae. Therefore, to make reliable assumptions about the differences in size dependent predation risk between these colouration strategies, it is necessary to consider both acceptability and detectability effects.

The inevitable trade-off between acceptability and detectability in aposematic animals leads to the evolution of “compromise” adaptations, such as sub-maximally expressed warning signals (Endler and Mappes 2004). An alternative strategy involves ontogenetic colouration shifts during the growth period, allowing animals to exhibit warning colouration only at the range of body sizes where it is efficient. In insects, this is typically interpreted as meaning that young small-bodied larvae should be cryptically coloured while larger older larvae should develop conspicuous colouration (Bernays and Montllor 1989, Ulmer et al. 2003, Sandre et al. 2007). However, assuming that there is a trade-off between acceptability and detectability, it could equally be predicted that an ontogenetic change in the opposite direction should occur: in order to reduce the high level of detectability resulting from their large size, late stage individuals should exhibit cryptic coloration in place of the warning colouration displayed by intermediate stages. Although the pupae of insect species with conspicuous larvae are typically cryptic (Wiklund and Sillen-Tullberg 1985), a change from conspicuous to cryptic during the larval stage has not been frequently documented (the few exceptions being causally related to switching from aggregated to solitary lifestyle) (Cornell et al. 1987, Costa et al. 2003). Nevertheless, each such example could contribute to our understanding of the role of colouration in the evolution of body size.

In addition to larval traits, seasonal changes in environment can also affect predation rate and its size-dependent components. *Per capita* predation risk can vary in relation to seasonal changes in predator communities (Ojala 2006), as well as the abundance of alternative prey (Cappuccino 1995, Harrison and Wilcox 1995, Tanhuanpää et al. 1999). Adult birds may choose smaller prey to feed the youngest nestlings (Moser 1986), or larger prey when food is abundant

(Grieco 1999, 2001, 2002). Moreover, the change in predation pressure throughout the feeding season may well differ for cryptic and conspicuous insect species. For example, Ojala (2006) found that models of *Parasemia* caterpillars with conspicuous warning colours suffered highest predation rates, compared with cryptic models, at the time in the year when the fledglings of most insectivorous birds start to forage. The likely reason for this is that the inexperienced fledglings had not yet learned to avoid warningly coloured prey. In addition to changes in the predator community, the varying abundance of alternative, palatable prey can differentially affect the predation risk of insects with different colouration strategies (Lindström et al. 2001a, Merilaita and Kaitala 2002). For these reasons, it is perhaps unfortunate that most classical optimality models used to explain age and size at maturity have treated the environment as constant in time (see review in Roff 2002). It is evident that incorporating seasonal changes has the potential to significantly affect the outcomes of such models (Abrams et al. 1996).

The goal of this thesis is to evaluate whether positively size dependent predation risk can counterbalance the high fecundity advantage of large size found in various insects. Particular attention is paid to the effects of different colouration strategies on the relationship between size and predation risk. Specifically, different parts of the study aim to: 1) provide an overview of empirical estimates of predation rates in folivorous insect larvae and the dependence of these figures on body size; 2) test the potential of prey acceptability and detectability to influence the risk of predation by birds in cryptic and warningly coloured larvae, and examine how these factors combine in natural situations; 3) test the trade-off hypothesis of the size-dependent colouration shifts in a moth species; 4) evaluate the relative importance of body size vs signal element size in warning colouration; and 5) provide quantitative estimates of predation risk in folivorous insect larvae throughout the feeding season. The results are used to construct an optimality model of body size for a particular moth species.

2. OVERVIEW OF SIZE-DEPENDENT PREDATION RATES

To construct optimality models of insect body size, realistic estimates of predation rates in juvenile stages are needed. Moreover, the dependence of predation risk on prey size has to be accounted for. To provide quantitative estimates for optimality models, I reviewed published papers reporting average daily predation rates in larvae that feed exposed on trees (**I**). Some of these papers provided direct measurements of daily predation rates; however, if predation rates were measured over a longer time period, I calculated the percent daily predation rate as $(1 - \text{survival}^{1/t}) \times 100$, where t is the number of days in the survey period. Similarly, if predation rates were provided for entire instars or the whole larval stage, I calculated approximate daily predation rates based on the average duration of the stage.

Additionally, the published data on size dependence of predation risk in Lepidopteran larvae were reviewed. Some of the respective papers report results of laboratory experiments, where bird or arthropod predators are offered different sized prey (e.g. Jones et al. 2005, Berger et al. 2006). Such experiments usually detect the predators' preference for prey size (especially in the case of birds), while ignoring any detectability differences. Other studies take the approach of predator exclusion in the field (e.g. Valenti et al. 1998, Hooks et al. 2003), providing perhaps more realistic information on size-dependent predation, as these studies account for both preference and searching efficiency of predators. A few studies have compared the size of caterpillars provided to nestlings by adult birds with the average caterpillar size found in their habitats (Gibb and Betts 1963, Naef-Daenzer et al. 2000). The latter type of data cannot be used to make quantitative estimates of the change in predation risk in response to unit change in body size; however, they serve to confirm the qualitative results found in other studies. The papers that did not provide satisfactory statistics for the dependence of predation risk on size were excluded.

A total of 23 papers were found that provide the information necessary to calculate daily predation rates, and another 34 that address larval size-dependent predation risk (**I**). The average bird predation risk (in non-outbreak populations) was found to be around 3.1% (± 2.3 SD) per day, and the average arthropod predation risk was about 10.5% (± 8.9 SD) per day. In the remaining papers that did not differentiate between predator guilds, an average daily predation rate of 8.4% (± 5.7 SD) was found. These figures are not in conflict, because the effects of bird and arthropod predation are not necessarily additive: birds are likely to remove some proportion of arthropod predators (Hooks et al. 2003, Mooney and Linhart 2006) or, conversely, avoid ant-infested trees (Philpott et al. 2005). Assuming a 30-day larval period, only about 38.9% (in case of bird predation) or 3.6% (arthropod predation) of the larvae would survive to pupate. However, it is likely that the figures of arthropod predation are somewhat exaggerated, as

some of the studies measure the predation rates in atypically dangerous situations, e.g. larvae have been exposed in direct vicinity of ant colonies. Additionally, arthropod predation is probably measured in habitats where it is assumed to be important, and neglected in other locations, which can also contribute to a bias in the estimates.

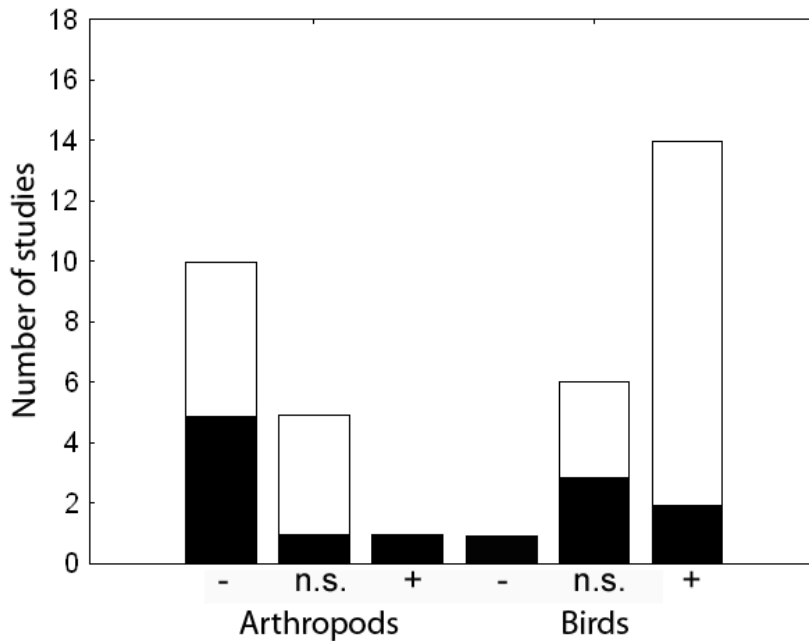


Figure 1. The number of studies reporting negative (–), non-significant (n.s.) and positive (+) arthropod- or bird-mediated size dependent predation risk in Lepidopteran larvae found in the field (white) or in laboratory experiments (black).

The studies investigating bird predation in the context of prey size variation almost invariably find positively size-dependent predation risk, with the only clear exception of aposematic species. In case of arthropod predation, the results tend to be opposite (Figure 1). However, even though laboratory experiments usually find negatively size-dependent predation risk posed by arthropod predators, the field results have often yielded less clear results, presumably because field conditions provide more diverse predator species and also better hiding opportunities for smaller larvae. From the results of field experiments, an average of 3.6-fold increase of bird predation risk was calculated to correspond to a 2-fold increase in body length. In studies of arthropod predation, a 2-fold increase in body length resulted in a 4.9-fold decrease of predation risk on average.

3. COMPONENTS OF PREDATION RISK

3.1. Overview

Body size and colour can affect predation risk in two major ways: by affecting the *detectability* or the *acceptability* of prey to predators. This implies that the predator either finds the prey animal or not, and having found it, the predator either attacks it or not. The third way relies on the ability of larger larvae to escape predator attacks, which is certainly important in many cases of arthropod predation (e.g. Chiravathanapong and Pitre 1980), but probably not much so in bird predation. To evaluate the size dependence of prey detectability and acceptability in determining its vulnerability to bird predation, these two mechanisms have to be tested independently, in controlled experiments. Therefore, separate experiments were conducted to investigate the size-dependent detectability and acceptability of cryptically and conspicuously coloured larvae, using great tits (*Parus major* L) as predators (II). However, laboratory experiments can not reliably predict how these mechanisms combine in natural situation, because they cannot determine the relative importance of detectability vs acceptability. To assess the net effect of size-dependent detectability and acceptability in the survival of cryptic and conspicuous larvae, a field study was carried out, in which different sized and coloured larvae were simultaneously exposed to forest birds (III).

3.2. Artificial prey

Numerous researchers have used artificial models of insect prey in predation experiments (e.g. Ham et al. 2006, Koh and Menge 2006, Ihalainen et al. 2007, Rowland et al. 2007a). These are easy to handle and devoid of unwanted species-specific morphological or behavioural traits. For these reasons, artificial prey can be preferred to real insects, especially when dealing with visually hunting predators and in experiments that aim to clarify the influence of a specific trait (such as colour, contrast, group size, *etc*) on prey survival. In the experiments conducted to test the effects of acceptability and detectability on bird predation risk, I used different prey models, because the separate experiments required different attributes of the prey. In all the experiments, however, half of the larvae were coloured green (cryptic colouration) and the rest black-yellow (warning colouration); there were four size classes in each colouration group, the largest larvae measuring 5 cm in length. The materials of artificial prey used in separate experiments are listed below.

- 1) In the detectability experiments (II), frozen mealworms of uniform size were hidden under different sized and coloured paper strips. Such design was

chosen because it was important that all prey items had a similar nutritial value, so that bird predators had no preferences for different looking items, and detectability could be measured without any confounding effects of acceptability. Before the experiments, all birds were trained to eat all prey types with similar frequency.

- 2) In the acceptability trials (**II**), artificial larvae were made of edible pastry (Church et al. 1997) and coloured with non-toxic fingerpaints. These models were designed to look reasonably natural, as the birds received no training prior to the experiment.
- 3) In the field experiments that tested the combined effect of detectability and acceptability, different prey types were used (Figure 1 in **III**). First, palatable pastry larvae and similar-looking unpalatable plasticine larvae were used in parallel to test for the potential effect of learning by resident birds. Second, in the later replicates of the experiments, palatable blowfly pupae were arranged in rows to form “larvae” of different lengths, and coloured with non-toxic water based colours.

3.3. Detectability

To test size-dependent detectability of prey items, experimental birds were first trained to accept prey items with conspicuous warning colouration as readily as cryptic ones. After the training, they were allowed to search for hidden individuals of both colouration types and four sizes in aviary from a) smooth green background, or b) potted *Philodendron* plants. The different backgrounds were used to test for the generality of the results. The time that the birds needed to find each larva was recorded.

It is no surprise that conspicuously coloured prey items were found sooner than cryptic ones (Table 1, Figure 1 in **II**). In both backgrounds, larger artificial larvae were found sooner than smaller ones, while no size dependence was detected in cryptic prey. The latter may have been a result of too narrow size range; however, as there was a significant interaction of size and colour in determining detection time, it can safely be concluded that the size-dependent detectability slope was steeper in conspicuous larvae.

3.4. Acceptability

Size-dependent acceptability of prey was tested in cage trials, by offering different sized prey (either cryptic or warningly coloured) sequentially to great tits in a random order. It was recorded if and when the birds attacked each item. The birds were considerably more reluctant to attack larger warningly coloured larvae, while larger cryptic larvae were attacked somewhat more readily (Table

2, Figure 2 in **II**). The overall attack rate was higher for cryptic items compared to conspicuous ones, as expected.

These results indicate a predominantly positively size-dependent predation risk in cryptic larvae, but opposing selection pressures in warningly coloured larvae, because, in the latter, detectability and acceptability change in opposite directions with increasing body size. The net outcome of these two factors may depend on their relative importance in natural habitats. In other words, both detectability and acceptability appear to depend on body size, but the way these two opposite effects combine under different conditions may well lead to both quantitative and qualitative differences in the correlation between body size and predation risk.

3.5. Combined effects of detectability and acceptability

I conducted field experiments to quantify the size-dependence of predation risk in a natural setting. In these trials, the predation risk depended on a realistic combination of detectability and acceptability of the prey items. In three years (2003, 2005–6), different sized and coloured artificial larvae were exposed to bird predation in a number of forest habitats. In 2003, either pastry (palatable) or plasticine (unpalatable) larvae were used at different locations to test for the possible learning effect of birds (see *Artificial prey*); however, as there was no difference between the two materials, the use of unpalatable material was abandoned in later experiments (2005–6).

In both colouration groups, larger larvae were attacked more often than smaller ones (Tables 1, 2, Figure 2 in **III**). However, the size-dependent slope of mortality was considerably steeper in the items with warning colouration compared to cryptic ones. This indicates that the positively size-dependent effect of detectability overrides the negatively size-dependent acceptability effect in warningly coloured larvae, and suggests that warning colouration is not necessarily the best option for largest larvae. These results were well consistent between years, locations and materials of artificial prey, which allows to consider the detected trends fairly general.

4. THE ROLE OF COLOUR PATTERNS

4.1. A case of size-dependent predation

Previous work has indicated that larvae with conspicuous warning colouration may suffer a much steeper rise in their risk of detection and predation by birds than cryptic larvae (**III**). This makes large body size risky for conspicuous larvae, because warning colouration never gives full protection against all avian predators (Exnerova et al. 2003, Endler and Mappes 2004, Sandre et al. 2007). Therefore, it is likely that warning colouration is not necessarily most beneficial for largest insect larvae, as it has been frequently suggested (Forsman and Merilaita 1999, Hagman and Forsman 2003, Nilsson and Forsman 2003). Instead, warning colouration might be a strategy that is best used within some intermediate size range, in which the advantages of effective warning signals exceed the detectability costs of large size. Indeed, interspecific comparisons seem to support such pattern. In particular, while it is well appreciated that the smallest insects are usually inconspicuous, also the largest ones are only rarely warningly coloured, at least in temperate areas. For example, among the European Macrolepidopteran larvae, clear warning colours occur most often among species of intermediate body sizes (about 200-500 mg of pupal weight) (Porter 1997). In contrast, the largest Lepidopterans, e.g. most Sphingids, Saturnids and Lasiocampids are typically characterised by cryptically coloured larvae.

A strategy frequently used to cope with the changing costs and benefits of warning colouration during growth involves ontogenetic shifts in colouration. Typically, the youngest and smallest larvae are cryptically coloured, and only the older stages develop conspicuous colouration (Inouye and Johnson 2005, Grant 2007, Sandre et al. 2007). However, opposite shifts – conspicuous larvae switching back to cryptic colouration – are not frequently documented, even though the high detectability risk of large size in conspicuous larvae seems to predict it. A species of Lymantriid moth, *Orgyia antiqua*, is among the few species, whose larvae can undergo several colouration shifts during their development, as indicated by the results of **IV**. The smallest larvae are cryptic, intermediate ones often display bright yellow hair tufts on blackish background, and in largest instars, the bright hair tufts are replaced with dull-coloured ones. The switching points are not fixed, and there is a considerable overlap between colour morphs at given sizes. A number of experiments was carried out to examine the adaptive value of such variability, and to test the hypothesis that the trade-off between warning effect and detectability can have lead to evolving these colouration shifts in *O. antiqua* larvae.

First, cage trials were conducted to confirm that the bright hair tufts function as warning signals. Different colour morphs of *O. antiqua* larvae in various sizes were offered to great tits, and the latency of attack was recorded. While

size had no effect on attack latency, it could be demonstrated that the bright morph was attacked with most delay (Table 2 in **IV**).

Second, a detectability experiment was carried out to test the size-dependent detection risk of the bright vs dull morph, using human subjects as “predators”. The use of humans avoided the confounding effect of differential acceptability of prey, which would be inevitable when using natural predators. Mainly for this reason, humans are frequently used in detectability experiments as a substitute for visually searching predators (Riipi et al. 2001, Sherratt and Beatty 2003, Gossum et al. 2004). The subjects were asked to search for pairs of similar sized bright and dull *O. antiqua* larvae from areas covered with semi-natural vegetation. Surprisingly, the dull larvae were generally found faster than similarly sized bright ones (Table 3 in **IV**). However, there was an interaction between size and colour in determining which morph was found first: the largest bright larvae had a disadvantage over dull ones, and were detected sooner (Table 2 in **IV**).

The finding that the detection risk increases more steeply with size in bright larvae compared to dull ones, is well consistent with the results of an earlier experiment (**II**) described in chapter 3.4. However, the lower detectability of intermediate-sized bright larvae suggests that the bright hair tufts may function as a disruptive pattern at longer viewing distances, as well as a warning signal at close view. Such dual function is often suspected in species that appear to display sub-maximal warning signals (Endler 1978, Ruxton et al. 2004, Tullberg et al. 2005, Bohlin et al. 2008). The likely explanation for the reversed detectability difference between morphs at largest body size is that the larger bodied individuals have also larger colour tufts, and the conspicuousness of large signal elements impairs the effect of disruptive colouration.

4.2. Body size or signal size?

It is generally appreciated that larger warningly coloured insects are more intimidating to bird predators than smaller ones (e.g. Forsman and Merilaita 1999, Hagman and Forsman 2003, Nilsson and Forsman 2003, **II**). However, most studies that have actually tested this assumption (Gamberale and Tullberg 1996b, **II**) have not separated the effect of body size from that of other prey characteristics, which tend to correlate with size. In particular, the number (Gamberale and Tullberg 1996b) or, perhaps more frequently, the size (**II**) of colour signal elements tends to increase with increasing body size (not necessarily for adaptive reasons), as in the larvae of *O. antiqua*, for example (**IV**). Therefore, it is not certain if body size has really a separate effect from that of signal element size. Such a separate effect might result e.g. from increased conspicuousness of larger animals, since conspicuousness *per se* can cause aversion in predators (Gittleman and Harvey 1980, Gamberale and Tullberg 1996b).

To test the relative importance of body size *vs* signal element size in determining the efficiency of warning colouration, a cage experiment was conducted, with great tits as predators. Different sized edible pastry larvae with either constant-sized warning signal elements, or signal element size increasing proportionally with body size, were offered sequentially to great tits. It was recorded if and when the birds attacked each larva. The slopes of size-dependent acceptability were thereafter compared between the two groups (constant *vs* proportional signal elements).

The probability of birds attacking the prey items was negatively size-dependent in the proportional-signal group, but no size dependence was detected in the larvae with constant-size signal elements (Table 1 in **V**). Moreover, an interaction between size and signal type (constant *vs* proportional) was found in determining the latency to attack the prey (**V**). These results suggest that the size of signal elements is, in fact, more important predictor of predation risk than body size, but fail to prove any independent effect of body size as such.

6. SEASONAL CHANGE IN PREDATION RISK

Important selective pressures on insect development time and body size arise from seasonally varying biotic interactions. For example, for tree-feeding insects, the often dramatic phenological change in the quality of the foliage is a major factor determining the most suitable period for larval development (Schroeder 1986, Awmack and Leather 2002, Haukioja 2003, Riipi et al. 2004, Ruusila et al. 2005, van Asch and Visser 2007). Similarly, the possible top-down effects of natural enemies can vary within season (Tammaru et al. 2001, Boyer et al. 2003, Gratton and Denno 2003). It is reasonable to assume that seasonal changes in the abundance and behaviour of natural enemies, such as insectivorous birds, may result in periodicity of mortality rates. In particular, during their breeding period, birds require higher levels of food, and after fledging, the number of foraging birds abruptly increases. Moreover, newly-fledged juveniles have been found to show behavioural differences from adults in their effect on different prey insects: they are perhaps less efficient foragers (Marchetti and Price 1989), and have yet to learn preference for or avoidance of certain food items (Lindström et al. 1999a, Exnerova et al. 2007). The latter can also affect the relative predation risk of cryptic and warningly coloured larvae.

Additionally, the *per capita* survival of insect larvae will be affected by the change in abundance of prey available to insectivores (for examples of predator saturation, see Cappuccino 1995, Harrison and Wilcox 1995, Tanhuanpää et al. 1999). Thus, assuming that the numbers and biomass of leaf-eating insects change throughout the season (van Balen 1973, Tremblay et al. 2003, Visser et al. 2006), their survival is likely to change accordingly (Veistola et al. 1995). Changes in the abundance of alternative prey can also affect the size selectivity of predators (Grieco 1999, 2001, 2002).

To provide quantitative estimates applicable for analysing these patterns from the perspective of insect life history evolution, artificial larvae were exposed to bird predation during four days in temperate forest habitats. The larvae were composed of live blowfly pupae arranged in rows (Figure 1 in VI). Such trials were repeated several times throughout the favorable season (May-August); the experiment was replicated in two years and two areas in Estonia (surroundings of Kilingi-Nõmme in 2005-6, and surroundings of Tartu in 2006).

The estimated daily predation rate of the artificial larvae peaked in mid-June (the approximate nesting time of most insectivorous birds in this area), and thereafter decreased rapidly to a low level (about 20–30% of the peak value, Figure 2 in VI). This trend was reasonably consistent between the years and areas. The decrease in predation rates roughly corresponded to a substantial increase in the caterpillar abundance, measured as frass fall in the study area (Figure 3 in VI). The quantitative estimates of daily predation rates were well consistent with those reported in other studies (I).

In this experiment, the artificial larvae were either cryptically or conspicuously coloured and divided between four size classes (see chapter 3.2.).

The purpose of such design was to test for the possible differences in the temporal mortality dynamics between larvae with different colouration strategies or varying sizes. However, no time×colour or time×size interactions were found, and all types of prey followed a similar dynamics of predation rates throughout the season (III).

7. DISCUSSION

The primary question addressed by this thesis was the potential of positively size-dependent predation risk to counterbalance the high fecundity advantage of large size in many insects, Lepidopterans in particular. In view of the notably high larval growth rates found in many species, detecting a selective pressure capable of reducing the optimal body size has proved to be a challenging task, indeed (Blanckenhorn 2000, Tammaru et al. 2002, Blanckenhorn 2005). In this thesis, the possible size dependence of predation risk was investigated separately for cryptic and conspicuous larvae.

Currently available published data (reviewed in **I**) allow one to expect an average bird predation rate of tree-feeding larvae of about 3% per day, and the average daily arthropod predation risk can be even higher, about 11%. However, since bird predation, unlike that of arthropods, appears to be predominantly positively size-dependent, birds can be considered more likely to cause an increasing mortality in the latest instars, which could reduce the optima for growth duration and final body size in insects. Considering the high variability of estimated predation rates (**I**, **III**), it is clearly necessary to vary the assumptions concerning predation pressure also in insect life-history models.

The colouration strategy of prey insects should be considered when analysing the factors determining their optimal body sizes. This is because both of the main components of size-dependent predation risk – *detectability* and *acceptability* by predators – were shown to differ for these two colouration groups (**II**). The warningly coloured larvae triggered the expected size-dependent response from birds: large artificial larvae were more easily found, but treated with more caution, than small ones. This confirms an often-suggested trade-off in the evolution of warning colouration: by increasing their warning effect, the conspicuous individuals also increase their risk of being detected and consumed by naïve predators (Endler 1988, Gamberale and Tullberg 1996b, Lindström et al. 1999a). In contrast, the results with cryptic larvae were rather unexpected: no correlation was found between body size and the risk of being detected. Birds attacked the larger cryptic prey slightly more readily, though.

Experiments investigating the different mechanisms constituting a particular selection pressure one by one, in controlled settings, are necessary to obtain a more profound understanding of the nature of that selective agent. However, these mechanisms should be studied jointly in order to learn how their effects combine in affecting the study organisms. Accordingly, since detectability and acceptability had opposite effects for the mortality of conspicuous larvae, it is not possible to infer from laboratory studies alone, how these two factors combine in natural situations: which are the resulting strength and direction of size-dependence of predation risk in conspicuous larvae and how these figures compare to those found in cryptic ones.

A field study designed to account for both detectability and acceptability of cryptic and conspicuous larvae revealed that, in both colouration groups, the predation risk was significantly size-dependent. However, the slope of size dependence in determining mortality was steeper for conspicuous prey: surprisingly, the largest warningly coloured larvae were attacked even slightly more frequently than equally sized cryptic larvae (Figure 2 in **III**). Therefore, it is clear that the warning colouration we used did not prevent many of the conspicuous models from being attacked. Our results suggest that, in field conditions, detectability is a far more important determinant of size-dependent predation rate in tree-feeding insect larvae than acceptability. This is because such a pattern is only possible if the size-specific increase in detectability overrides the decrease of acceptability.

The more strongly size-dependent predation risk found in conspicuous larvae contradicts the assumption that warningly coloured insects should benefit more from large size than cryptic ones, and should therefore evolve relatively larger sizes (Forsman and Merilaita 1999, Hagman and Forsman 2003, Nilsson and Forsman 2003). In view of the slightly higher attack rate on the largest conspicuous larvae compared to the largest cryptic larvae, it can be expected that warning colouration is most beneficial to larvae at some intermediate sizes (**IV**).

The results of the experiments with *O. antiqua* do not contradict the above conclusion. The larvae tended to obtain a bright warning colouration at intermediate sizes, but largely lost it again after a certain threshold size: the contrasting yellow tufts turned to dull brown (**IV**). The higher repellence of the brightly coloured morph was confirmed in the experiments with great tits as predators. However, the difference was not particularly large; this and the earlier results (**II**, **III**) confirm that even a classical black-yellow warning colouration may not provide reliable protection for aposematic larvae (see review in Endler and Mappes 2004). The reason why aposematic animals are in some cases eaten and in other cases not is probably that the predators' ability to overcome prey defences is different both within (Bowers and Farley 1990) and between bird species (Exnerova et al. 2003). Moreover, bird species differ in their ability to discriminate between aposematic and non-aposematic prey (Exnerova et al. 2003), and also the threshold signal strength that creates an aversion appears to vary (Exnerova et al. 2006). The birds' willingness to consume aposematic prey has also been shown to depend on their hunger level (Chai 1986, **IV**). In view of these findings, it is not surprising that a growing body of evidence is accumulating that many chemically defended species combine warning colouration with camouflage by expressing sub-maximal warning signals (Endler 1978, Ruxton et al. 2004, Tullberg et al. 2005).

However, even though the bright coloured larvae were shown to be repellent for birds, the ontogenetic colouration shifts of *O. antiqua* can also be explained with purely camouflage-related arguments. In particular, the bright morph turned out to be less effectively detectable than the dull morph at intermediate

sizes; this difference was reversed only in the largest size class. It is hard to see other explanation for such an outcome than a disruptive effect of the bright-coloured hair tufts. Indeed, since disruptive colouration (Cott 1940, Merilaita 1998) is thought to be most effective with high contrast between colour signal elements (Cott 1940, Merilaita 1998, Cuthill et al. 2005), this may well be the reason why yellow tufted larvae have a detectability advantage over the dull ones. The reversed detectability difference in the largest size class may be the result of larger colour tufts displayed by larger larvae: the large tufts may have appeared too conspicuous on the semi-natural background, as the efficiency of camouflage depends on the match between the size of signal elements and substrate patches (Poulton 1890). For these reasons, we cannot interpret the colouration shifts observed in this species as proving the trade-off between size-dependent warning effect and detectability. However, this trade-off may still have contributed to the evolution of the patterns observed. In particular, it is likely that the disruptive effect is a side-effect of the warning colouration used by these hairy caterpillars.

To better understand the evolution of warning colouration from the perspective of the predators' perception of colour signals, it is often advisable to distinguish between different aspects of warning colouration. The more frequently studied of such aspects include the colour of warning signal elements (Gamberale-Stille and Tullberg 1999, Gamberale-Stille and Guilford 2003, Ham et al. 2006, Aronsson and Gamberale-Stille 2008), as well as their symmetry (Forsman and Merilaita 1999, Forsman and Herrström 2004), contrast with adjacent colours (Prudic et al. 2007), conspicuousness in the environment (Gamberale-Stille 2001, Prudic et al. 2007, Stevens et al. 2008), and distinctiveness from other, palatable, species (Puurtilinen and Kaitala 2006, Merilaita and Ruxton 2007). Furthermore, other defenses, such as repellent odors (Rowe and Guilford 1999, Lindström et al. 2001b) and movements (Hatle and Salazar 2001), as well as hairiness (Mappes et al. 2005) or gregarious life style (Gamberale-Stille 2000, Hunter 2000, Hatle and Salazar 2001, Riipi et al. 2001) can function as warning signals of their own right, or interact with colouration.

However, in the context of the present study, it is more important to distinguish if the higher repellence of large bodied individuals found in warningly coloured prey (Gamberale and Tullberg 1996b, **II**) is caused by the effect of body size *per se*, or its allometric correlation with signal strength. In particular, in many warningly coloured larvae, such as *O. antiqua* (**IV**), the size of colour signal elements increases proportionally with body size. Larger signal elements, in turn, are found to cause higher aversion in birds or facilitate avoidance learning (Forsman and Merilaita 1999, Lindström et al. 1999b).

The results of this study (**V**) failed to prove an effect of body size, independent of signal element size, on the repellence of warningly coloured prey. This is because great tits showed a negatively size-dependent acceptance of the artificial baits only when the size of signal elements increased

proportionally with prey size, but not when the element size was kept constant across different prey sizes. Therefore, the apparent size dependence of prey acceptability is often probably just a side effect of the impact of signal variation. However, theoretically, body size may pose constraints on the signal strength, most obviously because very large signal elements cannot be displayed on very small animals.

More generally, this result illustrates the need to show caution towards seemingly self-evident assumptions, which in fact have very little experimental proof. For example, beside the experiments reported in this thesis, the study by Gamberale and Tullberg (1996b) is to my knowledge the only one that directly addresses size dependent rejection of aposematic prey by birds, although not controlling for signal element size. Nevertheless, the assumption that large body size promotes predators' rejection of warningly coloured prey appears to be widespread. Similarly common assumptions that have little or no experimental proof have also prevailed in other aspects of prey animal colouration, e.g. self-shadow concealment (Ruxton et al. 2004), an empirical confirmation of the adaptive value of which was provided only recently (Rowland et al. 2007b).

In addition to the effects of prey characteristics, this thesis addressed seasonal changes in predation risk. A distinct peak of *per capita* predation risk was found in the study area (boreal forests) in mid-June, suggesting a connection with the nestling provisioning of insectivorous birds in the area (Figures 2, 3 in **VI**). Later in the season, the predation rates dropped to a stably low level (about 20–30% of the peak mortality). This decline was most probably caused by the increasing abundance of caterpillars in the area. Additionally, the fledglings of small passerines suffer very high mortality in the first few days after leaving the nests (Naef-Daenzer et al. 2001), which can also account for the decline in predation rates.

The results of the field experiments (**III**, **VI**) were reasonably consistent across different replicates, and the patterns were unaffected by the material the artificial larvae were made of. Moreover, the quantitative results of mortality were well consistent with those found by other researchers in live caterpillars (**I**). The detected patterns of size-dependent mortality may therefore be considered fairly general, and can safely be used as realistic estimates in optimality models predicting adaptive values of adult body size in insects. The absence of an interaction between calendar date and body size or colouration in determining mortality risk also adds to the generality of the results, even if the seasonal dynamics in mortality risk itself cannot be ignored.

The present study was largely motivated by the need to obtain reliable, empirically based data for constructing life history models able to explain insect body sizes. Empirically based optimality models of insect growth need to integrate detailed knowledge about larval growth schedule, and, importantly, the possible size dependence of mortality risk. Such model is currently being constructed for a Lymantriid moth species *O. antiqua* (Tammaru et al., in preparation). The females of *O. antiqua* are capital breeders, implying a strong

size dependence of both potential and realized fecundity (Tammaru et al. 2002). The information on size-dependent mortality is primarily based on the results of the present thesis, and preliminary results will therefore be reported below.

The assumptions of growth curves are based on original experiments with *O. antiqua* (Esperk and Tammaru 2004, 2006, Sandre et al. 2007, Tammaru et al. in preparation). The experimental protocols included subjecting the larvae to various treatments to manipulate growth rates, with the larvae being weighed daily since their third instar. The obtained data on larval growth curve were used to construct an empirically based simulation model. The model pays explicit attention to larval instars, distinguishing a period of “free” growth in the beginning of each instar, and a subsequent period of minimal growth, an even decline in live weight as a consequence of preparation to the following moult (or pupation) (Esperk and Tammaru 2004). The period of free growth is best described by a power function (Tammaru and Esperk 2007). Growth rate, i.e. the parameter describing the free growth phase is considered an environmental variable, being determined by food quality and temperature.

The approach chosen in the present analysis was to examine the fitness of an imaginary mutant prolonging its “free” growth period of its last larval instar by one day. Combinations of average mortality rate and the strength of the dependence of mortality risk on body size, which would result in lower fitness of the mutant, as compared to a larva following the actual growth schedule were searched for. The lower fitness of the mutant would indicate that mortality risk constitutes a cost of large size high enough to explain actual body sizes in the optimality framework. In the model, fitness was calculated on the basis of fecundity determined by the final weight attained (Tammaru et al. 2002), and size-dependent survival integrated over the larval growth history. Corresponding functions were chosen on the basis of the findings of **III**.

As a result, we found that, for low growth rates, i.e. in inferior growth conditions, it would not pay to prolong the period of rapid growth (Figure 2) implying that the actual reaction norm may be considered optimal. In better conditions, however, it is hard to see the actual body sizes as optimal – it should pay to grow larger under of a wide array of parameter values. However, under the combination of a high average mortality rate (10% per day) and strong positive size dependence, the situation is different. Such high predation rates are frequently, though not predominantly, found in studies of larval mortality (**I**). In any case, the sensitivity of the results to assumptions of mortality patterns emphasizes the importance of studying these parameters in the present context.

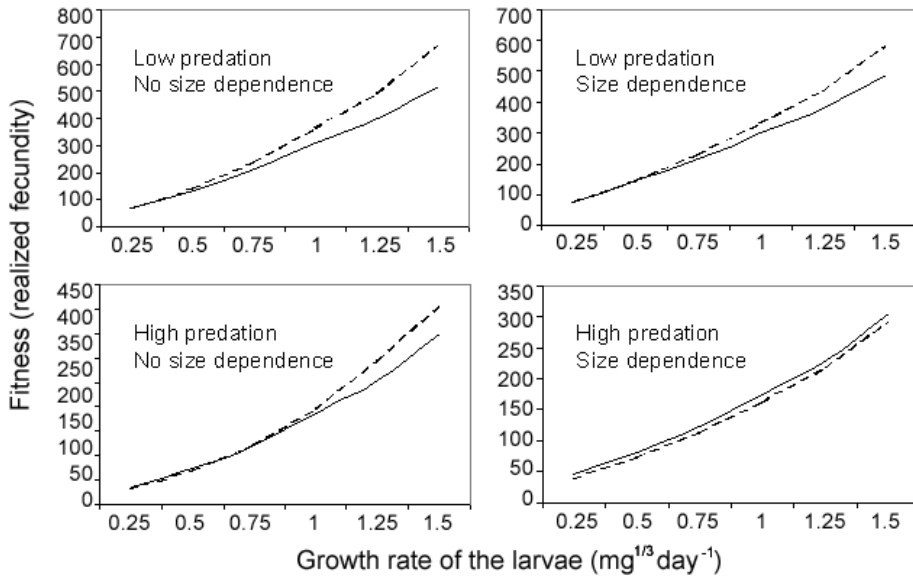


Figure 2. Estimated fitness (number of eggs laid) of *O. antiqua* larvae following the actual growth trajectory (solid line), and that of an imaginary mutant prolonging its larval growth by one day in its last instar (dashed line). Low predation rate means 5% predation per day; high predation rate is 10% per day. “Size dependence” quantitatively corresponds to the situation in Figure 3 (conspicuous larvae) in **III**; “no size dependence” implies equal daily mortality rate for all sizes during the last instar.

This thesis addressed bird predation as a possible driving force in the evolution of insect body size, as birds are likely the dominant predators for tree-feeding insect larvae causing positively size-dependent mortality. However, other evolutionary forces must not be ignored. For example, other natural enemies, mainly predatory arthropods and parasitoids, may also cause size-dependent mortality. Even though arthropods are generally thought to pose a higher risk for smaller larvae (e.g. Roger et al. 2000, Cogni et al. 2002, **I**), it is still worth investigating if they can substantially affect the optimal sizes in their prey. Similarly, some parasitoids can show clear preferences for host size (e.g. Teder et al. 1999, Lin and Ives 2003, Li et al. 2006), and may therefore create selection pressure favouring either smaller or larger individuals. These possibilities deserve separate attention in complementary studies. Furthermore, various thermal constraints, as well as those related to flight physiology may be present in different species (e.g. Oliveira 2005). Additionally, we cannot ignore the phylogenetic constraints on body size, since, typically, closely related species of Lepidoptera appear to show only small differences in body size. This is particularly obvious in view of the results of the simulation model described above, which show that, at a range of realistic assumptions, even positively size

dependent predation risk cannot explain the shortness of larval growth duration. Studies that evaluate the potential of different selective factors to affect the optimal growth schedules can provide indirect evidence for or against the existence of such constraints.

SUMMARY

The underlying aim of this thesis is to evaluate if positively size dependent risk of bird predation can counterbalance the high fecundity advantage of large size found in many insects, and thereby explain the seemingly nonadaptively short growth duration in these insects. In investigating this possibility, the colouration strategy of prey insects was accounted for, as it inevitably interacts with size in determining predation risk.

A review of published data revealed a between-studies average bird predation of tree-feeding larvae to be high, indeed (about 3% per day), even though the average arthropod predation rate was even higher (11% per day) (I). The studies investigating size-dependent predation rates by birds almost invariably found it to be positive, with the only clear exceptions found in warningly coloured larvae. In case of invertebrate predators, the direction of size-dependent predation was usually the opposite. Therefore, it is likely that birds have a higher potential to cause increased mortality in largest larvae, which may be necessary to counterbalance the fecundity advantage of further growth.

Size dependence of the two major components of predation risk – detectability and acceptability to predators – in both cryptic and warningly coloured larvae was studied in two laboratory experiments (II). Great tits attacked larger cryptic prey items more readily than smaller ones, but tended to avoid larger conspicuous prey. However, detectability trials revealed that the slope of positively size-dependent detection risk was substantially steeper for conspicuous larvae. This implies that in conspicuous, but not in cryptic larvae, detectability and acceptability cause opposing selection pressures on the optimal body size.

A field study was conducted to investigate the net outcome of the effects of detectability and acceptability on size-dependent predation rates in cryptic vs warningly coloured larvae (III). The results demonstrated that, in both colour groups, the risk of bird predation depended positively on size, but was more strongly size-dependent in the presence of warning colouration. This suggests that the effect of detectability may exceed that of acceptability in natural situations. This study appears to contradict the assumption that aposematic insects benefit more from large size than cryptic ones.

A species of moth, *O. antiqua*, displays bright colouration at intermediate larval sizes, and switches to duller morphology when approaching largest sizes. To test if such dynamics could be caused by the trade-off between acceptability and detectability, two experiments were conducted (IV). First, it was confirmed in a cage experiment that great tits regarded the bright morph with more caution than the dull morph. Second, a detectability experiment with human subjects revealed that, at intermediate sizes, the bright morph was actually better disguised. However, this difference was reversed in the largest size class. This is compatible with the findings of stronger size dependence in the detection risk

of warningly coloured larvae. However, even though these results do not contradict the trade-off hypothesis, they can also be explained with purely camouflage-related selection pressures.

In *O. antiqua*, as well as many other species and also the artificial larvae used in **II**, the size of signal elements of warning colouration increase proportionally with body size. Therefore, it is not clear if the increase of birds' aversion is caused by increasing body size or signal element size. A cage study using great tits as predators revealed negatively size-dependent acceptability when the warning signal elements increased with prey size (**V**). However, no size dependence was found when the size of signal elements was kept constant. This suggests a higher importance of signal size over body size; no independent effect of body size could be proved.

Most insect life-history models treat the environment as constant; however, incorporating seasonality could substantially alter the predictions of these models. To provide quantitative data on the seasonal dynamics of bird predation rates, artificial larvae were repeatedly exposed to predation during most of the feeding season (**VI**). A distinct peak of *per capita* mortality was found in mid-June, after which the mortality declined to a stably low level. These dynamics did not differ for larvae with different colouration or size (**III**).

An optimality model constructed for *O. antiqua*, based on empirical results partly obtained from this study, predicts that, in suboptimal growth conditions, the larvae would not benefit from growing a day longer. However, assuming reasonably high grow rates, it is hard to explain the shortness of the actual growth period with predation risk. Only when combining high overall predation rate with positive size dependence, can the effects of predation explain the existing growth curves even for fast growing larvae. The realistic parameters of larval predation rates estimated by this thesis constitute an important set of assumptions that are necessary for modelling and making inferences about insect life-history optimality.

SUMMARY IN ESTONIAN

Kiskluse roll putukate kehasuuruse evolutsioonis erinevate värvusstrateegiate korral

Käesoleva doktoriväitekirja eesmärk on hinnata kehasuurusest positiivselt sõltuva kisklusriski potentsiaali tasakaalustada paljudel putukatel leitud tugevat seost kehasuuruse ja viljakuse vahel. See võimaldaks selgitada niisuguste putukate esmapilgul mitteadaptiivselt lühikesena näivat kasvuperioodi. Uurimisel võeti arvesse eri värvusstrateegiate mõju kisklusriski suurusest-sõltuvuse suunale ja tugevusele.

Ülevaates avaldatud uurimustest leiti, et putuktoiduliste lindude poolt põhjustatud päevane suremus on ligikaudu 3% (üksikuurimuste keskmisena). Putuktoidulised selgrootud põhjustasid veelgi kõrgemat suremust – keskmiselt 11% päevas (**I**). Tööd, milles uuritakse saakputuka suurusest sõltuvat kisklusriski lindude poolt, on praktiliselt alati leidnud positiivse sõltuvuse suurusest; ainsaks selgeks erandiks on hoiatusvärvusega saakputukad. Suuruse mõju selgrootute poolsele kisklusele on aga enamasti vastupidine. Seetõttu on linnud märksa tõenäolisemaks teguriks, mis võiks põhjustada positiivselt suurusest sõltuvat suremust ja tasakaalustada edasisel kasvamisel oodatavat viljakuse tõusu.

Kehasuurus saab lindude vahendatud kisklusriski mõjutada peamiselt kahel moel – mõjutadas saaklooma silmatorkavust või kiskja otsust saaklooma rünnata. Laborikatsetes rasvatihastega (*P. major*) leiti, et linnud ründavad meelsmini suuremaid varjevärvusega, kuid väiksemaid hoiatusvärvusega saakloomi (**II**). Saaklooma leidmise kiirus sõltus aga suurusest hoiatusvärvuse puhul tunduvalt tugevamini kui varjevärvuse korral. Esimestel (kuid mitte viimastel) on silmatorkavusest ja kiskja eelistustest tulenevad valikusurved seega vastandlikud.

Hindamaks nende kahe valikusurve reaalselt tulemust kummagi värvustüübi puhul, viidi läbi välikatsed (**III**), mis andsid mõlema värvitüübi puhul tulemuseks positiivse sõltuvuse kehasuurusest. Suurus-sõltuvus oli hoiatusvärvusega mulaažidel aga tugevam. See lubab järeldada, et silmatorkavus mängib kiskjate eelistustest mõnevõrra suuremat rolli; need tulemused on aga vastuolus levinud arvamusega, et hoiatusvärvusega putukatel tasub kasvada suuremaks kui varjevärvuse puhul.

Liblikaliigi *O. antiqua* röövikutel arenevad keskmiste suuruste juures sageli erksavärvilised mustri-laigud, mis kõige suurematel isenditel asenduvad uuesti vähem silmatorkava mustri-ga. Selle varieeruvuse taga võiks olla ülalkirjeldatud lõivsuhe silmatorkavuse ja kiskja eelistuste vahel. Selle hüpoteesi testimiseks läbi viidud katsete tulemused lubavad seda aga seletada ka üksnes varjeomadustest tingitud valikusurve-ga (**IV**), sest selgus, et keskmiste suuruste korral

on erksavärviline muster eemalt vaadates tegelikult paremini varjatud kui (lähivaates) vähem silmatorkav muster.

O. antiqua ja paljude teiste liikide puhul suurenevad kehamõõtmete kasvades ka hoiatusvärvuse mustri-laigud. Seetõttu jääb selgusetuks, kumb neist tegelikult mõjutab lindude eelistust rünnata väiksemaid hoiatusvärvusega saakloomi. Selle selgitamiseks läbi viidud laborikatsetes leiti negatiivselt suurusest sõltuv kisklusrisk ainult juhul, kui mustri-laigud suurenesid proportsionaalselt kehasuurusega; kui mustri-laikude suurus jäi samaks, siis kisklusrisk kehasuurusest ei sõltunud (V). Siit võib järeldada, et mustri-laikude suurus on kehasuurusest olulisem kiskja eelistuse mõjutaja; mustri-laikudest sõltumatut kehasuuruse mõju ei õnnestunud tõestada.

Enamik putukate elukäigevolutsiooni kirjeldavaid mudeleid käsitlevad keskkonda konstantsena, kuid aastaajaliste muutuste kaasamine võib mudelite ennustusi märgatavalt mõjutada. Kisklusriski ajalise dünaamika uurimiseks korraldatud välikatses leiti tugev suremusmaksimum Juuni keskel (VI). See dünaamika oli mõlema värvustüübi ja kõigi suurusklasside puhul sarnane, kuid illustreerib sellegipoolest vajadust arvestada elukäigumudelites aastaajalisi fenoloogilisi muutusi.

Liigi *O. antiqua* kohta koostatud empiiriline optimaalsusmudel, mille aluseks on osaliselt käesoleva väitekirja kvantitatiivsed tulemused, näitas, et madala kasvukiiruse juures ei oleks sellel liigil päeva võrra pikem kasvuaeg adaptiivne. Kui aga eeldada kõrgemat kasvukiirust, siis ei piisa kiskluse mõjust, et tasakaalustada pikema kasvuaja puhul oodatavat viljakuse tõusu. Ainult üsna kõrge üldise suremuse korral, kombineerituna suremuse suurusest-sõltuvusega, osutuks päeva võrra kauem kasvamine ka kõrge kasvukiirusega isentitel mitteadaptiivseks. Selles väitekirjas leitud realistlikud suremusparameetrid moodustavad olulise osa eeldustest, mis on vajalikud putukate elukäikude modelleerimiseks ja nende optimaalsuse hindamiseks.

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Table 1. Contributions of different people to the accomplishment of this thesis.

<i>Person(s)</i>	<i>Contribution</i>
Toomas Tammaru	His resourceful, helpful and patient guidance.
Johanna Mappes	Providing me an opportunity to work at the University of Jyväskylä, and advising my research there.
Co-workers at the University of Tartu (Siiri-Lii Sandre, Toomas Esperk, Juhan Javoš, Tiit Teder, Ulvi Karu and many others), University of Jyväskylä and the Estonian University of Life Sciences	Creating a pleasant and enriching atmosphere.
Margret Sisask	Helpfulness in coordinating the logistic matters.
The members of the bird ecology study group at Tartu University (Raivo Mänd, Vallo Tilgar, Marko Mägi, Priit Kilgas, Elo Sisask and others)	Allowing me to use their data on the phenology of passerine birds and the estimates of caterpillar abundance in Kilingi-Nõmme.
The staff at Nigula Nature Reserve (especially Agu Leivits, Indrek Tammekänd and Jaak Tammekänd, as well as many voluntary assistants)	Providing me an opportunity to work at Kabli Bird Station, and their help in my experiments with wild birds.
Lab and field assistants:	
Helinä Nisu	Taking care of the experimental birds.
Oksana Gluško and Kaarel Mänd	Assistance in the field.
Tanel and Toomas Esperk, Kristiina Jürgens	Rearing the <i>Orgyia</i> larvae.
Students of Kilingi-Nõmme Highschool	Measurements of air temperatures.
Wolf Blanckenhorn, John Davison, John Endler, Andrew Higginson, Peeter Hõrak, Ann Kraut, Raivo Mänd, Lauri Saks, Tuul Sarv, Elin Sild, Siiri-Lii Sandre, Tom Sherratt, Tiit Teder and Marcel Visser	Making valuable comments to my manuscripts.
Human subjects, great tits and tussock moths	Participating in the experiments.
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II Research history

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- Sandre, S.-L., Tammaru, T. & **Mänd, T.** (2007) Size-dependent colouration in larvae of *Orgyia antiqua* (Lepidoptera: Lymantriidae): A trade-off between warning effect and detectability? *European Journal of Entomology*, 104, 745–752.
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III Improvement of skills

Introduction to ecological modelling (post-graduate course). 28. 11.–2. 12. 2005, University of Jyväskylä, Finland.

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Peamised uurimisvaldkonnad:

Putukaökoloogia, kehasuuruse ja hoiatusvärvuse evolutsiooniline ökoloogia

Publikatsioonide loetelu:

- Remmel, T.**, Tammaru, T. & Mägi, M. (2009) Seasonal mortality trends in tree-feeding insects: a field experiment. *Ecological Entomology* 21, 485–498.
- Mänd, T.**, Tammaru, T. & Mappes, J. (2007) Size dependent predation risk in cryptic and conspicuous insects. *Evolutionary Ecology*, 21, 485–498.
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Mänd, T., Tammaru, T., Mappes, J. "Size and colour affect mortality in insects" 10th Congress of the International Society of Behavioural Ecology (ISBE), 10.–15. 07. 2004, Jyväskylä, Soome (poster)

Mänd, T. "When is it good to be an aposematic caterpillar?" Finnish-Estonian Workshop on Animal Ecology. Apr 2005, Arbavere, Eesti.

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Mänd T., Tammaru T. "Within-season temporal variation in the predation risk of differently sized and coloured insect larvae" 11th International Behavioural Ecology Congress (ISBE 2006). 23.–29. 07. 2006, Tours, Prantsusmaa. (poster)

Mänd T., Tammaru T. "Within-season temporal variation in the predation risk of differently sized and coloured insect larvae" The Annual meeting of the Finnish Graduate School in Evolutionary Ecology 17.–19. 12. 2006, Konnevesi, Soome. (poster)

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III Erialane enesetäiendus

Introduction to ecological modelling (kursus). 28. Nov–2. det. 2005, Jyväskylä Ülikool, Soome.

Information theory and model selection (kursus). 5.–7. nov. 2007, University of Jyväskylä Ülikool, Soome.

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