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**INFLUENCE OF PREDATION ON THE
BODY SIZE EVOLUTION IN INSECTS.
IMPLICATIONS OF COLOUR**

Master thesis

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Introduction

Body size is among the traits most strongly correlated with fitness characters (Roff 1992, Stearns 1992). Other things being equal, large body is often believed to be profitable in various organisms; the latter idea is the cornerstone of Cope's law, which suggests that taxa evolve larger body sizes over evolutionary time (e.g. Jablonski 1997). In most ectotherms, for example, body size is correlated with female fecundity (Honk 1993). There are still reasons to believe that most values of body size are evolutionarily stable and not in the process of current evolutionary increase (in reference to body size canalization, see Nylin & Gotthard 1998 and Ahnesjö & Forsman 2003). We are thus justified to ask, what is the evolutionary force that balances the fecundity advantage, and thereby keeps body sizes from constantly increasing in time. Blanckenhorn (2000) has provided a review of the mechanisms that have been suggested to limit body size of various organisms. Among those is the general law that high mortality selects for shorter development time, which in turn results in smaller final body size (Roff 1992; Stearns 1992). A still stronger limitation to body size would be positively size dependent mortality, which may result from size-selective predation by natural enemies (Teder & Tammaru 2001). However, case studies dealing with size dependent mortality are comparatively scarce.

The present thesis comprises two studies, which address the problems of predation on insects in the context of body size evolution. The first study is a review of published data on predation rates in Lepidopteran larvae, which analyses general trends in the predation pressure associated with population density, gregariousness and aposematism. The second paper is a case study, which aims at evaluating the body-size dependence of predation rates in cryptic vs. aposematic insects.

In the first paper, I will provide a review of studies that have measured larval mortality due to predation in different species of Lepidoptera. Since the mortality of herbivorous insects appears to depend strongly on their population density, I will compare the different *per capita* predation rates found in studies that have measured mortality at different densities. At both high and low population densities, a crucial factor determining the optimal growth duration is the possible dependence of mortality risk on body size. If mortality were higher for larger individuals, the optimal body size at pupation, and consequently, the optimal growth

duration, would decrease. I will therefore discuss the potential sources of body-size dependence in predation on Lepidopteran larvae. It seems reasonable to assume that birds' preference for different food objects may depend, in one way or another, on the size of the latter. I therefore find it important to discuss also the prey size dependence of bird predation in greater detail in the current study. In the final part of the study, I will review the influence of the caterpillars' colouration on their survival. More precisely, I will discuss the influence of cryptic vs. aposematic prey colour on the intensity of bird predation, with special attention on the effect of colouration on the strength and direction of size dependence of the predation pressure.

The second study is based on an experimental approach to understanding the patterns of size dependence in the mortality of cryptic and aposematic insect larvae. It includes aviary experiments measuring firstly detectability, and secondly, acceptability of differently coloured and sized larvae to birds. A field experiment aimed at estimating how these two aspects combine in nature.

My contribution to the two articles constituting this thesis includes reviewing the relevant literature and participation in development of the work hypotheses and experimental designs. I carried out both laboratory and field experiments, and wrote the manuscripts.

Ahnesjö J, Forsman A (2003) Correlated evolution of colour pattern and body size in polymorphic pygmy grasshoppers, *Tetrix undulata*. *J Evol Biol* 16:1308-1318

Blanckenhorn WU (2000) The evolution of body size: what keeps organisms small? *Q Rev Biol* 75:385-407

Jablonski D (1997) Body-size evolution in cretaceous molluscs and the status of Cope's rule. *Nature* 385:250-252

Nylin S, Gotthard K (1998) Plasticity in life history traits. *Ann Rev Entomol* 43:63-83

Roff DA (1992) *The Evolution of Life Histories*. New York: Chapman & Hall

Stearns SC (1992) *The Evolution of Life Histories*. Oxford: Oxford University Press

Teder T, Tammaru T (2001) Large larvae of a flush-feeding moth (*Epirrita autumnata*, Lepidoptera: Geometridae) are not at a higher risk of parasitism: implications for the moth's life-history. *Eur J Entomol* 98:277-282

1. **Mänd T** “Predation on caterpillars and its impact in the evolution of body size in Lepidoptera”
2. **Mänd T, Tammaru T, Mappes J** “Size and colouration affect mortality in insects”

Conclusions

In the first study included in this thesis, I reviewed the data on mortality rates of Lepidopteran larvae caused by natural enemies, mainly birds and parasitoids. The available data reveals that both of these enemy guilds are responsible for a dramatic decline in the numbers of moth and butterfly larvae throughout the growing period. It has long been recognised that high juvenile mortality selects for earlier maturation, and thereby causes smaller adult body size. It is thus evident, that the impact birds and parasitoids is a significant evolutionary force reducing optimal body sizes in Lepidoptera.

Predation and parasitism rates depend on various characteristics of insect species, including ecological niche, life style and the means of antipredator defence. Additionally, the percent mortality is strongly dependent on the prey/host population density. At very high densities, the *per capita* predation risk is low, as well as at the lowest densities. This could imply temporal variations in the selection of body size, following the fluctuations in population density.

In some cases, the measured larval mortality has been found to be insufficient to balance the fecundity advantage of larger body size. We should therefore look for mechanisms that impose positively body-size dependent mortality in insect larvae, since the latter is likely to pose a much stronger selection pressure towards earlier maturation and smaller body size. I suggest that birds, as visual foragers, are more likely to cause size dependent mortality in Lepidopteran larvae, than parasitoids. Though the latter are reported to discriminate between host sizes, the size preferences of different parasitoid species are often converse to each other, resulting in weak overall size dependence in caterpillar mortality.

It seems reasonable to assume some differences in size dependent mortality between cryptically and aposematically coloured species. One could expect the latter to suffer lower predation rates, since they are typically protected with toxins or repellent taste. However, many birds are still reported to prey on aposematic larvae, and the much higher detectability of aposematic prey can effectively balance the advantage gained by their chemical defence.

The second paper included in this thesis is an experimental case study, which aims at evaluating the strength and direction of size-dependence in the predation on cryptic vs. aposematic insect larvae. I found that the detectability of aposematic larvae from both complex and smooth background by great tits was much higher than that of the cryptic ones. Additionally, detectability of aposematic larvae was positively related to body size, whereas no such correlation was found for the cryptic prey. Another experiment, however, revealed that the birds were less attracted to larger aposematic larvae, but preferred larger cryptic prey. In a field experiment, which was designed to assess the combined effect of detectability and acceptability, there was no evidence for size-dependent predation on cryptic larvae, though. In the aposematic colour class, there was a slight positive correlation between size and predation rate, suggesting that detectability may be a stronger determinant of their mortality than attractiveness.

These results provide an explanation to a somewhat surprising recent finding that aposematic Lepidopteran larvae are not larger on average than the cryptic ones. Since the warning effect of aposematic colouration is stronger in larger body sizes, it was widely believed that aposematic species should profit more from growing larger. If, however, the finding of aposematic prey by birds increases much more sharply with body size than in the cryptic prey, then the differences in their resultant optimal body sizes are not necessarily expectable.

Kokkuvõte

Käesolev töö koosneb kahest üksikuurimusest, millest mõlemad käsitlevad putukate vastseas toimuvat suuremust nende kehasuuruse evolutsiooni kontekstis. Üldise seisukoha järgi põhjustab noorjärkude kõrge suuremus kiirema suguküpsuse saabumisele suunatud valikusurve, millest omakorda paratamatult tuleneb väiksem optimaalne kehasuurus suguküpsuse saabumisel. Seetõttu on vastseperioodi jooksul avalduv kiskluse- ja parasitismisurve putukate kehasuuruse evolutsioonis määrava tähtsusega.

Esimene uurimus on ülevaade looduslike vaenlaste, peamiselt lindude ja parasitoidide poolt põhjustatud suuremusest liblikaröövikutel. Selles leidub kokkuvõtte erinevates töödes mõõdetud kiskluse ja parasitismi väärtustest ja mõnedest liblikaliikidele omastest tunnustest, nagu ökoloogiline nišš, üksik- või grupieluviis jms. Pikemalt käsitlem apoptoosilise värvuse mõju suuremusele selle erinevates aspektides, erilise rõhuga apoptoosiliste vastsete suurussõltuvuse erinevusele krüptiliselt värvunud röövikute omast.

Teine uurimus kujutab endast katset selgitada apoptoosiliste ja krüptiliste röövikute suurusest sõltuvat kisklusriski eksperimentaalselt, mõõtes kõigepealt selle erinevaid allikaid ning seejärel viimaste koosmõju. Suurus saab mõjutada rööviku riski langeda kiskja ohvriks kahel moel: 1) suuremad saakloomad on paremini leitavad ja 2) kiskjal võib esineda eelistus mingite suuruste suhtes. Nende kahe aspekti uurimiseks viisin läbi kaks eraldi laborikatset rasvatihaste ja kunstlikult valmistatud "vastsetega". Esimeses katses lasti lindudel otsida peidetud eri suurusega apoptoosilisi ja krüptilisi "vastseid" ning mõõdeti nende leidmise aeg. Teises katses pakuti lindudele eri suurust ja värvi kunstvastseid ja registreeriti nende ründamine või ignoreerimine. Kolmandaks eksponeerisin samade värvi ja suuruse kombinatsioonidega kunstvastseid lindudele looduses, tuvastamaks, kuidas laboris eraldi mõõdetud kaks mõju omavahel kombineeruvad.

Leidsin, et silmapaistva värvusega vastsete leitavus sõltus oluliselt nende suurusest, krüptilistel aga suurussõltuvust ei olnud. Lindude eelistus langes kokku oodatuga: eelistati pigem suuremaid krüptilisi, kuid väiksemaid apoptoosilisi saakobjekte. Välikatsetes tuvastati rohkem nokajälgi siiski suurematel apoptoosilistel vastsetel, mis võib tähendada, et saaklooma ülesleitavus on looduses suurema tähtsusega kui tema atraktiivsus. Mõlemad

seosed kehasuurusega (nii leitavuses kui atraktiivsuses) olid aposemaatilises grupis tugevamad; üsna ootuspäraselt eelistati krüptilisi vastseid aposemaatilistele, ehkki viimased

Kirjeldatud tulemused pakuvad seletuse hiljuti publitseeritud ja mõnevõrra ootamatule leiule, et aposemaatilised röövikud ei ole keskmiselt suuremad kui krüptilised. Kuna aposemaatilisi vastseid kaitseb eriti suuremates kasvujärkudes nende hoiatusvärvus, siis oli levinud seisukoht, et sellise värvusega liikidel tasub kasvada suuremaks kui krüptilistel. Kui aga nende leitavus tõuseb suurusega tunduvalt järsemalt kui krüptilistel vastsetel, nagu selgus käesolevas töös, siis võib see üles kaaluda hoiatussignaali tugevnemise kehasuuruse kasvades. Viimasel juhul ei ole põhjust enam eeldada, et aposemaatilised vastsed kannataksid nõrgema kisklussurve all ning peaksid vastavalt suuremaks kasvama.

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