Factors affecting life history variation in insects

by

Michelle Tseng

A thesis submitted in conformity with the requirements for the degree of Master of Science, Graduate Department of Zoology, University of Toronto

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Abstract

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Tseng, Michelle

Department of Zoology

University of Toronto

Given the fitness importance of age at and size at maturity in insects, it is intriguing that in nature, there exists a large amount of variation in these traits. In this thesis, I examine the role of predator risk and time constraints on life history variation in the mayfly *Ephemera subvaria*. Unlike many other mayfly species, *E. subvaria* is not known to exhibit anti-predator behaviours. This trait allows one to test for non-behaviourally mediated life history responses. I also use a meta-analysis to examine the overall effects of predator risk on insect growth and development. While time-constrained *E. subvaria* larvae tended to mature earlier than those that were not, there was no effect of predator risk on age at or size at maturity. In general, predator-induced life history shifts in insects were usually accompanied by changes in prey behaviour and growth rates.
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Prologue: background and objectives

The impetus behind this thesis was an observation introduced to me by Rowe and Berrill (1989). The authors noted that within a cohort of mayflies, those that metamorphosed earlier in the season invariably did so at a larger size than those that matured later in the season. This pattern had been noted by previous studies (Ide 1935, Vannote and Sweeney 1980, McCafferty and Pereira 1984) and has since been recorded to occur not only in mayflies, but in a number of other arthropods as well (mole crickets: Forrest 1987, butterflies: Nylin et al 1996, spiders: Higgins 2000). Given that in many of these organisms, size at maturity is positively correlated with fecundity (Sweeney and Vannote 1981), it is intriguing that there exists such large variation in this trait as well as pattern to this variation.

The optimal age and size at which an organism should mature has been the focus of numerous theoretical studies. Some of these have addressed the potential role of mortality (via predation, or other sources) in shaping this variation (Gilliam 1982, Werner and Gilliam 1984, Werner and Anholt 1993, Abrams and Rowe 1996) while others have focused on the effect of time constraints, or seasonality, on age and size at maturity (Rowe and Ludwig 1992, Rowe et al 1994). A few models have also considered the combined effects of both predation and time constraints on these life history traits (Ludwig and Rowe 1990, Houston et al 1993, Abrams et al 1996). Briefly, these models generally predict that with increased predator risk, or with decreased time available in the season, size at maturity usually decreases.

In chapter one of this thesis, I examine some of the predictions from the above models using *Ephemarella subvaria* (Ephemeroptera: Ephemerellidae). *E. subvaria* is a mayfly species found throughout temperate and sub-arctic streams of eastern North America. Larvae hatch in mid-August and grow until early winter. Little or no growth occurs over the winter but resumes in the spring. Emergence occurs from mid-May to June (Ciborowski 1976) and the cycle begins again. Like many other mayflies, this species also exhibits the pattern of decreasing size at emergence over time (Sweeney and Vannote 1981). To test the predictions from the time constraint models, I collect larval *E.
subvaria from a nearby stream and rear them in controlled laboratory conditions under two light/dark regimes. One regime matches the photoperiod that a mayfly would experience in early March (the “early” treatment), while mayflies in the other photoperiod experience day/night cycles of mid-April (the “late” treatment). The photoperiods are changed weekly to follow the natural light/dark progression of the particular treatment. I expect larvae in the “late” treatment to emerge at a smaller size than those in the “early” treatment.

I also examine the effect of predation on mayfly age and size at maturity. Abrams and Rowe (1996) and Abrams et al (1996) incorporate the possibility that to reduce the risk of mortality, prey may be able to alter growth rates in the presence of predators. For example, prey may reduce foraging rates if searching for food increases the risk of predation. Reduced food intake may result in a decrease in growth rate and a subsequent decrease in size at maturity. Depending on whether or not development rates are also flexible, decreased growth rates can also lead to an increased age at maturation. By including both constant and flexible growth rates into these models, predators are expected to induce both growth-mediated shifts in age at and size at maturity of prey, as well as growth-independent changes in these life history traits. I test for the presence of these two types of predator effects in E. subvaria by rearing individual larvae in the presence or absence of predator risk. Predator treatments are created by exposing larvae to chemical and visual cues of the fish Luxilus cornutus (the Common Shiner). Because E. subvaria are not known to exhibit anti-predator behaviours (Soluk 1993, Peckarsky 1990), I expect larvae not to display changes in growth rates in predator presence. Also, because of the paucity of empirical examples showing predator-induced growth-independent shifts in life history traits in insects (Ball and Baker 1996, Johansson et al 2000), I do not expect E. subvaria to alter age at or size at maturity.

Chapter two looks at the overall effects of predator risk on long-term insect growth and development. I use a meta-analysis to combine the results of independent experiments and for studies that rear insect prey to maturity in the presence of predators, I examine the frequency with which shifts age at and size at maturity are associated with
predator-induced changes in prey behaviour and growth rates. The main objective of this chapter is to ask whether insects share common growth and developmental responses to predators, and to explore the possible mechanisms behind these responses. I conclude this chapter by comparing the predator-induced life history responses of insects to those of amphibians and *Daphnia*.

Overall, I conclude by summarizing my findings and suggesting directions for future research. I hope this research furthers the understanding of the factors underlying the variation in age at and size at maturity in nature. These life history traits have important consequences not only for the fitness of individual organisms, but also to the growth and regulation of populations (Roff 1992). Please relax and enjoy the read...

References


Chapter 1

Life history stability in a predator-insensitive mayfly
Introduction

The age and size at which an organism matures can have important fitness consequences (Roff 1992, Stearns 1992). For example, size at maturity or metamorphosis is highly correlated with fecundity or other fitness measures in frogs (Smith 1987), mayflies (Vannote and Sweeney 1980) and odonates (Sokolovska et al 2000). Given the importance of these traits, it is curious that there exists a large amount of variation in age and size at maturity in nature (e.g. amphibians: reviewed in Werner 1986, insects: reviewed in Nylin and Gotthard 1998).

Most life history theory predicts the optimum size for maturity to be a balance between the costs (smaller size and thus reduced fecundity) and benefits (reduced probability of mortality) of earlier maturation (Roff 1992, Stearns 1992). Models have examined how this balance can be affected by varying levels of predation risk and resources (reviewed in Werner and Gilliam 1984 and Abrams and Rowe 1996). Some models (Gilliam 1982, Werner and Gilliam 1984) show that fitness is maximized by minimizing the ratio of mortality to growth rate across life history stages. Greater mortality rate or decreased growth during premetamorphic stages should favour decreased size at metamorphosis. More recent predator-prey theories have examined the direct effects of predators on prey life history, as well as the indirect effects (via increased food supply) of increased predator density (Abrams and Rowe 1996, Abrams et al 1996). The predictions of these generally depend on which life history traits are flexible and whether increased growth effort also increases predation risk (Abrams and Rowe 1996, Abrams et al 1996). Models that assume a flexible growth rate suggest that predators can directly affect prey life history in two ways: 1) via changes in prey growth rates or 2) independent of prey growth rate. This distinction is significant as it implies that predators can alter prey life history through behaviourally mediated shifts in prey growth rates, or independent of prey behaviour. Growth-independent changes in prey development rates is an example of a non-behaviourally mediated prey response.
Theory has also demonstrated that optimal age and size at maturity can be influenced by time constraints as well as biotic factors (Rowe and Ludwig 1991, Rowe et al 1994, Abrams et al 1996). These time constraints can be imposed by seasonality. For example, adult insects may need to emerge before a set time in the season and tadpoles may need to metamorphose prior to pond drying. Delaying emergence may carry with it the benefit of attaining further size, and thus fecundity, but also the cost of delayed reproduction. These costs may include decreased available time for larvae to attain a minimum overwintering size, and an increased probability of adult mortality (Rowe and Ludwig 1991). In general, if growth rate is constant, these models predict a decrease in size at maturity and increase in age at maturity as the time horizon approaches (Rowe and Ludwig 1991, Rowe et al 1994). If growth rate is flexible, the most likely effect of reduced time is that growth becomes faster and emergence size smaller (Abrams et al 1996). Rowe and Ludwig (1991) also predict that smaller individuals should delay emergence longer than larger individuals, as the relative fitness gain per increment of delay may be greater for a smaller individual than a larger individual.

Numerous empirical studies have examined the independent effects of predators (e.g. Ball and Baker 1995, Crowl and Covich 1990, Skelley and Werner 1990) or seasonality (e.g. Higgins 2000, Plaistow and Siva-Jothy 1999, Johansson and Rowe 1999) on an organism’s life history characteristics. Most “predator” studies that include behavioural observations have found that in the presence of predators, prey reduce foraging activity and growth rate and thus metamorphose at a smaller size (e.g., Skelley and Werner 1990, Ball and Baker 1996, Scrimgeour and Culp 1994b; reviewed in Tseng unpublished thesis). Studies that have examined the effect of seasonality or time constraints on an organism’s life history usually do so by manipulating photoperiod (Tauber et al 1986, Nylin and Gotthard 1998). In response to photoperiod manipulations, individuals usually increase development rate, but final body size has been shown to either decrease (Johansson and Rowe 1999, Plaistow and Siva-Jothy 1999), or remain constant (Leimar 1996).
There have been only a few empirical studies that have examined the combined effects of both seasonality and predators on life history characteristics (Johansson et al 2000, Laurila and Kujasalo 1999). Johansson et al (2000) found that predators induced a behaviourally-mediated decrease in size at emergence on the damselfly *Lestes sponsa* but a time constraint decreased size at emergence independent of behavioural changes. Laurila and Kujasalo (1999) found that common frog (*Rana temporaria*) larvae are able to respond to pond-drying by speeding up development and that pond-drying seems to be a more important determinant of development rate than the presence of odonate predators.

The objective of this study is to examine experimentally the combined effects of time constraints and predation on age and size at maturity in the mayfly *Ephemera subvaria* (Ephemeroptera: Ephemerellidae). *E. subvaria* possesses a number of key characteristics that make it an ideal organism in which to ask these types of questions. The first is that unlike most mayfly species, larval *E. subvaria* are remarkably behaviourally unresponsive to both vertebrate and invertebrate predators (Soluk and Collins 1988, Peckarsky 1996). This trait is significant because most studies that have examined the effect of predation on insect life histories have used prey organisms that are known to exhibit anti-predator behaviours even at low levels of risk (Scrimgeour and Culp 1994b, Ball and Baker 1995, 1996, Lima and Dill 1990, Lima 1998). For example, larvae of the mayfly *Paraleptophlebia heteronea* abruptly increase drift rates by 30 fold in the presence of foraging fish (Culp et al 1991). Larval chironomids respond to predators by rapidly pulling back into their tubes and reducing activity (Macchiusi and Baker 1991, 1992). Mayflies of the genus *Baetis* respond to the presence of sculpins by significantly reducing time spent on top surfaces of substrates, and by decreasing movement rate when moving within and between food patches (Kohler and McPeek 1989). In the field, baetids were also able to detect and respond to changes in fish odour concentration within five minutes of odour addition (McIntosh et al 1999). Because *E. subvaria* are not known to exhibit anti-predator behaviours, this species allows for the testing of direct predator effects on life history traits. Although theory predicts that both behavioural and life history traits are expected to respond independently to predator risk.
(Abrams and Rowe 1996, Abrams et al 1996), few studies have been able to disentangle those effects due to behaviourally-mediated changes in prey growth rate, and those due to growth independent effects (Johansson et al 2000).

The second trait that makes E. subvaria a model organism with which to test theories of life history variation is that the life cycle of this species follows closely with temperate climate seasons (Ciborowski 1976) and that there is large variation in size at emergence (Sweeney and Vannote 1981). The correlation of the life cycle with the seasons suggests that larvae may use an abiotic cue (e.g. photoperiod or temperature) to gauge the time of year. Thus, manipulating this cue in the laboratory should alter a larva’s perception of the time of year. The existence of a wide range of emergence sizes, of the pattern that larger individuals emerge earlier in the year than smaller individuals, and of the positive correlation between size at emergence and female fecundity (Sweeney and Vannote 1981), suggests growth and development are flexible and can potentially respond to experimental manipulations.

In the present study, I conduct an experiment that examines the combined effects of predators and time constraints on life history of the mayfly E. subvaria. Larvae are reared in a photoperiod mimicking “late” in the growing season and a photoperiod mimicking “early” in the season. Theory predicts that E. subvaria larvae facing a time constraint will metamorphose at a smaller size than non-time constrained individuals and that initially smaller individuals will emerge at a later date than their larger counterparts (Rowe and Ludwig 1991).

The effects of predators on this mayfly are less predictable. Although theory predicts that predators can alter prey life history through changes in prey behaviour as well as independent of prey behaviour, few studies have been able to rule out changes in behaviour as the causal agent of shifts in prey life history (but see Skelly and Werner 1990, Hetchel and Juliano 1997). Given the absence of anti-predator behaviours in this species, and the lack of data supporting the existence of non-behaviourally-mediated
direct predator effects, I expect this species not to show strong life history shifts in response to predation risk.
Methods

Study organism

*Ephemerella subvaria* is a riffle-inhabiting species found in north-temperate and sub-arctic streams in eastern North America (Allen and Edmunds 1965). Nymphs hatch in mid-August and growth in head width is linear until early winter. Little or no growth occurs over the winter but resumes in the spring. Emergence occurs from mid-May into June (Ciborowski 1976).

*Ephemerella subvaria* larvae were collected on March 22 and 23, 2000 from Reesor Creek, Durham County, Ontario, Canada. Mayfly larvae were held for six days in plastic 10-L containers filled with aerated dechlorinated tap water before being transferred to individual rearing containers, one day prior to the start of the experiment. During these six days, the temperature of the environmental chamber was slowly increased from 4°C (water temperature at time of collection) to 15°C (water temperature during regular emergence period), where it remained for the duration of the experiment. Rearing containers consisted of transparent plastic cups with two 4x5 cm$^2$ squares cut out and replaced with 0.25 mm Nitex screen. The screen allowed water to flow through the rearing containers. The cups were held afloat with a styrofoam collar. Twenty cups were grouped into a larger black plastic holding bin (62 cm long x 40.5 cm wide x 14.5 cm deep) which was filled 10 cm deep with aerated dechlorinated tap water. Five litres of the water in these holding bins were replaced every 5-6 days.

Larvae were provided with a 4x4 cm$^2$ piece of maple leaf for food as well as for substrate. In an experiment examining the effect of different food types on growth and survival of *E. subvaria*, Bird and Kaushik (1984) found that larvae reared on maple leaf discs had both intermediate growth and survival. Larvae reared on *Cladophora* had high survival but low growth, while those reared on periphyton had high growth but low survival. Maple leaves were collected in October 1999 and stored in a clear plastic bag until approximately three weeks before their use. At this time, they were conditioned in
dechlorinated tap water mixed with water from Reesor Creek and enriched with 2.7g KH$_2$PO$_4$ and 4.0g KNO$_3$ per 25L water (following Bird and Kaushik 1984). During conditioning, water was changed every three to four days. Larvae received freshly conditioned leaves every 3-4 days. When eating these decomposing leaves, larvae consume all but the veins of the leaf (Tseng, personal observation). Thus, it is possible to observe whether had larvae had consumed all or part of this food source before leaves were replaced. In no case did larvae consume the entire leaf before it was replaced.

Predation risk on *E. subvaria* was imposed by exposing larvae to the fish *Luxilus cornutus* (the Common Shiner). The distribution of *L. cornutus* overlaps extensively with that of *E. subvaria* and it is a predator of larval and adult aquatic insects (Scott and Crossman 1998). In the predator present treatments, two *L. cornutus* were placed in the large holding bins and were allowed to swim freely amongst the rearing containers. The fish could not prey directly on the mayfly larvae in the individual cups. Predation risk was thus imposed indirectly on mayfly larvae via chemical and visual cues. Many species of insects have been shown to respond to these cues (e.g. chironomids: Ball and Baker 1996; mayflies: McIntosh et al 1999). Fish were fed Tetra Tropical Fish Staple Flakes daily along with *E. subvaria* larvae every three days.

**Experimental design and statistical analysis**

Two photoperiod treatments (early, late) and two predator treatments (present, absent) were used in the experiment. A single environmental chamber was divided into two halves with larvae in one half of the room exposed to one photoperiod treatment and those in the other side of the room exposed to the other treatment. The start of the “early” treatment mimicked that of early March, while the start of the “late” treatment mimicked that of mid-April. *E. subvaria* have an emergence period of about one month in nature (Sweeney and Vannote 1981). This range in emergence dates should translate into about a one-month difference between larvae hatching out from eggs of earlier emergers and those of eggs of later emergers. Thus, the six-week difference in starting photoperiods in
this experiment is a reasonable approximation to what early and late E. subvaria larvae would experience in nature.

Lights were controlled using digital timers and adjusted weekly to follow the natural light/dark progression of the particular treatment. The photoperiod and predator treatments were crossed to form four treatments in total (early/predator, early/no predator, late/predator, and late/no predator). Each treatment was replicated twice. Thus, there were eight holding bins, each containing 20 individual rearing containers. The experiment began on March 28, 2000 with 40 individuals in each treatment. Halfway through the experiment, all bins were rotated to minimize effects due to bin positioning. The half of the room receiving the “early” light treatment became the “late” light treatment and vice versa. The order of the holding bins within each treatment was haphazardly reordered during this transfer.

Larval head widths were measured as the farthest distance between the eyes, with a dissecting microscope fitted with an ocular micrometer. Head widths were measured on days 8, 18, and 32 of the experiment as well as when larvae reached the black wing pad (BWP) stage. The BWP stage is the last larval stage (Brittain 1982). Larval mouthparts have completely degenerated by this time; larvae cease growing and emerge 1-2 days after reaching this stage. Size and age at the BWP stage are commonly used as measures of age and size at maturity in studies of mayfly life history (e.g. Peckarsky et al 1993, Scrimgeour and Culp 1994a).

Age at maturity was the number of days needed to reach the BWP stage in the lab. This duration is not the actual age of the larvae, but because each treatment received a random sample of the collected larvae, the variation in age or size at maturity that is due to variation in starting size can be accounted for statistically (see below). Growth rate was calculated as (BWP head width - initial head width)*1000/age at maturity. Data were transformed when necessary to meet the assumptions of analysis of variance. Specific transformations are indicated in the results and table legends. All analyses were performed using Systat version 6.0 (Wilkinson 1989).
Because the larvae at the start of the experiment were not all the same age or size, and because there is a linear relationship between larval age and size during this part of the season (Waters and Crawford 1973), I conducted all statistical analyses on the residuals of the regression of the variable of interest on initial head width (Sokal and Rohlf 1995, pg 489). For example, in the analysis of the effect of photoperiod and predation on size at maturity, the dependent variable of the ANOVA was the residuals of the regression of BWP head width on initial head width.
Results

Mean head widths did not differ among treatments or between sexes at the start of the experiment (table 1.1: photoperiod: F=0.29, p=0.59; predation: F=0.02, p=0.88, sex: F=3.63, p=0.06). Males have slightly larger head widths than females because they develop compound eyes towards the middle of larval development (Ciborowski 1976). Unequal sample sizes across cells are attributable to deaths in the first few days of the experiment.

A nested ANOVA with bins nested within treatments revealed no significant bin effects on age at maturity (p>0.05), size at maturity (p>0.5) and growth rate (p>0.5). Therefore, each rearing container was considered a replicate for all statistical analysis.

Initial size was a significant predictor of age at maturity ($r^2=0.25$, p<0.0001), size at maturity ($r^2=0.50$, p<0.0001) and growth ($r^2=0.25$, p<0.0001). The pattern of the regressions revealed that initially smaller individuals reached maturity at a later date, grew less, and attained a smaller size at maturity than initially larger individuals.

Growth rates in each treatment were highest in the first week and leveled off after weeks three and four (fig. 1.1). Male head widths grew significantly faster than females (males: 6.70 ± 0.5 μm/day, females: 4.83 ± 0.5 μm/day) but neither predator risk nor photoperiod affected these rates significantly (fig. 1.2a, table 1.2a,b).

Males emerged with larger head widths than females (males: 1.85 ± 0.01mm, females: 1.77 ± 0.01mm), but there was no significant treatment effect of either photoperiod or predation on size at emergence in either sex (table 1.3a, b, fig. 1.2b). Predator risk did not have a significant effect on larval time to emergence in either sex (table 1.4a,b, fig. 1.2c). Larvae reared in the “late” photoperiod reached the BWP stage 2-3 days earlier than those in the “early” photoperiod, as expected but this effect was not significant (p=0.09). A power test (Sokal and Rohlf 1995) revealed a $\beta=0.4$, suggesting that there was a 40% chance of committing a type II error in this test. Thus, it is highly
likely that a statistically significant effect of photoperiod on age at maturity would have been found had there been a larger sample size. There was no effect of sex on age at maturity (table 4b). To further verify that there was no significant effect of predation or photoperiod on size at emergence, I also used dry weight as a measure of final size. Larvae were dried at 60°C for 24 hours and then weighed on a microbalance. Females emerged slightly heavier than males (females: 2.09 ± 0.1mg, males: 1.80 ± 0.1mg; F=2.71, p=0.1) but there was also no effect of either predation or photoperiod on final larval dry weights (predation: F=0.342, p>0.5; photoperiod: F=0.089, p>0.5).

Overall, there was a negative relationship between age at maturity and size at maturity ($r^2=0.46$, n=94), with smaller individuals emerging later in the season than larger individuals (fig. 3).
Discussion

The objectives of this study were to examine the combined effects of predation and time constraints on life history characteristics of the mayfly *E. subvaria*. Predator risk was imposed by rearing larvae in the non-lethal presence of fish, and time constraints were simulated using two photoperiod treatments. Neither predators nor photoperiod had significant effects on mayfly larval life history.

**Predator risk**

*E. subvaria* did not alter its growth rate, age at maturity or size at maturity in the presence of predators. Although there are few examples in the literature showing non-behaviourally mediated shifts in prey life history, the lack of effect of predators on larval life history was somewhat unexpected, as theory suggests that predators can affect prey life history independent of shifts in prey growth rate (Abrams and Rowe 1996). There are three possible reasons for this result. First, because I used mayfly larvae that had completed over half of their development before the start of the experiment, they may have no longer been able to respond to the cues provided by the experimental manipulation. Studies of the age and size at metamorphosis in amphibians (Hensley 1993) and crustaceans (Twombly 1996) have shown that developmental pathways may become fixed towards the end of larval development. For example, Twombly (1996) found that early changes in food concentrations had significant effects on size at metamorphosis in the freshwater copepod *Mesocyclops edax* but changes initiated during the penultimate larval stage had no effect on metamorph size.

Second, because the predators and prey were kept in close proximity, over time, mayfly larvae may have acclimated to the presence of predators. A recent theoretical paper by Lima and Bednekoff (1999) suggests that optimal prey behaviour in any given situation may depend on the overall pattern of risks experienced by that individual. Prey responses to predators may depend on the proportion of time that they are exposed to high risk versus low risk situations. The model also predicts that anti-predator behaviour
in a high-risk environment will decrease, as high-risk situations become more frequent or lengthy. This model may not directly apply to *E. subvaria* larvae, as they are not known to exhibit anti-predator behaviours, but this type of temporal variation in prey response described by Lima and Bednekoff (1999) may also be applicable to life history responses. If life history responses of prey depend on the previous exposure to predators, this may help explain the weak response of *E. subvaria* to *L. cornutus* predation. I performed an ad-hoc test of this prediction by dividing the data into three categories: those that emerged earliest, those that emerged in the middle, and those that emerged last. If mayflies do acclimate to predator presence, then I would expect strength of the predator effect to decrease as time passed, and that the effect may be weakest on the mayflies that emerged last. I did not find such an effect (the effect of predators on size of early emergers: \(F_{(1,22)} = 0.894, p > 0.1\); mid-emergers: \(F_{(1,26)} = 3.64, p > 0.05\); late-emergers: \(F_{(1,22)} = 0.109, p > 0.5\).

A better way to test this hypothesis would be to hatch mayfly larvae in the laboratory and then begin predator exposure at different ages. This method could also be used to ask whether larvae become developmentally fixed after a certain age or size. Another way to examine whether larvae acclimate to the presence of predators would be to ask whether larvae responded differently to continuous versus discrete exposure to predators. If, while holding the total predator exposure time constant, it was found that prey under continuous predator risk responded less than those exposed to discrete units of predator risk, than this would lend support to some of the predictions of the Lima and Bednekoff (1999) model.

The third explanation for the lack of response to predator presence is that the threat of predation in nature is so low that there has not been selective pressure for *E. subvaria* to develop life history responses to this type of predator. The documented absence of anti-predator behaviours in *E. subvaria* (Soluk and Collins 1988, Peckarsky 1996) supports this argument. However, the presence of a thicker than average cuticle in this species (Soluk 1993, Peckarsky 1990) suggests that the risk of predation in nature
does exist, and that perhaps *E. subvaria* has evolved morphological defenses, rather than behavioural or developmental plasticity, as an anti-predator response.

Prior studies that have examined predator effects on prey life history argue that predators induce a decrease in prey activity, which usually translates into a decreased size at maturity and an increased or constant development time (Johansson et al in press, Scrimgeour and Culp 1994a, Scrimgeour and Culp 1994b, Werner and Anholt 1996, Peckarsky et al 1993, reviewed in Tseng unpublished thesis). One question that needs more exploration is how often predators cause life history changes independent of these behavioural changes. In this experiment, mayfly larvae that did not show anti-predator behaviours also did not exhibit life history shifts in response to predators. This result supports the argument that most predator-induced life history changes are behaviourally mediated. The frequency with which these behavioral vs. non-behaviourally mediated effects occur needs to be examined.

**Time constraints**

I also did not find a significant effect of photoperiod on growth rate, age at maturity or size at maturity in *E. subvaria*. There was a tendency for larvae in the "late" treatment to emerge 2-3 days earlier than those in the "early" treatment (fig. 2c), but this effect was not significant. The results of the power test suggest that had a larger sample size been used, I would likely have found a significant effect of photoperiod on age at maturity. The absence of response in size at maturity was unexpected, as it has been both predicted by theory (Rowe and Ludwig 1991, Abrams et al 1996) and documented empirically (Johansson et al in press, Johansson and Rowe 1999, Plaistow and Siva-Jothy 1999, Higgins 2000) that organisms approaching a time constraint tend to increase development rate and suffer a decrease in size at maturity. This response to photoperiod may be due to mechanisms similar to those behind the lack of larval response to predation. As discussed above, larvae used in this experiment may have already reached a stage in their life history after which development rates are fixed. One way to test this hypothesis would be to conduct the experiment with different age classes of larvae and then examine whether there is an effect of starting age on developmental flexibility.
Finally, a very interesting result was that despite the fact that photoperiod and predation did not have strong effects on mayfly life history, there still existed the pattern of decreased size at emergence over time (fig. 3). This pattern is similar to that seen in nature (Sweeney and Vannote 1981). Rowe and Ludwig (1991) hypothesized that smaller individuals do not emerge at the largest possible size because of the costs associated with delayed emergence. This hypothesis hinges on the ability of organisms to gauge the time of year, and it was proposed that photoperiod or temperature might provide such a cue (Sweeney et al. 1995, Rowe et al 1994). Temperature has been demonstrated to affect larval development rates (Sweeney and Vannote 1978) but it could not explain the pattern of decreasing size of emergence over time (Sweeney et al 1995). Future experiments could investigate the combined effects of temperature, photoperiod and predation on age and size at emergence in mayflies.

In summary, this study examined the effects of a time constraint and predation on an organism not known to exhibit anti-predator behaviours. The magnitude of the effect of the approaching end of season on age and size at maturity was larger that that of predation, but neither effect was statistically significant. This study is significant because it suggests that not all aquatic insects are responsive to predation risk, in contrast to recent literature (Johansson et al in press, Ball and Baker 1995, Ball and Baker 1996, Scrimgeour and Culp 1994b, Peckarsky et al 2000, Peckarsky et al 1993). Further understanding of the effect of predators on organisms from a wide range of taxa is necessary to better understand the variation of prey to predators in nature.
References


Peckarsky, B.L., B.W. Taylor, A.R. McIntosh, M.A. McPeek and D.A. Lytle. 2000. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology. in press.


Table 1.1. Initial head widths (mean ± SE) and sample sizes for the four treatments.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Predator</th>
<th>Photoperiod</th>
<th>early</th>
<th>late</th>
</tr>
</thead>
<tbody>
<tr>
<td>male</td>
<td>absent</td>
<td>1.63 ± 0.03 (17)</td>
<td>1.64 ± 0.04 (15)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>present</td>
<td>1.61 ± 0.03 (20)</td>
<td>1.65 ± 0.03 (18)</td>
<td></td>
</tr>
<tr>
<td>female</td>
<td>absent</td>
<td>1.58 ± 0.03 (19)</td>
<td>1.59 ± 0.03 (20)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>present</td>
<td>1.60 ± 0.04 (16)</td>
<td>1.59 ± 0.03 (19)</td>
<td></td>
</tr>
</tbody>
</table>
Table 1.2a. Comparison of growth rates (mean μm/day ± SE) for male and female *Ephemerella subvaria* reared in early or late photoperiods and in the absence or presence of predators. Sample sizes are listed in parentheses.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Predator</th>
<th>Photoperiod</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>early</td>
</tr>
<tr>
<td>male</td>
<td>absent</td>
<td>6.67 ± 1.1 (12)</td>
</tr>
<tr>
<td></td>
<td>present</td>
<td>6.61 ± 0.9 (16)</td>
</tr>
<tr>
<td>female</td>
<td>absent</td>
<td>5.25 ± 1.1 (11)</td>
</tr>
<tr>
<td></td>
<td>present</td>
<td>4.18 ± 1.3 (8)</td>
</tr>
</tbody>
</table>

Table 1.2b. Effect of photoperiod and predation on growth rate. ANOVA performed on the residuals from the regression of growth rate on initial head width (n=94).

<table>
<thead>
<tr>
<th>Factor</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>photoperiod</td>
<td>0.00035</td>
<td>0.98517</td>
</tr>
<tr>
<td>predation</td>
<td>0.03334</td>
<td>0.85556</td>
</tr>
<tr>
<td>sex</td>
<td>9.592</td>
<td>0.00264</td>
</tr>
<tr>
<td>sex x photoperiod</td>
<td>0.02923</td>
<td>0.86465</td>
</tr>
<tr>
<td>sex x predation</td>
<td>0.58720</td>
<td>0.44560</td>
</tr>
<tr>
<td>photoperiod x predation</td>
<td>0.11899</td>
<td>0.73097</td>
</tr>
<tr>
<td>sex x photoperiod x predation</td>
<td>0.03117</td>
<td>0.86028</td>
</tr>
</tbody>
</table>
Table 1.3a. Comparison of size (mean ± SE) at maturity (mm head width) for male and female *Ephemerella subvaria* reared in early or late photoperiods and in the absence or presence of predators. Sample sizes are listed in parentheses.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Predator</th>
<th>Photoperiod</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>early</td>
</tr>
<tr>
<td>male</td>
<td>absent</td>
<td>1.83 ± 0.03 (12)</td>
</tr>
<tr>
<td></td>
<td>present</td>
<td>1.86 ± 0.02 (16)</td>
</tr>
<tr>
<td>female</td>
<td>absent</td>
<td>1.76 ± 0.03 (12)</td>
</tr>
<tr>
<td></td>
<td>present</td>
<td>1.80 ± 0.03 (8)</td>
</tr>
</tbody>
</table>

Table 1.3b. Effect of photoperiod and predation on size at maturity. ANOVA performed on ln transformed residuals from the regression of head width at maturity on initial head width (n=95).

<table>
<thead>
<tr>
<th>Factor</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>photoperiod</td>
<td>0.0389</td>
<td>0.84406</td>
</tr>
<tr>
<td>predation</td>
<td>0.9154</td>
<td>0.34133</td>
</tr>
<tr>
<td>sex</td>
<td>15.990</td>
<td>0.00013</td>
</tr>
<tr>
<td>sex x photoperiod</td>
<td>0.01038</td>
<td>0.91909</td>
</tr>
<tr>
<td>sex x predation</td>
<td>0.49071</td>
<td>0.48548</td>
</tr>
<tr>
<td>photoperiod x predation</td>
<td>0.22977</td>
<td>0.63290</td>
</tr>
<tr>
<td>sex x photoperiod x predation</td>
<td>0.43055</td>
<td>0.51345</td>
</tr>
</tbody>
</table>
Table 1.4a. Comparison of age at maturity (days to BWP stage ± SE) for male and female Ephemerella subvaria reared in early or late photoperiods and in the absence or presence of predators. Sample sizes are listed in parentheses.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Predator</th>
<th>Photoperiod</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>early</td>
</tr>
<tr>
<td>Male</td>
<td>absent</td>
<td>30.6 ± 2.4 (12)</td>
</tr>
<tr>
<td></td>
<td>present</td>
<td>31.6 ± 2.1 (16)</td>
</tr>
<tr>
<td>Female</td>
<td>absent</td>
<td>32.9 ± 2.5 (11)</td>
</tr>
<tr>
<td></td>
<td>present</td>
<td>33.0 ± 2.9 (8)</td>
</tr>
</tbody>
</table>

Table 1.4b. Effect of photoperiod and predation on age at maturity. ANOVA performed on the residuals from the regression of age at maturity on initial head width (n=94).

<table>
<thead>
<tr>
<th>Factor</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>photoperiod</td>
<td>2.9851</td>
<td>0.0876</td>
</tr>
<tr>
<td>predation</td>
<td>1.6780</td>
<td>0.1985</td>
</tr>
<tr>
<td>sex</td>
<td>2.1368</td>
<td>0.1477</td>
</tr>
<tr>
<td>sex x photoperiod</td>
<td>0.2461</td>
<td>0.6210</td>
</tr>
<tr>
<td>sex x predation</td>
<td>0.0002</td>
<td>0.9886</td>
</tr>
<tr>
<td>photoperiod x predation</td>
<td>0.0066</td>
<td>0.9354</td>
</tr>
<tr>
<td>sex x photoperiod x predation</td>
<td>0.0137</td>
<td>0.9070</td>
</tr>
</tbody>
</table>
Figure 1.1. Mayfly head widths from the start of the experiment until maturity. Circles = predator absent, x = predator present, solid lines = early photoperiod, dashed lines = late photoperiod.
**Figure 1.2a.** The effect of photoperiod and predation risk on growth rate. Growth rate is measured as the residuals of the regression of growth rate on initial head width. The original growth rate is measured as: \((\text{head width at BWP} - \text{initial head width}) \times 1000 / \text{days to maturity}\). (Circles = predators present, x = predators absent, dashed lines = male, solid lines = female, error bars = standard error.)
The graph shows the growth rate as a function of photoperiod, with early and late photoperiod categories on the x-axis and growth rate on the y-axis. The data suggests a stable growth rate for both early and late photoperiods.
**Figure 1.2b.** The effect of photoperiod and predation risk on size at maturity. Size at maturity is measured as the ln of the residuals of the regression of head width at maturity on initial head width. (Circles = predators present, x = predators absent, dashed lines = male, solid lines = female, error bars = standard error.)
Figure 1.2c. The effect of photoperiod and predation risk on age at maturity. Age at maturity is measured as the residuals of the regression of age at maturity on initial head width. (Circles = predators present, x = predators absent, dashed lines = male, solid lines = female, error bars = standard error.)
Figure 1.3. Relationship between size at maturity and ln age at maturity in *Ephemerella subvaria* \((r^2=0.46, \ n=94)\).
Chapter 2

The effect of predator risk on long-term growth and development in insects
Introduction

The ability of prey to respond plastically to predator risk has been the focus of several recent predator-prey experiments. Prey have been demonstrated to alter behaviours (reviewed in Lima and Dill 1990, Lima 1998), morphologies (Arnqvist and Johansson 1998, Boersma 1998, Van Buskirk et al 1997) and life histories (Crowl and Covich 1990, Peckarsky et al 1993, Skelly and Werner 1990) in the presence of predators. Particular attention has been paid to the effect of predators on the size and timing of metamorphosis in organisms with complex life cycles (Ball and Baker 1995, 1996, Laurila et al 1998, Peckarsky and McIntosh 1998, Skelly and Werner 1990, Nicieza 2000) with hopes that any variation in prey responses can help explain the variation seen in these life history traits in nature. Given that in many of the organisms that undergo these ontogenetic transitions, size at metamorphosis or maturity is highly correlated with overall fecundity or fitness (e.g. frogs: Smith 1987; mayflies: Sweeney and Vannote 1981; odontates: Sokolovska et al 2000), it is intriguing that there exists such large variation in age and size at maturity (amphibians: reviewed in Werner 1986, arthropods: reviewed in Higgins 2000) as well as pattern to this variation. For example, in univoltine arthropods, late-maturing individuals are often smaller than early-maturing individuals (spiders: Higgins 2000; butterflies: Nylin et al 1996; mayflies: Vannote and Sweeney 1980; mole crickets: Forrest 1987).

The potential role of predators in maintaining selection for plasticity in prey growth and development has been central to numerous theoretical models. Generally, most models assume the optimal age at or size at maturity to be a balance between the costs (smaller size and thus, reduced fecundity) and benefits (reduced probability of mortality) of early maturation in varying resource levels and predator risk (reviewed in Werner and Gilliam 1984 and Abrams and Rowe 1996). Some studies (Gilliam 1982, Werner and Gilliam 1984) predict that fitness is maximized by minimizing the ratio of mortality rate to growth rate across all life history stages, and if all else is equal, greater mortality rate or decreased growth rate during juvenile stages should favour decreased size at metamorphosis. Although these models have been used to accurately predict prey
life history responses under certain conditions, these models assume fixed growth rates within life history stages and have not taken into consideration the possibility that prey may exhibit plasticity in growth rates in response to predators. For example, growth rates can be affected by changes in prey behaviour. The effects of predators on prey behaviour have been widely documented (reviewed in Lima and Dill 1990, Lima 1998) and thus including this trait in predator-prey models can only serve to increase their predictive power.

More recent models have investigated the possible effects of anti-predator behaviour on long-term growth and development of prey (Abrams and Rowe 1996, Abrams et al 1996, Werner and Anholt 1993, Houston et al 1993). These models incorporate the assumption that changes in prey foraging rates or activity rates in the presence of predators may result in corresponding changes in prey growth rates. Anti-predator behaviour is built into these models by allowing growth rates to be flexible as well as fixed. Specific model predictions of prey responses to increased predator risk mostly depend the following characteristics: 1) whether growth rate, age at maturity or size at maturity are fixed or plastic, 2) whether mortality rate is a linear, decelerating, or increasing function of growth rate, and 3) the relationship between increased predator density and food availability (Abrams and Rowe 1996, Abrams et al 1996). Abrams and Rowe (1996) also consider shifts in prey age and size at maturity that may be caused by predators consuming prey. Here, surviving prey experience an increase in per capita food supply. These types of predator effects are considered to be “indirect”, versus the “direct” effects discussed above.

An interesting result that arises from the inclusion of flexible growth rates into these models is the prediction that predators can induce shifts in prey life history via a) changes in growth rates, or b) independent of growth rates. Decreases in prey growth rate in predator presence can lead to delayed maturity and smaller size at maturation. The response of *Bufo americanus* to odonate predation risk provides an example of behavioural- and growth-mediated prey life history responses. In the presence of predator chemical cues, *B. americanus* tadpoles exhibited a decrease in activity rate, growth rate
and size at maturity (Skelly and Werner 1990). Prey may also show life history responses to predator risk without increases or decreases in growth rate if development rate is flexible. Although this non-growth mediated effect of predators on prey is predicted by theory (Abrams and Rowe 1996), empirical examples of these facultative life history shifts are not common (Johansson et al 2000, Ball and Baker 1996).

The objectives of this review are to a) use meta-analysis to investigate the overall effect of predator risk on long-term insect growth and development and to examine how often shifts in prey age at and size at maturity are also accompanied by changes in prey behaviour and growth rates. Insects are an ideal system with which to ask these types of questions, as there has been a recent increase in the number of and taxonomic breadth of studies exploring the effect of predator risk on growth and developmental plasticity in insects. Studies of the metamorphic responses of amphibians to predators have been confined to relatively few species. (*Bufo americanus*: Skelly and Werner 1990; *Rana temporaria*: Laurila et al 1998, Laurila and Kujasalo 1999, Nicieza 2000; *Bufo bufo*: Laurila et al 1998), while the effects of predators on *Daphnia* life history have recently been synthesized (Riessen 1999). I conclude by comparing predator-induced life history responses of insects to those of amphibians and *Daphnia*. 
Methods

I use a meta-analysis (MA) to examine the effect of predator risk on long-term growth and development in insects. MA is a statistical technique that can be used to combine the results of independent experiments. In more traditional and qualitative reviews, the importance of an effect is judged based on how frequently it occurs in the literature. This "vote-counting" approach is flawed because the significance level of a study is a function not only of the magnitude of the effect, but also of its sample size (Gurevitch and Hedges 1993). A meta-analysis allows for quantitative analyses of the results of similar experiments and has a high degree of objectivity because it is based on a standardized set of statistical procedures and thus is able to control for variation in effect sizes due to sample sizes (Arnqvist and Wooster 1995).

All analyses were carried out as in Gurevitch and Hedges (1993). For each comparison, an estimate of the magnitude of the treatment effect (effect size, $d$) was calculated as the difference between the means of the experimental and control groups divided by the pooled standard deviation, and weighted by a correction term that removes small-sample biases. Effect sizes were combined using the mixed-effects model to obtain a grand mean effect size for development, and one for growth. Predator risk was considered to have a significant effect if the 99% confidence interval of the effect size did not overlap zero. Cohen (1969) provides a conventional interpretation of the absolute magnitude of effect sizes: 0.2 is a small effect, 0.5 is a medium effect, 0.8 is large, and any effect greater than 1 is considered very large.

To conduct the MA, sample size, means and standard deviations for each prey's growth and development in the presence and absence of predators was taken from published studies. Growth was defined as: final mass - initial mass, and development was defined as the number of days needed to complete a given instar, or number of days until maturity. Data had to have been available in the article as numerical or graphical data, or they had to have been available from the authors. Graphical data that were not available
in numerical form were scanned and then extracted with DataThief (Huyer and Van der Laan 1994).

In total, 11 studies were included in the analysis. Only studies that exposed prey to predation risk for seven days or greater were included. Traditional methods used to investigate this effect involve rearing prey in the sub-lethal (sensu Peckarsky et al 1993, also termed “non-lethal” by Skelly and Werner 1990) presence of predators. Prey have visual or chemical contact with predators, but are not in direct danger of being eaten. This rearing method allows for the disentangling of predator effects due to selective mortality or to decreases in prey density as a consequence of predation, from the direct effect of risk perception.

Eight of the 11 reviewed experiments reported results separately for males and females. Three studies did not distinguish between sexes. Because some studies separated the sexes while others did not, I analyzed the overall effect size for growth and development and then divided the data into three classes (Females, Males, Both) and asked whether there were significant differences in effect sizes, within traits, between classes. This was done by calculating $Q_B$ (between-class homogeneity) and testing it against a Chi-square distribution with the degrees of freedom equal to the number of classes minus one. I further tested for significant differences in effect sizes between the sexes (classes Female and Male) using a t-test. Because different sets of data (e.g. male data and female data) reported in the same publication are not necessarily independent of one another, I used a very conservative significance level ($p<0.01$) to assess the significance of the effect sizes (Gurevitch et al 1992). The results should be interpreted with some caution because most of the studies used in the review are published, and there might be a potential bias for researchers to submit, and journals to publish, significant results more often than non-significant results (Gurevitch and Hedges 1993, Wooster and Sih 1995).

For those studies that reared prey to maturity, I also examine how often shifts in age at and size at maturity in response to predators are accompanied by plastic responses.
in behaviour and growth rates. Growth rate (increase in size divided by number of growing days) data were not included in the meta-analysis because although the final statistical results were usually reported (e.g. Anova or t-test results) the raw data needed for the MA (means, variances, sample sizes) were usually omitted. Raw MA data are listed in Appendix A.
Results

Development

In this category, all studies but one (*Ishnura verticalis*: Dixon and Baker 1987) reared prey to maturity and thus development time can largely be thought of as age at maturity. *I. verticalis* was reared for one instar and while damselflies in the predator present treatment tended to take longer to complete the instar, no significant effect of predator risk on instar duration was found (Dixon and Baker 1987). In the other studies, age at maturity increased in the presence of predator risk for all species except in *Baetis bicaudatus* females (Peckarsky and McIntosh 1998). Combining the effect sizes of all the experiments resulted in a large, positive and significant overall effect size (table 2.1). There was significant heterogeneity between the three classes of data (table 2.1) and while the Male class tended to delay development longer than the Female class, this difference was not statistically significant (t=0.92, p>0.1).

Growth

In this category, all but two studies reared prey to maturity. The two species that were not reared to metamorphosis were *Hemileuca lucina* (Stamp and Bowers 1991), and *Chironomus tentans* (Macchiusi and Baker 1992). In the 11 day experiment, *H. lucina* in the predator present treatment grew less than those in the predator absent treatment but no statistical tests were performed (Stamp and Bowers 1991). In contrast, there was no significant effect of predator treatment on seven-day growth of *C. tentans* (Macchiusi and Baker 1992). Similar to the effects of predators on development of *I. verticalis*, although *C. tentans* individuals in predator present treatments tended to gain less mass than those in predator absent treatments, small sample sizes may have contributed to the non-statistically significant result (Macchiusi and Baker 1992).

Overall, predator risk had a large and significantly negative effect on insect growth (table 2.1). All but two of the reviewed studies reported decreases in prey growth. Predator risk did not have a negative effect on size at maturity in males of two
populations of *Aedes triseriatus* (Hetchel and Juliano 1997), and on size at maturity in both sexes of *Ephemera subvaria* (Tseng unpublished thesis). There was significant heterogeneity between classes of data (table 2.1). Also, predator risk had a significantly greater effect on female growth than on male growth (t=2.79, p<0.01). A closer examination of this difference reveals that while females grew significantly less in the presence of predators, there was no significant effect of predators on male growth.

**Behaviour and growth rate**

Behavioural and growth rate data for the seven reviewed species that were reared to maturity revealed that in all cases, a change in behaviour in predator presence was associated with a decrease in growth rate (table 2.2). Both *Baetis bicaudatus* and *B. tricaudatus* increased drift activity. This increase in movement decreased foraging opportunities for both mayfly species (Peckarsky 1996, Kratz 1996). *Chironomus tentans* and *Lestes sponsa* decreased movement rates in the presence of predators. *Junonia coenia* moved from the young leaves of the plant exterior to the interior of the plant in predator presence (Stamp and Bowers 1988). This area provided refuge from predators but also contained lower quality leaves (Stamp and Bowers 1988).

Neither behavioural responses nor growth rate responses to predators were observed for *Aedes triseriatus* (Hetchel and Juliano 1997) and *Ephemera subvaria* (Tseng, unpublished thesis). Interestingly, as noted above, these two species also did not show shifts in age at or size at maturity in the presence of predators.
Discussion

General effects

This review reveals that the overall effect of predator risk is to delay development and decrease growth in insects. Because most of the experiments reviewed reared prey to maturity, these changes in growth and development translate into a delayed age at maturity and a decreased size at maturity in insects. These results suggest that growth rates decrease in predator presence. Although growth rate was not included in the MA, a separate survey of the effect of predators on insect behaviour and growth rate demonstrated that in most cases (Baetis bicaudatus, B. tricaudatus, Chironomus tentans, Junonia coenia, Lestes sponsa), species of insects that exhibited life history shifts in predator presence have also been shown to display anti-predator behaviours and predator-induced decreases in growth rates. Predation risk did not have a significant effect on activity rates, growth rates, age at maturity and size at maturity in Aedes triseriatus and Ephemerella subvaria. Although males and females from the four populations of A. triseriatus used in that experiment did not respond to the non-lethal presence of predatory mosquitoes, significant behavioural, growth and life history shifts were seen in the lethal presence of predators (Hetchel and Juliano 1997). E. subvaria has been described as having a heavier than average cuticle (Soluk 1993, Peckarsky 1990) and thus this species may have evolved morphological defenses in response to predators, rather than plasticity in behaviours or life history traits.

The observation that prey exhibit shifts in life history traits in the non-lethal presence of predators, combined with reports revealing that these species also show behavioural changes and decreases in growth rates in predator presence, suggest life history shifts in insects are behavioural- and growth-mediated. Prey likely trade off risky foraging activities for increased survival and thus experience a decrease in growth rates, smaller sizes at maturity and delayed maturity.

Although the mechanisms behind predator-induced life history shifts in a variety of insects seem to be similar, the same is not true for amphibians and Daphnia. In the
presence of odonate predator risk, *Rana temporaria* decreased activity levels, delayed in time to metamorphosis and metamorphosed at a larger size, but experienced no change in growth rates (Laurila et al 1998, Laurila and Kujasalo 1999). Nicieza (2000) also demonstrated the presence of anti-predator behaviours in *R. temporaria*, but prey life history and growth rates were dependent on food level. Both *Bufo americanus* and *Bufo bufo* decreased activity rates in the non-lethal presence of odonate predators. However, while decreased activity was correlated with lower growth rates and a smaller size at metamorphosis in *Bufo americanus* (Skelly and Werner 1990), *Bufo bufo* had a shorter larval period, a slight decrease in size at maturity, and no change in growth rate (Laurila et al 1998). While the life history responses of *B. americanus* were attributed mainly to behaviourally mediated growth effects (Skelly and Werner 1990), life history responses of *B. bufo* tadpoles were independent of behaviour (Laurila et al 1998).

A meta-analysis of the effects of predator risk on *Daphnia* life history traits demonstrated that prey responses were predator-specific (Riessen 1999). Similar to the effect of predators on *R. temporaria*, in the presence of *Chaoborus* kairomones, *Daphnia* increased age at maturity and matured at a larger size than in the absence of predator chemical cues. Unlike that of insects or amphibians, in the presence of *Notonectid* or fish cues, *Daphnia* responded by decreasing both age at maturity and size at maturity.

In general, while the life history responses of insects to predator risk appear to be mediated primarily by behaviourally driven changes in growth rates, the mechanisms of life history responses of amphibians and *Daphnia* seem to be less clear. Predator risk induces species specific, growth-independent and growth-dependent life history responses in amphibians while life history shifts of *Daphnia* appear to be predator specific. The frequency with which predators affect *Daphnia* life history responses via changes in behaviours has not been investigated. Likewise, life history shifts of amphibians may also predator specific, but more experiments are needed to test this hypothesis. Finally, these amphibian studies also suggest that the assumption of changes in behaviour also resulting in changes in growth rates (discussed in Abrams and Rowe
1996) may not apply to all taxa. While anti-predator behaviour and growth rate seem to be linked in insects, the same is not true in amphibians.

**Sex-specific responses**

As well as providing an objective method of determining overall effect sizes, a meta-analysis also allows one to compare effect sizes amongst groupings of data. A closer examination of the MA reveals significant differences in effect sizes, between the sexes. Predators had a significantly larger effect on female growth than on male growth (table 2.1) but while predators affected male development slightly more than female development, this difference between the sexes was not statistically significant. These results should be interpreted with caution, however, as they may be biased by the method by which the effect size, \( d \), was calculated. A more robust method would be to use the response ratio, \( R \), as a measure of effect size (Osenberg et al 1997). \( R \) is the ratio of the treated and control means, rather than the difference between the means. The effect size \( d \) is still an adequate measure to use to examine the overall effect of predators on prey life history, but \( R \) is likely a better measure for comparing the sexes, as the ratio is a relative measure, rather than an absolute measure.

Sexual dimorphism in the response to predation was not predicted, but is nonetheless interesting. Past tests of the effect of predators on metamorphosis in amphibians or cladocerans have not evaluated intersexual differences (Werner 1986, Figiel and Semlitsch 1990, Skelly and Werner 1990, Skelly 1992, Laurila et al 1998, Riessen 1999). I know of no theoretical studies that have examined when sexually dimorphic life history responses would be expected. Presumably, it is equally beneficial for both males and females to mature at the largest possible size. Larger females are usually more fecund than smaller ones (Peckarsky et al 1993, Scrimgeour and Culp 1994) and larger males may obtain more matings (Flecker et al 1988). Although selection for large male size may be countered by the benefits of early maturity connected with protandry (Roff 1992), here it appears that the costs associated with delayed emergence may not be as great as those associated with small body size. It is possible that the
significant difference in size effects is a by-product of the effect of predators on
development time. If the relationship between size and age in females is different from
that in males, a per unit decrease in development time may not have the same effect on
male size as it does on female size. It is currently not know whether the sex-specific
growth trajectories in these species of insects are significantly different.

Future directions

This study suggests two areas for future research. First, although I have shown that the
general increase in development time and decrease in growth shown by some insects in
response to predators is usually correlated with changes in behaviour and decreased
growth rates, whether or not predators affect prey life history traits independent of
changes in prey behaviour and growth rates is still unclear. Theory predicts the existence
of both growth-dependent and growth-independent predator effects (Abrams et al 1996,
Abrams and Rowe 1996, Werner and Anholt 1993). However, most current experiments
(but see Johansson et al 2000, Skelly and Werner 1990) have not tested for growth-
independent effects. To do this, experiments must be able to tease apart the effects of the
 predator that are due to decreased foraging opportunities, from those that are not due to
decreased food levels. Future experiments could test for this response by examining
whether decreases in growth rates caused by predator presence are equivalent to
decreases in growth rates caused by food deprivation (Johansson et al 2000).

The second area is the one of intersexual differences in life history responses of
prey to predators. According to this meta-analysis, sex-specific responses are not rare
events; rather, they seem to be quite common, at least within insects. What is needed is a
theoretical framework that maps out the conditions under which sexually dimorphic
responses could be expected. Whether these types of responses occur in other taxa also
needs to be examined.
References


Table 2.1. Results for the meta-analysis of the effects of predator risk on insect age at maturity and size at maturity. (n = sample size, d = effect size, v = effect size variances, $Q_{B(df=2)}$ = heterogeneity between classes MALE, FEMALE and BOTH. * = not significant).

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Table 2.2. Summary of the anti-predator responses of the eight insect species reviewed in the meta-analysis. The first reference listed for each species is the reference for the anti-predator behaviour data and the second is for the growth rate data. See text for further details.

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Denouement: summary and future directions

This thesis examined a) the effects of predator risk and time constraints on age at and size at maturity in the mayfly *EphemereUa subvaria* and b) the effects of predator risk on growth and development of insects. Mayflies reared in the "late" light treatment matured slightly earlier than those reared in the "early" light regime but the presence of fish predators did not influence mayfly age at maturity or size at maturity. The review chapter revealed that insects that exhibited shifts in life history traits tended also to display anti-predator behaviours and decreased growth rates in the presence of predators.

Although theory predicts that predators can induce both growth-mediated and growth-independent shifts in life history traits, the results from this thesis suggest that life history responses in insects in the presence of predators are likely caused by decreases in growth rates arising from lost foraging opportunities. However, it is still too early to rule out the possible role of non-behaviourally, or non-growth mediated predator effects, as many predator-prey experiments have not tested for these effects. Future experiments need to compare the growth rates of prey reared with predators, to the growth rates of prey reared in a range of food levels. If the growth rates experienced by prey in the presence of predators are lower than those of prey reared at the same food level, but in the absence of predators, then this would suggest that predators also have non-behaviour or non-growth mediated effects on prey.

As well as separating the effects of food deprivation from the effects of predator perception, future experiments need to examine the consequences of rearing prey in close proximity to predators for extended periods of time. Traditionally the effects of predation risk on prey life history are investigated by rearing prey under continuous chemical or visual predator cues. Theoretical considerations of the effect of temporal variation in predator risk on prey behaviour (Lima and Bednekoff 1999) suggest that optimal prey behaviour in any given situation may depend on the overall pattern of risks experienced by that individual. The response of prey to predators may depend on the proportion of time that they are exposed to high versus low risk situations. If this prediction is true,
then experiments that expose prey to predators for a short amount of time may overestimate the predator effect, while those that hold predators and prey together for a lengthy period of time may underestimate the true effect. The effect of predator exposure time on prey behaviours and the consequences of these behaviours need to be tested.

Finally, the results of the meta-analysis reported in Chapter Two reveal sex-specific life history responses of prey to predators. Although Ball and Baker (1996) and Hetchel and Juliano (1997) briefly address this topic, I am not aware of any models that specify conditions under which sex-specific responses are to be expected. Given the strength of these effects in insects, it is worthwhile to investigate the frequency with which these effects occur in other organisms.

References


Appendix A. Meta-analysis data (class: m=male, f=female, b=both; Xc=control mean; SDe=control standard deviation; Ne=control sample size; Xe=predator treatment mean; SDe=predator treatment standard deviation; Ne=predator treatment sample size; dij=effect size; vij=effect size variance)

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