Competition in caddis larvae

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This thesis deals with behavioural strategies used by caddis larvae in pairwise contests and when selecting microhabitats. Effects of caddis larvae on survival and habitat selection of other insect taxa have also been studied.

The behaviours used by *Arctopsyche ladogensis* larvae fighting for nets, and *Agrypnia pagetana* larvae fighting for cases, agreed well with predictions from the sequential assessment game, which is an ESS model of animal fighting behaviour.

Establishment by net-spinning *Hydropsyche siltalai* larvae on artificial substrates was highest at intermediate densities of residents. Emigration/mortality was density independent, and it was higher at a poor site (low food availability) than at a rich site. Establishment was unaffected by site quality. Growth was density dependent because larvae in upstream positions reduced both current velocity and concentration of food particles for larvae in downstream positions.

A field experiment involved manipulations of the density of *H. siltalai* larvae and their nets in a lake outlet stream. *H. siltalai* larvae affected all abundant taxa, but the mechanism involved varied between taxa. *Rhyacophila nubila* (Trichoptera) and chironomid larvae benefited from the presence of *H. siltalai* nets. Negative effects on nymphs of the mayfly *Ephemerella ignita* were due to predation by *H. siltalai* larvae, while a combination of predation and increased emigration in response to nets depressed densities of *Simulium truncatum* blackfly larvae.

**Key words**

*Agrypnia pagetana*, *Arctopsyche ladogensis*, emigration, fighting behaviour, habitat selection, *Hydropsyche siltalai*, Hydropsychidae, immigration, predation, resource competition, sequential assessment game
List of papers

This thesis is based on the following papers, which will be referred to by their Roman numerals.


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- Summary of the thesis -

Introduction

One of the main propositions of Darwin's theory of evolution by natural selection is that only a small fraction of each generation survives to reproduce, as a consequence of competition for resources in short supply. The winners of this struggle for existence should often be individuals with the highest competitive abilities. In some situations, competitive ability could be due to physical strength, but often the success of an individual is affected by the behavioural strategies it uses. Thus, we expect that many behaviours have been shaped by natural selection. Ecologists tend to ask two kinds of questions about behaviours:

1. What selection pressures have shaped the behaviours we see?
2. How do the behaviours of individuals affect population and community properties?

A common approach to the first question is to use models, which incorporate what are thought to be the most important constraints and selection mechanisms, to predict what kinds of behaviours should be favoured under these assumptions. Observations are then compared to predictions. In this thesis I have compared predictions from a model of pairwise contests, the sequential assessment game, with observations of the behaviours of caddis larvae.

In terms of the second question, many ecologists believe that models which incorporate properties of individuals, such as behaviour, physiology and morphology, can substantially increase our understanding of patterns that emerge at the population and community levels (Schoener 1986, Persson and Diehl 1990). Good examples are models of habitat selection that are used to predict the distribution of individuals between patches of different quality (e.g. Fretwell and Lucas 1970, Gilliam and Fraser 1988). These models are based on the assumption that individuals select habitat so as to maximize their fitness,
and properties of individuals, such as competitive ability, hunger state and vulnerability to predators have been incorporated (see review in Milinski and Parker 1991). I have studied the behavioural strategies used by net-spinning caddis larvae when selecting habitat and related their behaviours to models of habitat selection. I have also studied how the behaviours of net-spinning caddis larvae affect the survival and habitat selection of other lotic species.

Models of pairwise contests
What is the best behavioural strategy an individual can use in pairwise contests? In many situations the answer depends on what strategies other competitors use, because the pay off for different strategies is dependent on their frequency in the population. The strategy favoured by selection in this situation is called an evolutionary stable strategy or ESS (Maynard Smith and Price 1973). A strategy is an ESS if, when fixed in a population, it cannot be invaded by a rare mutant strategy. Early ESS models of pairwise contests such as the hawk and dove game, and the war of attrition, were based on obviously conspicuously unrealistic assumptions about how real animals behave during fights (Maynard Smith and Parker 1976, Parker and Rubenstein 1981, Hammerstein and Parker 1982). Nevertheless they were quite successful in predicting aspects of real contests (Riechert 1979, Oronen 1984, Austad 1983, Crespi 1986). This success seems to be due to the fact that many predictions about pairwise contests from ESS models are robust in the sense that they are insensitive to assumptions about the competitive mechanism involved. Thus, most models predict that fights should be more costly if the resource value is increased.

The first ESS model that included a detailed representation of behaviours performed during real contests was the sequential assessment game (Enquist and Leimar 1983). In this model, it was recognized that assessment of relative fighting ability is a major activity during fights. The basic idea is that information about relative fighting ability is gained by repeating a potentially dangerous contest behaviour, and decisions about whether to give up or to continue fighting are based on this information. The basic prediction is that fights should be longest when the opponents are equally sized. This is because it is more difficult to detect a small difference. The most important variable affecting the fighting strategy is the value of the contested resource relative to contest
cost. When the resource value is low relative to contest cost, role asymmetries should be used to settle contests (Davies 1978, Hammerstein 1981, Leimar and Enquist 1984). Usually, this means that owners are not challenged or that owners are more persistent and win most of the fights. At intermediate resource values, we expect to see longer fights in which the contestants try to assess their relative fighting ability (Parker 1974, Maynard Smith and Parker 1976, Enquist and Leimar 1983, 1987). When the resource value is so high that a major part of the expected reproductive success is at stake, we expect fatal fights, i.e. fights do not end until one of the contestants is injured or killed (Grafen 1987, Enquist and Leimar 1990).

Models of habitat selection
Often the fitness that an individual can attain when staying in a habitat, depends on both the inherent quality of the habitat and the density of competitors. How should an individual select a habitat in this situation? The answer to this question is, again, that it depends on what the other individuals do. The fundamental model of density dependent habitat selection is the ideal free distribution model by Fretwell and Lucas (1970). They assumed that individuals can move between habitats freely, without cost, and that fitness of individuals within a habitat decreases with increasing density. If individuals try to maximize their fitness, a stable distribution will be reached when density matches habitat quality so that fitness is equal in all habitats. This solution is essentially an ESS because no individual can do better by changing strategy. Other important models are the ideal despotic distribution model and the ideal preemptive distribution model (Fretwell and Lucas 1970, Fretwell 1972, Pulliam and Danielson 1991). In these models, it is assumed that individuals are constrained in their habitat selection by the activities of dominant (usually territorial) individuals. The resulting distribution differs from that of the ideal free distribution in that mean fitness and density will be highest in high quality patches and dominant individuals will have higher fitness than subordinate ones.

If risk of predation is spatially variable, it can also affect the distribution of individuals between habitats. In this situation we expect individuals to balance the risk of predation against the benefit of obtaining food when selecting a habitat (Gilliam and Fraser 1988, Abrahams and Dill 1989).
For many species, the assumption of no search cost is obviously unrealistic. Models of optimal patch use have shown that an animal should leave a site only if the expected gain from moving is larger than the cost of moving (Charnov 1976, Janetos 1982). This means that if the search cost is high, then individuals will remain in inferior habitats in spite of a low potential fitness, and it is expected that mean fitness should vary substantially between habitats. In fact, it has been suggested that the variation in mean fitness between habitats could be used as measure of search cost (Morris 1987).

An alternative way of examining how behavioural decisions affect distribution patterns, is to measure how immigration and emigration rates depend on patch quality (food and predators) and density of competitors, and use colonization models to examine how distribution patterns are affected. The colonization models used in this thesis have the form

\[ \frac{dN}{dt} = I(N,q) - E(N,q) \]

where \( \frac{dN}{dt} \) is the rate of change of the numbers of individuals within the patch, \( I(N,q) \) is the number of individuals arriving in the patch, and \( E(N,q) \) is the number of individuals lost from the patch as functions of density within the patch \( (N) \) and quality of the patch \( (q) \).

Questions addressed

Predictions generated from the sequential assessment game were tested in papers (I) and (II). In the first paper, I examined how factors such as size differences, ownership and differences in information about the value of the contested resource affected the duration and outcome of contests over nets in Arctopsyche ladogensis larvae. The value of the nets in terms of the amount of silk invested and food availability were varied, and it was assumed that only the owner was aware of the true value of the net and could adjust its behaviour accordingly. In paper (II), the emphasis was on a comparison of the fighting behaviours in two different populations of cased Agrypnia pagetana caddis larvae.

The basic assumptions in models of density dependent habitat selection are that fitness is density dependent and that individuals are somehow able to evaluate both density of competitors and habitat
quality, and use this information to select a habitat so that fitness is maximized. In papers (III) and (IV), these assumptions were examined for the net-spinning caddis larvae *Hydropsyche siltalai*. Paper (III) examined the competitive mechanism that caused growth (and presumably also fitness) to be density dependent, while paper (IV) examined how establishment and growth were affected by density, food availability, current velocity and larval size.

Hydropsychid larvae are not only aggressive against conspecifics. All invertebrates that are of equal or smaller size are attacked. However, the effects of hydropsychid larvae are not only negative. Some insect taxa are favoured by the presence of hydropsychid nets (Diamond 1986). In paper (V), I examined how *H. siltalai* larvae and their nets affected the distribution of other insect larvae.

**Study organisms**

Larvae of the caddisfly *Hydropsyche siltalai* Döhler (Hydropsychidae) are found in small and medium sized streams, and they are particularly abundant in lake outlet streams. In northern Sweden, *H. siltalai* is usually univoltine, and winged adults are found from July to September. Larvae of *Arctopsyche ladogensis* (Kolenati) (Hydropsychidae) are found in medium sized streams. This species is usually univoltine, and adults are found in June. The larvae of these two species feed on particles captured from the passing current with silken nets. The most fundamental habitat requirements are physical structures that can be used as support for the nets, suitable current velocity, and food particles in the water (Richardson and Mackay 1991). Hydropsychid larvae are very aggressive, and fights over catch nets are common (Jansson and Vuoristo 1979).

The caddisfly *Agrypnia pagetana* Curtis (Phryganeidae) is univoltine, and adults are found in June in northern Sweden. The larvae of this species live in the littoral zone of lakes, and they construct cases from small pieces of plants or hollow stems. They are predacious and a variety of invertebrates, including conspecifics, comprise their diet.
Summary of papers I-V

(I) Fighting and assessment in the net-spinning caddis larva *Arctopsyche ladogensis*: a test of the sequential assessment game

In this paper, the behaviours used by *Arctopsyche ladogensis* larvae fighting for nets were examined to test predictions from the sequential assessment game. The fighting behaviours used by this species agreed well with predictions regarding the effects of relative size and ownership status. Contests were usually won by the larger opponent and both contest durations and the standard deviations of contest duration were largest when opponents were equally sized. Owners were more persistent than intruders and they won more fights than intruders. Contests, where both opponents regarded themselves as owners, were longer than ordinary owner-intruder contests. Predictions regarding the effects of the value of the contested resource were not upheld. Neither the outcome nor the duration of contests were affected by variation in the amount of silk invested or the amount of food obtained in the net.

(II) Effects of ownership status, weight asymmetry, and case fit on the outcome of case contests in two populations of *Agrypnia pagetana* (Trichoptera: Phryganeidae) larvae

In this paper, behaviours expressed during contests for cases were examined in a sparse and a dense population of the cased caddis larva, *Agrypnia pagetana*. Most contests were very short and won by the case owner, suggesting that the value of cases was low relative to contest costs. The fighting strategies differed between the two populations: Owners were more successful in the sparse population, but contest duration did not differ between the two populations. Relative size was most important in the dense population, and here the larger contestant usually won. However, when the intruders were much larger than the owners, cases were seldom taken over, and this was because the cases were too small for the large intruder.
(III) Asymmetric resource competition in a filter-feeding stream insect (*Hydropsyche siltalai*; Trichoptera)

An interesting property of resource competition in lotic net-spinning caddis larvae is that it is unidirectional. Larvae in upstream positions can affect food availability for those in downstream positions, but not the reverse. In this paper, I examined the importance of resource competition in dense aggregations of *H. siltalai* larvae. Marked larvae were implanted in the upstream or downstream end of dense aggregations and recovered after 17 days. Growth was higher in the upstream end of aggregations, and more marked larvae were recovered from this position. Naturally colonizing large *H. siltalai* larvae were more abundant in the downstream position, while the abundance of small first and second instar *Hydropsyche angustipennis* and/or *Hydropsyche pellucidula* larvae were highest in the upstream end of aggregations. Current velocity as well as density of drifting prey were lower behind aggregations. The food delivery rate, calculated from these two measurements, was about 50% lower behind aggregations.

(IV) Effects of density and food availability on habitat selection in a net-spinning caddis larva, *Hydropsyche siltalai*

The aim of this study was to examine how establishment and growth of *H. siltalai* larvae were affected by density of competitors, habitat quality and individual size. At two sites, differing in food availability, I released marked IV and V instar larvae on artificial substrates with different densities of residents. After one day, establishment was highest at intermediate densities, but it did not differ between the two sites. Growth of larvae, measured after ten days, decreased with increasing density and it was highest at the site with rich food supply. The number of larvae that emigrated or died was not affected by density, but peaked at the low food site.

In a laboratory study, the behaviours expressed during establishment were examined in detail. For large (V instar) larvae, the establishment rate increased with density of competitors, while establishment of smaller (IV instar) larvae was high irrespective of density. The mechanism behind this pattern was complex. The physical structure of the moss habitat seemed to be suitable for small but not for large larvae.
At high densities, large larvae sometimes found abandoned retreats and they could take over occupied retreats, while small larvae never took over abandoned retreats and they suffered from cannibalism from large larvae.

A simple colonization model was used to examine how the behaviours used by *H. siltalai* larvae could affect the distribution of individuals between patches of different quality. I concluded that the distributions should tend to be aggregated in poor areas with low population density, and more even in rich areas. An ideal free distribution cannot be reached for two reasons. First, emigration/mortality was density-independent and establishment was independent of patch quality. Thus, no feedback mechanism between density and fitness was found. Second, search cost is likely to be very high in *H. siltalai* larvae.

(V) Interactions in a lake outlet stream community: Direct and indirect effects of net-spinning caddis larvae

In this study, I examined the effects of *H. siltalai* larvae and their nets on the local distribution of other lotic insects. Artificial substrates that held either high densities of *H. siltalai* larvae and their nets, nets only or that were devoid of both larvae and nets, were exposed for 17 days to colonizing insects. Nymphs of the mayfly *Ephemerella ignita* were negatively affected by the presence of *H. siltalai* larvae, while larvae of the blackfly *Simulium truncatum*, were negatively affected by the nets. Colonization by *Rhyacophila nubila* caddis larvae and chironomid larvae increased due to the nets of *H. siltalai* larvae. Laboratory experiments showed that predation was the most important mechanism whereby *H. siltalai* larvae affected *E. ignita* nymphs and *S. truncatum* larvae. However, the presence of *H. siltalai* larvae did not influence the emigration rate of the two species. The presence of *H. siltalai* nets increased both immigration and emigration rates for *S. truncatum* larvae.

A colonization model and the results from the laboratory experiment were used to derive quantitative predictions of the effects of *H. siltalai* larvae and nets in the field. Predicted effects agreed fairly well with observed field effects in *E. ignita* nymphs. In *S. truncatum* larvae, on the other hand, significant differences between predicted effects and field effects were found. I hypothesized that in addition to the mechanisms
observed in the laboratory, indirect effects mediated by other species also affected the density of *S. truncatum* larvae.

**Discussion**

**Pairwise contests**

In general, I found good agreement between the predictions of the sequential assessment game and the fighting behaviours shown by *A. ladogensis* and *A. pagetana* larvae. Other explicit tests of this model have also found confirmed the predictions (e.g. Enquist et al 1990), and there are many earlier studies that support these findings (see reviews in Enquist and Leimar 1983, 1987, Leimar and Enquist 1984). In *A. ladogensis*, all predictions regarding the effects of relative size and ownership status were confirmed, but contrary to the predictions, there were no effects of variation in the value of nets in terms of amount of silk or food availability. It is difficult to interpret this result as it is not known how much the value of nets varied in the experiments. The value of a resource should be defined as the difference in expected future reproductive success between the two alternatives of winning and losing the fight (Grafen 1987). This means that the value of a contested net is determined not only by its quality, but also by costs incurred by the losing individual when trying to obtain another net. Thus, it is possible that the differences in the quality of the nets, produced in the experiment, actually made up a very small fraction of the actual value of nets.

When comparing the two populations of *A. pagetana*, we found that ownership was more important in the sparse population. Because ownership should be used to settle contests when the resource value is low relative to contest cost (Leimar and Enquist 1984), this result suggests that cases were of lower value (or that contest costs were higher) in this population. However, no firm conclusion could be reached, as it was not possible to make accurate estimates of the value of cases in the two populations.

When a model is tested it is important to examine not only how the predictions agree with the data, but also whether the model is based on realistic assumptions about how animals behave. Do the animals really base their decisions about giving up or continuing, on information about relative fighting ability that is obtained during the fight? Alternative
assumptions are that they determine, in advance, how long they are willing to fight, or that differences in motivation rather than fighting ability are assessed (Hansen 1986, Enquist 1985). The prediction that fights should be longest when the opponents are equal is central, and it should not be fulfilled if animals fight for a predetermined time, or if they assess differences in motivation. This prediction was confirmed in *A. ladogensis* larvae but not in *A. pagetana* larvae, suggesting that something else may occur in fights over cases in this species.

**Habitat selection**

A fundamental assumption made in the ideal free distribution model is that fitness should be density dependent (Fretwell 1972). This seemed to be true in *H. siltalai* larvae. Growth rate (and presumably also fitness) decreased with increasing density. Other density dependent mechanisms that affect fitness include cannibalism and interference competition for nets. Another important assumption is that immigration and/or emigration rates should depend on density and patch quality. Establishment by *H. siltalai* larvae was affected by density, but not by habitat quality. The density response was dome shaped, i.e. establishment rate increased with density at low densities and then declined again at high densities. Thus, it is clear that facilitating mechanisms were more important than competitive ones at low densities. Emigration/mortality was affected by habitat quality, but not by density. Taken together, these results suggest that density cannot, even in theory, be regulated so that fitness is equal in patches of different quality. The reason is that density only affects establishment rate and patch quality only affects emigration/mortality rate. A third assumption in the ideal free distribution model is that there is no search cost. This is certainly not true in hydropsychid larvae. They have to make an expensive investment in a net before an accurate assessment of patch quality can be made. Moreover, small larvae experienced substantial mortality when searching for a net-spinning site in high density patches.

**Effects of *H. siltalai* larvae on other taxa**

*H. siltalai* larvae seem to be a key species in the examined lake outlet stream community, because all abundant species were affected. A variety of mechanisms were responsible for these effects. *R. nubila* and
chironomid larvae increased their local density in response to the nets of *H. siltalai* larvae. Similar positive effects have been found by Diamond (1986). Direct mortality was the most important mechanism affecting *E. ignita* nymphs and *S. truncatum* larvae. Predation risk should affect habitat selection (e.g. Gilliam and Fraser 1988, Abrahams and Dill 1989). However, neither of the two species suffering high mortality from *H. siltalai* larvae, increased their emigration rate in response to these predators. It is possible that they lacked the capabilities necessary to assess the risk of predation. The *S. truncatum* blackfly larvae increased their emigration from net mats probably because the nets interfered with the blackflies' feeding activities (cf. Hart 1986).

Since the densities of hydropsychid larvae in lake outlet streams are regulated primarily by the concentration of lake derived zooplankton in the water (Petersen 1987), this study suggests that hydropsychid larvae constitute an important link between the lake ecosystem and the lake outlet stream community (cf. Perry and Sheldon 1986).

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