

Intraguild predation, cannibalism, and microhabitat use in *Calopteryx virgo* and *Somatochlora metallica* larvae: a laboratory experiment

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Abstract

Intraguild predation (IGP) and cannibalism among co-occurring lotic odonate species was studied in Central Finland. A laboratory experiment was performed to assess the microhabitat use and cannibalism between intermediate and late instars of *Calopteryx virgo* larvae and predation by larger *Somatochlora metallica* larvae on the intermediate *C. virgo* instars. The experiment was run in small running-water aquaria where the larvae were able to divide their mutual habitat vertically by clinging onto artificial perches or crawling on the bottom. Life span of the small *C. virgo* larvae and attack rate on them were compared between the cannibalism and IGP treatments. The effect of predation on the activity, habitat use and spatial distribution of the small *C. virgo* larvae was examined. The IGP rate was 36%. The prey larvae spent the most of their time on the perches, whereas the *S. metallica* preferred the substrate. The large *C. virgo* larvae did not cannibalise smaller conspecifics. The presence of a predator (*S. metallica*) had no effect on the habitat use or activity of the prey (*C. virgo*) larvae. Habitat use differed more between those species than between conspecifics of different size classes of *C. virgo*. The spatial distribution between *S. metallica* and *C. virgo* showed a completely random pattern, whereas the two size classes of *C. virgo* aggregated in the vegetation. Absence of cannibalism and behavioural observations indicate that *C. virgo* may have a low tendency for intraspecific aggressions.

Introduction

Intraguild predation (IGP) is a complex combination of predation and competition occurring in a guild of species which compete for mutual resources (review by Polis et al. 1989). Polis et al. (1989) use the term 'guild' broadly to include all taxa in a community that use similar resources and compete for them. In this study, the term is used to define coexisting lotic communities of dragonfly

(Odonata: Anisoptera) and damselfly (Odonata: Zygoptera) larvae. According to Polis et al. (1989, p. 305) Relative body size and degree of trophic specialization are the two most important factors influencing the frequency and direction of IGP. In most cases IGP occurs in communities with size-structured populations by generalist predators, and the predators are usually larger than their intraguild prey. Often such generalist predators also prey on smaller conspecifics (Polis et al.

1989), and thus both intraguild predation and cannibalism may occur.

Larval odonates (Odonata) are generalist predators with size-structured populations, and they often are the dominant invertebrate predators in freshwater littoral zones (Johnson 1991). They live among vegetation or on the substrate (Corbet 1980) and may under sufficient densities compete for space and act aggressively towards other larvae (Baker 1981a; Baker and Dixon 1986; Suutari et al. 2004). When the size difference between the encountering larvae increases, the probability of intraguild predation increases (Wissinger 1992). Especially in the slow-lifestyle species, where larval development takes several years, many distinct size classes are simultaneously present. Some direct evidence for IGP has been found in larval odonate diets (Thompson 1978a; Baker and Clifford 1981; Blois 1985), and IGP or its probable effects have been observed in field experiments (Crowley et al. 1987a; Fincke 1994). Both IGP (e.g. Robinson and Wellborn 1987; Wissinger and McGrady 1993) and cannibalism (e.g. van Buskirk 1989; Hopper et al. 1996) has been reported in odonate larvae.

The key factors that influence intraguild predation and cannibalism in odonate larvae appear to be larval density, availability of alternative food and habitat structure. Increasing larval density usually increases the level of larval encounters and thus increases the opportunity for predation between larvae (Benke 1978; Johnson et al. 1985; McPeck and Crowley 1987; Wissinger 1989; Anholt 1990). Low availability of alternative food forces the larvae to move around more when searching for food, which increases the probability of encounters and thus increases predation between larvae (Anholt 1990; Johansson 1993a). Increasing habitat complexity reduces interference between larvae by either providing the animals with more space, or allowing them to use a wider array of habitats and avoid IGP by habitat partitioning (Gribbin and Thompson 1990; Anholt 1994; Suutari et al. 2004).

Habitat shift is a possible short-term response to intraguild predation (Polis et al. 1989; Suutari et al. 2004). Interspecific interference influences larval habitat use (Suhling 1996; Suutari et al. 2004) and larvae have been reported to exclude conspecifics from feeding areas through aggressive interactions (Baker 1981a). Prey can also avoid predation by decreasing their activity. Decreasing

activity reduces the risk of being detected by a predator or encountering one (Sih 1987). Decreased activity of odonate larvae has been reported as a response to both non-odonate (Heads 1985; Pierce 1988) and odonate (Johansson 1993a and 1993b) predation.

Our aim was to study the small-scale habitat use, IGP, and cannibalism in lotic odonate communities. So far, IGP and cannibalism and their effects on larval odonates have mostly been studied in standing water communities. However, Suhling (1996) studied the interspecific competition and habitat selection by a running water dragonfly species, *Onychogomphus uncatatus*. In our laboratory experiment the larvae were provided with a three-dimensional environment which consisted of the two major components in a larval odonate habitat: the substrate and the vegetation. We studied the mortality, activity and habitat use of small *Calopteryx virgo* (L.) (Zygoptera) larvae on their own, and under the presence of larger conspecific or *Somatochlora metallica* (Van der Linden) (Anisoptera) predators. Our main questions were: (1) Does the predation rate on small *C. virgo* larvae differ between IGP and cannibalism, and (2) How do the small *C. virgo* larvae respond to IGP and cannibalism? We expected cannibalism to be more frequent than IGP, resulting from species-specific habitat use and a higher encounter rate between conspecifics. We anticipated the prey larvae to respond to intraguild predation by decreasing their activity, changing their habitat use, or actively escaping their predators.

Materials and methods

Study area and species

We ran the experiment in June 1998 in the Konnevesi Research Station in Central Finland (62°37' N, 26°20' E). We collected the larvae used in the experiment in the stream Myllypuro (62°34' N, 25°52' E) 24 km west of the station. Myllypuro is a second-order forest stream about 2 km long, running between two lakes (stream classification by Vannote et al. 1980). In the study section at the halfway between the lakes the stream is approximately 2–3 m wide and surrounded by cultivated land. In this stream both *C. virgo* and *S. metallica* were abundant, and we did not find

any larvae of other odonate species during the collection.

Calopteryx virgo and *S. metallica* are the most common and abundant lotic odonate species in Central Finland and they frequently co-occur in the vegetated zone of rivers (Valle 1945; Bagge 1983; Ilmonen 1999). Gomphidae spp. larvae, mostly represented by *Onychogomphus forcipatus* (L.) and *Ophiogomphus cecilia* (Fourcroy), are also abundant but usually use somewhat different habitats than *C. virgo* and *S. metallica* (Ilmonen 1999). Gomphids prefer sand and gravel substrate and moderate to high current velocity in the mid-section and current-exposed areas of the stream, whereas *S. metallica* and *C. virgo* co-occur in the slow flowing littoral zone, usually within vegetation.

In the vegetated littoral zone of a stream, *C. virgo* larvae cling to the vegetation or other suitable perches, whereas *S. metallica* larvae are more commonly bottom-dwellers crawling on or burrowing in the substrate (Valle 1945; Bagge 1983). Therefore the species use different microhabitats in their common environment. Both species are semi- or partivoltine and various larval size classes can be found at any time, and thus the opportunity for intraguild predation and cannibalism is always present. *Somatochlora metallica* larvae are more robust than *C. virgo* larvae, which enhances their potential as intraguild predators (Wissinger 1992).

Laboratory experiment

We used plastic running-water aquaria with opaque walls in the experiment. Water for the aquaria was continuously pumped from the Lake Konnevesi next to the research station. Water temperature during the experiment was 8.8–11.6 °C. Water was pumped into an open 50-l plastic container where it was aerated to ensure a sufficient oxygen level for the larvae. From the container water drained through 12 plastic hoses (diameter 4 mm) to the 12 aquaria 1 m below the container. Water entered the aquaria through T-shaped plugs placed near the bottom, creating a symmetric, turbulent slow (about 10 cm s⁻¹ near the sides and almost standing in the middle) flow in the square aquaria (Figure 1). From the opposite side of the aquaria overflow water exited through plastic hoses (diameter 8 mm) 9 cm above the bottom.

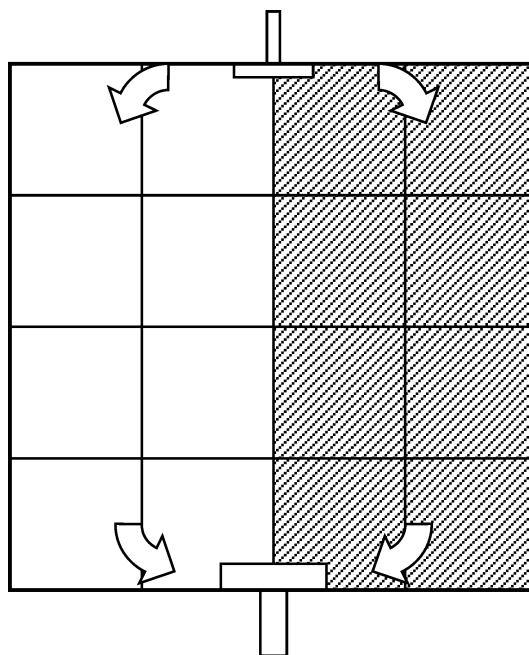


Figure 1. The experimental aquarium. The shaded area represents the vegetated side, where twelve perches were arranged in a regular pattern on the sand substrate. The other side was only covered with fine sand. The squares represent the grid marked on the sides of the aquarium. The arrows indicate where the water entered and exited the aquarium.

We arranged the aquaria in two rows with six units in each row. Each experimental aquarium was 16×16 cm wide with a water volume of 2.5 l. We marked a 4×4 cm grid on the sides of the aquarium (Figure 1). On the bottom there was a 1-cm layer of fine sand and twelve 7 cm long perches were attached in a regular pattern on one half of the aquarium, hereafter referred to as the vegetation. The sand and the perches were to provide the larvae with the possibility to burrow into the substrate or to cling onto the perches. We used nine of the aquaria in the experiment, and the additional three for acclimatising predators before the experiment. The three treatments were (1) one small *C. virgo* larva alone (control for mortality, habitat use and activity), (2) one small *C. virgo* larva with one large *C. virgo* larva (cannibalism) and (3) one small *C. virgo* larva with one large *S. metallica* larva (IGP). The larvae used in the experiment represented the natural size distribution in the river Myllypuro during the time we ran the experiments. The small *C. virgo* larvae represented the intermediate and large larvae the latest

instars (Table 1). We used the largest *C. virgo* and *S. metallica* larvae found as predators. We assigned the treatments randomly in the nine experimental aquaria, and ran a set of three replicates per treatment four times, so the total amount of replicates per treatment was 12.

We collected the larvae used in the experiment with a dip net between 8.00 and 11.00 a.m. from the river Myllypuro and brought them to the laboratory by 12.00 h. We then examined the small *C. virgo* larvae to see if any legs or caudal gills were missing and measured their length excluding caudal gills. We recorded injuries to the larvae, and placed them into the aquaria. We kept the larvae used as predators in separate aquaria, and starved all larvae for 24 h to ensure an equal hunger level. The light–dark regime was 18:6, and day ranged from 4.00 a.m. to 22.00 p.m. The room was lit with fluorescent tubes during the day and a red darkroom light during the night.

The experiment began at 12.00 h on the second day, when we added the predators into the middle section of each aquarium assigned for predation treatment. We then surveyed each aquarium for 1 min to record the position and activity of the larvae. We determined their habitat use by two factors: (1) horizontal habitat use (among the vegetation or not) and (2) vertical habitat use (on the substrate or on a perch). We recorded a direct predator–prey encounter if the larvae were within the distance of a leg or antenna length from each other or if they clearly reacted to the presence of the other larva in any way (e.g. orientation towards prey, attack, escape, threatening postures). We repeated the 1-min survey for all nine aquaria six times, respectively, and the surveillance period lasted for about one h. We performed five surveillance periods at 12.00–13.00, 18.00–19.00, 23.00–0.00 (night), 7.00–8.00 and 12.00–13.00 h and the experiment lasted for 25 h. After the experiment, we kept the larvae in the aquaria for

the proceeding 23 h until the next run began. The larvae were not fed with alternative prey during the experiment, and we used each larva only once in the experiment.

We rejected one replicate in the IGP treatment because the prey larva moulted during the experiment, and one replicate in the cannibalism treatment because the labium of the predator larva was missing. It looked like the labium had been missing for some time. For analyses of encounter rate as well as total activity, vegetation use and perch use, we used only data from cases where no predation occurred.

We compared the means of proportional predator–prey size difference between predation treatments and analysed them by two-sample *t*-test, and we used Fisher’s exact test for analysing the attack rate (number of eaten + injured larvae out of all replicates per treatment) on the small *C. virgo* larvae in the predation treatments. For other analyses, we used Mann–Whitney *U*-test for two independent samples when comparing differences between the two predation treatments, and Kruskal–Wallis test for comparisons between all the treatments.

We determined the life span of the prey larvae by summing up how many surveillance periods the larvae had survived through. Thus, the life span of a given larva was one, if the larva had been eaten between the first and the second period, and two, if the larva had been eaten between the second and the third period, etc. No larvae were eaten during the surveillance periods. We compared the life span ranks of the prey larvae between all treatments and between the predation treatments. We compared the mean number of observed predator–prey encounters between predation treatments. We determined the total activity, vegetation use and perch use of the larvae by summing up how many times during the 30 observations in each replicate the larva was recorded as active,

Table 1. Length, head width and labium width (mm) of the larvae used in the experiment.

Larva		Length		Head width		Labium width		N
		Mean	SD	Mean	SD	Mean	SD	
Small	<i>C. virgo</i>	10.4	2.1	2.1	0.3	1.8	0.3	34
Large	<i>C. virgo</i>	20.8	2.1	3.8	0.1	3.0	0.2	11
Large	<i>S. metallica</i>	17.6	3.1	5.1	0.8	4.5	0.6	11

Small *C. virgo* larvae were used as prey and large larvae as predators.

among the vegetation or on the perch, respectively. We used pairwise scatter plots to examine total activity, vegetation use and perch use of predator and prey larva in each replicate, and compared the deviation from a 1:1 ratio, where both predator and prey larva would behave similarly, between predation treatments.

After the experiment, we preserved the larvae in 75% ethanol. We examined the small larvae for new injuries and measured all the larvae. Injuries that had appeared during the experiment were interpreted as attacks (Baker and Dixon 1986). We measured the total length (*C. virgo* excluding caudal gills, *S. metallica* to the tip of the abdominal spines), head width and labium width for each larva. For the small larvae that had been killed and eaten during the experiment, we used the body length measured before the experiment and estimated their head width and labium width based on the data from fully measured larvae of the same species. We calculated the proportional size difference between the labium (gape) width (g) of the large larva and the head width (h) of the small larva ($(g-h)/g$) to estimate the relative likelihood of predation for each predator–prey pair. Probability of predation among odonate larvae increases when the size difference increases (Wissinger 1992), and we used the $(g-h)/g$ values to estimate the predation risk for each pair and to compare the predation risk between treatments. According to Wissinger (1992), intraguild predation is likely when $(g-h)/g > 0.20$. Predation rates increase as a function of the proportional size differences, and predation is always likely when $(g-h)/g > 0.80$. The proportional size difference between predator labium width (g) and prey head width (h) ranged between 0.19 and 0.57 in the cannibalism (small and large *C. virgo*) treatment, and between 0.38 and 0.69 in the IGP (small *C. virgo* and large *S. metallica*) treatment. Proportional size difference was greater in the IGP treatment (mean = 0.50, SD = 0.09) than in the cannibalism treatment (mean = 0.37, SD = 0.12) (t -test, $t = -3.07$ df = 20, $p = 0.006$).

Statistical analyses

We calculated the distance between predator and prey larva in the 4×4 squares grid during each observation from the position data using one

square as the unit of distance, and compared the mean distance between predator and prey larva between predation treatments. We also counted the frequencies of every possible distance in the grid and the observed distances in both treatments, and transformed the numerical frequencies of the expected and observed distances into proportional frequencies. We then plotted the cumulative curves of the expected distances and observed distances in both treatments together to see if the larvae were spacing out or showing a clumped distribution pattern.

Results

The mean survival of the small larvae was 100% in the cannibalism treatment and in the control treatment, and 64% (SD = 15%) (7 out of 11) in the IGP treatment. Four prey larvae were eaten in the IGP treatment, two after the first surveillance period, one after the third period and one after the fourth period. Life span of the prey larvae was the lowest in the IGP treatment both when compared to the other two treatments (Kruskal–Wallis-test, $H = 9.20$, df = 2, $p = 0.010$) and when compared to the cannibalism treatment (Mann–Whitney U -test, $U = 38.5$, $n_1 = n_2 = 11$, $p = 0.032$). Attack rate was higher in the IGP treatment (7 out of 11) than in the cannibalism treatment (2 out of 11), the difference being nearly statistically significant (Fisher's exact test, $p = 0.08$). Observed predator–prey encounter rate was higher in the cannibalism treatment (69 observed encounters/330 observations) than in the IGP treatment (7 observed encounters/210 observations) (Mann–Whitney U -test, $U = 16.5$, $n_1 = 11$, $n_2 = 7$, $p = 0.041$).

Total activity of the small *C. virgo* larvae was not significantly different between treatments (Kruskal–Wallis-test, $H = 2.35$, df = 2, $p = 0.31$). Neither total use of vegetation (Kruskal–Wallis-test, $H = 2.85$, df = 2, $p = 0.24$) nor perches (Kruskal–Wallis-test, $H = 1.45$, df = 2, $p = 0.48$) of the small *C. virgo* larvae showed any difference between treatments. In the pairwise predator–prey plots, predator larvae showed a low level of activity, whereas prey larvae showed intermediate or low activity (Figure 2a). Deviation from a 1:1 ratio in the activity between predator and prey larva showed no significant difference between the treatments (Mann–Whitney U -test, $U = 20.5$,

$n_1 = 11$, $n_2 = 7$, $p = 0.10$). All the larvae mostly used the vegetation (Figure 2b), but only small and large *C. virgo* larvae used the perches frequently; a large *S. metallica* larva was only seen twice out of 330 observations trying to climb a perch (Figure 2c). Deviation from a 1:1 ratio in total use of vegetation between small and large larvae was greater in the IGP treatment than in the cannibalism treatment (Mann–Whitney *U*-test, $U = 9.5$, $n_1 = 11$, $n_2 = 7$, $p = 0.008$), as was the case in total use of perches (Mann–Whitney *U*-test, $U = 5$, $n_1 = 11$, $n_2 = 7$, $p = 0.002$).

The distance (unit = one cell in the grid) of predator and prey larva was longer in the IGP treatment (mean = 1.87, SD = 0.50) than in the cannibalism treatment (mean = 1.32, SD = 0.37) (Mann–Whitney *U*-test, $U = 14$, $n_1 = 11$, $n_2 = 7$, $p = 0.026$). The comparison of observed and expected frequencies of distances revealed that this was not caused by antipredatory behaviour; larvae showed a clumped distribution in the cannibalism treatment, whereas in the IGP treatment they were randomly distributed (Figure 3). The observed distribution of distances in the IGP treatment was almost identical to that expected.

Discussion

In our laboratory experiment *S. metallica* larvae occasionally preyed on small *C. virgo* larvae, but the species used different microhabitats which resulted in a low encounter rate and the predation rate was quite low. *Somatochlora metallica* larvae did not climb onto the perches, where the small *C. virgo* larvae spent most of their time. Thus the perches provided the small *C. virgo* larvae with a spatial refuge in the sense used in Peckarsky's (1982) review on predation in aquatic insects. The different microhabitat use of the two species studied here is apparently more a species-specific feature that has developed over the course of evolution, rather than a short-term response to intraguild predation (Polis et al. 1989). Predation risk may have influenced the differentiation in the habitat use of the species, or decreased predation risk may have come as a by-product of habitat differentiation caused by some other evolutionary forces.

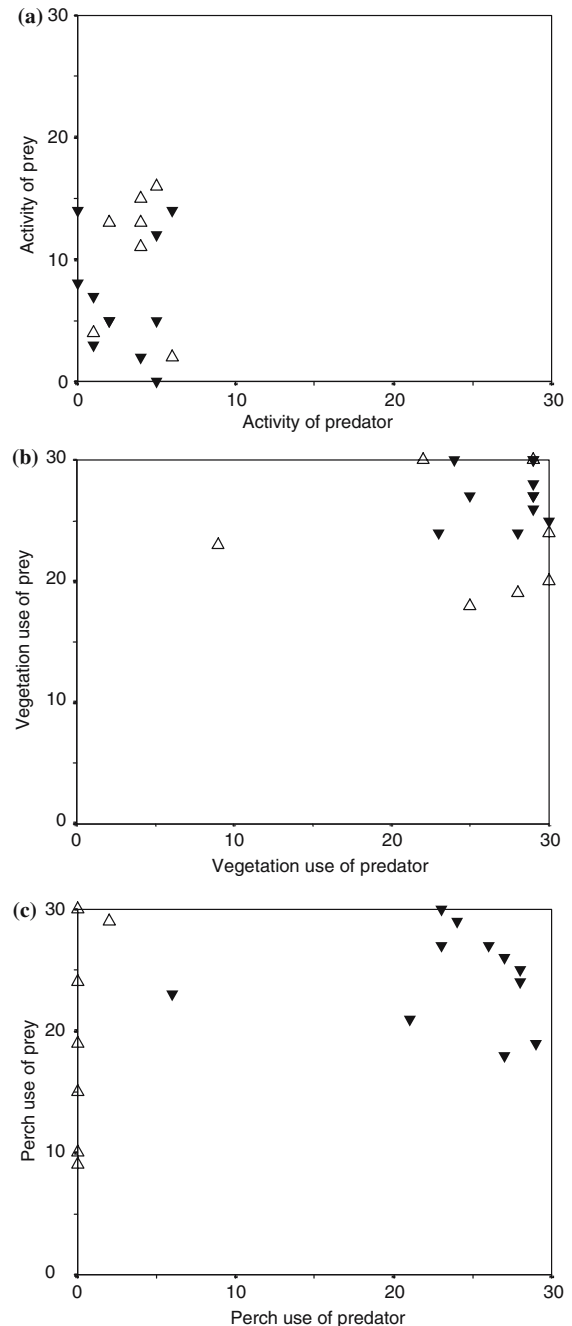


Figure 2. Pairwise scatter plot of total (a) activity, (b) vegetation use and (c) perch use for each predator–prey trial. The values are totals for each predator and prey larva recorded active, among vegetation or on a perch out of 30 observations. The symbols are: solid triangle = cannibalism treatment (small and large *C. virgo*, $n = 11$), open triangle = IGP treatment (small *C. virgo* and large *S. metallica*, $n = 7$).

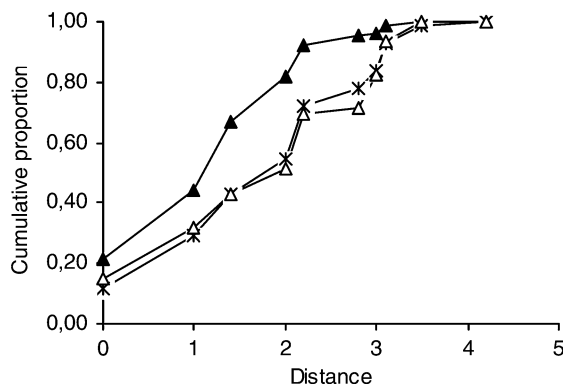


Figure 3. Cumulative curve of the expected and observed frequencies of possible larval distances in a 4×4 grid between predator and prey. The symbols are: asterisk = expected curve ($n = 136$), solid triangle = cannibalism treatment (small and large *C. virgo*, $n = 330$) and open triangle = IGP treatment (small *C. virgo* and large *S. metallica*, $n = 210$).

The encounter rate was higher between conspecifics, as we predicted, but this did not show in the predation or attack rates. Instead, interspecific predation was more common than intraspecific predation. Large *C. virgo* larvae did not kill any smaller conspecifics though they were frequently in touch with each other, whereas large *S. metallica* larvae encountered the small *C. virgo* larvae scarcely but attacked them frequently. The reason for heavier interspecific rather than intraspecific predation could be that the proportional size difference between predator and prey was greater in the interspecific rather than in the intraspecific treatment, and that the larvae used as prey might have been too big for the large *C. virgo* larvae to prey on. An alternative explanation would be that *C. virgo* larvae tend to avoid aggressive interactions when encountering a conspecific.

The proportional size difference between predator and prey was within the range (see Wissinger 1992) for intraguild predation to be likely in both treatments. The size difference was smaller in the intraspecific treatment, and in one case with conspecific predator and prey, the value was slightly below the range (0.19). Furthermore, in the two cases when a small *C. virgo* larva had been attacked by a larger conspecific, the size difference was the greatest in the intraspecific predation treatment (0.53 and 0.57). These facts suggest that if the overall size difference between conspecifics had been greater, cannibalism could have occurred. However, the size distribution of the

species represented the natural size distribution at the moment, and thus the results indicate that *C. virgo* larvae have a weak tendency for cannibalism at least in these circumstances. Cannibalism may occur later on in the summer, between late and early instars or between early instars. The density is high in the earliest larval instars and most of larval mortality occurs in these stages (Crowley et al. 1987b).

In other studies, cannibalism has been reported between dragonfly larvae when their size difference is only one or two instars (Wissinger 1988; Hopper et al. 1996). In damselflies, cannibalism has been reported even within an instar in early-instar larvae, when their density was very high (Johansson 1996). The *C. virgo* larvae used in this experiment as predators were on average twice as large as the conspecifics used as prey. The large larvae were at least 3–4 instars older than the small, determined by an increase factor of 1.15–1.25 in head width between instars (Norling and Sahlén 1997), and had hatched a year before the smaller larvae.

Unfortunately, there are no accurate data on prey selection or field data on cannibalism by *C. virgo* larvae, so the questions as to whether the conspecific larvae used as prey were too large for the predators to prey on and whether cannibalism in *C. virgo* occurs in natural conditions cannot be explicitly answered. During the experiment, though, we made some observations of predation by *C. virgo* larvae on mayfly (Ephemeroptera) and stonefly (Plecoptera) nymphs and different stages of *Asellus aquaticus* in an extra aquarium. We saw large *C. virgo* larvae attacking and consuming prey roughly of the same size class as the small *C. virgo* larvae used as prey. Thus, it does not seem likely that too small a size difference alone resulted in the absence of predatory behaviour between conspecifics.

The behavioural observations we made during the experiment gave us the impression that the absence of cannibalism in our experiment was due to some other reasons than the prey being too large. If not cannibalistic, the *C. virgo* larvae also did not seem to behave aggressively towards each other. Mostly the larvae encountered each other when one was entering a previously occupied perch. Usually the larvae stared at each other for a while, after which either one of the larvae moved to the other side of the perch, and the entering larva climbed onto the perch. The small larva sometimes

even crawled over the larger conspecific. The larvae could sit still on the same perch for hours, and they did not seem to compete for the perches. In other studies, larval intraspecific aggressions have been reported in many damselfly species (Baker 1981a; Convey 1988; Gribbin and Thompson 1990). Usually damselfly larvae defend an occupied perch against an intruder, but the occurrence of intraspecific aggressions seems to vary between species. Absence of agonistic behaviour has been previously reported for *Lestes disjunctus* (Baker 1981b), and also *C. virgo* larvae seem to have a low tendency for cannibalism between the intermediate and late instars. Furthermore, Schütte and Schrimpf (2002) suggest that *C. virgo* larvae are less aggressive than larvae of *C. splendens*, based on the two species' occurrence in the field.

The small larvae did not decrease their activity or change their habitat use in either of the predation treatments, compared to the control treatment. Anti-predatory responses should be stronger if predation risk increases (Sih 1987), and thus we expected some differences between the treatments. However, the predation risk in this experiment seems to have been too low to affect the behaviour of the small larvae. Larger conspecifics were not a threat to the small *C. virgo* larvae, and against *S. metallica* larvae they had an effective refuge, the perches. The low water temperature probably inhibited the overall activity of the larvae to some degree (Thompson 1978b), and thus affected the level of larval interactions. On the other hand, absence of alternative food in the experiment should have enhanced the interactions between larvae (Johansson 1992 and 1993b).

The pairwise predator–prey plots reveal that the large larvae on the whole showed a low level of activity, and that the predation treatment did not have a significant effect on the activity of the small larvae. In habitat use, the difference was clear between the species, but not between conspecifics of different stages. All larvae preferred the same horizontal habitat among the vegetation, but only *C. virgo* larvae used the vertical dimension of the environment, the perches. Thus the species divided their mutual habitat efficiently, and the presence of a larger conspecific had no negative effects on the small larva.

The spatial distribution of the larvae differed between treatments, but this did not result from anti-predatory behaviour. In fact, the larvae

appeared to be positively associated in the cannibalism treatment, whereas in the interspecific predation treatment they showed a random distribution. But, since the *C. virgo* larvae preferred the vegetation and and clinged onto the perches, they mostly used only one half of the aquarium and thus were expected to aggregate to some degree. Also, projecting a two-dimensional grid in a three-dimensional environment does not reveal the whole truth about larval distribution. This is especially so if the two species can divide their mutual habitat as efficiently as the species used here. Thus the observed aggregated spatial distribution of the *C. virgo* larvae in the experiment cannot be held as explicit evidence of the species' tendency to form aggregations.

The results of our laboratory experiment were in congruence with an earlier observation, that not all odonate larvae are such mechanical predators as they are usually considered, preying on anything of suitable size, including conspecifics. Species-specific variation in intraspecific aggression obviously occurs. However, these results should be further tested by examining the diet of *C. virgo* in the field and by conducting more behaviour-oriented laboratory experiments.

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