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Intraguild predation and interference competition on the endangered dragonfly *Aeshna viridis*

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Abstract We examined the effects of intraguild predation (IGP) and interference competition on an endangered dragonfly, *Aeshna viridis* Eversm. (Odonata: Anisoptera). *A. viridis* is rare in Europe due to the decrease in suitable habitats harboring the macrophyte *Stratiotes aloides* L. *Stratiotes* plants are the principal oviposition substrate for *A. viridis* females and protect the larvae of *A. viridis* from fish predation. In our study lakes *A. viridis* larvae are sympatric with larvae of *Aeshna grandis* and *Aeshna juncea*. The susceptibility of *A. viridis* larvae to IGP by similar-sized larvae of *A. grandis* and *A. juncea* was tested in a laboratory predation experiment. Microhabitat use of *A. viridis* and *A. grandis* was studied in the laboratory to determine the possible effects of interference competition on the spatial distribution of *A. viridis* larvae. Our results show that at least in laboratory conditions, *A. viridis* is susceptible to IGP and interference competition. In competition, *A. grandis* larvae dominated the middle and outer portion of *S. aloides* rosettes whereas *A. viridis* stayed in the inner parts. When *A. grandis* larvae were absent, *A. viridis* colonized the middle and outer parts of the rosettes. We conclude that asymmetric predation between odonate larvae of equal size can be intense, and that both IGP and interference competition affect *A. viridis*. Although natural habitat complexity diminishes their impact, these interactions may nevertheless influence the distribution of *A. viridis* in *S. aloides* waters and restrict its microhabitat use in *S. aloides* rosettes.

Keywords Odonata · Anisoptera · Asymmetric predation · Microhabitat distribution · Equal sized larvae

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Introduction

Understanding the interspecific interactions controlling for species coexistence and their spatial distribution is a fundamental topic in both terrestrial and aquatic ecology. A crucial interaction that has often been neglected in the study of freshwater ecosystems is intraguild predation (IGP) (Koperski 2002). IGP is a taxonomically widespread interaction affecting significantly the functioning of aquatic food webs as well as the distribution, abundance, and evolution of numerous species (Polis et al. 1989; Holt and Polis 1997; Koperski 2002).

IGP occurs when species using similar, often limiting, resources kill and eat each other (Polis et al. 1989). Species can interact as competitors, intraguild predators or both, and consequently IGP can be seen as a combination of competition and predation (Wissinger 1992). It can be asymmetrical, one species being the predator on another species, or symmetrical with species mutually preying on each other. It occurs commonly in size-structured populations of omnivorous predators and includes cannibalism (Polis et al. 1989).

IGP and cannibalism are frequent among size-structured assemblages of odonate larvae (e.g., Benke 1978; Anholt 1990; Van Buskirk 1992; Johansson 1993; Corbet 1999, pp 137–139; Suhling 2001). At mid-temperate or higher latitudes most dragonfly species have semivoltine life histories and larvae of many size classes occur simultaneously. Intraodonate predation is usually size- and density-dependent and can occur routinely especially in the shallow, littoral zone of eutrophic lakes and ponds (Corbet 1999, pp 137–139). Odonate species also differ in their vulnerability to intraodonate predation (Johansson 1993). It has been suggested that larvae equal in size are potential competitors, whereas larvae disparate in size interact mainly as predator and prey (Benke 1978). Little or no predation has been observed to occur between odonate larvae similar in size (Wissinger 1988; Hopper et al. 1996).

In addition to IGP, other interactions operate among larval assemblages of odonates. Numerous studies support

the idea that competition plays an important role in odonate communities (e.g., Benke 1978; Johnson et al. 1985; Pierce et al. 1985), interference competition being especially important (Pierce et al. 1985; Van Buskirk 1992). Interference competition is caused by behavioral interactions between individuals and it can be divided into food- and mortality-related interference. Both of these forms of interference competition are often density-dependent, and can have consequences at the individual as well as assemblage level (McPeck 1990a; Van Buskirk 1992).

In this study we wanted to elucidate the effects of IGP and interference competition on the habitat use of the endangered dragonfly *Aeshna viridis* Eversm. *A. viridis* occurs in eutrophic, neutral or slightly alkaline ponds and lakes (Askew 1988) with the water macrophyte *Stratiotes aloides* L. (Rantalainen and Kanervo 1928; Gibbons 1986; Rantala et al. 2004). *Stratiotes* rosettes provide *A. viridis* larvae with refuges from fish predation (Rantala et al. 2004), and *A. viridis* females oviposit almost exclusively in *S. aloides* leaves (Rantalainen and Kanervo 1928; Münchberg 1930; Askew 1988). Larvae and emerging individuals have been recorded only from *Stratiotes* waters (e.g., Valle 1952; Valtonen 1997). During the last decades, *S. aloides* has considerably declined (Smolders et al. 1996; Rassi et al. 2001). The rarity of *A. viridis* is a consequence of its extraordinary habitat requirements and the decline of suitable reproduction areas (Rassi et al. 2001).

The distribution of *A. viridis* is highly overlapped with those of other dragonfly species, especially *Aeshna grandis* L. (Schmidt 1975; Gibbons 1986; Heidemann and Seidenbusch 1993). *A. grandis* is a reasonably common and widespread species in Europe, and occurs frequently in *S. aloides* lakes in Finland (E. Suutari, unpublished data). Another common holarctic aeshnid, *Aeshna juncea* L., can also be sympatric with *A. viridis*. Because of the similarities in their ecology and occurrence, *A. grandis* and *A. juncea* were chosen to be our study species with *A. viridis*.

We conducted a field study to examine the co-occurrence of *A. viridis* with other *Aeshna* species. Coexistence would indicate that aggressive interspecific interactions can take place also in natural conditions. In our first laboratory experiment we tested the vulnerability of *A. viridis* larvae to IGP by similar-sized larvae of *A. grandis* and *A. juncea*. IGP by larvae of equal size is not as extensively studied as mortality-related interactions between larvae of different instar (e.g., Crowley et al. 1987; Wissinger 1988; Anholt 1990; Van Buskirk 1992; Johansson 1993) or cannibalism within a year-class of a species (Fincke 1994; Hopper et al. 1996). In our second experiment we examined how the presence of a potential competitor, an *A. grandis* larva, affected the microhabitat use of similar sized *A. viridis* larva in a *Stratiotes* rosette.

Materials and methods

Field study

To verify the co-occurrence of *A. viridis* with *A. grandis* and *A. juncea*, we sampled eight eutrophic *S. aloides* lakes in southern Finland. Sampling was performed in late May and early June 2000. Sweep samples from *S. aloides* stands were taken with a pond net (D-shape, width 35 cm, height 25 cm and mesh size 0.4 mm), each sampling lasting 2 min. Eight samples were taken from each lake. The distance between samples was ca. 10 m, varying slightly due to variation in stand size. All odonate larvae obtained in the samples were identified in situ and released back to the lake.

Obtaining study objects

A. viridis, *A. grandis* and *A. juncea* larvae used in experiments were collected from Lake Saarioisjärvi in southern Finland in June 1999 and 2000. Lake Saarioisjärvi is a shallow eutrophic lake supporting a vital population of *A. viridis*. The body length of collected larvae varied between 17 and 42 mm. When not used in the experiments, the larvae were kept in 60-l plastic containers and fed with *Asellus aquaticus* L. and *Baetis* sp. larvae daily. During the experiments no food was available to the larvae. After the experiments, all surviving larvae were released back to their home lake.

Vulnerability experiment

To study the susceptibility of *A. viridis* to IGP, *A. viridis* larvae were placed into plastic jars with either *A. grandis* or *A. juncea* larvae. The experiment was performed under natural light conditions at 20 ± 1°C in June 1999 in Jyväskylä. For the experiment, we used twenty 1.5-l plastic jars (10×12×12.5 cm) each filled with 1 l tap water. One plastic drinking straw was set into each jar to provide a climbing substrate for the larvae. No bottom substrate was added. Before introducing the larvae into the jars their lengths were measured from the front of the head to the tip of the abdomen (excluding anal appendages). The most similar-sized larvae were chosen to form pairs. Pairs of *A. viridis* and *A. grandis* were placed in 12 jars and pairs of *A. viridis* and *A. juncea* were placed in eight jars. The maximum size difference between paired *A. viridis* and *A. grandis* was 5.5 mm (one pair, *A. grandis* larger) and the maximum size difference between *A. viridis* and *A. juncea* was 2.0 mm (*A. viridis* larger). In six of 12 *viridis*–*grandis* pairs *A. viridis* was slightly (0.5–1.6 mm) larger, and in five of eight *viridis*–*juncea* pairs, *A. viridis* was larger (0.3–2.0 mm). The larvae were placed on the water surface and left to float or swim to the bottom of the jar. The condition of larvae was surveyed after 3 h and 11 h (10 a.m. and 6 p.m. respectively) from the beginning of the experiment. In all the experiment lasted for 3 days, that is until predation had occurred in every jar, with surveillance twice a day.

Microhabitat-use experiment

In the microhabitat-use experiment we wanted to determine if the presence of *A. grandis* larvae affects the spatial distribution of *A. viridis* larvae in *S. aloides* rosettes. This was studied in eighteen 50×30×30-cm glass aquaria filled with water from mesotrophic Lake Jyväsjärvi. *Stratiotes* plants used in the experiment were selected randomly and removed from a large patch of vegetation in Lake Saarioisjärvi. One *S. aloides* plant with a diameter of ca. 30 cm was placed in each aquarium. Similar-sized dragonfly larvae, one *A. viridis* and one *A. grandis*, were placed in a random position on the surface of nine aquaria. In each nine control aquaria, one *A. viridis* larva was present. The locations of larvae on the plants were surveyed once a day at 1200 hours for 8 days. A total of 64 location

observations were made of *A. grandis* larvae and 71 and 72 of *A. viridis* larvae in competition and control situation, respectively. In order to facilitate the documentation of larval positioning, four location categories were designated: (1) the inner third of the plant near the center of the rosette, (2) the middle third of the leaves, (3) outer parts up to the tips of the leaves, and (4) in the water away from the rosette.

Statistical tests

In the vulnerability experiment, we used the binomial test to study the frequencies of negative and positive differences in predatory behavior of the three *Aeshna* species. In the microhabitat-use experiment, mean location of each individual in a *Stratiotes* rosette was calculated using location categories. Mean locations of *A. viridis* and *A. grandis* larvae within an aquarium were compared using the Wilcoxon signed ranks test. When comparing the mean locations of *A. viridis* in competition and control situations, each aquarium was used as a statistically independent observation unit. Comparison was performed using the Mann–Whitney *U*-test. SPSS version 11.5 for Windows was used for all statistical tests.

Results

Field study

Five of eight *S. aloides* lakes supported *A. viridis* larvae, and total of 42 larvae was discovered (Table 1). *A. grandis* was present in six lakes (26 individuals) and in three of these it was sympatric with *A. viridis*. One *A. juncea* individual was found from the sampled *S. aloides* lakes and it co-occurred with both *A. grandis* and *A. viridis*.

Vulnerability experiment

Larvae of *A. viridis* were very vulnerable to IGP. In all 12 cases, *A. grandis* killed *A. viridis* (binomial test, $P < 0.001$). The result was similar with *A. juncea*, in all eight cases *A. juncea* killed *A. viridis* (binomial test, $P = 0.008$). In most cases predation occurred within 24 h from the beginning of the experiment, in the case of one pair predation took place after 2 days. The *A. viridis* larva was killed although

Table 1 Total numbers of *Aeshna viridis*, *A. grandis* and *A. juncea* larvae in the sampled *Stratiotes aloides* lakes in southern Finland. Eight sweep-net samples were taken from *S. aloides* patches in each lake

Lake	<i>A. viridis</i>	<i>A. grandis</i>	<i>A. juncea</i>
Pitkäjärvi	8	12	1
Hepojärvi		3	
Peltolampi		5	
Ilmoilanselkä		2	
Tykölänjärvi	1		
Saarioisjärvi	18	2	
Luukonperä	4	2	
Lehijärvi	11		
Total	42	26	1

it was the slightly larger individual of the pair. None of the larvae moulted during the experiment.

Microhabitat-use experiment

Microhabitat use of *A. viridis* and *A. grandis* differed when both species were present in a plant rosette (Wilcoxon signed ranks test, $T = 1.5$, $n = 8$, $P = 0.02$) (Fig. 1). In the competition situation, *A. grandis* preferred the middle and outer parts of the *Stratiotes* rosette whereas *A. viridis* occupied the inner portion of the plant more frequently than *A. grandis*. On the last experimental day, one *A. viridis* was killed by an *A. grandis* larva.

The site preference of *A. viridis* differed when the competitor was present and when it occupied the *Stratiotes* rosette alone (Mann–Whitney *U*-test, $U = 13.5$, $n_1 = 9$, $n_2 = 9$, $P = 0.017$). In competition, nearly 30% of observed *A. viridis* were located in the inner third of a rosette (Fig. 1). In control aquaria *A. viridis* larvae preferred the middle and outer parts of plants, occupying inner areas in <10% of observations.

Discussion

Co-occurrence of *Aeshna* species

Our field study confirmed that *A. viridis* is sympatric with other *Aeshna* species in Finland. Larvae of *A. grandis* and *A. juncea* were found from *S. aloides* zones of lakes inhabited by *A. viridis*. *A. viridis* was the most abundant and *A. juncea* was the scarcest when all three species coexisted. A low occurrence of *A. juncea* can be due to the fact that although the species is able to breed in eutrophic, often alkaline lakes and ponds supporting *S. aloides*, it usually prefers more oligotrophic and even slightly acid waters (Askew 1988). Thus, in areas inhabited by *A. viridis*, encounters with *A. grandis* are more likely than encounters with *A. juncea* or other aeshnids, which has been reported also in odonatological literature (Gibbons 1986; Heidemann and Seidenbusch 1993).

IGP and interference competition

Results of the vulnerability experiment indicate that *A. viridis* is very sensitive to IGP. Even a slightly larger size of *A. viridis* does not assure its survival in aggressive interspecific interactions. This is exceptional because usually little or no predation occurs between similar-sized dragonfly larvae (Wissinger 1988; Van Buskirk 1992; Hopper et al. 1996; but see Fincke 1994).

Behavioral adaptations that reduce the susceptibility of odonate larvae to fish predation may make them more vulnerable to other predators, such as large dragonfly larvae (see Johnson 1991). Antipredator behavior of *A. viridis* is thought to have evolved mainly to enable its existence in areas with high fish predation pressure

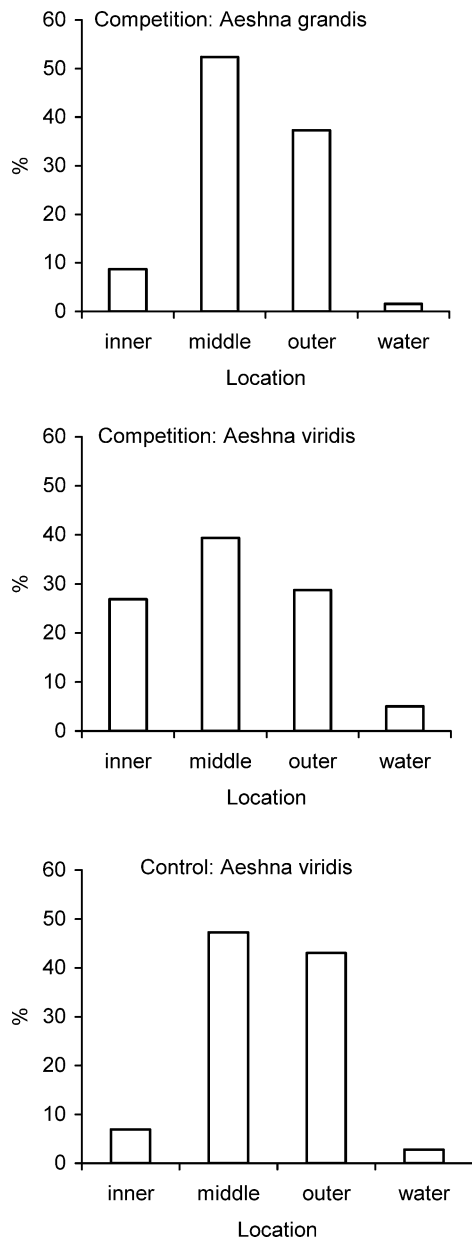


Fig. 1 Microhabitat use of *Aeshna viridis* and *A. grandis* in *Stratiotes aloides* rosettes. The bars represent the percent occupancy in each location. Location categories (starting from the center of the rosette) are inner third (*inner*), middle third (*middle*), outer third (*outer*), and open water (*open*). Nine competition aquaria and nine control aquaria were surveyed once a day for an 8-day period

(Rantala et al. 2004). Dragonfly larvae in habitats with fish typically restrict their activity (Henrikson 1988) and stay motionless even when attacked (McPeck 1990b; Stoks et al. 2003). Inactivity of *A. viridis*, which helps it to avoid fish predation, can increase its risk of being preyed upon by other dragonfly larvae.

Interference competition stimulated the withdrawal of *A. viridis* larvae to the inner portion of *S. aloides* rosettes. In the absence of a competitor they preferred the middle and outer parts of plants, sites occupied mostly by *A. grandis* in the competition situation. Interference compe-

tion is the most usual mechanism of interaction between odonate larvae of similar size (Johnson et al. 1985; Crowley et al. 1987; Johnson 1991; but see Van Buskirk 1989). In large *Aeshna* species, interference is often mortality-related and can lead to IGP, especially when encountering larvae are of different instars (Van Buskirk 1992; Corbet 1999, pp 137–139). In laboratory conditions, *A. viridis* was very sensitive to IGP. Because of this, interference competition and especially the threat of mortality-related interference affects the microhabitat distribution of the species.

In the IGP experiment, our experimental design provoked the predation to take place because the larvae could not avoid encountering each other in the jar where neither refuges nor alternative prey items were available. In natural conditions the spatial complexity of *S. aloides* rosettes provides refuges where *A. viridis* larvae can hide from other odonates and vertebrate predators. This most likely strongly diminishes the effects of IGP, and may also explain the existence of *A. viridis* in areas with other *Aeshna* larvae as well as fish. The fact that during the microhabitat experiment, only one *A. viridis* larva was preyed on, supports the importance of spatial complexity and the role of *S. aloides* rosettes as refuges. In nature microhabitat shifts induced by other odonate larvae may enable the coexistence of *A. viridis* with them. In the inner parts of *S. aloides* rosettes *A. viridis* larvae may stay undetected and are able to avoid aggressive interactions. It has been found that macrophytes of an appropriate form can reduce the likelihood of larval encounters, and therefore inhibit agonistic behavior between odonates (Corbet 1999, pp 164–169). Wellborn and Robinson (1987) have also shown that a within-plant larval distribution pattern can be highly non-random, with the most preferred sites providing effective refuges from fish predation.

Conclusions

IGP is usually size-dependent, with small larvae being most vulnerable to this phenomenon (Wissinger 1988; Van Buskirk 1989). Predation between dragonfly larvae similar in size and belonging to the same family has been very little studied (but see Fincke 1994; Hopper et al. 1996). Our results show that asymmetric predation by similar-sized odonate larvae can be intense and induce an increased risk of mortality-related interference competition. *A. viridis* proved to be very vulnerable to IGP, but in nature the spatial complexity of *Stratiotes* stands and the microhabitat shifts within *S. aloides* rosettes reduce the risk of IGP and most likely enable its coexistence with other *Aeshna* species.

To further understand the ecology of *A. viridis* and interspecific interactions between odonates, it would be informative to compare the vulnerability of *A. viridis* and other *Aeshna* species to fish predation. Green, inconspicuous and inactive *A. viridis* might be superior in staying undetected from fish compared to other, brown aeshnids.

This could explain the fact that although *A. viridis* is a poor competitor against other dragonfly larvae, it is able to occupy *S. aloides* rosettes in areas with intense fish predation.

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References

- Anholt BR (1990) An experimental separation of interference and exploitative competition in a larval damselfly. *Ecology* 71:1483–1493
- Askw RR (1988) *The dragonflies of Europe*. Harley Books, Martins
- Benke AC (1978) Interactions among co-existing predators—a field experiment with dragonfly larvae. *J Anim Ecol* 47:335–350
- Corbet PS (1999) *Dragonflies: behavior and ecology of odonata*. Harley Books, Martins
- Crowley PH, Dillon PM, Johnson DM, Watson CN (1987) Intraspecific interference among larvae in a semivoltine dragonfly population. *Oecologia* 71:447–456
- Fincke OM (1994) Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. *Oecologia* 100:118–127
- Gibbons B (1986) *Dragonflies and damselflies of Britain and Northern Europe*. Hamlyn, London
- Heidemann H, Seidenbusch R (1993) *Die Libellenlarven Deutschlands und Frankreichs*. Handbuch für Exuviansammler. Bauer, Keltern
- Henrikson B-I (1988) The absence of antipredator behaviour in the larvae of *Leucorrhinia dubia* (Odonata) and the consequences for their distribution. *Oikos* 51:179–183
- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745–764
- Hopper KR, Crowley PH, Kielman D (1996) Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. *Ecology* 77:191–200
- Johansson F (1993) Intraguild predation and cannibalism in odonate larvae: Effects of foraging behaviour and zooplankton availability. *Oikos* 66:80–87
- Johnson DM (1991) Behavioral ecology of larval dragonflies and damselflies. *Trends Ecol Evol* 6:8–13
- Johnson DM, Crowley PH, Bohanan RE, Watson CN, Martin TH (1985) Competition among larval dragonflies: a field enclosure experiment. *Ecology* 66:119–128
- Koperski P (2002) Factors determining diversity in diet composition: multivariate analysis of a guild of epiphytic predators. *Arch Hydrobiol* 155:291–314
- McPeck MA (1990a) Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* 71:83–98
- McPeck MA (1990b) Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. *Ecology* 71:1714–1726
- Münchberg P (1930) Zur Biologie der Odonatengenera *Brachytron* Evans und *Aeschna* Fbr. *Z Morphol Ökol Tiere* 20:172–232
- Pierce CL (1988) Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. *Oecologia* 77:81–90
- Pierce CL, Crowley PH, Johnson DM (1985) Behavior and ecological interactions of larval Odonata. *Ecology* 66:1504–1512
- Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330
- Rantala MJ, Ilmonen J, Koskimäki J, Suhonen J, Tynkkynen K (2004) The macrophyte, *Stratiotes aloides*, protects larvae of dragonfly *Aeshna viridis* against fish predation. *Aquat Ecol* 38:77–82
- Rantalainen E, Kanervo E (1928) *Aeschna viridix*ns esiintymisestä ja elintavoista Suomessa. *Luonnon Ystävä* 32:161–170
- Rassi P, Alanen A, Kanerva T, Mannerkoski I (2001) Threatened species in Finland in 2001. Ministry of the Environment and Finnish Environment Institute, Helsinki
- Schmidt EB (1975) *Aeshna viridis* Eversmann in Schleswig-Holstein, Bundesrepublik Deutschland (Anisoptera: *Aeshnidae*). *Odonatologica* 4:81–88
- Smolders AJP, Roelofs JGM, Den Hartog C (1996) Possible causes for the decline of the water soldier (*Stratiotes aloides* L.) in the Netherlands. *Arch Hydrobiol* 136:327–342
- Stoks R, McPeck MA, Mitchell JL (2003) Evolution of prey behavior in response to changes in predation regime: damselflies in fish and dragonfly lakes. *Evolution* 57:574–585
- Suhling F (2001) Intraguild predation, activity patterns, growth and longitudinal distribution in running water odonate larvae. *Arch Hydrobiol* 151:1–15
- Valle KJ (1952) Suomen eläimet 7. Sudenkorennot. WSOY, Turku
- Valtonen P (1997) Suku *Aeshna* Suomessa ja Pirkanmaalla. 1. osa. *Diamina* 6:6–12
- Van Buskirk J (1989) Density-dependent cannibalism in larval dragonflies. *Ecology* 70:1442–1449
- Van Buskirk J (1992) Competition, cannibalism, and size class dominance in a dragonfly. *Oikos* 65:455–464
- Wellborn GA, Robinson JV (1987) Microhabitat selection as an antipredator strategy in the aquatic insect *Pachydiplax longipennis* Burmeister (Odonata: Libellulidae). *Oecologia* 71:185–189
- Wissinger SA (1988) Effects of food availability on larval development and inter-instar predation among larvae of *Libellula lydia* and *Libellula luctuosa* (Odonata: Anisoptera). *Can J Zool* 66:543–549
- Wissinger SA (1992) Niche overlap and potential for competition and intraguild predation between size-structured populations. *Ecology* 73:1431–1444