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INTRAGUILD PREDATION AND COMPETITION BETWEEN LARVAL DRAGONFLIES: DIRECT AND INDIRECT EFFECTS ON SHARED PREY[1]

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Abstract. We conducted manipulative field experiments in artificial ponds to quantify the predatory impact of larvae of a migratory dragonfly (*Tramea lacerata*) on a common resident dragonfly species (*Erythemis simplicicollis*), and on damselflies as shared prey of the two dragonflies. We found that the combined predatory effects of the two dragonflies on damselflies were not additive. To determine the underlying cause of non-additive predation rates in the field, we conducted a second experiment in laboratory aquaria to isolate the impact of each predator on the consumption rates of the other. Dragonfly consumption rates of damselflies in single-predator treatments were compared to those in the presence of heterospecifics or conspecifics with their menta (mouthparts) surgically modified so that they could not capture prey.

In the laboratory experiment, de-mented *Tramea* reduced the consumption rates of *Erythemis* to less than half of that observed when *Erythemis* foraged alone. *Erythemis* numbers were also reduced by *Tramea* predation. *Erythemis* had neither effect on *Tramea*. Both of the negative effects of *Tramea* on *Erythemis* will have indirect positive effects on damselflies. The "behavioral" component (reduced *Erythemis* foraging rate) should be more important than the "trophic link" (reduced *Erythemis* numbers) indirect effect. Together these indirect positive effects will allay, but not completely compensate for, the direct negative effects of *Tramea* predation on damselflies.

These results illustrate how an asymmetric potential for intraguild predation can lead to asymmetries in interference competition and to non-additive effects on prey mortality. The addition or removal of predators that interact in this manner to or from communities should have only a small net effect on prey because of compensating direct and indirect effects. This may explain why predator manipulations have often had unpredictable or undetectable effects on freshwater benthic communities.

Key words: behavioral interference; benthic freshwater invertebrates; dragonflies; Erythemis; *field experiments; indirect effects; interference competition; intraguild predation; ponds;* Tramea.

INTRODUCTION

Competition and predation have historically been considered as interactions within and between trophic levels, respectively. However, ecologists now realize that many species interact concurrently as competitors and intraguild predators (reviews by Werner and Gilliam 1984, Ebenman and Persson 1989, Polis et al. 1989; recent articles by Cortwright 1988, Hurd 1988, Wissinger 1989, Cortwright and Nelson 1990, Hurd and Eisenberg 1990, Spiller and Schoener 1990). Although theory (e.g., Polis et al. 1989) predicts that coexistence in guilds of these species should depend on an interplay between the two types of interactions, the details of mixed competition–predation interactions are well studied in only a few systems (reviews by Polis 1989, Polis et al. 1989).

The purpose of this study was to explore one type of complex interaction between intraguild predators—the interaction between competition for shared resources and the threat of intraguild predation. We were particularly interested in quantifying how this interaction might indirectly affect the overall mortality of shared prey. The importance of indirect effects has been well established during the past decade, but most experimental studies have focused on interactions among prey that share a common predator (reviews by Holt 1977, Sih et al. 1985, Kerfoot and Sih 1987; recent examples by Schmitt 1987, Huang and Sih 1990, Strauss 1991). In this study we focus on a second, less well-studied, class of indirect effects in which interactions between predators influence the net predation rate on a common prey species (Huang and Sih 1991). Previous studies suggest that there is considerable varia-

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tion among taxa in whether the combined effects of predators on shared prey can be predicted by their separate effects, and therefore whether prey are being indirectly affected by predator–predator interactions (Charnov et al. 1976, Sih 1979). In some cases the combined effects of two or more predators on shared prey are: (1) additive, suggesting no indirect effects (e.g., Van Buskirk 1988, Wilbur and Fauth 1990), (2) more than additive, indicating facilitation among the predators and/or resource enhancement (e.g., Soluk and Collins 1988, Martin et al. 1989), or (3) less than additive, indicating negative interactions between predators (interference, intraguild predation) and/or resource depression (Soluk and Collins 1988, Fauth 1990, Huang and Sih 1991). Ecologists have long been interested in knowing whether pairwise interactions between species can be used to predict outcomes in a multi-species context (Wilbur 1972, Fowler and Rausher 1985, Wilbur and Fauth 1990), yet the conditions under which predator–predator interactions have additive or non-additive effects on prey remain poorly understood.

Our study focused on the interactions among larvae of a large migratory dragonfly (*Tramea lacerata*), a smaller dragonfly (*Erythemis simplicicollis*), and damselflies as shared prey. We conducted two types of experiments to quantify interactions between *Tramea* and *Erythemis* while they were foraging for damselflies. In a field experiment conducted in artificial ponds, we found that the predatory effects of these two dragonfly species on damselflies were not statistically additive. Such non-additive effects may or may not be indicative of a complex interaction between these two predators (Fowler and Rausher 1985). The purpose of the second experiment, which was conducted in the laboratory, was to test hypotheses about the underlying cause(s) of the non-additive effect we observed in the field.

Methods

Natural history

Tramea spp. and other large dragonflies (e.g., *Pantala, Anax, Aeshna*) are only common in ponds and wetlands without fish, which they replace as the top predators on resident odonates, other benthic and planktonic invertebrates, and amphibian larvae (Caldwell et al. 1980, Morin 1984*a, b,* Travis et al. 1985, Robinson and Wellborn 1987, McPeek 1990*a, b,* Skelly and Werner 1990, Johnson 1991). *Tramea* are residents in the southern and central United States, but northern populations in North America are maintained or supplemented by spring immigrants, which complete one generation before returning south (Walker and Corbet 1978, Corbet 1984, Wissinger 1988*b*). Size-specific overlap data suggest that when *Tramea* immigrate to these ponds, larvae should have a predatory and competitive advantage over most resident odonates, both because of their larger body size at a given instar, and because of a developmental headstart related to breeding phenology (Wissinger 1988*b,* 1992). We chose to study interactions between *Tramea* and *Erythemis* because *Erythemis* is often among the most abundant resident species that, like *Tramea,* also spends most of its time climbing among the stems of submergent vegetation (McPeek 1990*a,* S. Wissinger and A. Droz, *unpublished data*). Laboratory experiments in simple predation arenas indicated that both *Tramea* and *Erythemis* will readily consume damselfly larvae, and will also prey on each other (McGrady 1989).

Field experiment

Experimental ponds.—The field experiment was conducted during the fall of 1989 in round, galvanized cattle tanks (1.5 m diameter; 0.6 m depth) at Allegheny College's Environmental Research Reserve in western Pennsylvania. The 48 tanks (6 × 8 array) are partially sunk in the ground and are all contained in a large (15 × 25 × 3 m) screened (2.5-cm mesh) enclosure that prevents colonization by dragonflies and amphibians. Adults of a variety of small aquatic insects can readily pass through the screen, allowing for natural immigration from nearby ponds. The benthic habitat in each tank was initially created in May 1988 when 10 cm of sandy soil from an adjacent dry lake basin was added to each tank. Organic detritus, submergent vegetation (*Ceratophyllum demersum, Najas flexilis*), and aquatic invertebrates from a nearby pond on the reserve were subsequently added to each tank in approximately equal amounts. Aquatic vegetation and invertebrates from the same source ponds were added again in the spring of 1989. We sampled the tanks just prior to the experiment and found they contained a diverse invertebrate assemblage dominated by chydorid cladocerans, chironomid larvae, mayfly larvae (*Caenis* sp.), adult corixids, dytiscid beetles, and a gammarid crustacean (S. Wissinger, *unpublished data*). The semi-natural conditions of habitat heterogeneity and resource renewal in the tanks provided the conditions for ecologically relevant encounter rates and behaviors.

Experimental design and setup.—The purpose of the field experiment was to: (1) quantify the effects of predation by *Tramea* on *Erythemis,* and/or *Erythemis* on *Tramea,* (2) compare the effects of predation by *Tramea* and *Erythemis* on damselfly larvae, and (3) to determine if the effects of these predators on damselflies were additive. We compared damselfly survival across four predator treatments: no predators, *Tramea* only, *Erythemis* only, and *Tramea* + *Erythemis* (Table 1). The total density in the combined-predator treatment was doubled because we wanted to focus on the degree to which the predatory effects of the two species were additive. Predatory interactions between *Tramea* and *Erythemis* were inferred by comparing the survival of each species between single- and combined-predator treatments. Twelve tanks were chosen from the 48-tank array based on similarity in percentage of vege-

tation cover, and randomly assigned to one of the four dragonfly–damselfly treatments. Resident damselflies and other invertebrate predators such as dytiscid beetle larvae were removed from the tanks prior to the experiment.

Nearby sources of *Tramea* contained larvae of both *Tramea lacerata* and *T. carolina*, which can be distinguished reliably only after inspection of each individual. To facilitate the rapid collection of large numbers of organisms of known taxonomic identity, the *Tramea* and *Erythemis* larvae used in the experiment were collected from a small farm pond in central Indiana. Life history studies at this pond over the past 10 yr indicate that 99% of all *Tramea* that emerge at this site are *Tramea lacerata* (S. Wissinger 1988*b*, *c*, and *unpublished data*). The density used for single-species treatments was based on the average abundance of the two species at the time of collection (6–8 October 1989). We used only the last three instars in proportion to their relative abundances to minimize the confounding effects of cannibalism (Van Buskirk 1989, Wissinger 1989) (Table 1). Feeding trials conducted in simple laboratory arenas indicated that all dragonflies could prey on all instars of the damselflies used in the experiments (McGrady 1989).

The damselfly larvae (mainly *Ischnura verticalis* and *Enallagma aspersum*) were collected in Pennsylvania from a small pond in the Erie National Wildlife Refuge. This pond contained a diverse dragonfly fauna including *Tramea* spp. and *Erythemis simplicicollis*. Late-instar damselflies were collected from 10–20 October 1990 and added daily in equal numbers to each tank during the 10-d period. The species composition and overall density of damselflies used in the experiment reflected those of the source pond. The experiment was terminated in early December, 6 wk after the experimental setup was completed, at which time damselfly and dragonfly larvae were removed from the tanks. The larvae were sorted live from vegetation and detritus in the laboratory in large (60 × 40 cm) enamel pans.

The expected rate of damselfly survival in the combined-predator treatment was calculated using an addition probability theorem that assumes finite sample space and independence between the foraging rates of the two predators (after Soluk and Collins 1988). Specifically, we predicted that damselfly mortality in the absence of interactions between the predators should be $= n(p_T + p_E - p_T p_E)$, where n is the initial number of damselflies and p_T and p_E are the proportions of damselflies consumed in *Tramea* and *Erythemis* single-predator treatments, respectively.

The field experiment was analyzed using a two-way ANOVA with the interaction term as a test for additivity of the predatory effects of *Tramea* and *Erythemis* on damselflies. We compared the observed and expected values for the combined predator treatment using one-way ANOVA. Three expected values were generated from pairs of *Tramea* and *Erythemis* predation rates blocked by replicate number. Student-Newman-Keuls (SNK) multiple-comparison tests ($P < .05$) were used to compare treatment means, and a Bartlett–Box test was used to test for homoscedasticity.

TABLE 1. Experimental design parameters of the field experiments conducted to quantify the predatory effects of *Tramea* and *Erythemis* on damselfly survival. There were three replicates = 12 cattle tanks.

Treatment	No. predators	No. prey
Damselfly control	0	250
Tramea predation	60	250
Erythemis predation	60	250
Tramea + *Erythemis*	60 + 60	250

Predator size distributions

Species	Instar*	Mean head width (mm) (n = 10)	Number
Tramea	F	7.55	6
	F-1	6.40	37
	F-2	5.30	17
		Total =	60
Erythemis	F	4.90	25
	F-1	3.95	22
	F-2	3.15	13
		Total =	60

* F = final instar, size F-1 = penultimate instar, etc. Sizes are from Wissinger (1992).

Laboratory experiment

Experimental design.—This experiment was designed to determine whether lower-than-expected foraging rates observed in combined-predator treatments in the field experiments were due to changes in *Erythemis* and/or *Tramea* consumption of damselflies in the presence of the other species. To do this we measured the per-capita consumption rate of each species alone and compared it to that in treatments containing additional larvae with the distal lobes of their menta cut (hereafter referred to as "de-mented" dragonflies). The mentum of a larval dragonfly is the extendable mouthpart used to capture prey, and we found in preliminary experiments that larvae with the palpal lobes of this structure removed could not capture damselflies (after Van Buskirk 1989). Thus, de-mented larvae could potentially elicit changes in the foraging rates of other dragonfly larvae with intact menta, but could not themselves affect the response variable used to assay consumption rates (damselfly survival).

The design of the experiment consisted of nine treatments in which we manipulated dragonfly density and species and measured the foraging rates of the larvae with intact menta (Table 2). For each dragonfly we compared consumption rates on damselflies when alone to those in the presence of either de-mented heterospecifics or de-mented conspecifics. This enabled us to measure the effects of both inter- and intraspecific in-

TABLE 2. Experimental design of the laboratory experiment to test for interference effects between *Tramea* and *Erythemis* while they were foraging for damselfly prey. Menta = dragonfly trophic apparatus. There were four replicates of each treatment = 36 aquaria.

Treatment	Manipulations	Total no. dragonflies	No. damselfly prey
1. *Tramea* control	8 with menta intact	8	80
2. *Erythemis* control	8 with menta intact	8	80
3. Combined predator	8 *Tramea* and 8 *Erythemis* with menta intact	16	80
4. *Tramea* interference with *Erythemis* foraging	8 de-mented *Tramea* 8 *Erythemis* with menta intact	16	80
5. *Erythemis* interference with *Tramea* foraging	8 de-mented *Erythemis* 8 *Tramea* with menta intact	16	80
6. *Tramea* interference with *Tramea* foraging	8 de-mented 8 with menta intact	16	80
7. *Erythemis* interference with *Erythemis* foraging	8 de-mented 8 with menta intact	16	80
8. Efficacy of de-mentation	8 de-mented *Tramea* 8 de-mented *Erythemis*	16	80
9. Damselfly mortality control	No dragonflies	0	80

teractions on foraging rates. We also repeated the combined-predator treatment with all intact larvae to determine if the non-additive effect observed in the field could be detected under the conditions of the laboratory setup. Additional control treatments included: (1) measuring damselfly survival in the presence of demented larvae to ensure that this procedure was effective in eliminating predatory capabilities throughout the duration of the experiment, and (2) measuring damselfly survival in the absence of all dragonflies.

Experimental setup and excision of palpal lobes of mentum.—The experiment was conducted during October 1990 in 36 38-L aquaria (bottom area 0.125 m^2) under a 12L:12D light regime and at 15° ± 2°C. The density and structure of macrophyte beds is known to affect predator avoidance and spacing in damselflies (Convey 1988, Anholt 1990), and can mediate behavioral interference among odonates (Crowley et al. 1987*b*, Wellborn and Robinson 1987, Crowley and Martin 1989, Johnson 1991). Thus, we re-created a semi-natural macrophyte bed in the tanks using washed vegetation from the source pond. The bottom of each tank was covered with 5 cm of silica sand that was used to root 100 stems (cut to 40 cm lengths) of *Myriophyllum spicatum*. We chose stems with a similar density and vertical distribution of leaf whorls. By washing the stems vigorously in two separate wash buckets we reduced the number of incidentally added damselflies to ≤2 per tank. A few tube-dwelling chironomid larvae were added with the plants.

To encourage damselflies to perch in their typical "fishing positions" in the vegetation (see Crowley 1979, Baker 1980, 1981, Rowe 1980, Anholt 1990), we supplemented prey resources by adding five gravid *Daphnia magna* when we vegetated the tanks and again at days 5 and 10 during the experiment. In addition, we added a concentrate of filtered zooplankton from the source pond at the beginning of the experiment and on day 7. The concentrate was obtained by first pouring pond water from the littoral zone through a 1-mm mesh D-shaped aquatic net to remove detritus and large macroinvertebrates, and then filtering the plankton from that water through a zooplankton net (152-μm mesh). The zooplankters were mainly cyclopoid copepods, and daphniid and chydorid cladocerans.

All damselfly and dragonfly larvae were collected from a small pond in central Indiana (described in Wissinger 1988*b*, *c*). Late instars of mainly *Ischnura verticalis* and *Enallagma civile* (these two species constitute >75% of all coenagrionids that emerge at this site) were collected from the pond and randomly added to the appropriate tanks during 1–4 October 1990. *Tramea* and *Erythemis* larvae were collected on 5–7 October and housed separately while we excised menta and acclimated de-mented larvae to the aquaria.

Menta were excised by first anesthetizing larvae with CO_2 (one 3.3-g seltzer tablet per 200 mL of pond water). The labium was easily extended from the relaxed larva and the distal lobes were cut with dissecting scissors at their point of attachment with the prementum. The procedure had almost no mortality effect on *Tramea*, but was lethal to ≈25% of the *Erythemis* (see also Van Buskirk 1989). We avoided using final instars of either species because in preliminary trials we found that the procedure often stimulated unsuccessful metamorphosis in *Tramea*. De-mented larvae were held separately in the presence of *D. magna* for 24 h before they were added to the experimental arenas. This recovery/observation period was used to ensure that the procedure was effective for disabling their capture abilities and

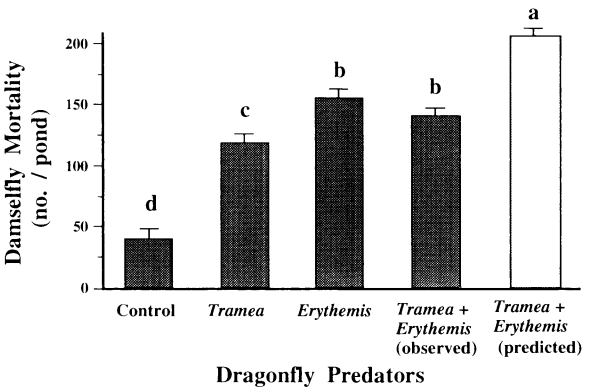

FIG. 1. Damselfly mortality (mean and 1 SE; $n = 3$) in the field experiment with *Tramea* and *Erythemis* predators. The adjusted predicted value accounts for changes in predator densities across treatments. Means are grouped into statistically different subsets (a–d) based on a Student-Newman-Keuls multiple-comparison test for one-way ANOVA on observed and predicted values.

to remove tramautized larvae that did not recover from the procedure.

After 2 wk the experiment was terminated, at which time all dragonflies and damselflies remaining in the tanks were counted by removing and repeatedly washing the vegetation and detritus. Damselfly survival in each treatment was used to calculate an instantaneous consumption rate (after Dodson 1975 and Peckarsky and Penton 1989) as

$$c = \frac{-\ln(P_t/P_0)}{Rt}$$

where P_t is the number of prey at time t (corrected for losses from the damselfly control), P_0 is the initial number of prey, R is the number of predators surviving to the end of the experiment, and t is the duration of the experiment. Consumption rates are in units of number of prey eaten per predator per day. Treatment effects on consumption rates were analyzed using a one-way ANOVA. SNK multiple-comparison tests were used to compare means, and a Bartlett–Box procedure was used to test for the assumption of homogeneity of variances. The observed and expected values (see *Methods: Field Experiment: Experimental design and setup,* above) for consumption rates in the combined-predator treatment were compared with one-way ANOVA. Four expected values were generated from pairs of *Tramea* and *Erythemis* consumption rates blocked by replicate number.

RESULTS

Field experiment

Tramea and *Erythemis* both had a significant negative effect on damselfly mortality (Fig. 1). However, their combined effects were not statistically additive, as illustrated by the significant two-way interaction (Table 3). To further explore the nature of this interaction, we compared the observed damselfly mortality in the combined-predator treatment to that expected assuming no interaction between the two predators, and found it was significantly lower than expected ($F = 20.9$, df = 2, 8, $P = .02$; Fig. 1). One explanation for the disparity in expected vs. observed prey mortality in the combined-predator treatment was that *Erythemis* survival in the presence of *Tramea* was lower than in the single-predator treatment (37 ± 1.5 vs. 51 ± 2.1 damselflies consumed per tank, respectively [$\bar{X}$ ± 1 SD]; $F = 120.1$, df = 1, 5, $P < .001$). To account for this reduction in *Erythemis* in the combined-predator treatment, we corrected the predicted prey mortality using mortality rates based on the final density of *Erythemis* species in the combined-predator treatment. However, even after accounting for *Erythemis* mortality we found that prey mortality in the combined-predator treatment was still less than that predicted by the additive model (SNK, $P < .05$).

Laboratory experiment

Damselfly mortality varied dramatically among the different treatments in the laboratory experiment ($F = 75.3$, df = 8, 35, $P < .001$; Fig. 2). Mortality in the damselfly control and in the treatment containing only de-mented larvae was significantly less than in any predator treatments (SNK, $P < .05$). The negligible mortality in these two controls suggests that damselfly cannibalism was not a factor in this experiment, and that dragonfly larvae with excised menta were not able to capture damselflies. We corrected the consumption rates in the subsequent analyses to account for the losses in the damselfly control.

The results of the single- and combined-predator treatments in the laboratory were consistent with the non-additive effect observed in the field experiment. The per-capita consumption rate of damselflies in the presence of both predators was again much lower than that predicted from consumption rates in the single-predator treatments (SNK, $P < .05$; Fig. 3). In contrast to the results of the field experiment, *Tramea* consumption rates on damselflies were greater than those of *Erythemis* in single-predator treatments.

Comparing results of single-predator treatments to those with de-mented larvae revealed the underlying cause for the non-additive consumption rates in com-

TABLE 3. ANOVA of the effect of dragonfly predators on damselfly mortality in field experiment conducted in artificial ponds.

Source	df	SS	F	P
Main effects	2	17557.6	44.0	<.001
Tramea	1	3131.3	15.7	.004
Erythemis	1	14421.3	72.3	<.001
2-way interaction, *Tramea* × *Erythemis*	1	6627.0	33.2	<.001
Explained	3	24184.6	40.4	<.001
Error	8	1596.0	...	...

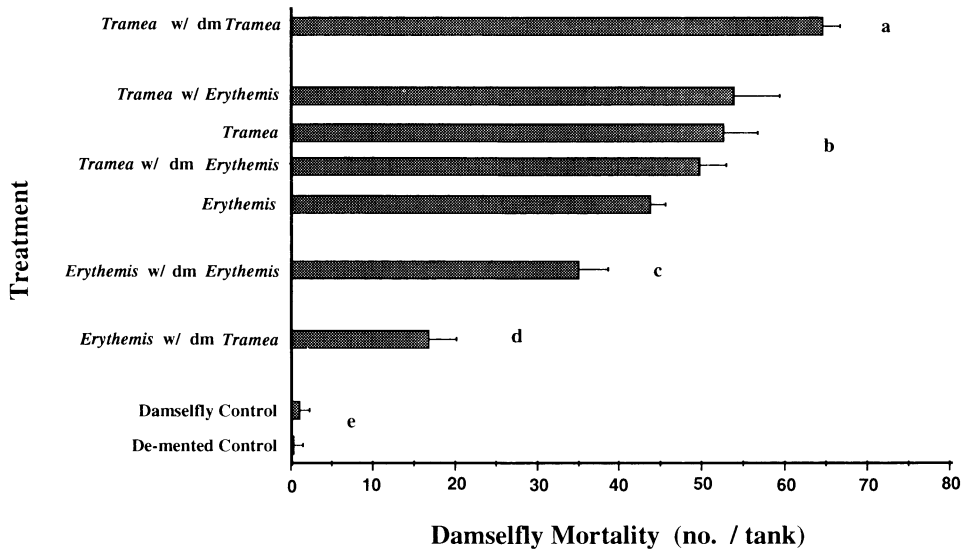

FIG. 2. Damselfly mortality (mean and 1 SE; $n = 4$) in all treatments of the laboratory experiment. dm = de-mented = trophic apparatus removed. Means are grouped into statistically different subsets (a–e) based on a Student-Newman-Keuls multiple-comparison test.

bined-predator treatments. The cause was not due to a change in *Tramea* consumption rates. *Tramea* consumption rates in single-predator treatments were nearly identical to those of *Tramea* larvae in combination with de-mented *Erythemis* (SNK, $P < .05$; Fig. 4). Although *Tramea* was also foraging on *Erythemis* (see paragraph below), this did not have a negative effect on the capture rate of damselflies. In contrast, *Erythemis* predation on damselflies was affected by the presence of *Tramea*. *Erythemis* per-capita consumption in the presence of de-mented *Tramea* was significantly less than when foraging alone (SNK, $P < .05$; Fig. 5). On average there was a 61% decrease in damselfly consumption by *Erythemis* in the presence of de-mented *Tramea* as compared to the *Erythemis* treatment (Fig. 2).

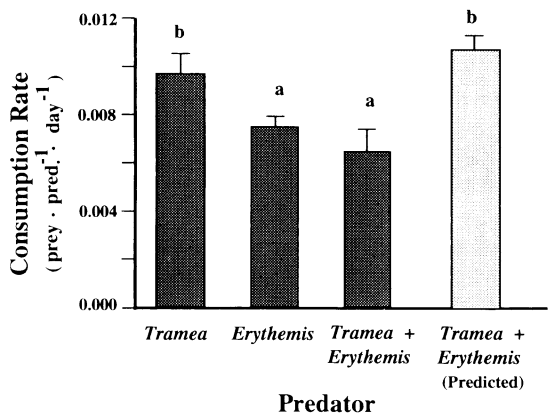

FIG. 3. Per-capita consumption of damselfly larvae (mean and 1 SE; $n = 4$) by dragonfly predators in the laboratory experiment. Means are grouped into statistically different subsets (a, b) based on a Student-Newman-Keuls multiple-comparison test for the overall analysis.

Tramea also had a significant mortality effect on *Erythemis* with intact menta and on de-mented *Erythemis* ($F = 7.69$, df = 3, 11, $P = .004$ and $F = 18.3$, df = 2, 8, $P < .001$, respectively; Fig. 6). On average, *Tramea* reduced the density of *Erythemis* by ≈25%, which would be the magnitude of the trophic-linkage component of an indirect positive effect on damselfly survival. Thus, in this system, it appears that the behavioral component of the non-additive effects of two predators on the mortality of common prey is more than twice (61%) that of the trophic-linkage component.

It is possible that the degree to which interference was asymmetric in this experiment was affected by the de-mentation procedure. *Erythemis* appear to be more sensitive than *Tramea* to mentum excision (Fig. 6). However, in mixed assemblages of odonates in aquaria, *Tramea* are qualitatively more aggressive towards both conspecifics and heterospecifics than are *Erythemis* (S. Wissinger, *unpublished data*). In addition, while being collected as larvae in the field, *Tramea* often attack and consume other larvae in the sorting pans, whereas *Erythemis* are rarely aggressive and are more difficult to sort because of their "freeze" response to disturbance (S. Wissinger, *personal observation*). Thus, while we cannot eliminate the possibility that the de-mentation procedure exacerbated the observed results, the degree of asymmetry we observed in the experiments is consistent with our natural-history observations of these two species.

Finally, the results of the intraspecific comparisons suggest that an increase in predator density, irrespec-

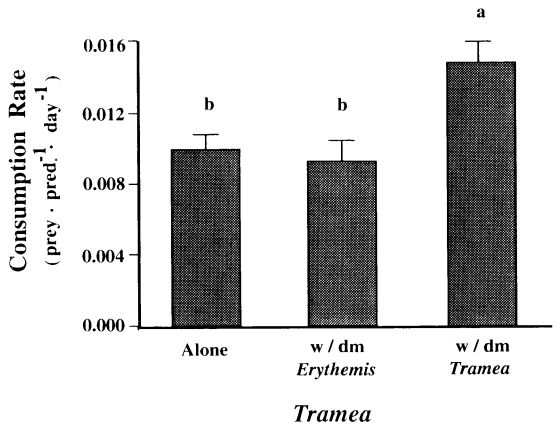

FIG. 4. Per-capita consumption of damselfly larvae (mean and 1 SE; $n = 4$) by *Tramea* when alone, in combination with de-mented *Erythemis*, and with de-mented conspecifics. (dm = de-mented = trophic apparatus removed.) Means are grouped into statistically different subsets (a, b) based on a Student-Newman-Keuls multiple-comparison test for the overall analysis.

tive of species composition, does not result in decreased prey availability. In the case of *Tramea*, consumption rates were actually higher in the presence of de-mented conspecifics than when this species was foraging at lower densities (Fig. 4). Damselfly mortality was greater in this treatment than in any other, with an average of only 15 of the 80 damselflies remaining to the end of the experiment. In contrast, *Erythemis* consumption rates were depressed in the presence of de-mented conspecifics, although to a much lesser degree than was seen in the presence of de-mented *Tramea* (SNK, $P < .05$; Fig. 5).

DISCUSSION

Asymmetric intraguild predation and interference

In the field experiment we found that (1) *Tramea* and *Erythemis* both significantly reduced the density of damselfly larvae, (2) in combined-predator treatments, the total prey mortality was less than predicted from the results of single-predator treatments, and (3) this lower-than-expected mortality was only partly due to *Tramea* predation on *Erythemis*. These interactions should be ecologically relevant (cf. Connell 1983) because they were detected in the field at natural densities, under semi-natural conditions of habitat complexity, and in the presence of alternative prey.

The laboratory experiment was designed to determine the extent to which the reduced mortality of damselflies in combined-predator treatments in the field was due to changes in *Erythemis* foraging in the presence of *Tramea* and/or to changes in *Tramea* foraging in the presence of *Erythemis*. The most revealing result of this experiment was the dramatic reduction in *Erythemis* consumption of damselfly prey in the presence of *Tramea* larvae. This type of behavioral interference has previously been demonstrated for a variety of aquatic invertebrates, including stonefly larvae, aquatic bugs, caddisfly larvae, true fly larvae, damselfly larvae, and crayfish (see recent review by Peckarsky [1991]). In most of these studies, interference is motivated by competition for common resources rather than avoidance of intraguild predation (e.g., Wilson et al. 1978, Hildrew and Townsend 1980, Wilcox and Ruckdeschel 1982, Walde and Davies 1984, Hart 1985, 1986, Peckarsky and Penton 1985, Peckarsky 1991). Even for damselfly larvae, behavioral interference appears to be more related to the defense or acquisition of foraging perches and refuges than to avoiding intraguild predation (Baker 1980, 1981, Rowe 1985, Baker and Dixon 1986, Harvey and Corbet 1986, McPeek and Crowley 1987). In contrast, the interference effect of *Tramea* on *Erythemis* is probably a case in which *Erythemis* faces a tradeoff between foraging for damselflies and being eaten by *Tramea* (see Sih 1978, 1980, Abrams 1984). This type of tradeoff has been described for many aquatic and terrestrial organisms, but in most cases predator and prey are not also competitors (reviews by Dill 1987, Mittlebach and Chesson 1987, Sih 1987, Kohler and McPeek 1989, Turner and Mittlebach 1990, Lima and Dill 1991). In this study, it is likely that the interference effect on *Erythemis* is a result of avoiding *Tramea* predation, which secondarily affects foraging rates and hence competition for shared prey.

In a previous study documenting interference effects between dragonfly larvae, Crowley et al. (1987*a*) found that the presence of large *Tetragoneuria* reduced the movements and capture rates of smaller conspecifics. The other studies describing interference effects in odonates have focused on damselflies and their behavioral response to other odonates or fish (Heads 1985, 1986,

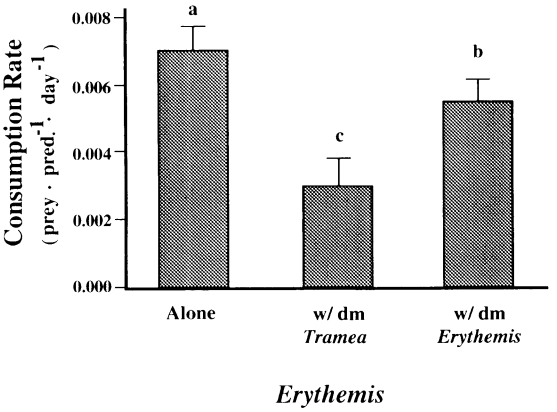

FIG. 5. Per-capita consumption of damselfly larvae (mean and 1 SE; $n = 4$) by *Erythemis* when alone, in combination with de-mented *Tramea*, and with de-mented conspecifics. (dm = de-mented = trophic apparatus removed.) Means are grouped into statistically different subsets (a–c) based on a Student-Newman-Keuls multiple-comparison test for the overall analysis.

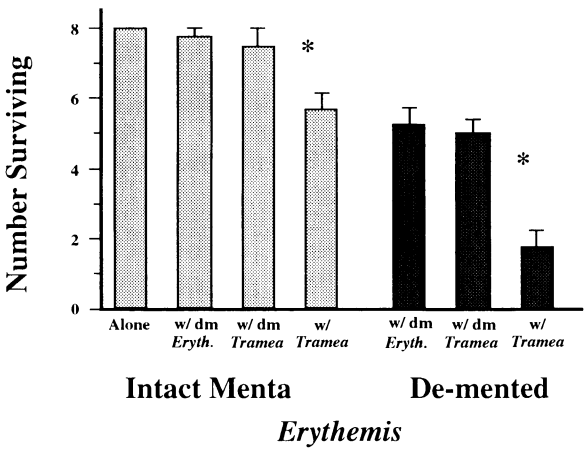

FIG. 6. Number of *Erythemis* and de-mented *Erythemis* surviving (mean and 1 SE; $n = 4$) in the laboratory experiment. (dm = de-mented = trophic apparatus removed.) Asterisks indicate a significant difference between treatments based on Student-Newman-Keuls multiple-comparison test for a one-way ANOVA for each type of *Erythemis* larvae.

Pierce et al. 1985, Crowley et al. 1987*b*, McPeek and Crowley 1987, Dixon and Baker 1988, Pierce 1988, Blois-Heulin et al. 1990, Gribben and Thompson 1990, Jeffries 1990, Johansson 1991, McPeek 1990*b*). Depressed movement is the most common response, although this does not always have a demonstrable cost in terms of feeding rate (Chowdury and Corbet 1988, Baker 1989, Anholt 1990, Jeffries 1990, McPeek 1990*a, b,* Johansson 1991). In this study, we showed that *Erythemis* feeding rates were dramatically reduced by *Tramea,* but our study does not resolve the underlying mechanism(s). Possible mechanisms include depressed movement, increased movement (fleeing), shift in habitat, and/or retreat to a refuge (as in Pierce et al. 1985, Pierce 1988, McPeek 1990*b,* Blois-Heulin et al. 1990). The degree to which *Tramea* reduces the overall food intake of *Erythemis* will depend on the type of behavioral response of *Erythemis* to *Tramea.* For example, a shift in microhabitat that allows the exploitation of alternative prey might have a lower impact on *Erythemis* prey consumption than a depressed movement response (Holbrook and Schmitt 1988 and references therein). Future experiments will focus on the underlying mechanism(s) for reduced *Erythemis* feeding rates in the presence of *Tramea.*

Irrespective of the mechanism, previous studies with odonates suggest that reduced foraging rates can lead to slower growth (Hassan 1976, Lawton et al. 1980, Baker 1982, Wissinger 1988*a,* Pickup and Thompson 1990), which in turn (1) increases the time larvae remain vulnerable to gape-limited predators (Banks and Thompson 1987, Wissinger 1989, Blois-Heulin et al. 1990), (2) increases generation time (Banks and Thompson 1987), and (3) delays emergence, which increases the likelihood of asymmetric competition and intraguild predation in the subsequent generation (Gribben and Thompson 1990; review by Johnson 1991).

Presence of *Erythemis* larvae had no effect on *Tramea* consumption rates despite the fact that foraging time was divided between capturing *Erythemis* and damselflies. This suggests that *Tramea* is not distracted by *Erythemis,* neither in the sense of having its attention divided between a competing predator and shared prey (as in Crowley and Martin 1989), nor in the sense that foraging for *Erythemis* involved a shift in *Tramea*'s foraging mode, search image, or some other aspect of predatory lifestyle (Huey and Pianka 1981, Sih 1987, Johansson 1991) that might detract from detecting and capturing damselflies. Thus, we did not find an indirect positive effect ("apparent mutualism," Holt 1977) between damselflies and *Erythemis* as a result of sharing *Tramea* as a predator (see Huang and Sih 1990, McNeeley et al. 1990).

The absence of an *Erythemis* interference effect on *Tramea* implies that the interference component of the interactions between these two species is amensal. Amensalism—asymmetric competition in which one species adversely affects another, but the second species has no effect on the first—characterizes competitive interactions in the majority of studies involving insects (Lawton and Hassell 1981). The degree to which predator–predator interactions are asymmetric may determine whether their combined effects on prey are additive or less than additive. For example, in a previous study with dragonflies similar in size at a given instar, the combined effects of different species were additive with no apparent interference (Van Buskirk 1988). In contrast, in this study the asymmetric threat of predation between *Tramea* and *Erythemis* results in strong interference and a non-additive effect on total prey mortality. Studies with centrarchid fishes (Werner et al. 1983) and terrestrial arthropod predators (Hurd and Eisenburg 1990) support the prediction that predator–predator interactions are especially likely to have non-additive effects on prey when they include an asymmetric threat of intraguild predation.

Finally, our results add to the growing evidence that an interplay between predation and competition determines coexistence in many guilds of predators (see references in *Introduction*). From this study we can conclude that *Tramea* and *Erythemis* will at least interact (1) as intraguild predators, with asymmetric benefits to *Tramea* both in terms of energy gain and the elimination of a competitor, and (2) as interference competitors, with the negative effect manifested as reduced rates of prey consumption for *Erythemis.* These two types of interactions are interrelated in that the threat of intraguild predation should enhance the asymmetry in the competitive effect. These data support the general observation that larger species are typically superior interference competitors (Morin and Johnson 1988, Peckarsky 1991), and are consistent with the hypothesis that this should be especially true

when the larger competitor also poses a predatory threat (Persson 1985, 1989, Polis 1989).

Intraspecific interactions

The two dragonfly species responded differently to de-mented conspecifics. *Erythemis* per-capita consumption of damselflies was reduced in the presence of de-mented conspecifics, but not as dramatically as in the presence of de-mented *Tramea.* This reduction could be due either to some change in prey behavior that reduces prey availability (i.e., to resource depression; Charnov et al. 1976), or to a change in predator behavior (i.e., intraspecific interference). In contrast, *Tramea* consumption rates increased in the presence of de-mented conspecifics, perhaps as a result of increased movement of prey at higher densities of predators (i.e., "resource enhancement"; Charnov et al. 1976, Sih 1979). The contrasting intraspecific results suggest that the interspecific effects we observed between *Tramea* and *Erythemis* were not due solely to resource depression. Preliminary behavioral observations suggest that the opposite responses of *Tramea* and *Erythemis* to increased densities of conspecifics might be related to differences in foraging mode (stalking vs. sit-and-wait, respectively). *Tramea* are generally more active climbers, and this activity may flush damselflies from their perches.

Indirect effects and keystone predation

Most predators are polyphagous (Hassell 1978), and polyphagy appears to be especially common in freshwater ecosystems where many predators are generalists within a size/year class and, in addition, also shift ontogenetically in prey use (Werner 1984, 1986, Werner and Gilliam 1984, Wilbur 1984, Vadas 1990). As a result, omnivory (sensu Pimm 1978), including intraguild predation, is common, and food web connections will be characterized by redundancies (sensu Bradley 1983) and loops (Jeffries 1975). The manipulation of one predator in such a food web will have numerous indirect and direct effects (see reviews by Kerfoot and Sih 1987, Carpenter 1988), so that the net impact on the community or on any one other species may be difficult to detect (Sprules and Bowerman 1988).

The results of this study provide an empirical demonstration of how the direct effects of predator addition on a known prey species can be reduced by compensating indirect interactions with other predators. Considering only direct effects, foraging rates from single-predator treatments suggest that *Tramea* immigration would result in a 118% increase in damselfly mortality as compared to a system with only resident *Erythemis.* However, *Tramea* will also have two types of negative effects on *Erythemis,* which should positively affect damselfly survival. The first is a trophic-link indirect effect (Miller and Kerfoot 1987, Kotler and Holt 1989) in which *Tramea* predation on *Erythemis* reduces the number of *Erythemis* preying on damselflies (by 25%). The second is a behavioral indirect effect (Miller and Kerfoot 1987, Kotler and Holt 1989, Skelly and Werner 1990, Huang and Sih 1991) through which *Tramea* reduces the foraging rates of the remaining *Erythemis* (by 61%). Under the spatial and temporal conditions in our experiments, indirect effects would reduce the net effect of *Tramea* invasion on damselfly mortality from 118% to only 32%. The direct negative effect of *Tramea* predation on damselflies still exceeds the indirect positive effects on prey through reduced *Erythemis* predation, but by much less than if those indirect effects were ignored. This result differs from that of Huang and Sih (1991) who found that the total indirect positive effects on prey of interactions between predators were greater than the direct negative effects of predation.

Compensatory effects need not be predictable from the strength of trophic links if interference between predators is mainly behavioral (Turner and Mittlebach 1990). Huang and Sih (1991) found that the behavioral component of an indirect interaction (reduced salamander foraging for isopods in the presence of fish) is more important than the trophic-link component (fish predation on salamanders). Similarly, in this study, the behavioral component of the indirect effect of predator–predator interactions (reduced *Erythemis* foraging for damselflies in the presence of *Tramea*) is more than twice as strong as the trophic-link component (intraguild predation by *Tramea* on *Erythemis*). Behavioral interference is often an important mediator of interactions among aquatic invertebrates (see review by Peckarsky 1991), and between fish and invertebrate predators (Pierce et al. 1985, Pierce 1988, Soluk and Collins 1988, Kohler and McPeek 1989, McPeek 1990*a, b*). Thus, even though trophic-link connections among these predators may appear to be weak, the net effects of top-predator removal (or addition) should be difficult to detect because behavioral responses will lead to increased (or decreased) predation rates by other predators. Such compensatory responses among competing predators may explain why predator manipulations in freshwater invertebrate communities have often had unpredictable or undetectable effects on community composition (Allan 1982, Gilinsky 1984, Thorp 1986, Yodzis 1988).

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