

# The influence of an ecosystem-level manipulation on prey consumption by a lotic dragonfly

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Received March 31, 1986

WALLACE, J. B., T. F. CUFFNEY, C. C. LAY, and D. VOGEL. 1987. The influence of an ecosystem-level manipulation on prey consumption by a lotic dragonfly. *Can. J. Zool.* **65**: 35–40.

Pesticide application to a small headwater stream (treatment stream) resulted in massive invertebrate drift and altered community structure with respect to both biomasses and densities. The community changed from one dominated by insects to one of primarily noninsects. Insects represented 71 to 78% of total abundance and about 95% of total biomass in an adjacent reference stream during 2 years of study. During the initial treatment year, insects, mainly Chironomidae, composed less than 20% of total invertebrate biomass (<10% of abundance) in litterbags in the treatment stream. Within 2 years of the initial disturbance, invertebrate biomass in the treatment stream was again dominated by insects (90% of total) although insects represented only 36% of total abundance. *Lanthus vernalis* Carle (Odonata: Gomphidae) was among the insect taxa least affected by the treatment. Diets of larval *Lanthus* (gut analyses) reflected changes in community structure within the treatment stream, with insects representing only 13% of the prey during the initial treatment year and more than 82% during the 2nd year of recovery. In contrast, *Lanthus* in the reference stream consumed primarily insects (73 to 78%) in both years. These data indicate that generalist predators such as *Lanthus* can readily shift to alternative prey when confronted by massive changes in community structure. The results suggest that this disturbance reduced the abundance of the more profitable prey to a level where less profitable prey increased in the diet. Following the disturbance, *Lanthus* consumption reflected the recovery of more profitable prey in the environment. Secondary production of *Lanthus* approached 27% of average standing stock biomass of invertebrates in litterbags in each stream and, based on literature values for bioenergetic efficiencies, *Lanthus* consumed about 65% of the average standing stock biomass of invertebrates. Total consumption necessary to support production of all invertebrate predators may exceed the average standing stock prey biomass by 2.5 to 2.7 times. However, when prey turnover is considered, the potential impact of this predation on invertebrate community structure may be quite modest.

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L'application d'un pesticide à un petit ruisseau de tête (ruisseau traité) a entraîné une dérive massive des invertébrés et modifié la structure de la communauté, tant du point de vue de la biomasse que du point de vue de la densité. La communauté, surtout dominée par les insectes au départ, est devenue dominée surtout par les organismes autres que les insectes dans le ruisseau traité. Dans un ruisseau voisin considéré comme ruisseau témoin, les insectes constituaient 71 à 78% de l'abondance totale et environ 95% de la biomasse totale durant les 2 années qu'ont duré l'étude. Au cours de la première année de traitement, la communauté d'insectes, surtout des Chironomides, constituait moins de 20% de la biomasse totale d'invertébrés (<10% de la densité totale) dans des sacs de litière. En moins de 2 ans, la biomasse des invertébrés dans le ruisseau traité est redevenue dominée par les insectes (90% du total), mais les insectes ne constituaient que 36% de l'abondance totale. *Lanthus vernalis* Carle (Odonata: Gomphidae) était l'une des espèces d'insecte le moins affectées par le traitement. Le régime alimentaire des larves de *Lanthus* (analyse des contenus stomacaux) reflétait bien les changements dans la structure de la communauté; les insectes ne constituaient que 13% des proies au cours de la première année qui a suivi le traitement, mais 82% des proies au cours de la seconde année. Dans le ruisseau témoin, *Lanthus* a consommé surtout des insectes au cours des 2 années (73 à 78%). Ces résultats indiquent que les prédateurs généralistes tels *Lanthus* peuvent s'accommoder facilement de proies de rechange lorsqu'il se produit des changements massifs dans la structure de la communauté. Il semble que le traitement ait diminué l'abondance des proies les plus profitables jusqu'à un point à partir duquel des proies moins profitables sont venues constituer le régime alimentaire. Par la suite, le régime alimentaire de *Lanthus* s'est mis à refléter la réapparition des proies plus profitables dans le ruisseau. La production secondaire de *Lanthus* représentait près de 27% de la biomasse moyenne d'invertébrés dans des sacs de litière dans chacun des ruisseaux et, d'après les données de la littérature sur l'efficacité bioénergétique, *Lanthus* consommait environ 65% de la biomasse moyenne d'invertébrés. La consommation totale nécessaire à la production de tous les prédateurs d'invertébrés semble dépasser la biomasse moyenne de proies par un facteur de 2,5 à 2,7. Cependant, lorsqu'on tient compte du remplacement des proies, le potentiel d'impact de cette prédation sur la structure de la communauté des invertébrés est probablement assez limité.

[Traduit par la revue]

## Introduction

Larval odonates are regarded as generalist predators that feed on a variety of prey species (Koslucher and Minshall 1973; Thompson 1978a; Corbet 1980; Johnson 1982; Johnson *et al.* 1984, 1985; Folsom and Collins 1984; Merrill and Johnson 1984; Thorp and Cothran 1984). Some workers have reported that, within limits, some species of odonates appear to consume prey taxa in roughly the same proportions as their relative abundances in the environment (Thompson 1978a). In contrast,

other workers have found some disparity between prey consumed and their abundance in the environment (Lawton 1970; Johnson 1982; Folsom and Collins 1984).

The relative proportion of a given prey type consumed may be influenced by factors such as encounter rates between predator and prey (Lawton *et al.* 1974; Thompson 1978a; Akre and Johnson 1979; Folsom and Collins 1984; Cothran and Thorp 1985), handling time for prey of various types and sizes (Thompson 1975, 1978b), hunger (Lawton *et al.* 1974; Akre and Johnson 1979), and the presence or absence of refugia for prey species (Benke 1976, 1978; Folsom and Collins 1984; Cothran and Thorp 1985). Some odonates also have the remarkable ability to survive through periods of extreme food

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stress (Lawton *et al.* 1980). Profitability (energy yield per unit handling time) is probably also important and, although not studied directly for odonates, Charnov (1976) demonstrated its importance for mantid predators.

Habitat complexity and prey behavior may have a profound influence on prey selection by odonates and many of the above results were obtained in laboratory experiments which do not necessarily reflect results obtained in the field (Folsom and Collins 1984). Several studies have attempted to estimate the influence of *in situ* odonate predation on their prey either by inference (Benke 1976), or through direct field manipulations (Benke 1978; Johnson *et al.* 1984, 1985; Thorp and Cothran 1984; Pierce *et al.* 1985). However, as pointed out by Allan (1983), "without a laboratory or very fortuitous field experimental design, it is extremely difficult to generalize on prey choice by invertebrate predators."

Ecosystem disturbances may alter growth rates, abundances, and biomass of potential prey species available to consumers. It has been hypothesized that such disturbances may reduce the abundance of more profitable prey items to a level where less profitable prey items are included in the diet (Glasser 1979). In 1980, insecticide application to a small headwater stream (treatment stream, TS) resulted in massive insect drift and reduced aquatic insect densities and biomass in litterbags to <10% of those found in an adjacent, untreated, reference stream (RS). Subsequently, noninsect invertebrate densities and biomass increased in the TS compared with the RS (Wallace *et al.* 1982; Cuffney *et al.* 1984). Densities and biomass of the larval dragonfly predator, *Lanthus vernalis* Carle (Odonata: Gomphidae) in the TS were only 50% of those of the RS. Although reduced in biomass and density, *Lanthus* was the least-affected insect predator in the TS, where it represented 74% of total insect predator biomass compared with 33% in the RS.

Our objectives are to examine the influence of this severe ecosystem-level manipulation on dragonfly prey consumption. Specifically, we will address the following questions. Do severe ecosystem-level disturbances, which affect prey densities and biomass, influence a predator's pattern of prey consumption? How consistent are the predator's consumption patterns in undisturbed and manipulated streams between years? What is the estimated influence of *Lanthus* predation on litterbag fauna in these streams?

### Site description and methods

The two first-order streams studied drain catchments 53 (TS: catchment area = 5.2 ha) and 54 (RS: catchment area = 4.2 ha) at the Coweeta Hydrologic Laboratory of the United States Forest Service in the Blue Ridge Province of the southern Appalachian Mountains in Macon County, North Carolina. Normal discharge on the two study streams ranges from about 0.2 to 2.3 L/s and temperatures range from about 4 to 17°C in each stream. Additional site descriptions can be found in Wallace *et al.* (1982), Cuffney *et al.* (1984), and Wallace *et al.* (1986).

#### Treatment

Treatment consisted of applications of the pesticide methoxychlor (1,1,1-trichloro-2,2-bis(*p*-methoxyphenyl)ethane) to the TS on each of four dates: 16 February, 10 May, 20 August, and 8 November 1980. Since the last date, there have been no additional treatments applied to this stream. Details of treatments can be found in Wallace *et al.* (1982) and Cuffney *et al.* (1984).

#### Collection and processing of samples

All invertebrates were collected from litterbags (35 × 18 cm; mesh size = 5 mm) that were each filled with about 15 g dry weight of leaves.

In 1980, litterbags were placed in each stream on 16 February and 12 litterbags were removed on eight dates between 4 March 1980 and 8 February 1981 ( $n = 96$  per stream). In 1982, litterbags were placed at the same location in each stream on 20 February and 16 bags were removed on each of nine dates between 28 February 1982 and 14 March 1983 ( $n = 144$  per stream). See Wallace *et al.* (1982, 1986), and Cuffney *et al.* (1984) for additional details.

In the 1980 samples, invertebrates, detritus, and sediments washed from the litterbags were retained on a 250- $\mu$ m sieve. Invertebrates were removed by hand from this material and from leaf material that remained in bags after washing. In 1982, samples were processed similarly except that the material retained on 250- $\mu$ m mesh sieves was subsampled (1/8 to 1/16 of original sample) using a sample splitter (Waters 1969). Invertebrates were removed from these subsamples by handpicking under 10 × magnification. This subsampling procedure greatly increased the efficiency of recovery of small invertebrates (especially Copepoda, Acarina, and early instars of Chironomidae) as overall abundances were greater in *both* streams during the 1982 study. Similar enhanced recovery of small organisms has been found for other benthic sampling programs at Coweeta following introduction of this sample splitter (J. B. Wallace, D. Vogel, and T. F. Cuffney, unpublished data). In the 1980 study, ash-free dry mass (AFDM) of representative organisms in each taxon were used to determine biomass (mg AFDM) in each sample, whereas in the 1982 study AFDM of invertebrates was calculated and summed for each sample using taxon-specific size-weight regressions for each genus.

#### Lanthus gut contents

Head widths of *Lanthus* were measured using a dissecting microscope equipped with an ocular micrometer. Foreguts were extracted and contents filtered onto membrane filters, which were then mounted on microscope slides (Cummins 1973). The average head widths of RS specimens used for gut analyses were 2.3 mm (SD = 0.8,  $n = 28$ ) for 1980 and 2.7 mm (SD = 1.1,  $n = 43$ ) for 1982, versus 2.1 mm (SD = 0.7,  $n = 29$ ) for 1980 and 2.1 mm (SD = 1.1,  $n = 69$ ) for 1982 for TS specimens. Prey were identified by scanning each slide at 100× and 300× using a compound microscope. Thompson (1978a) has discussed some of the problems involved with prey identification and techniques to resolve them. The presence of chaetae (e.g., Pennak 1978; Thompson 1978a) were regarded as evidence for consumption of oligochaetes. Turbellarians were not discernible in any guts examined because of the absence of recognizable body parts. Hence, turbellarians were deleted from comparisons of gut contents with prey abundances in litterbags.

#### Data analysis

The following invertebrates, which represented 93 to 96% of total abundances and 92 to 98% of total biomass in litterbags, were considered: Nematoda, Oligochaeta, Copepoda, Acarina, Odonata, Ephemeroptera, Plecoptera, Trichoptera, Chironomidae, and other Diptera. Each group was treated on the basis of its relative contribution to total litterbag abundances, proportional contribution to total litterbag biomass, and proportional contribution to gut contents of *Lanthus*.

Data were compared by proportional similarity and correlation based on a maximum of 10 prey categories listed above. Proportional similarities (PS) were calculated using Whittaker's (1975) method:

$$PS = 1 - 0.5 \sum |P_a - P_b| = \sum \min(P_a \text{ or } P_b)$$

where  $P_a$  = decimal importance value for a given taxa in sample A,  $P_b$  = the same for sample B. For correlation, all percentages were arcsine transformed (Zar 1984).

#### Secondary production

In the 1982–1983 study, head widths were used to sort larvae into seven size classes, which were used to construct larval size class distributions for *Lanthus* on each sample date. Weights for each size class were estimated with size-weight regressions. The mean weight of individuals in each size class and their abundance in each litterbag on each date were used to calculate size-frequency production estimates ( $\pm 95\%$  CI) per litterbag (Krueger and Martin 1980).

TABLE 1. Proportional similarities (PS) and correlation coefficients ( $r$ ) for invertebrate abundances and biomasses in litterbags in the reference stream (RS) and pesticide-treated stream (TS) based on 10 prey categories

	PS ( $r$ )		
	RS 80	TS 80	RS 82
Invertebrate abundances in litterbags			
TS 80	0.299(0.36)		
RS 82	0.653(0.76**)	0.228(0.16)	
TS 82	0.393(0.24)	0.217(0.17)	0.567(0.72**)
Invertebrate biomass in litterbags			
TS 80	0.188(0.03)		
RS 82	0.897(0.97***)	0.169(-0.07)	
TS 82	0.747(0.78**)	0.156(-0.03)	0.819(0.86**)
<i>Lanthus</i> gut contents			
TS 80	0.358(-0.10)		
RS 82	0.821(0.82**)	0.343(-0.38)	
TS 82	0.620(0.48)	0.305(-0.33)	0.686(0.60*)

NOTE: RS 80 and TS 80, initial treatment year (1980–1981); RS 82 and TS 82, 2nd year recovery (1982–1983). The levels of significance for the correlation coefficient ( $r$ ) are as follows: \*,  $0.01 < P < 0.05$ ; \*\*,  $0.001 < P < 0.01$ ; \*\*\*,  $P < 0.001$ .

## Results

### *Litterbag fauna 1980–1981 versus 1982–1983*

Abundances and biomasses of invertebrates occurring in the RS litterbags were significantly correlated between the two study periods (abundance  $r = 0.76$ ,  $P < 0.01$ ; biomass  $r = 0.97$ ,  $P < 0.001$ ) (Table 1, Fig. 1). Proportional similarity indices followed similar trends between years in the RS with values of 0.653 and 0.897 for abundances and biomass, respectively. The differences in abundances and biomass are partially attributed to increased sampling efficiency of small invertebrates, e.g., copepods, Acarina, and early instars of chironomids, during the 2nd year. These small animals contribute relatively little to total standing stock biomass within litterbags. Thus, biomasses were more similar than abundances between years in the RS.

During the initial treatment year, there was a shift in fauna in the TS from an invertebrate community dominated by insects to one dominated by the Oligochaeta (Fig. 1) (see also Wallace *et al.* 1982; Cuffney *et al.* 1984). Trophic structure (functional group biomass) had recovered in the TS within 2 years (Wallace *et al.* 1986). Thus, there was little similarity in abundance (PS = 0.217,  $r = 0.17$ ) or biomass (PS = 0.156,  $r = -0.03$ ) in the TS between years (Table 1, Fig. 1).

Between-stream comparisons during the initial treatment year show little similarity in abundance (PS = 0.299,  $r = 0.36$ ) or biomass (PS = 0.188,  $r = 0.03$ ) for the 10 prey categories considered here. Conversely, 1982–1983 between-stream comparisons of abundance (PS = 0.567,  $r = 0.72$ ,  $P < 0.01$ ) and biomass (PS = 0.819,  $r = 0.86$ ,  $P < 0.01$ ) were more similar, reflecting dramatic changes during recovery of the TS. Despite the recovery of insect biomass (and to a lesser extent abundances) in the TS (Fig. 1), considerable differences remained within our 10 prey categories for individual taxa colonizing each stream. These generic and specific differences are discussed elsewhere (Wallace *et al.* 1986).

### *Lanthus* gut contents: 1980 versus 1982

Between-year within-stream comparisons of gut contents of

*Lanthus* were similar for the RS (PS = 0.821,  $r = 0.82$ ,  $P < 0.01$ ) whereas those for the TS were not (PS = 0.305,  $r = 0.33$ ). Within-year between-stream comparisons indicate that *Lanthus* consumed different proportions of prey items between streams in 1980–1981 (PS = 0.358,  $r = 0.10$ ) compared with 1982–1983 (PS = 0.686,  $r = 0.60$ ,  $P < 0.05$ ) (Table 1).

In the RS, insects were the major prey of *Lanthus* in both years, comprising 73% of total prey items in 1980–1981 and 78% in 1982–1983. Plecopteran larvae were the most frequent items consumed (27.1 to 29% of all prey) followed by larvae of Chironomidae (16.3 to 20.8%) and Trichoptera (10.4 to 11.6%). Oligochaetes (8.1 to 12.5%) and copepods (8.1 to 10.4%) were the most frequently consumed noninsect prey in the RS (Fig. 1).

In the TS, *Lanthus* underwent a large dietary shift between years. Noninsects represented 87% of total prey during the treatment year (1980–1981) but only 17.8% during post-treatment (1982–1983). During 1980–1981, copepods comprised 28.3% of all prey followed by oligochaetes (26.1%) and nematodes (23.9%). Conversely, during 1982–1983, Trichoptera (26.7%), chironomids (24.7%), and other Diptera, primarily tipulids and ceratopogonids (14.6%), were the most frequently consumed items in the TS (Fig. 1).

### *Environmental prey abundances versus frequencies in guts*

Prey items consumed by *Lanthus* (gut analyses) were significantly correlated with prey abundances in litterbags only during 1980–1981 (RS:  $r = 0.77$ ,  $P < 0.01$ ; TS:  $r = 0.64$ ,  $P < 0.05$ ) (Table 2). Nematodes, which composed over 20% of the prey items in the TS in 1980–1981, were not adequately sampled in the litterbag by our methods. Gut contents were poorly correlated with abundances in 1982–1983 in both streams when recovery of small individuals, especially copepods, was enhanced (RS:  $r = 0.50$ ,  $P > 0.05$ ; TS:  $r = 0.31$ ,  $P > 0.10$ ). However, *Lanthus* consumed insects in greater proportion than their relative abundances in litterbags during the 2nd year of recovery (1982–1983) in the TS (Fig. 1).

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