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THE DIET OF ANISOPTERAN LARVAE FROM TWO STREAMS IN NORTH-EASTERN VICTORIA, AUSTRALIA*

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The diets of larvae of 7 spp. from the Kiewa River and Middle Creek, Victoria were examined and compared from faecal pellet examination. Differences between spp. instars and season reflect a high degree of opportunism among these polyphagous predators, with differences in prey spectrum reflecting habitat and feeding method.

INTRODUCTION

As part of a study of the factors influencing numbers and distribution of Odonata in the Kiewa River system and associated water bodies in north-eastern Victoria, Australia (Fig. 1) (HAWKING, 1994), series of larvae of the more abundant Anisoptera were subjected to dietary analysis by examining the prey remains in faecal pellets (PRITCHARD, 1964; LAWTON, 1970; THOMPSON, 1978; BLOIS, 1985). The aims were (1) to document, in part, the natural diets of these taxa, (2) to compare diets of co-occurring species and investigate the extent of dietary overlap, and (3) to examine temporal variation in diet within and between species and instars. Collectively, these parameters may suggest whether differences in prey spectrum are significant in ecological segregation of these aquatic predators.

METHODS

SOURCE OF LARVAE. – Larvae of Anisoptera were collected during regular monthly or bimonthly samples (March 1989 - February 199) by kick sampling (five samples/site, each 0.5 m^2 area, 5-10 cm depth, agitated for 30 seconds, specimens recovered in 500 m mesh net downstream), log picking

* This paper is dedicated to the memory of our good friend and colleague, the late Dr J.A.L. (Tony) Watson.

(examination of any available submerged wood) and sieving (dredging mud and detritus from depositional sections and sieving through a 2 mm mesh sieve). Three sites were used (Fig. 1), Killara and Upper Gundowring on the Kiewa River, and Bandiana on Middle Creek. These sites are similar in altitude but differ in topography and substrate:

(a) Killara (K_1) (36°08'S, 146°-5/'E). River width 20-35 m, with average belowbank depth of 3.6 m; substrate of gravel and sand in erosional sections and fine sediments in depositional sections; submerged wood common on margins. Altitude 160 m.

(b) Upper Gundowring (K_2) (36°-30'S, 147°03'E). River width 45-50 m; substrate of cobbles in the riffles, cobbles and gravels in the depositional zones, fine silt in backwater pools; small amounts of fallen wood. Altitude 225 m.

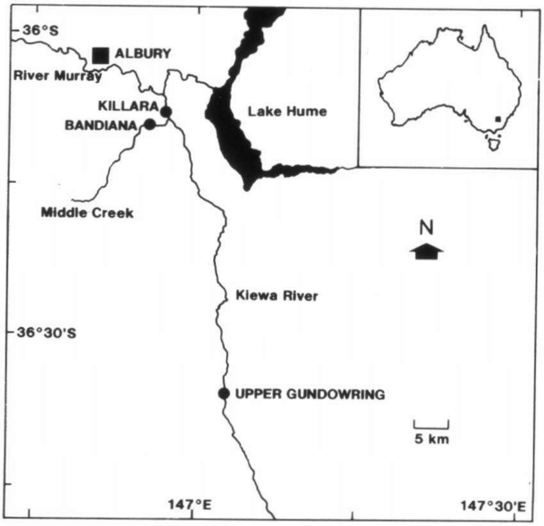

Fig. 1. Map of the study area; – Collection sites, Killara and Upper Gundowring (Kiewa River), and Bandiana (Middle Creek), north-eastern Victoria.

(c) Middle Creek (MC) (36°10'S, 146°56'E). Small third order stream with between-bank width of 1.5-3 m; channel of sand, with accumulated detritus and mud in backwater areas. Altitude 172 m.

TREATMENT OF LARVAE. – Living larvae were transported individually, maintained at 10°C during field storage. Each was then maintained in a 28 ml McCartney bottle for up to 48 h to allow passage of any faecal pellet present. Pellets were preserved individually, with the host larva, in 70% alcohol. Each was later broken up and contents mounted in a PVA medium on a microscope slide; larvae were identified to species and instar using HAWKING (1986) and measurements of growth stages obtained by rearing larvae for instar determination. In this paper, 'f' is the final instar; 'f-1' 'f-2' etc refers to the penultimate instar, the second last instar, and so on.

ANALYSIS OF DIET. – Contents of the faecal pellets were examined under a standard Zeiss compound microscope at 100 or 400 x magnification, and a photographic index of all identifiable prey remains developed for comparison with all gut contents. Prey items were allocated to nine major groups (Tab. I), some of which were later subdivided into family or subfamily components. Numbers were determined by summation of parts to give minimum numbers of individuals (BAKER & CLIFFORD, 1981); for Oligochaeta, abundance was more subjectively based on chaeta numbers: <60 chaetae was assessed as one individual, 60 or more chaetae as two individuals. 'Unidentified' represents chitinous fragments which could not be allocated reliably to order. Incidence of sand or other inorganic material in pellets was also noted. A prey per pellet index was derived by dividing the total number of prey individuals by the number of pellets containing prey.

RESULTS

The prey recorded from the seven most abundant species of Anisoptera (Tab. I) was derived from about a quarter of the 1305 larvae collected, and prey remains were found in more than 70% of the pellets of each species.

Table I

Summary of prey (number) incidence in faecal pellets of seven species of Anisoptera larvae from the Kiewa River (K_1, K_2 see text) and Middle Creek (MC), Victoria. – [*A.u.*: *Austroaeschna u. unicornis*; – *H.p.*: *Hemianax papuensis*; – *A.c.*: *Austrogomphus cornutus*; – *A.o.*: *A. ochraceus*; – *H.g.*: *Hemigomphus gouldii*; – *A.m.*: *Apocordulia macrops*; – *D.h.*: *Diplacodes haematodes*]

Prey category	Species (site)							
	A.u. (K_1)	*A.u.* (MC)	*H.p.* (MC)	*A.c.* (MC)	*A.o.* (K_1)	*H.g.* (K_2)	*A.m.* (K_1)	*D.h.* (MC)
Ephemeroptera	27	35	24	13	7	8	3	14
Odonata	5	0	2	0	0	1	1	1
Plecoptera	1	0	1	0	0	4	0	0
Hemiptera	6	0	4	3	1	2	0	4
Coleoptera	10	6	8	3	4	0	2	8
Diptera	58	13	12	44	14	5	13	1
Trichoptera	8	2	2	0	1	4	2	0
Acarina	2	2	0	0	0	3	0	0
Oligochaeta	0	0	0	47	5	6	0	0
Unidentified	4	4	2	23	7	15	0	3
No. larvae tested	167	102	116	546	55	199	51	69
% with pellets	19	24	23	17	42	20	22	28
No. pellets with prey	31	24	27	93	23	39	11	19
No. prey	121	62	55	133	39	48	21	31
Average prey/pellet	3.90	2.58	2.04	1.43	1.70	1.23	1.91	1.63

The prey categories are ranked in order of abundance in Table II. Major results for each taxon are as follows:

AESHNIDAE. – *Austroaeschna u. unicornis* (Martin): Both populations sampled had fed heavily on Diptera and Ephemeroptera larvae, with Coleoptera the third-ranked food category. Other foods were eaten only in very small quantities, and no Oligochaeta were found in the diet of either population.

Hemianax papuensis (Burm.): Very similar trends to *A. u. unicornis*, with Ephemeroptera the predominant food item.

GOMPHIDAE. – *Austrogomphus cornutus* Watson: This was the only species sampled which had eaten substantial numbers of Oligochaeta. Diptera larvae followed closely in abundance and only Ephemeroptera was otherwise eaten commonly.

A. ochraceus (Sel.) and *Hemigomphus gouldii* (Sel.): These species had both also eaten Oligochaeta but other food categories (Ephemeroptera, Diptera) were slightly more frequent in the samples examined. The three gomphid species had also eaten numbers of 'unidentified' prey.

CORDULIIDAE. – *Apocordulia macrops* Watson: Other than Diptera, all food categories were sparsely represented or not found in the sample.

LIBELLULIDAE. – *Diplacodes haematodes* (Burm.): Unusually, Diptera were a very small dietary component, and Ephemeroptera and Coleoptera both much more frequent.

There seemed to be similarities and differences between the diets of Aeshnidae and Gomphidae, from the limited evidence of three samples of each family. No traces of Oligochaeta were found in the 82 aeshnid pellets containing prey, whereas oligochaetes were ranked in the top three food categories of the three Gomphidae (Tab. II), all of which were from different sites. The 'unidentified' category was

Table II

Ranking of prey abundance in faecal pellets of seven species of Anisoptera – [Abbreviations of species as in Tab. I; – C: Coleoptera; – D: Diptera; – E: Ephemeroptera; – H: Hemiptera; – O: Oligochaeta; – Od: Odonata; – P: Plecoptera; – T: Trichoptera; – Un: unidentified]

		Species (site)							
		A.u. (K_1)	*A.u.* (MC)	*H.p.* (MC)	*A.c.* (MC)	*A.o.* (K_1)	*H.g.* (K_2)	*A.m.* (K_1)	*D.h.* (MC)
Most abundant prey	1	D	E	E	O	D	Un	D	E
	2	E	D	D	D	E/Un	E	E	C
	3	C	C	C	Un	O	O	C/	H
	4	T	Un	H	E	C	P/T	Od	Un
No. of prey categories		*9*	*6*	*8*	*6*	*7*	*9*	*5*	*6*

also high in this family. Only one species (*A. u. unicornis*) was collected in the Kiewa River and Middle Creek, and diets of the two populations were reasonably consistent. Of the four co-occurring Middle Creek species, there were clear differences in diet as noted above, although the two aeshnids had the same ranking of Ephemeroptera over Diptera. The three Killara species all had diptera as the most frequent food category, and Ephemeroptera as the second-ranked, although numbers of the latter were sometimes small. Sand was also present in a high proportion of pellets from the Gomphidae, but found only occasionally in the other species.

However, all species were clearly polyphagous. *A. u. unicornis* and *H. gouldii* had each eaten nine different prey categories, and the smallest number, five, was taken by *A. macrops*. Overall, Diptera and Ephemeroptera were the highest ranked food items, being first for seven/eight samples and second in six. Further dietary influences can be made by considering variations over the sampling period and differences between instars of the more abundant species, as follows, with the Diptera category subdivided into major components.

Numbers of faecal pellets listed in Table III differ from some values given earlier because small samples from other sites, in themselves insufficient to give sound comparative information, are included where available. Incidence of pellets on different dates, and from different species, varies greatly. Discussion of

Table III

Seasonal representation of pellets analysed for prey contents (all samples). – [Number of pellets on each occasion given for sampling periods from March 1989 - January/February 1990; – months designated by initial letter]

species	Number of faecal pellets in									
	M	A	M	J	J	A/S	O	N	D	J/F
A. u. unicornis (K_1)	13	-	-	-	7	7	-	6	3	9
A. u. unicornis (MC)	-	-	-	-	-	-	-	-	8	16
H. papuensis	6	8	3	-	1	-	-	-	-	8
A. cornutus	9	13	5	1	17	22	33	26	12	3
A. ochraceus	5	-	-	-	-	1	-	4	7	8
H. gouldii	-	-	6	-	4	3	2	16	10	3
A. macrops	3	-	-	-	-	-	-	1	6	1
D. haematodes	-	4	-	2	-	-	-	-	-	13
No. species	*5*	*3*	*3*	*2*	*4*	*4*	*2*	*5*	*5*	*7*
No. pellets	*36*	*25*	*14*	*3*	*29*	*33*	*35*	*53*	*46*	*61*

results is thereby limited; for any given sampling date only samples of 9 or more pellets are noted for assessment below.

On this basis, no more than two samples can be compared on a sampling date, and only four months allow for direct comparison:

March: *A. cornutus* (9 pellets), *A. u. unicornis* (13 pellets). Chironominae were the predominant prey of both species, comprising 64% (45/70 items) in *A. u. unicornis* and 60% (6/10) in *A. cornutus*. Both species had diverse diets: 4 categories in *A. cornutus* and 7 categories in *A. u. unicornis*.

November: *A. cornutus* (26 pellets), *H. gouldii* (16 pellets). *A. cornutus* had a predominance of Chironominae and Oligochaeta: 38% and 29.4%, respectively of 34 prey items representing 6 prey categories. No Chironominae were among the 9 prey categories (20 items) recovered from *H. gouldii* pellets.

December: *A. cornutus* (12 pellets), *H. gouldii* (10 pellets). Oligochaeta (16/19

Table IV

Diet analysis of *Austrogomphus cornutus* larvae from faecal pellet contents, March - December 1989. – [Months indicated in sequence, only for samples with 10 or more pellets]

Prey	Number prey items					
	Ap	Jy	A/S	O	N	D
Diptera						
Orthocladiinae	-	-	2	33	-	-
Chironominae	2	-	1	1	13	-
Unidentified	-	-	1	-	1	-
Coleoptera	-	-	1	1	-	1
Ephemeroptera	1	-	2	4	2	1
Hemiptera	-	1	-	2	1	-
Oligochaeta	2	1	11	10	10	16
(Unidentified)	1	5	6	-	7	1
No. pellets	13	17	22	33	26	12
No. prey	5	7	24	51	34	19
No. empty pellets	8	2	2	11	4	1

prey) dominated the diet of *A. cornutus*, and only singletons in three other categories occurred. Small numbers of three insect categories comprised the 10 prey items from *H. gouldii*.

January/February: *A. u. unicornis* (MC, 16 pellets), *D. haematodes* (13 pellets). Both species had Ephemeroptera as the predominant prey: 26/41 and 9/25, respectively, with small numbers of seven other categories making up the balance for each.

Within a species, only *A. cornutus* was sufficiently represented to allow any analysis of temporal variation in diet (Tab. IV). Empty pellets were obtained in all samples. Oligochaeta were recovered from all samples, but were abundant from August to December. Most other food items were more sporadic, but Diptera (Orthocladiinae) were abundant in October only. On each occasion a variety of different prey items was eaten.

Table V

Dietary composition of larvae of *Austrogomphus cornutus*, from analysis of faecal pellets of instars f to f-4; percentage composition given for major food items

Prey category	% incidence of total diet of instar				
	f	f-1	f-2	f-3	f-4
Diptera					
Orthocladiinae	23	19	14	22	50
Chironominae	9	12	18	17	31
Oligochaeta	41	33	43	35	6
No. pellets	*15*	*30*	*35*	*23*	*16*

A. cornutus pellets were also analysed by larval instar, to allow comparison of the diets of the final five instars (Tab. V). Dipteran larvae (Orthocladiinae, Chironominae) and Ephemeroptera were also frequent in instars f-1 to f-4.

DISCUSSION

The results presented here confirm the widespread inference that larvae of Anisoptera are commonly polyphagous predators, with the prey spectrum reflecting that in the habitat but modified by opportunism and larval feeding habitats. A high proportion of larvae produced 'empty' pellets of shed peritrophic membrane, and one practical difficulty of studying large Anisoptera in this way is that of obtaining sufficient material for analysis. In their studies of Zygoptera larvae, LAWTON (1970) and THOMPSON (1978) did not comment on this aspect and, like PRITCHARD (1964; Anisoptera), concentrated on the positive results obtained. Indeed, Pritchard commented that Anisoptera larvae collected at different times during daylight hours 'always had food in their guts', though later noted that 11% (of 1015 larvae) collected had empty guts. Nevertheless, the work reported here provides the important caveat that larval samples may need to be large in order to obtain reasonable numbers of pellets for analysis. Presence of sand or other inorganic material, may reflect several sources: covering of prey items (caddis larva cases, for example), gut contents of prey, and the scooped substrate. It is possible that this material helps in internal maceration of prey and might thereby have adaptive value. When food is scarce, some odonate larvae can survive for considerable periods without it (TILLYARD, 1910).

In general, relative abundance of prey in a species diet may reflect relative abundance in the habitat, and differences between species therefore reflect habitat specificity or segregation rather than prey selection. Dominant prey categories were Diptera: Chironomidae larvae and Ephemeroptera larvae, with the former generally more frequent in the Kiewa River samples and the latter in Middle Creek samples. These prey groups are the predominant food of most taxa appraised, and are widespread in the waterbodies. PRITCHARD (1964) noted that chironomid larvae, as well as being abundant, are conspicuous by their movement, of convenient size and texture, and can be captured easily and eaten rapidly. Mayfly larvae are also accessible easily, especially by Odonata on vegetation or active on the substrate. Oligochaeta are confined to the substrate and their abundance in the diet of Gomphidae (especially *A. cornutus*) reflects their bottom-dwelling habit and 'scooping' feeding action. *A. cornutus* larvae are burrowers. By contrast, 'sprawlers' such as *D. haematodes, A. u. unicornis* and *H. papuensis* utilise prey occurring on logs or submerged macrophytes.

The higher numbers of prey/pellet found for *A. u. unicornis* probably reflect, simply, the greater size of the larvae than any other larvae studied here. Evidence of feeding opportunism is given by the data on Orthocladiinae eaten by *A. cornutus*, with the peak in October foreshadowed in the previous sample. This is most likely to reflect seasonal incidence, of short duration, of these prey. Absence of crustaceans from the diets was unexpected, though their generally small size may render many copepods and ostracods more attractive to young odonate larvae than to later instars, but may reflect their relative scarcity in flowing waters. Likewise, the few Acarina found may represent 'casual' ingestion rather than deliberate feeding. Large water mites cannot be chewed easily by dragonfly larvae (PRITCHARD, 1964). However, large odonate larvae can indeed ingest small prey items: for *Ischnura elegans* (Vander L.) (Coenagrionidae), the penultimate instar still takes large numbers of particularly small prey (THOMPSON, 1978). PRITCHARD (1964) suggested that very small prey are 'often missed' by Anisoptera larvae. Prey 'selection' is probably governed mainly by the abundance and accessibility of the prey items, and the work noted here supports this general conclusion advanced by PRITCHARD (1964). Thus, although the nature of the food itself may not be limiting to a given odonatan species, separation of habitats and habits may render different food taxa accessible, so that particular dietary components reflect habitat segregation reasonably clearly. Whether the coexisting predators may then exhibit interspecific behavioural and/or physiological specialisations rendering any given prey group more suitable than others is yet to be addressed except at the gross level of labial form.

Nevertheless, coexisting Odonata in the same riffle-reach in a Hong Kong stream had rather different diets, although two species of Gomphidae made similar use of resources (DUDGEON, 1989). Niche partitioning by dietary differences in the Anisoptera studied here seems to be interlinked intimately with microhabitat differences, and patterns of food item use are likely to reflect a strong component of opportunism.

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