

## RESOURCE PARTITIONING AMONG LARVAE OF SIX COEXISTING ODONATE SPECIES OF THE KALI GANDAKI RIVER, CENTRAL NEPAL (ANISOPTERA)

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Odon. larvae were collected from 50-1190 m elevation in central Nepal's Gandaki River from 1984 to 1986. Resource partitioning among coexisting odon. spp. at high (>500m) and low (<500m) elevations was investigated by examining their gut contents. At both elevations, diet differences between *Anisogomphus occipitalis* and *Davidius* sp. were statistically significant. *A. occipitalis* ate mostly midges whereas *Davidius* sp. ate mayflies and caddisflies as well as midges. At low elevation there was no diet difference between *A. occipitalis* and *Paragomphus lineatus* nor between the libellulids *Crocothemis servilia* and *Trithemis festiva*. Analyses of niche breadths indicate overlap between *Davidius* sp., *Macromia moorei*, *C. servilia*, and *T. festiva*, and between *A. occipitalis* and *P. lineatus*. Significant diet differences in both *A. occipitalis* and *Davidius* sp. between low and high elevations may indicate negative interactions in the presence of other coexisting species at low elevation. Similarly, at low elevation both spp. have a narrow niche breadth, a low average number of prey items per gut, and also more empty guts than at high elevation. Mean body weights of studied odon. were relatively higher at lower elevation than at higher elevation. Predatory interactions seemed to be of little or no importance in structuring this lotic odon. assemblage, in contrast with lentic Odonata in other studies.

### INTRODUCTION

Resource partitioning among coexisting species plays a very important role in structuring communities (PACALA, 1982; TOFT, 1985). It commonly occurs along the ranked axes of habitat > food > temporal dimension (SCHOENER, 1974) or by the influence of competition and predation within community structure (MOYLE & SENANAYAKE, 1984; MARTIN, 1988). MOYLE & SENANAYAKE (1984) reported that species not segregated by habitat tend to show low dietary overlap. Similarly TOWNSEND & HILDREW (1979) reported that groups of ecologically

similar species usually show a partitioning of resources.

Larval odonates are often the dominant invertebrate predators in littoral zones of aquatic habitats. Although odonate larvae are usually generalist predators of the littoral zone (PRITCHARD, 1964; THOMPSON, 1978; DUDGEON & WAT, 1986), selective predation has been reported by LAWTON (1970), JOHNSON (1982), and BLOIS (1985), and resource partitioning among coexisting species of odonate larvae may also play an important role in community assemblage. Coexistence of odonate larvae with vertebrate predators is determined by differential vulnerability to fish predation and the simultaneous effects of interspecific competition and intraguild predation (BENKE, 1978; MORIN, 1984; JOHNSON et al., 1987; VAN BUSKIRK, 1989; WISSINGER, 1989; McPEEK, 1990). Niche partitioning among coexisting species of odonate larvae may reduce competitive interactions by diet partitioning (CARCHINI & NICOLAI, 1984; BLOIS, 1985; DUDGEON, 1989; MAHATO & JOHNSON, 1991), by habitat partitioning (JOHNSON & CROWLEY, 1980), and by seasonal segregation (SCHOENER, 1974; CROWLEY & JOHNSON, 1982a). BENKE & BENKE, (1975)

reported that seasonal segregation of life histories may reduce interspecific competition. CROWLEY & JOHNSON, (1982b) reported that competitive exclusion rarely occurs among odonates.

The streams and rivers of the Himalayan country of Nepal are typically unstable environments for aquatic organisms because of monsoonal floods in summer. Most river systems arise from the Himalaya and monsoonal rains often cause unpredictable fluctuations in water levels, water currents, and other river physical characteristics. Such floods typically cause major rearrangements of substrates and other aspects of the stream bed. Despite the unstable nature of the

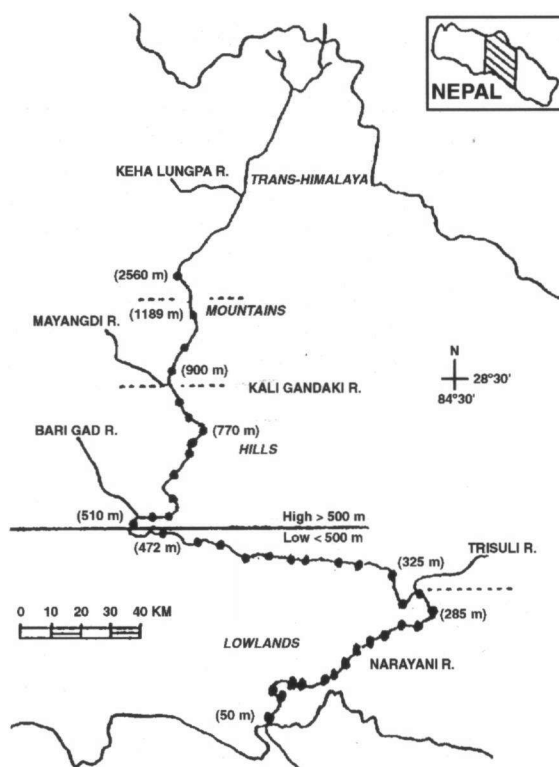


Fig. 1. Map of the Gandaki River, Nepal. Black dots indicate odonate collection sites.

environment, some species of odonate larvae are adapted to that kind of environment. The species in these assemblages generally show morphological specialization (CORBET, 1983) as well as dietary and habitat specialization. They provide good opportunities to study resource partitioning among co-existing species in lotic habitats.

Odonate specimens were collected from Nepal's Gandaki River

between 50 and 2560 m elevation from 1984 to 1986 (Fig. 1). Detailed information on the distribution of odonate taxa are presented elsewhere (MAHATO & EDDS, 1993). Of 19 taxa collected, only six had more than 25 specimens (Tab. I). All specimens from these six taxa were collected below 1190 m. Below 500 m the environment significantly changes: the water current slows when the river turns eastward in the plains region where warmer climate predominates.

*Anisogomphus occipitalis* and *Davidius* sp. (Gomphidae) were collected both above and below 500m whereas *Paragomphus lineatus* (Gomphidae), *Macromia moorei* (Corduliidae), and *Crocothemis servilia* and *Trithemis festiva* (Libellulidae) were collected only below 500 m. These species were selected for diet analysis.

#### METHODS

I removed the guts by pulling the head apart from the rest of the body, separated the head capsule, teased apart the gut on a microscope slide, and mounted in Pro-Texx mounting media. I identified prey fragments to the lowest possible taxon at 100x magnification, recording total prey items based on the convention described in MAHATO & JOHNSON (1991). Detailed diet data are presented in Appendices A and B. Due to low numbers of prey taxa in some odonate taxa, I further combined prey taxa into 11 prey categories for data analysis. The prey categories were: (a) chironomids separated into burrowing, sprawling, and climbing midges (CUMMINS & COFFMAN, 1984); (b) oligochaetes; (c) among arthropods, prey items were separated as Macrocrustacea, Ephemeroptera, Trichoptera, Odonata, Coleoptera, Hemiptera, and Acarina.

I also measured the head width of each odonate specimen. I then placed the whole body, along with its head capsule but excluding the digestive system, in an oven at 60°C for two days. Later, I weighed the dried odonate specimens to determine the correlation between head width and body weight.

Table I

Total number of specimens studied for diet analysis from Nepal's Gandaki River

Species	High (above 500m)	Low (below 500 m)
G o m p h i d a e		
<i>Anisogomphus occipitalis</i>	99	72
<i>Davidius</i> sp.	210	248
<i>Paragomphus lineatus</i> #	0	24
C o r d u l i i d a e		
<i>Macromia moorei</i> *	0	88
L i b e l l u l i d a e		
<i>Crocothemis servilia</i> *	0	60
<i>Trithemis festiva</i> *	0	68

# = Only five specimens were collected from high altitude hence not used for diet analysis.

\* = None of these species were collected from high altitude.

DATA ANALYSIS. – I compared the frequencies of various prey taxa in diets using Chi-square contingency tests partitioned into independent components, each with one degree of freedom. Due to low frequencies, Coleoptera, Hemiptera, and Acarina were combined as miscellaneous arthropods in the Chi-square analysis.

I calculated niche breadth (B) for each odonate species using the index proposed by SIMPSON (1949),  $1/\sum P_i^2$ , where  $P_i$  is the proportionate use of the  $i^{\text{th}}$  prey item. This niche breadth value ranges from 1 to the maximum number of prey categories. A larger value indicates a wider niche breadth. Niche overlap ( $O_{xy}$ ) between studied species was calculated as proposed by PIANKA (1973):

$$O_{xy} = \frac{\sum_i^n P_{xi} P_{yi}}{\sqrt{\sum_i^n P_{xi}^2 \sum_i^n P_{yi}^2}}$$

$P_{xi}$  and  $P_{yi}$  represent percentage use of the same prey category by species  $x$  and  $y$ . Values  $>0.75$  may be considered to indicate high niche overlap (MATTHEWS et al., 1982). I also analyzed diet similarity between species using cluster analysis (NEMEC, 1991). The same 11 prey categories were used for all calculations.

Differences in average number of prey items per gut between taxa and correlation coefficients (SOKAL & ROHLF, 1981) between head width and dry body weights were calculated. Average body weight per head width size group was also determined.

## RESULTS

Eight hundred and sixty nine specimens were used for gut content analysis (Tab. I). This comprises approximately 87% of the specimens collected from the river (MAHATO & EDDS, 1993); the remainder were either rare species or damaged and poorly preserved specimens. A detailed summary of the gut contents separated by species is presented in Appendices A and B.

Data on percentage of guts containing prey are presented in Table II. *C. servilia* had the highest percentage (78%) and *A. occipitalis* at low elevation had the lowest percentage (44%) of guts with prey. *A. occipitalis* and *Davidius* sp. had more than 60% guts with prey at high elevation and less than 50% of guts with prey at low elevation, although these values varied with larval size. Values for both taxa at both elevations tended to decrease with larval size. This trend was not apparent in the

Table II  
Percentage of odonate guts with some prey, separated by size, collected from the Gandaki River, Nepal. – [Number in parenthesis represents total number of specimens studied]

Head width mm	<i>Anisogomphus occipitalis</i>		<i>Davidius</i> sp.		<i>Paragomphus lineatus</i>	<i>Macromia moorei</i>	<i>Crocothemis servilia</i>	<i>Trithemis festiva</i>
	High	Low	High	Low				
<2.9	61.7 (47)	64.3 (28)	70.2 (47)	61.9 (42)	60.0 (5)	50.0 (6)	100.0 (1)	80.0 (5)
3-3.9	92.3 (13)	53.9 (13)	74.0 (77)	44.4 (81)	62.5 (8)	76.3 (38)	70.6 (17)	47.1 (17)
4-4.9	57.6 (33)	46.2 (13)	52.4 (84)	46.3 (108)	50.0 (10)	66.7 (15)	82.1 (28)	62.2 (45)
>5	16.7 (6)	5.6 (18)	50.0 (2)	35.3 (17)	100.0 (1)	64.29 (28)	78.6 (14)	100.0 (1)
All	61.6 (99)	44.4 (72)	64.3(210)	47.2 (248)	58.3 (24)	69.3 (88)	78.3 (60)	60.3 (68)

Table III  
Average number of prey items/taxa per odonate species with standard error, collected from the Gandaki River, Nepal

Species	No. examined	No. of empty guts	No. of prey items	No. of prey taxa	Avg. No. prey per gut	Standard error
<i>Anisogomphus occipitalis</i> (high)	99	38	425	30	4.29	0.83
<i>Anisogomphus occipitalis</i> (low)	72	40	202	22	2.81	0.56
<i>Davidius</i> sp. (high)	210	75	438	19	2.09	0.18
<i>Davidius</i> sp. (low)	248	131	272	20	1.10	0.11
<i>Paragomphus lineatus</i>	24	10	137	23	5.71	1.89
<i>Micromia moorei</i>	88	27	150	20	1.70	0.19
<i>Crocothemis servilia</i>	60	13	80	17	1.33	0.14
<i>Trithemis festiva</i>	68	27	96	13	1.41	0.19

other four taxa.

The analysis of average number of prey items per gut for each taxon from all studied odonate larvae, indicates that at low elevation *P. lineatus* and *A. occipitalis* had more prey items ( $P < 0.05$ ) per gut than other species (Tab. III). These species had mostly midges in their guts. Midges are much smaller than Ephemeroptera and Trichoptera, hence odonates may have to eat more midges to maintain their body metabolism. These two species also had higher variability in the total number of prey items per gut than other species. Up to 12 prey items per gut were recorded from 10% of the *A. occipitalis* and 21% of the *P. lineatus* larvae. *Davidius* sp. had fewer prey items per gut ( $P < 0.01$ ) at low elevation. No significant difference in average number of prey items was found in *A. occipitalis* between high and low elevations. However, more prey taxa were counted at low elevation than at high elevation from

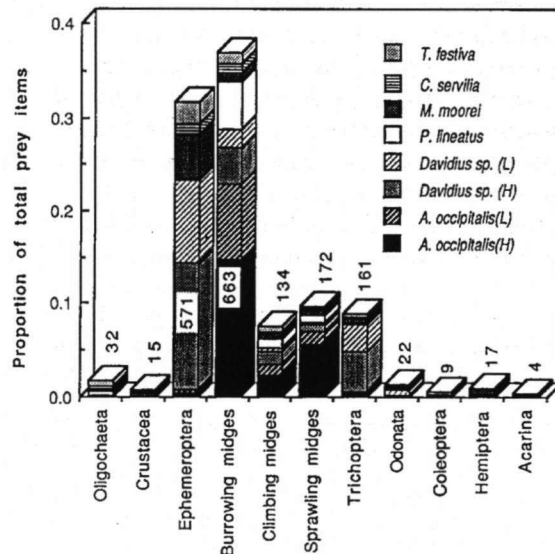


Fig. 2. Proportion of total prey items separated by major prey categories and also by different species of odonates collected from the Gandaki River, Nepal.

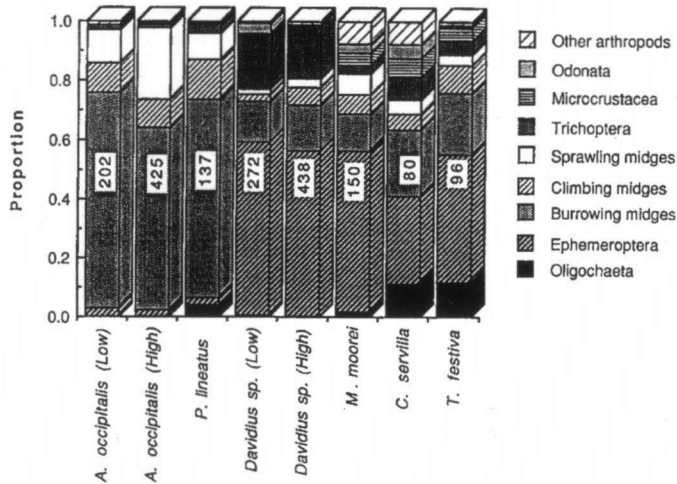


Fig. 3. Proportion of prey categories in each odonate species collected from the Gandaki River, Nepal.

both *A. occipitalis* and *Davidius* sp. diets.

The majority of the prey were midges, Ephemeroptera, and Trichoptera (Fig. 2). Burrowing midges ( $n = 663$ ) were present in the highest number and the second highest were ephemeropterans ( $n = 571$ ). However, the composition of these prey items was different between species (Fig. 3). The major prey items for *A. occipitalis* and *P. lineatus* were midges (>95%), and of these, more than 50% were burrowing midges. Diets of *M. moorei*, *C. servilia*, and *T. festiva* were similar to those of *Davidius* sp.: Ephemeroptera, Trichoptera and midges were the common prey items. However, *M. moorei*, *C. servilia*, and *T. festiva* also had a higher number of oligochaetes and other arthropod prey items than gomphids (*A. occipitalis*, *Paragomphus*, and *Davidius* sp.).

Dietary differences between species and within species at high and low elevations are shown in Table IV. There is no significant difference between *A. occipitalis* collected from low elevation and *P. lineatus* ( $\chi^2 = 12.55$ ,  $DF=7$ ,  $P>0.05$ ). Similarly, the difference between *C. servilia* and *T. festiva* was also nonsignificant ( $\chi^2 = 11.49$ ,  $DF=8$ ,  $P>0.05$ ). All other diet differences were statistically significant, including the comparisons for both *A. occipitalis* and *Davidius* sp. between high and low elevation. At low elevation the diet of *A. occipitalis* shifted from sprawling midges to burrowing midges, and the diet of *Davidius* sp. shifted from midges to other insect items.

*M. moorei*, *C. servilia*, and *T. festiva* had a larger niche breadth than *A. occipitalis*, *P. lineatus*, and *Davidius* sp. (Fig. 4). Both *A. occipitalis* and *Davidius* sp. had a slightly smaller niche breadth at low elevation than at high elevation.

Cluster analysis results are presented in Figure 5. The grouping of species is similar to the results above. Intra- and interspecific niche overlap values ( $O_{xy}$ ) reflect

Table IV

Chi-square contingency tests for significant differences between diets of odonate species collected from the Gandaki River, Nepal. - Ao(H) = *A. occipitalis* (>500m); - Ao(L) = *A. occipitalis* (<500m); - D(H) = *Davidius* sp. (>500m); - D(L) = *Davidius* sp. (<500m); - Pl = *P. lineatus*; - Mm = *M. moorei*; - Cs = *C. servilia*; - Tf = *T. festiva*]

	Ao(L)	D(H)	D(L)	Pl	Mm	Cs	Tf
Ao(H)	*	***	***	***	***	***	***
Ao(L)		***	***	ns	***	***	***
D(H)			*	***	***	***	***
D(L)				***	***	***	***
Pl					***	***	***
Mm						**	**
Cs							ns

ns,  $P > 0.1$ ; \*,  $0.05 > P > 0.01$ ; \*\*,  $0.01 > P > 0.001$ ; \*\*\*,  $P < 0.001$

similar results to the cluster analysis (Tab. V).

The correlation of head-width with body weight shows no difference in correlation coefficient values between high and low elevations for *A. occipitalis* and *Davidius* sp. (Fig. 6). Similarly, when data were tabulated by different size categories, no consistent trend was observed for either species (Tab. VI).

## DISCUSSION

Coexisting species may reduce competition by separation along one or more niche axes (SCHOENER, 1974). Resource partitioning may be a by-product of a series of evolutionary changes in species in response to selection pressure generated by inter- and intra-specific competition and predatory interactions within a particular community (WALTER, 1991). SCHOENER (1974) also suggests habitat may be the frequently partitioned niche axis. In this present study, all three factors are potentially important for coexistence of these several

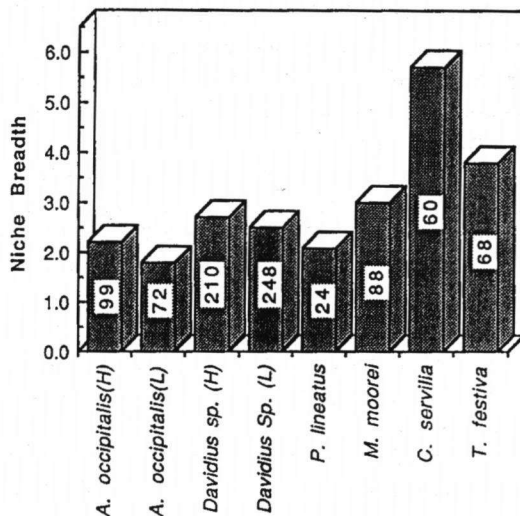


Fig. 4. Niche breadth with respect to diet for each odonate species collected from the Gandaki River, Nepal.

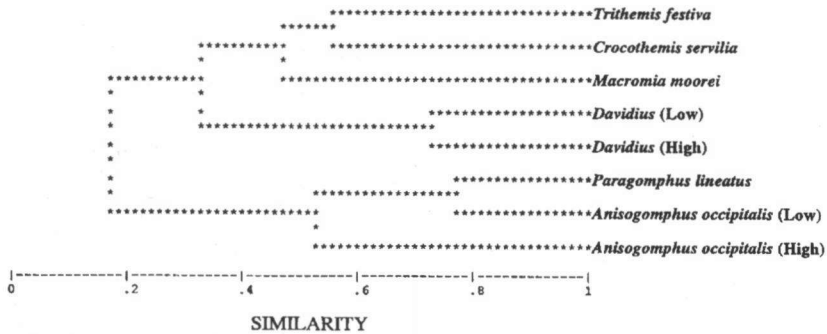


Fig. 5. Cluster analysis indicating levels of diet similarity among odonate taxa collected from the Gandaki River, Nepal.

odonate species. However, diet analysis in the present study shows the potential for competitive interactions but provides very little evidence of predatory interactions among coexisting dragonfly larvae.

Resource partitioning may be a result of morphological differences. *A. occipitalis*, *P. lineatus*, and *Davidius* sp. larvae have the general characteristics of burrowing odonates (short flattened bodies and short legs) as described by WRIGHT (1943) and CORBET (1983). By contrast *M. moorei*, *C. servilia*, and *T. festiva* are sprawling odonate larvae with broadly rounded and somewhat flattened bodies and extremely long legs which enable them to move freely over complex substrates. PRITCHARD (1964) suggested that there is a correlation between odonate labium morphology and the biological characteristics of the prey. Libellulid labia are cup-shaped with many crenulations in their palpal lobes, which help them capture a variety of prey taxa including smaller worms and microcrustacea. Gomphids have a flat labium,

Table V

Intra- and Interspecific niche overlap values ( $O_{xy}$ ) with respect to diet composition (cf. PLANKA, 1973) of odonates collected from the Gandaki River, Nepal. - [Ao(H) = *A. occipitalis* (>500m); - Ao(L) = *A. occipitalis* (<500m); - D(H) = *Davidius* sp. (>500m); - D(L) = *Davidius* sp. (<500m); - Pl = *P. lineatus*; - Mm = *M. Moorei*; - Cs = *C. servilia*; - Tf = *T. festiva*]

	Ao(L)	D(H)	D(L)	Pl	Mm	Cs	Tf
Ao(H)	<b>0.978</b>	0.296	0.238	<b>0.970</b>	0.278	0.581	0.450
Ao(L)		0.312	0.258	<b>0.996</b>	0.277	0.592	0.468
D(H)			<b>0.995</b>	0.311	<b>0.956</b>	<b>0.861</b>	<b>0.934</b>
D(L)				0.256	<b>0.951</b>	<b>0.847</b>	<b>0.920</b>
Pl					0.274	0.610	0.483
Mm						<b>0.853</b>	<b>0.943</b>
Cs							<b>0.955</b>

$O_{xy} > 0.75$  is "high overlap" (MATTHEWS et al., 1982) and indicated by bold type font



with hooks on the palpal lobe, which allows them to capture only larger prey items.

In general, members of the same family have similar morphological characteristics and thus we also expect a similar diet. However, *Davidius* sp. consumes different prey items than *A. occipitalis* and *P. lineatus*; there is very low interspecific dietary overlap and highly significant diet difference. This is contrary to results suggested by PRITCHARD (1964) and observations made by DUDGEON (1989) among two gomphids. KUMAR (1973) described *A. occipitalis* and *P. lineatus* larvae as very sluggish, and found lying in muddy substrate. Based on the diet analysis, it seems *A. occipitalis* and *P. lineatus* remain buried in the substrate and depend mostly upon burrowing midges for food, whereas *Davidius* sp. crawl around rather than burrow, and feed mostly on Ephemeroptera and Trichoptera larvae and any other prey items they come across. At low elevation, these two gomphids also coexist with other odonates and share similar prey taxa. Cluster analysis clearly indicates that at low elevation *P. lineatus* had a diet similar to *A. occipitalis*, whereas *Davidius* sp. had a diet similar to *M. moorei*, *C. servilia*, and *T. festiva* (the true sprawling odonate larvae). This similarity in diet with Libellulidae and Corduliidae rather than with other gomphids indicates that *Davidius* sp. is probably a sprawler rather than a burrower.

ALLAN (1983) did not find any strong evidence of predator effects on stream benthos community structure. DUDGEON (1989) suggested that lotic odonates are unlikely to deplete their prey significantly; such lack of prey depletion has also been demonstrated in a lentic habitat (JOHNSON et al., 1987). However, both *A. occipitalis* and *Davidius* sp. had a higher percentage of empty guts at low elevation than at high elevation. This may indicate some negative impact on prey in the presence of other odonate species at low elevation. High resource diversity, high resource productivity, warmer climate, and stable environmental conditions at low

Table VI

Average body dry mass (mg) of odonate larvae, separated into different head width groups collected from the Gandaki River, Nepal. – [Number in parenthesis represents total number of specimens studied]

HW group	<i>Anisogomphus occipitalis</i>		<i>Davidius</i> sp.		<i>Paragomphus lineatus</i>	<i>Macromia moorei</i>	<i>Crocothemis servilia</i>	<i>Trithemis festiva</i>
	High	Low	High	Low				
1.6-2.0	3.22 (5)	3.07 (3)		2.70 (1)				1.30 (1)
2.1-2.5	3.97 (9)	6.13 (5)	6.04 (8)	4.60 (7)	5.00 (2)	11.03 (4)		
2.6-3.0	9.62 (9)	12.39 (11)	9.34 (28)	9.59 (10)	8.60 (1)	19.19 (10)	2.33 (3)	4.80 (3)
3.1-3.5	14.95 (2)	19.25 (2)	15.53 (17)	24.87 (3)	10.40 (3)	26.10 (4)	2.90 (10)	7.16 (7)
3.6-4.0	17.20 (1)		17.87 (3)	24.23 (17)		30.97 (11)	5.99 (13)	17.62 (10)
4.1-4.5	24.75 (2)		36.71 (26)	47.19 (15)	33.50 (5)	37.20 (1)	5.46 (5)	16.22 (13)
4.6-5.0	28.22 (13)	44.00 (1)	58.68 (16)	58.01 (27)	38.50 (3)	72.90 (4)	9.38 (4)	16.00 (1)
5.1-5.6	60.00 (1)	71.55 (2)	83.50 (1)			76.38 (6)	26.80 (1)	
>5.6				99.90 (5)	72.30 (1)	86.50 (1)		

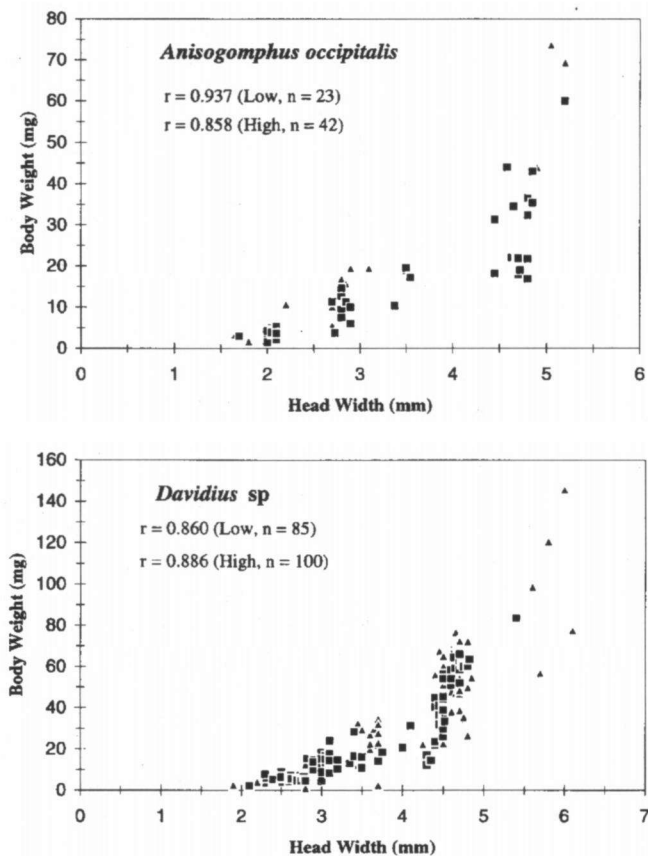


Fig. 6. Relationship between head width and body weight for two odonate larvae collected from both high (>500m) and low (<500m) elevation of the Gandaki River, Nepal.

elevation may support the higher odonate species richness at low elevation (cf. LAWTON et al., 1987).

KUMAR & KHANNA (1983) reported that the gomphids, *A. occipitalis*, *P. lineatus*, and *Davidius* sp., and the corduliid, *M. moorei*, take more than one year to complete their life cycle, whereas the libellulids, *C. servilia* and *T. festiva*, have more than one generation per year. In winter the libellulids may remain in the larval stage in nearby lentic habitat, and in spring they emerge and lay eggs in lotic habitats where they complete several generations in the summer. This temporal segregation (BENKE & BENKE, 1975; CROWLEY & JOHNSON, 1982a) has the potential to reduce year-round competition for resources (WISSINGER, 1992).

CROWLEY & JOHNSON (1982b) reported that competitive exclusion rarely occurs among odonates. High niche overlap values between *A. occipitalis* and *P.*

*lineatus* and among *C. servilia*, *T. festiva*, *Davidius* sp., and *M. moorei*, and the lack of significant diet differences between *A. occipitalis* and *P. lineatus* and between *C. servilia* and *T. festiva* at low elevation, may indicate that there is the potential for exploitation competition (HANSSON, 1995) if resources are limited. But in the presence of sufficient prey items, competitive interactions may rarely occur at low elevation.

However, although competitive exclusion may not have occurred, competition may have had some impact on diet shift in *A. occipitalis* and *Davidius* sp. At low elevation in the presence of other species, *A. occipitalis* has significantly shifted its diet from sprawling midges to burrowing midges ( $\chi^2 = 15.13$ , DF=6,  $P < 0.05$ ). This is similar to what was reported by MAHATO & JOHNSON (1991). They reported that successful invasion of one lotic species into a lentic community shifted dietary niche for one of the dominant lentic species and may have had a negative impact on population size. The present study suggest that competitive interaction for food with coexisting odonate larvae at low elevation may have caused *A. occipitalis* to remain buried and subsequently feed mostly on burrowing midges. However, this will have led to a diet similar to that of *P. lineatus* ( $\chi^2 = 11.17$ , DF=6,  $P > 0.05$ ) and the higher percentage of empty guts may indicate some competitive interaction for food. The diet of *Davidius* sp. shifted significantly from midges to other insects ( $\chi^2 = 15.99$ , DF=6,  $P < 0.05$ ) at low elevation and also had a higher percentage of empty guts than at higher elevation. Relatively lower niche breadth at low elevation than high elevation for both *A. occipitalis* and *Davidius* sp. indicates interaction with other coexisting species. This interpretation is also supported by lower numbers of prey items at low elevation than at high elevation.

Only a few cases of inter-odonate predation were recorded in the present study. As studied in lentic odonates (BENKE et al., 1982; CROWLEY et al., 1987) predatory interactions, including intraguild predation (POLIS & MYERS, 1989), seem to be of little importance in lotic odonate assemblages (cf. DUDGEON, 1989).

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## APPENDIX A

Frequency of identifiable prey remaining in gut contents of *Anisogomphus occipitalis*, *Davidius* sp., and *Paragomphus lineatus* collected from Gandaki River, Nepal

Prey taxa	<i>Anisogomphus occipitalis</i>			<i>Davidius</i> sp.			<i>Paragomphus lineatus</i>
	Low	High	Total	Low	High	Total	Total
Oligochaeta	0	1	1	2	0	2	6
EPHEMEROPTERA							
<i>Baetis</i>	5	7	12	116	219	335	3
<i>Ecdyones</i>	1	1	2	38	23	61	0
<i>Ephemerellia</i>	0	0	0	2	2	4	0
<i>Eporus</i>	0	0	0	2	2	4	0
<i>Rithrogenia</i>	0	0	0	2	0	2	0
DIPTERA							
Burrowing midges							
Tanitarsini	131	185	316	11	27	38	55
Ceratopogonidae	0	1	1	0	0	0	3
<i>Alotanypus</i>	0	2	2	0	0	0	0
<i>Brilla</i>	6	15	21	12	16	28	26
<i>Chironomus</i>	0	0	0	0	0	0	3
<i>Constempella</i>	3	1	4	0	0	0	1
<i>Cricotopus</i>	0	3	3	3	6	9	1
<i>Paratendipes</i>	4	1	5	0	0	0	0
<i>Pseudochironomus</i>	0	0	0	0	0	0	1
<i>Rheotantarsus</i>	3	56	59	10	18	28	2
<i>Trissoc</i>	0	0	0	0	1	1	0
Climbing midges							
<i>Micropsectra</i>	9	16	25	2	10	12	4
<i>Microtendipes</i>	5	4	9	0	3	3	8
<i>Polypedilum</i>	6	21	27	5	12	17	6
Sprawling midges							
<i>Archeopelepia</i>	0	1	1	0	3	3	1
<i>Cryptochironomus</i>	7	6	13	0	0	0	2
<i>Diamesa</i>	5	3	8	1	0	1	1
<i>Eukefferella</i>	2	3	5	0	2	2	2
<i>Larsia</i>	0	5	5	0	0	0	0
<i>Micropelopia</i>	1	1	2	0	0	0	0
<i>Nilotanipus</i>	1	0	1	0	0	0	0
<i>Parachironomus</i>	2	46	48	1	0	1	0
<i>Paracricotopus</i>	2	17	19	0	6	6	0
<i>Procladius</i>	1	4	5	1	3	4	0
<i>Psectrocladius</i>	2	2	4	0	0	0	0
<i>Stemple</i>	0	0	0	0	0	0	2
<i>Thienemani</i>	0	11	11	0	0	0	3
<i>Zavrelinyia</i>	0	3	3	1	0	1	1
TRICHOPTERA	4	5	9	52	80	132	4
COLEOPTERA	0	0	0	0	1	1	0
HEMIPTERA	1	0	1	0	4	4	0
ANISOPTERA	0	1	1	9	0	9	1
ZYGOPTERA	0	2	2	1	0	1	1
ACARINA	1	1	2	1	0	1	0

## APPENDIX B

Frequency of identifiable prey remaining in gut contents of *Macromia moorei*, *Crocothemis servilia*, and *Trithemis festiva* collected from Gandaki River, Nepal

Prey taxa	<i>Macromia moorei</i>	<i>Crocothemis servilia</i>	<i>Trithemis festiva</i>
MICROCRUSTACEA	6	5	4
OLIGOCHAETA	3	9	11
EPHEMEROPTERA			
<i>Baetis</i>	63	22	38
<i>Ecdyones</i>	9	0	4
<i>Ephemerellia</i>	7	2	0
<i>Apobat</i>	3	0	0
DIPTERA			
Burrowing midges			
Tanitarsini	15	5	11
Ceratopogonidae	1	8	6
<i>Brilla</i>	1	1	0
<i>Chironomus</i>	0	1	0
<i>Cricotopus</i>	1	0	0
<i>Dicrotendips</i>	0	3	0
<i>Rheotanytarsus</i>	0	0	3
Climbing midges			
<i>Micropsectra</i>	8	0	9
<i>Microtendipes</i>	1	0	0
<i>Polypedilum</i>	1	4	0
Sprawling midges			
<i>Archeopelepia</i>	1	2	2
<i>Cryptochironomus</i>	7	0	0
<i>Diamesa</i>	0	0	1
<i>Larsia</i>	1	1	0
<i>Nilotanipus</i>	0	1	0
<i>Parachironomus</i>	1	0	0
TRICHOPTERA	5	6	5
COLEOPTERA	0	6	1
HEMIPTERA	12	0	0
ANISOPTERA	4	2	1
ZYGOPTERA	0	2	0