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Diet of *Gambusia affinis holbrooki*, *Xiphophorus helleri*, *X. maculatus* and *Poecilia reticulata* (Pisces: Poeciliidae) in Streams of Southeastern Queensland, Australia

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Abstract

The diets of four introduced Poeciliidae, *Gambusia affinis holbrooki, Xiphophorus helleri, X. maculatus* and *Poecilia reticulata*, were studied in subtropical streams, southeastern Queensland, Australia. The prey of greatest importance in *G. affinis* diets was usually of terrestrial origin, i.e. ants and adult nematoceran Diptera, but aquatic Hemiptera and other aquatic taxa were also important in some habitats. *G. affinis* ate invertebrate prey that were small relative to body size and mouth gape (mean prey width 0.3 x mouth gape, mean prey length 1.28 x mouth gape) and relative to the size range of prey present (mean prey ingested = 0.597 x mean length and 0.702 x mean width of availability prey in the environment equal to or smaller than the largest prey eaten). Some aquatic taxa (e.g., immature Trichoptera and Ephemeroptera, Oligochaeta, Crustacea and Mollusca) of the preferred size range which were abundant in the streams were eaten infrequently. *X. helleri* was omnivorous, consuming aquatic plant tissue, filamentous and other algae and aquatic and terrestrial invertebrates. *X. maculatus* consumed Crustacea and aquatic and terrestrial insects, with dominance of the atyid shrimp, *Caridina*. *P. reticulata* had a more diverse diet composed largely of terrestrial insects, particularly ants; chironomid larvae were the dominant aquatic taxon eaten. The four species of poeciliids had significantly different mean diet composition. The implications of poeciliid feeding for sympatric endemic fishes are briefly discussed.

Introduction

Six species of Poeciliidae have become established in Australia inland waters and there is evidence that the mosquito fish, *Gambusia affinis holbrooki* Girard, has had adverse effects on endemic fishes, particularly small-bodied species with similar habitat and dietary requirements (see Arthington et al. 1983; Lloyd 1987). Although there is worldwide concern about the ecological impacts of introduced poeciliids (e.g., Courtenay and Stauffer 1984; Meffe and Snelson, in press) and a general belief that interspecific competition for food has been a major process affecting endemic fishes in the presence of *G. affinis* (Schoenherr 1981, but see also Meffe 1985; Arthington and Lloyd, in press), there is a surprising lack of data on the dietary ecology of these fishes in areas of introduction.

The diet of *G. affinis* has been studied in relation to the species' role in mosquito control (see Lloyd 1986) and its impact on invertebrates in pond and experimental ecosystems (e.g., Hurlbert and Mulla 1981; Meffe 1985; Bence and Murdoch 1986); the adaptive and evolutionary significance of cannibalism have also been explored (e.g. Dionne 1985; Meffe and Crump 1987). Information on the diet of *G. affinis* in streams is very limited. Cadwallader (1979) examined nine individuals from the Seven Creeks River System in Victoria, Australia, and found that terrestrial insects were the main component of gut contents.

The guppy, *P. reticulata* Peters, has also been widely distributed as an aquarium fish and for mosquito control (Reddy and Shakuntala 1979; Haas and Pal 1984) yet its natural diet has been studied only in two countries of introduction (Yamagishi et al. 1967; Green et al. 1976, 1978). The diets of the swordtail, *X. helleri* (Gunther), and the platy, *X. maculatus* Heckel, in nature are also not well known but species of *Xiphophorus* are omnivorous in aquaria (Alexander 1967; Kallman 1976). Dussault and Kramer (1981) suggest that opportunistic feeding with a major component of benthic algal material may be the common pattern in poeciliids, particularly genera with protractible jaws, such as *Poecilia* and *Xiphophorus*.

This study compares the diets of *G. affinis*, *X. helleri*, *X. maculatus* and *P. reticulata* in subtropical streams. Since *G. a. holbrooki* is the most widespread and abundant introduced poeciliid in Australia, particular attention was given to its diet composition as a basis for assessing impacts on endemic stream fishes. Prey selection, defined as the difference in dietary and environmental size and taxonomic distribution of prey (Eggers 1982), was examined. Another aspect of the study was to determine whether gut content analysis revealed any evidence that poeciliids prey on the eggs and fry of endemic fishes, as the mosquitofish reportedly does in other countries (Myers 1965; Johnson 1976; Shakuntala and Reddy 1977; Meffe 1985).

Materials and Methods

The study area included sites where the poeciliids were abundant in 1982, i.e., sites on Kedron Brook, Enoggera Creek, Moggill Creek, Gold Creek, Oakey Creek, Seven Hills Creek and Manchester Creek, and Kholo and Colleges Crossing on the Brisbane River (see Fig. 1, Arthington et al. 1983). Most of these creeks lie to the north of the Brisbane River, draining predominantly eastward from the foothills of the southern part of the D'Aguilar Range to discharge into Moreton Bay or the Brisbane River. Kholo and Colleges Crossing are large shallow pools and backwaters with extensive macrophyte growth situated on the upper Brisbane River and Manchester Creek drains southward from below Lake Manchester, a water storage, into the Brisbane River.

Towards their headwaters, most of the streams retain their natural features, draining forested catchments (dry sclerophyll forest dominated by species of *Eucalyptus, Tristania* and *Acacia*), but they are increasingly modified in rural, suburban and urban areas by removal of riparian vegetation, invasion of introduced, semiterrestrial and aquatic plants (Arthington et al. 1983), various river improvement works (Boughton and Neller 1981) and water pollution (McIvor 1966; Arthington et al. 1982).

The Brisbane region has a subtropical climate with a mean annual temperature of 20.6°C and extreme air temperatures of 2.3°C and 43.2°C (Anon. 1970). The annual rainfall ranges from 750 to 1,500 mm, with about 70% falling in summer months (October-March). Cyclonic storms cause severe and sudden summer flooding in most of the streams studied, but water levels usually subside rapidly. Data on the variability of discharge have been published for most of the study sites (Milton and Arthington 1983, 1984, 1985).

Dietary studies were largely confined to March-July 1981 but some additional data were gathered in February 1988. By March-July in Brisbane the poeciliids and all common small-bodied endemic species have completed most of their breeding activity. Thus, the population densities of *G. affinis, X. helleri* and common endemic species were high at a time when the diversity and abundance of aquatic invertebrates tend to be lower than in the early part of the summer (McIvor 1966; Arthington et al. 1982). This was possibly a period of limited resource availability for stream fishes and an opportune time to study trophic interactions with endemic fishes.

The sites selected for the dietary studies were all relatively clear, unpolluted stream pools less than 1.5 m deep, usually with an associated riffle, but two sites on the Brisbane River at Kholo and Colleges Crossing consisted of weedy pools isolated from the main course of the river. Major details of sites and habitats sampled, dates of sampling, fish numbers and standard lengths are given in Table 1.

Table 1. Habitats, creeks, 1981 sampling dates and number and standard length range of 514 *G. affinis* and 314 *X. helleri* examined for diet in Brisbane creeks.

Habitat type	Creek code*	Date of sampling	Fish examined Number	Standard length (mm)
G. affinis				
Open water	A	3 April	36	12-35
	B	13 April	45	14-33
	C	8 May	45	12-34
	D_1	17 March	56	17-37
Edge areas	B	15 April	54	13-31
	C	8 May	39	16-33
	E_1	13 May	50	22-39
	E_2	23 May	45	12-32
Weed beds	D_2	17 March	28	17-32
	D_3	17 March	56	14-33
	F	25 March	30	19-35
	G	14 March	30	23-29
X. helleri				
Edge areas	C_1	14 April	25	20-36
	C_2	8 May	100	11-47
	C_3	8 May	29	11-36
	E_1	27 July	30	20-39
	E_2	13 May	30	33-59
	H	17 June	100	14-42

*A - Moggill Creek; B - Gold Creek; C_1 - Upper Kedron Brook; C_2 - Middle Kedron Brook; C_3 - Lower Kedron Brook; D_1 - Kholo Crossing on Brisbane River; D_2 - Backwater at Kholo Crossing; D_3 - Colleges Crossing on Brisbane River; E_1 - Middle Enoggera Creek; E_2 - Lower Enoggera Creek; F - Oakey Creek; G - Manchester Creek; H - Ithaca Creek.

Fish were sampled from three major types of habitat - the open water of pools; edge areas sheltered by overhanging banks and root masses or partially overgrown by sedges *(Typha, Cyperus, Lomandra)* and semiterrestrial grasses *(Cynodon, Brachiaria);* and areas with beds of aquatic macrophytes *(Vallisneria, Hydrilla, Nymphoides).* Fish populations were sampled during daylight (1100-1600 hours) using an electrofishing apparatus (1981) or by dragging a small seine net through weed beds (1988). Details of stream habitats and sampling methods are provided by Arthington et al. (1983).

Fish were fixed in formalin and transferred to 70% alcohol for identification, measurement and storage. Fish standard length was measured to the nearest 0.5 mm. Whole guts were removed and their contents emptied into a petri dish divided into 1-mm^2 grids by a circular piece of graph paper glued to the underside of the dish. Gut contents were separated into up to 15 major food categories within which lower taxonomic groups were recorded. Since gut volumes and food items were generally too small to permit rapid volumetric analysis of the diet, an approximation of the volumetric method of Hellawell and Abel (1971) was developed. The items within each major food category were firmly squashed together to a depth approximating 1 mm; the area of each squash was then measured in mm^2 by counting the number of grid units covered by the squash similar to the area method of Hyslop (1980).

The importance of each food category was then expressed in two of three ways: frequency of occurrence (% representation of each food category in the guts of all fish in a sample), the total area of each food category (expressed as % of the total area of all identifiable food plus digested matter found in the fish of a sample) and the % numeric contribution of each food category to the total number of food items (i.e., whole or identifiable prey). Quantitative dietary comparisons are based on all fish examined regardless of stomach fullness.

The horizontal width of mouth gape of *G. affinis* was the maximum gape between the inner sides of the mouth to the nearest 0.002 mm (Bence and Murdoch 1986). The size of whole prey items in mosquitofish guts was also determined as width to the nearest 0.002 mm of the widest part of the body or head capsule, whichever was larger and as total body length (minus cerci).

The range of food items potentially available to poeciliids and endemic fishes was determined at four representative sites by standardized sampling of invertebrates in benthic substrata, beds of aquatic macrophytes and in the drift. Macrobenthos was sampled by taking three random Macan scoop samples (see Arthington et al. 1982) in each type of habitat and sieving the material through a brass mesh sieve of 0.25 mm mesh size. The invertebrates of weed beds and edge habitats were sampled by dip-netting along the length of a habitat unit several times for approximately 30 seconds, using 30-cm diameter nets of ≈ 1-mm mesh size. Drift and terrestrial insects falling into the water were sampled using a 0.25-mm mesh drift net with a 0.1-m^2 square mouth and steel frame, anchored above the bottom on long steel prongs. Nets were placed in shallow riffle areas immediately downstream from each fish sampling site, and were cleared twice daily after 12 and 24 hours.

Benthic invertebrate and drift samples were preserved in 70% ethanol and sorted into major taxa for uncommon groups and into families for groups of more frequent occurrence in samples. The body widths and lengths of whole invertebrates were measured as described above.

Differences in composition of *G. affinis* gut contents within and between habitat types and differences between the four species were examined by the Mann-Whitney U-test. The relationships between fish standard length, fish mouth gape and food size were examined by regression analysis.

Results

Diet of **G.a. holbrooki**

The composition of the diet of *G. affinis* is shown in Table 2 as the mean frequency of occurrence and % area of 13 dietary components plus digested matter in fish collected from three habitats, and for all fish collected. The taxa occurring most frequently in mosquitofish guts were ants (Formicidae), adults of small Diptera, the nymphs and adults of aquatic Hemiptera, and the larvae and adults of aquatic Coleoptera.

By the % area method of gut analysis, ants on average composed 29.68% of the gut contents of the mosquitofish and aquatic Hemiptera plus terrestrial Diptera another 20% (Table 2). All other identifiable food categories individually comprised less than 5% of the gut contents by area. Although some taxa such as aquatic Coleoptera and other aquatic insects occurred quite frequently in the diet, they were relatively unimportant in volumetric contribution.

G. affinis collected from open water and edge habitat had similar gut contents at each site, but gut contents in fish collected from weed beds were significantly different from those in open water and water weed (Table 3). The ratios of % areal contributions of aquatic to terrestrial taxa in gut contents of fish from weed beds were: site D_2 = 8.46 : 76.68, D_3 = 49.21 : 23.79, F = 0.40 : 97.60, site G = 13.2 : 8.7.

Examination of mosquitofish guts gave only the most incidental evidence of piscivory. Fish scales were found in less than 1% of the fish collected, and only at one site. Attempts to evacuate the guts of

Table 2. Mean composition of the gut contents of 514 *G. affinis* caught in open water, edge areas and weed beds expressed as frequency of occurrence (%) and % area of 13 food categories and digested matter.

Food category Habitat type	Open water	Mean frequency of occurrence (%) ± S.D. Edge area	Weed	Overall mean
Aquatic				
Hemiptera	13.45 ± 14.87	35.22 ± 29.84	5.70 ± 5.29	18.12 ± 21.94
Coleoptera	19.82 ± 18.54	15.10 ± 13.35	11.42 ± 10.28	15.45 ± 13.56
Chironomidae	12.30 ± 7.86	6.45 ± 4.82	0.45 ± 0.90	6.40 ± 6.85
Trichoptera	10.17 ± 10.44	0.47 ± 0.95	4.02 ± 5.90	4.89 ± 7.55
Odonata	7.60 ± 15.20	0.47 ± 0.95	10.15 ± 11.57	6.07 ± 10.86
Ephemeroptera	4.82 ± 6.48	1.30 ± 1.60	5.72 ± 9.38	3.95 ± 6.32
Other Taxa	4.22 ± 5.89		4.02 ± 5.90	2.75 ± 4.81
Terrestrial				
Formicidae	24.10 ± 22.54	26.67 ± 5.83	30.10 ± 39.69	26.96 ± 24.16
Other Hymenoptera	4.70 ± 2.50	8.20 ± 5.62	5.18 ± 4.59	6.02 ± 4.23
Diptera	21.65 ± 14.62	27.27 ± 10.96	25.10 ± 19.18	24.67 ± 14.05
Thysanoptera	2.22 ± 3.16	0.65 ± 1.30	0.90 ± 1.80	1.26 ± 2.14
Other Insecta	3.47 ± 5.25	5.65 ± 5.80	13.98 ± 6.79	7.70 ± 7.18
Araneae	8.02 ± 8.96	7.45 ± 4.71	4.00 ± 4.68	6.49 ± 4.44
Digested matter	48.75 ± 18.65	24.10 ± 24.61	42.98 ± 30.76	38.61 ± 25.27
		Mean % area ± S.D.		
Aquatic				
Hemiptera	8.30 ± 11.87	20.30 ± 18.80	1.16 ± 1.83	10.07 ± 13.99
Coleoptera	6.75 ± 6.55	2.60 ± 4.09	2.96 ± 2.17	4.09 ± 4.62
Chironomidae	4.97 ± 3.21	4.35 ± 2.57	0.48 ± 0.96	3.27 ± 3.05
Trichoptera	4.32 ± 6.27	1.12 ± 1.56	0.86 ± 1.23	2.10 ± 3.81
Odonata	4.70 ± 9.40	0.90 ± 1.80	5.62 ± 6.41	3.74 ± 6.38
Ephemeroptera	2.65 ± 2.37	0.15 ± 0.30	1.84 ± 3.03	1.55 ± 2.32
Other taxa	3.10 ± 4.90		4.42 – 7.01	2.50 – 4.87
Terrestrial				
Formicidae	22.67 ± 24.13	29.02 ± 15.67	37.33 ± 44.97	29.68 ± 28.56
Other Hymenoptera	1.42 ± 0.74	2.30 ± 1.35	1.15 ± 0.59	1.63 ± 1.25
Diptera	8.75 ± 7.54	12.65 ± 9.66	6.37 ± 10.03	10.06 ± 8.49
Thysanoptera	0.67 ± 1.16	1.37 ± 1.49	0.10 ± 0.21	0.72 ± 1.13
Other Insecta	1.52 ± 2.66	2.57 ± 1.90	3.51 ± 3.64	2.54 ± 2.70
Araneae	4.23 ± 2.45	1.35 ± 1.98	0.69 ± 118	2.09 ± 2.37
Digested matter	25.70 ± 13.30	21.22 ± 11.84	30.75 ± 33.29	25.89 ± 20.13

Table 3. Significant differences in gut contents of *G. affinis* within and between habitat types by the frequency of occurrence methods (lower left sector) and the % area method (upper right sector), according to the Mann-Whitney U-test. * = $P < 0.05$, ** = $P < 0.001$, ns = not significantly different.

Habitats compared	Sites compared	Open water				Edge areas				Weed beds			
		A	B	C	D_1	B	C	E_1	E_2	D_2	D_3	F	G
	A	-	ns	ns	*	ns	ns	ns	ns	ns	*	ns	ns
	B	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	**	ns
Open water	C	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	*	ns
	D_1	*	ns	ns	-	*	ns	ns	ns	ns	ns	**	*
	B	ns	ns	ns	*	-	ns	ns	ns	ns	*	*	ns
	C	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	*	ns
Edge areas	E_1	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	*	ns
	E_2	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns
Weed beds	D_2	ns	ns	ns	ns	ns	ns	ns	ns	-	*	ns	ns
	D_3	*	ns	ns	ns	*	ns	*	ns	ns	-	**	*
	F	ns	ns	*	**	ns	*	ns	ns	*	**	-	ns
	G	ns	ns	*	*	ns	ns	ns	ns	ns	**	ns	-

freshly caught *G. affinis* and *X. maculatus* by injecting a concentrated saline solution down the esophagus using a fine syringe were unsuccessful; the procedure caused the gut to rupture.

There was very little distinguishable plant or algal material in the guts of *G. affinis* collected from streams. Digested material examined microscopically contained mainly amorphous matter with some algal cells.

Width of mouth gape in *G. affinis* was correlated with fish standard length ($r = 0.9285$, $P < 0.01$, $n = 514$). It could be expected that if *G. affinis* is a gape-limited predator (*sensu* Zaret 1980), the ability to handle progressively larger prey items could account for some of the observed dietary variability.

Prey length was correlated with fish width of mouth gape ($r = 0.217$, $P < 0.01$, $n = 217$) but prey width was not ($r = 0.025$, $P > 0.05$, $n = 217$). The mean length of whole prey items in all fish examined was 2.305 mm and mean prey width was 0.543 mm; the mean width of mouth gape in the same fish was 1.804 mm (Table 4). Thus, on average, mosquitofish ingested prey of widths about 0.3 x width of mouth gape and of lengths 1.28 x width of gape, i.e., rather small prey relative to mouth size. The frequency distributions of length and width of all whole prey taken from fish guts (Fig. 1b and c) confirm that *G. affinis* showed a bias towards small prey even though mouth size (Fig. 1a) varied sufficiently to allow larger prey to be ingested. Mouth size set morphological constraints on the upper limits of prey size; the largest prey items collected from the stream environment (>9.5 mm long and >2.6 mm wide) were absent from the guts of mosquitofish.

The apparent selection of small prey could be a direct consequence of their relative abundance (and encounter rate) as suggested by similar size-frequency distributions of prey in fish guts and in the four streams sampled (Fig. 1b-e). To determine if active size selection had occurred I used the method of Gerking and Plantz (1980). I compared the mean size of prey ingested by all fish (L_1, W_1) with the mean size of prey from the four stream sites that were of equal size or smaller than the largest prey eaten (L_2, W_2). When the ratios of mean L_1/mean L_2 and mean W_1/mean W_2 are less than one, a preference is shown for smaller prey amongst those present (not necessarily available in the sense of encounter rate), whereas ratios greater than one indicate preferential feeding on larger prey within the prey size range imposed by fish mouth size (Gerking and Plantz 1980). Results are given in Table 4.

Table 4. Statistics describing the frequency distributions of *G. affinis* width of mouth, length and width of all whole prey items in 514 fish guts and at four stream sites, and frequency distributions of length and width of taxa of prey items collected at the four stream sites but occurring in fish guts with a mean frequency <5% (i.e., Chironomidae and Odonata; see Table 2). All measurements are in mm. N = number of fish or prey measured.

Data	Mean ± S.D.	Mode	Skewness	Kurtosis	N
		Fish mouth width			
Mouth width	1.804 ± 0.518	1.768	-0.112	-0.504	315
		All prey items in fish guts			
Prey length (L_1)	2.305 ± 1.462	2.480	2.331	7.463	217
Prey width (W_1)	0.543 ± 0.391	0.480	1.518	3.717	218
		All prey at four stream sites			
Prey length	4.723 ± 3.670	2.480	2.401	8.410	438
Prey width	1.023 ± 0.973	0.480	2.014	4.118	394
		Prey in streams < or = largest prey ingested			
Prey length (L_2)	3.861 ± 2.068	2.480	0.880	0.200	401
Prey width (W_2)	0.773 ± 0.530	0.480	1.066	0.441	359
		Prey at four stream sites eaten by <5% of fish			
Prey length	5.351 ± 4.237	2.480	2.233	6.350	259
Prey width	1.350 ± 1.082	0.960	1.659	2.419	215

Mean L_1/mean L_2 = 0.527 Mean W_1/W_2 = 0.702

The ratio values of 0.527 for prey length and 0.702 (Table 4) for prey width show clearly that overall, *G. affinis* fed selectively on the small prey in its environment, even though it was able to ingest larger prey within the limits imposed by mouth size. Small prey were consumed in greater proportion than their relative abundance in the environment.

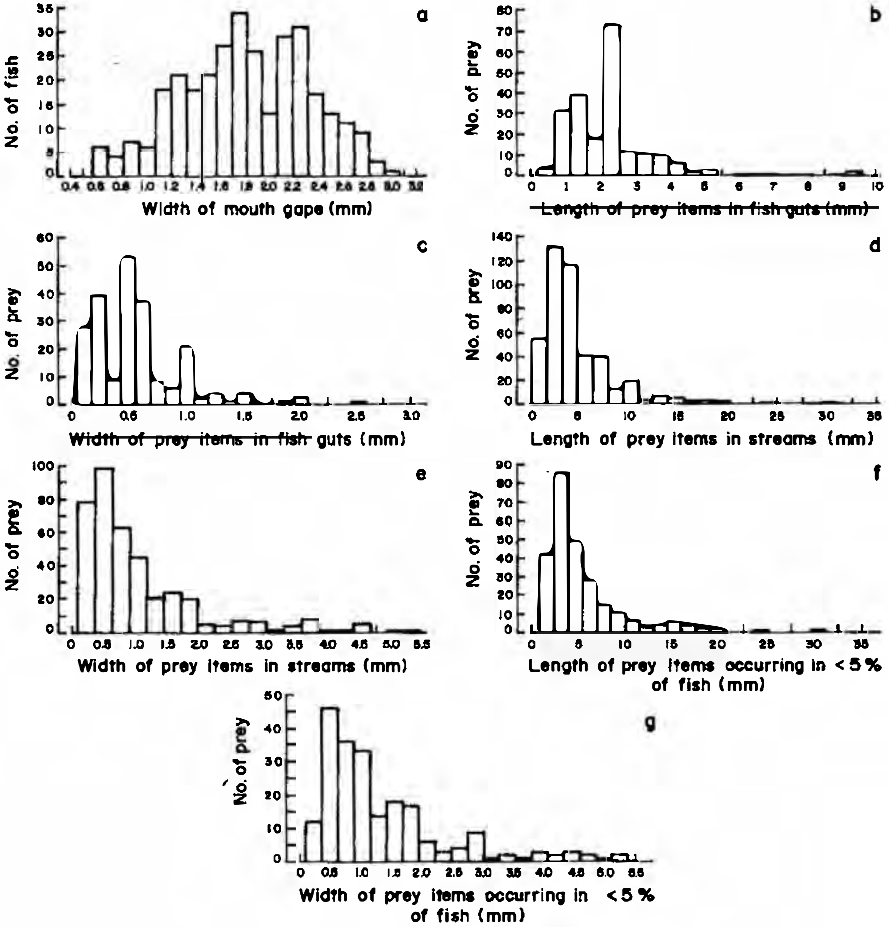

Fig. 1. Frequency distributions of (a) *G. affinis* width of mouth gape, (b) and (c) length and width of all whole prey in fish guts, (d) and (e) length and width of all whole prey in four stream sites, (f) and (g) length and width of whole prey taxa in stream sites which occurred in <5% of fish guts.

This analysis takes no account of the taxonomic composition of prey of different sizes; a low frequency of occurrence of certain taxa could be due to their size relative to the fish's feeding preferences. To examine this I plotted (Fig. 1f and g) the size-frequency distributions of all prey taxa collected at the four stream sites but occurring in fish guts with a mean frequency less than 5% (i.e., immature Trichoptera, Ephemeroptera and other aquatic taxa exclusive of Hemiptera, Coleoptera, Chironomidae and Odonata, see Table 2). Again the distributions were skewed in favor of small prey items (Table 4). Thus, although small prey were selected by *G. affinis* from amongst the array of prey present in its environment, some taxa of the preferred size range which were abundant in the streams were seldom eaten, most notably the immature stages of Trichoptera and Ephemeroptera; other taxa of the appropriate small size were almost completely neglected, e.g., small Oligochaeta, Bivalvia, Gastropoda, small Crustacea (Copepoda, Ostracoda, Cladocera) and simuliid larvae.

Diet of X. helleri

The guts of *X. helleri* were frequently filled with amorphous, partly digested material and were difficult to analyze; also many fish guts were empty (particularly fish collected in open water and weed habitat). Quantitative data are presented only for fish collected from edge habitat (Tables 1 and 5). Identifiable algal remains, especially

Table 5. Mean composition of the gut contents of *X. helleri* caught in edge areas expressed as frequency of occurrence (%) and % area of 15 food categories and digested matter.

Food category	Frequency of occurrence (%)	% area
	Mean ± S.D.	
Aquatic		
Hemiptera	1.15 ± 2.82	0.27 ± 0.65
Coleoptera	2.87 ± 7.02	0.22 ± 0.53
Trichoptera	1.40 ± 2.23	0.21 ± 0.33
Chironomidae	3.22 ± 5.00	0.29 ± 0.56
Simuliidae	0.50 ± 1.23	0.42 ± 1.02
Oligochaeta	3.05 ± 4.78	2.74 ± 5.86
Mollusca	0.72 ± 1.33	0.13 ± 0.28
Fish scales	0.67 ± 1.63	0.02 ± 0.04
Algae	12.83 ± 15.18	4.21 ± 5.91
Plants	2.00 ± 3.35	1.14 ± 2.32
Terrestrial		
Hymenoptera	2.45 ± 3.18	0.08 ± 0.12
Diptera	1.15 ± 2.82	0.17 ± 0.41
Hemiptera	0.55 ± 1.35	0.03 ± 0.08
Other Insecta	3.62 ± 2.76	0.19 ± 0.18
Arachnida	1.67 ± 2.77	1.67 ± 2.78
Digested matter	80.62 ± 23.43	89.61 ± 9.34

filamentous forms, were found in the guts of 0-36% of fish from individual collections (mean 12.83 ± 15.18) and plant fragments were found in 0-8% (mean 2.0%) of all fish. In addition, fish guts contained quite a range of aquatic and terrestrial invertebrates (Table 5) but these were relatively unimportant components of the diet, all occurring on average in less than 4% of fish examined.

For all fish examined the mean % areal contribution of amorphous, partly digested material in guts was 88.23%, of algae 4.21% and of plants 1.14% (Table 5). Microscopic examination of amorphous material revealed plant fragments, filamentous algae *(Spirogyra and Oscillatoria)*, *Closterium* and diatoms. Invertebrates collectively comprised about 6.42% by area of the mean gut contents. However, in the fish collection from Lower Kedron Brook, aquatic Oligochaeta comprised 14.60% of the gut contents and the mean areal contribution of Oligochaeta was 2.74%. Fish scales were found in <1% of all fish examined.

The gut contents of *X. helleri* did not differ significantly in composition between sites by either method of analysis ($P > 0.05$).

Diet of X. maculatus *and* P. reticulata

The composition of the diet of five collections of *X. maculatus* collected from Kholo and College Crossing on the Brisbane River in 1981 and 1988, and of 31 *P. reticulata* collected from Seven Hills Creek in 1981 is given in Table 6.

Table 6. Composition of the gut contents of 30 *X. maculatus* caught in weed beds at Colleges Crossing (17 March 1981) and of 31 *P. reticulata* caught in the edge areas and weeds at Seven Hills Creek (15 May 1981) expressed as frequency of occurrence (%), number of prey items (N) and % N of 15 food categories and digested matter.

Species Standard length (range mm)	*X. maculatus* 21.05 - 39.43			*P. reticulata* 15.65 - 21.50		
Food category	Frequency of occurrence (%)	N	% N	Frequency of occurrence (%)	N	% N
Aquatic						
Chironomidae	3.33	1	5.56	16.12	27	23.27
Ceratopogonidae	-	-	-	3.23	15	12.93
Culicidae	-	-	-	6.45	2	1.72
Odonata	6.67	2	11.11	-	-	-
Ephemeroptera	6.67	2	11.11	-	-	-
Curstacea *(Caradina)*	20.00	6	33.33	-	-	-
Terrestrial						
Hymenoptera	-	-	-	54.84	54	46.55
Hemiptera	3.33	1	5.56	9.67	3	2.59
Diptera	-	-	-	9.67	3	2.59
Other Insecta	20.00	6	33.33	22.58	12	10.34
Digested matter	70.96			48.38		

X. maculatus consumed Crustacea (Family Atyidae, *Caridina*) and various aquatic and terrestrial insects, but with a distinct predominance of *Caridina* and aquatic insects. In 20% of the 1981 and 36% of the 1988 collections, the stomach was fully distended by a single *Caridina* plus the remains of one or two insects. Partly digested material included unidentifiable amorphous material and a few algal cells. *P. reticulata* had a more diverse diet which was composed largely of terrestrial insects, particularly ants. Larval Chironomidae dominated the aquatic component of the gut contents.

Comparison of Poeciliid Diets

The gut contents of *G. affinis* and *X. helleri*, *X. maculatus* and *P. reticulata* were significantly different in terms of mean frequency of occurrence of food categories (Mann-Whitney U-test, $P < 0.01$). The diets of *G. affinis* and *X. helleri* also differed significantly by the % area method ($P < 0.01$). *X. maculatus* and *P. reticulata* differed in the % representation of number of food items in gut contents ($P < 0.01$).

Discussion

Diet of **G. affinis**

The most striking feature of the diet of *G. affinis* is the diversity of prey consumed and the variability of the diet under different circumstances. In ponds *G. affinis* forages on crustacean zooplankton (Cladocera, Copepoda and Ostracoda), snails found on aquatic plants, larval chironomids, floating terrestrial insects and certain benthic insects (Hurlbert et al. 1972; Rees 1979; Walters and Legner 1980; Hurlbert and Mulla 1981). Studies on the rice field ecosystem have demonstrated feeding on Rotifera, Mollusca, Crustacea, Insecta, Chlorophyceae and Desmidaceae (Sokolov and Chvaliova 1936) and the impact of mosquitofish predation on Cladocera, Odonata, Ephemeroptera, Corixidae, Belostomatidae and aquatic beetles (Farley and Younce 1977; Miura et al. 1984). Harrington and Harrington (1961) found that *G. affinis* in a Florida salt marsh ate vascular plants and algae, Copepoda, crab zoeae, *Aedes* larvae, other aquatic insects, aquatic invertebrate eggs, mites, ants and fishes. However, in small experimental systems *G. affinis* has survived on quite restricted diets such as pure *Tubifex tubifex* (Shakuntala and Reddy 1977; Vondracek et al. in press), *Daphnia* (Bence and Murdoch 1986), various species of mosquitoes (e.g., Reddy and Pandian 1972; Wurtsbaugh et al. 1980), notonectids (Bence and Murdoch 1982), frog eggs (Grubb 1972) and fish (by cannibalism, Dionne 1985 and on other species, Meffe 1985).

This study confirms that *G. affinis* is a generalist predator *sensu* Keast (1979) in stream habitats, taking a wide range of invertebrate prey of aquatic and terrestrial origin but very little algal and plant material. When digested matter was excluded from total gut contents, terrestrial insects collectively contributed 63% of mean total gut contents and ants comprised 40%. The feeding site had an influence on the composition of *G. affinis* gut contents, particularly on the relative proportions of aquatic and terrestrial taxa eaten in weed bed habitat (Tables 2 and 3).

G. affinis showed a preference for small prey, a finding in direct contrast to several field studies but consistent with experimental data. Farley (1980) suggested that Cladocera and Copepoda were unattractive to *G. affinis* in rice fields because of their small size, implying preference for large prey. Wurtsbaugh et al. (1980) concluded that individual *G. affinis* will select the largest prey they can successfully capture, but prey movement, visibility and palatability affected prey choice in aquarium experiments.

G. affinis given a choice between larvae of *Aedes aegypti* and *Culex fatigans* preferred the former species, a behavior attributed by Rajasekharan and Chowdaiah (1972) to smaller size, vertical position occupied in the water and a tendency to aggregate. Bence and Murdoch (1982) showed that all sizes of *G. affinis* that could consume more than one instar of *Notonecta* preferred the first instar. They subsequently demonstrated active choice of small *Daphnia* by *G. affinis* in an experimental study of feeding in relation to optimal diet theory (Bence and Murdoch 1986).

The absence or infrequent occurrence of certain aquatic taxa in the preferred size range (i.e., small Crustacea, Oligochaeta, Gastropoda, immature Trichoptera and Ephemeroptera) in the guts of *G. affinis* in spite of their abundance in the stream environment contrasts with other studies where Gastropoda, zooplanktonic and littoral Crustacea and benthic invertebrates were important components of the diet (e.g., Crustacea and Ephemeroptera - Sokolov and Chvaliova (1936); Hurlbert et al. (1972); planktonic Crustacea - Hurlbert and Mulla (1981); Gastropoda - Rees (1979); benthic insects

- Farley and Younce (1977); Cladocera and Ephemeroptera - Miura et al. (1984). Although *G. affinis* is particularly well adapted morphologically to feeding at the water's surface, having a flattened head and terminal, upwardly directed mouth (Scott et al. 1974), the mouth morphology of Poeciliidae in general does not preclude feeding on benthic invertebrates and grazing on algae and detritus (Dussault and Kramer 1981). The paucity of immature Ephemeroptera and Trichoptera from the diet of *G. affinis* in streams could be due to their cryptic behavior in the benthos. However, both taxa were abundant in drift samples especially those taken at night, and it is known that *G. affinis* feeds on drifting fauna (e.g., McDowall 1980). A possible explanation for these feeding biases may lie in the relative encounter rate (e.g., drifting Ephemeroptera were more abundant at night), difficulty of capture of some taxa and unpalatibility. Sokolov and Chvaliova (1936) noted that female *G. affinis* did not eat Trichoptera larvae.

The foraging strategy of *G. affinis* appears to be flexible, well tuned to spatial and presumably also temporal variations in food availability, and highly adaptive for life in the variable stream environment. *G. affinis* is considered to be one of the world's most successful colonizing species and undoubtedly a foraging strategy of the type described here has contributed significantly to its establishment in many environments (see Arthington and Mitchell 1986). Shakuntala (1977) suggested that the ecological success of *G. affinis* in competitive situations may be largely dependent on the availability of food and the ability of individuals to successfully regulate food intake. Other features which have proved highly adaptive for the mosquitofish, especially in areas of introduction, are described by Arthington and Mitchell (1986).

The Diet of **X. helleri, X. maculatus** *and* **P. reticulata**

X. helleri was consistently omnivorous in the study streams, as it is in aquaria (e.g., Kallman 1976), but showed a preference for plant foods. *X. maculatus* was also omnivorous but preferred animal foods, particularly large individuals of the atyid *Caridina* and various aquatic and terrestrial insects. Green et al. (1978) found *X. maculatus* to be primarily a detritivore in Indonesian lakes, although consuming a small quantity of cyclopoid copepods and chironomid larvae.

The data of this study on *P. reticulata* present a contrast with data from Trinidadian streams, where immature aquatic insects, unicellular algae, diatoms and plants were eaten (Dussault and Kramer 1981). In Brisbane streams the diet of *P. reticulata* was similar to that of *G. affinis* in its taxonomic diversity and the importance of terrestrial insects, particularly ants, but larval Chironomidae were more important than for *G. affinis*. Very little algal or plant material was found in the guts of *P. reticulata*. Dussault and Kramer (1981) found that *P. reticulata* can live and grow on an exclusive diet of the green alga *Chlorococcum* but not on the filamentous green *Oedogonium;* growth was slower in fish fed on algae than in fish fed *Daphnia* and fish food (Tetra-min). Other studies suggest that *P. reticulata* is primarily carnivorous (Davis 1968) and a surface feeder (Murdoch et al. 1975; Ballin 1973). Green et al. (1978) commented that shifts from surface to plankton to benthic food sources by *P. reticulata* may be a major factor contributing to its success in Indonesian lakes.

Dussault and Kramer (1981) concluded that opportunistic feeding on a variety of animal foods with a major component of benthic algal material may be the common feeding pattern in poeciliids. This is consistent with intestinal morphology, i.e., unusually long and coiled, varying in length from one to two times standard length in *P. reticulata* (Dussault and Kramer 1981) and the two *Xiphophorus* species (this study), an adaptation for digesting algae and detritus (De Silva et al. 1980). Nevertheless, the flexibility of poeciliid mouth position during feeding, which involves the protraction of the premaxilla so that the mouth opening shifts from a dorsal terminal to a ventral terminal position, is adaptive for all styles of feeding, i.e., surface, midwater and benthic feeding (Alexander 1967; Dussault and Kramer 1981).

The generalized structure and flexibility of use of the mouth apparatus explains the breadth and variability of poeciliid diets, very selective feeding when necessary and food resource partitioning by poeciliids in sympatry (e.g., Odum and Heald 1972; Vrijenhoek 1978).

The differentiation of poeciliid diets amongst sympatric species is borne out here. In Brisbane streams *G. affinis* and *X. helleri* most often occurred together and showed high overlap in habitat use (mean $C_{xy} = 0.76$, Arthington et al. 1983), although *G. affinis* was more likely to be found in surface waters than *X. helleri*. Both species showed a preference for edge habitat sheltered by introduced grasses, but their mean diets differed significantly; *G. affinis* was primarily carnivorous and *X. helleri* omnivorous, with only a small amount of feeding on invertebrates. Where *X. maculatus* was sympatric with *G. affinis* these species also consumed different food resources. *G. affinis* and *P. reticulata* both use surface waters for foraging, but their diets were significantly different in this study. Haas and Pal (1984) describe *P. reticulata* as having food and habitat requirements almost identical to those of *G. affinis*.

Impact of Poeciliid Feeding on Stream Food Resources

The observed patterns of resource use by poeciliids may have a considerable impact on the *in situ* food resources of streams, especially where poeciliids are numerous. *G. affinis* alone may have profound impacts on aquatic ecosystems (e.g., Hurlbert et al. 1972). The frequent occurrence of large populations of *G. affinis* and *X. helleri*, or *G. affinis* and *P. reticulata*, in many subtropical streams represents a significant disturbance. These poeciliid species pairs seem to depress populations of certain endemic fish species, possibly as a result of feeding interactions (Arthington et al. 1983). Dietary overlap between poeciliids and endemic stream fishes, and evidence of interspecific competition for food, will be examined elsewhere.

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