

Seasonal, sexual and ontogenetic variations in the diet of the ‘declining’ frogs *Litoria nannotis*, *Litoria rheocola* and *Nyctimystes dayi*

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Abstract. Faecal analyses were used to investigate the diets of the endangered frogs *Litoria nannotis*, *L. rheocola* and *Nyctimystes dayi* in Tully Gorge, North Queensland. Comparisons of diet and food availability indicate that these species feed indiscriminately on a range of terrestrial and aquatic invertebrates. Changes in morphology and foraging behaviour significantly influenced diet composition and created subtle shifts in the degree of selectivity displayed in prey choice. Interspecific differences in numeric and volumetric diet composition were attributed to variations in gape size and microhabitat selection. Within the diets of *L. nannotis* and *L. rheocola*, a decline in prey selectivity observed during the dry season reflected a reduction in foraging activity. Differences in the gape size and foraging behaviour of males and females of *L. nannotis* were responsible for sex-specific differences in diet composition. *L. nannotis* also displayed an ontogenetic shift in prey size and type. As snout–vent length increased, *L. nannotis* consumed fewer, but larger prey and increasingly discriminated against dipterans, dipteran larvae and hemipterans. Importantly, *L. nannotis*, *L. rheocola* and *N. dayi* demonstrated the capacity to compensate for fluctuations in food availability by feeding on less lucrative prey.

Introduction

Most animals experience some variation in dietary intake and feeding efficiency throughout their lives. While predators tend to feed on the most optimal prey available (Emlen 1966; Schoener 1971; Pyke *et al.* 1977), they rarely encounter a constant and unwavering supply of prey. Instead, the rate at which optimal prey are encountered and consumed tends to vary with changes in food availability, foraging behaviour and predator morphology. Selection pressures that restrict the time available for foraging, such as the need to reproduce, avoid predators and shelter from adverse environmental conditions, can also affect the rate at which optimal prey are encountered (Regal 1983; Lucas 1985). For a given species, the abundance and quality of prey encountered may therefore vary seasonally, between males and females and through ontogeny. Predators therefore rarely feed at maximum efficiency and must have the capacity to adapt to these changes in order to survive.

Foraging behaviour can have a strong influence on dietary composition. In frogs and lizards, foraging behaviour spans a continuum between active foraging and sedentary, sit-and-wait predation (Toft 1980, 1981). Predators that forage actively tend to encounter more prey than those that

employ a sedentary, sit-and-wait feeding strategy. Active foragers can therefore afford to specialise on optimal prey. In contrast, sedentary predators tend to be more indiscriminate, or opportunistic, in their selection of prey, since they encounter prey less frequently (Emerson 1976; Huey and Pianka 1977; Toft 1980, 1981; Taigen and Pough 1983; Magnusson *et al.* 1985).

Predators may regulate their feeding efficiency by altering foraging behaviour; however, most predators can achieve this only within narrow limits. This is due to the fact that foraging behaviour is often correlated with other ecological characteristics such as predator defence, reproductive strategies, aerobic capacity and general physiology (Seymour 1973; Emerson 1976; Vitt and Congdon 1978; Huey and Pianka 1981; Toft 1981; Taigen and Pough 1983; Strussman *et al.* 1984; Magnusson *et al.* 1985). Any dramatic change in foraging behaviour would therefore compromise species fitness by increasing exposure to predation, reducing reproductive opportunities or leading to physiological deterioration (Seymour 1973; Emerson 1976; Vitt and Congdon 1978; Huey and Pianka 1981; Toft 1981; Taigen and Pough 1983; Strussman *et al.* 1984; Magnusson *et al.* 1985). Given this limitation, a predators’

capacity to adapt to changes in food availability will be largely dependent on the degree to which it can compromise its diet and accept a broader range of less lucrative prey.

Three species of frogs, *Litoria nannotis*, *Litoria rheocola* and *Nyctimystes dayi*, have declined from upland regions of north Queensland's Wet Tropics since the early 1990s (Richards *et al.* 1993; Trenerry *et al.* 1994). While potential causal factors for their decline have been proposed and widely investigated (Laurance 1996; Laurance *et al.* 1996; Alford and Richards 1997; Hero and Gillespie 1997), many aspects of their basic ecology remain unknown. Existing information on the ecology of *L. nannotis*, *L. rheocola* and *N. dayi* (habitat specialisation, range restriction and low fecundity) indicates that they are particularly susceptible to localised extinction (Williams and Hero 1998). There is, however, no information on the diet of these three species. This study aimed to describe and compare the diets of *L. nannotis*, *L. rheocola* and *N. dayi* and investigate their capacity to compensate for fluctuations in feeding efficiency.

Information on the behavioural ecology of these frogs and their environment suggests that they may experience considerable variation in feeding efficiency. Within the tropics, the availability of invertebrate food items often increases substantially during the wetter months, in response to rainfall (Wolda 1980; Stamps and Tanaka 1981). Many tropical predators therefore experience seasonal diet shifts that simply reflect a change in food availability (Pianka 1970; Sexton *et al.* 1972; Vitt and Lacher 1981; Schoener *et al.* 1982; Burquez *et al.* 1986; Van Sluys 1995; Rocha 1996). *L. nannotis*, *L. rheocola* and *N. dayi* inhabit an environment that is characterised by distinct wet and dry seasons (Hodgkison and Hero 2001, 2002). They may therefore experience some seasonal variation in feeding efficiency.

The diets of *L. nannotis*, *L. rheocola* and *N. dayi* may also be affected by variations in their own morphology. Like most frogs, *L. nannotis*, *L. rheocola* and *N. dayi* swallow their prey whole and can therefore only consume prey that fit inside their mouth. Variations in gape size have been responsible for ontogenetic and sex-specific diet shifts in many frogs and lizards (Labanick 1976; Christian 1982; Schoener *et al.* 1982; Donnelly 1991; Van Sluys 1993) and may influence the diet of *L. nannotis*, *L. rheocola* and *N. dayi*.

Finally, *L. nannotis* and *L. rheocola* display sex-specific variations in foraging behaviour that may lead to a difference in the diet of males and females. Compared with those of females, the foraging activities of males of both species are somewhat restricted, males displaying greater fidelity to the breeding site (Hodgkison and Hero 2002). Sex-specific differences in foraging behaviour often cause variations in the choice of prey of frogs (Pengilly 1971; Christian 1982; Woolbright 1985; Donnelly 1991) and lizards (Parmelee and Guyer 1995). *L. nannotis* and *L. rheocola* may therefore experience sex-specific variations in prey selection.

This study aimed to describe and compare the diets of *L. nannotis*, *L. rheocola* and *N. dayi* from faecal analysis and investigate potential interspecific, seasonal, sex-specific and ontogenetic changes in numeric and volumetric diet composition and prey selectivity.

Methods

This study was conducted within Tully Gorge (17°46'S, 145°35'E), north Queensland, Australia. Tully Gorge experiences distinct wet and dry seasons, with rainfall increasing dramatically between January and April (Hodgkison and Hero 2001). Three fast-flowing rainforest streams, lying approximately 4 km apart, were surveyed for frogs and food availability. All streams contain large granite boulders that create many short waterfalls. Streams were lined by simple notophyll-vine forest.

Diet

Faecal analysis is the least destructive method of diet analysis currently available and was considered the most appropriate, given the endangered status of the frogs involved. In all, 298 *L. nannotis*, 121 *L. rheocola* and 18 *N. dayi* were captured over 14 months for dietary analysis. Once captured, frogs were measured for snout-vent length and then held in individual plastic bags for 12–36 h. Frogs were then released at the site of capture and any faeces preserved in alcohol. Prey remains were identified to family and the number of individuals in each family counted. Lengths of prey were reconstructed, using intact specimens as a scaling guide. Volumes (mm³) of prey were estimated using the procedure described by Schoener (1967), after measuring the length, width and height of prey remains to the nearest 0.1 mm using Vernier callipers.

Food availability

Data on availability of terrestrial and aquatic food were collected from each of the three streams monthly for 14 months (June 1996 – July 1997). Terrestrial-food availability was measured using ground-level and hanging adhesive traps. Traps were used to measure food availability in three terrestrial microhabitats: (i) on boulders within the stream, (ii) within streamside vegetation (<5 m from stream edge) and (iii) within the adjacent forest (15–20 m from stream edge). Each month, terrestrial food-availability traps were left for 12 h (0700–1900 hours) to measure diurnal food availability. Traps were then replaced and left for a further 12 h (1900–0700 hours) to measure nocturnal food availability.

Aquatic food availability was sampled in three microhabitats: (i) in pools, (ii) on rocks beside calm water and (iii) on rocks beside turbulent water. Food availability in pools was sampled using 1-min random sweeps with a 0.5-mm-mesh net. Rocks were sampled for invertebrates by haphazardly placing a 1 m × 1 m quadrat on rocks and scraping invertebrates from the area within. Each of the three aquatic microhabitats was sampled at 10 locations per stream per month (June 1996 – July 1997). All invertebrates found in terrestrial and aquatic food-availability surveys were identified to family and preserved in alcohol. Seasonal variation in food availability was investigated by comparing data collected in the peak three months of the wet season (December–February) with those of the dry season (June–August).

Analysis

A 2-way MANOVA was used to investigate the effect of season (wet, dry) and microhabitat (pools, rock beside calm water, rock beside fast-flowing water) on aquatic food availability, where independent variables were individual food items, grouped by taxa. A 3-way MANOVA was used to investigate the effect of season (wet, dry), time

of day (day, night) and microhabitat (stream, stream-side vegetation, forest) on terrestrial food availability. Again, the dependent variables were individual food items, grouped by taxa. Two-way MANOVAs (Hair *et al.* 1995) were used to test the effect of species (*L. nannotis*, *L. rheocola*, *N. dayi*) and season (wet, dry) on the numeric and volumetric prey compositions of male frogs. Two-way MANOVAs were used to investigate the effect of season (wet, dry) and sex (juvenile, male and female) on the numeric and volumetric dietary composition of *L. nannotis*. The numeric and volumetric diet data were multiplicative, and therefore log-transformed prior to analysis. Bonferroni corrections were used when assessing the significance of all MANOVA results. To avoid overlap between seasonal diets, all investigations of seasonal diet change were conducted using data collected during the peak three months of the wet season (December–February) and dry season (June–August).

Simpson's diversity indices (Zar 1984) were calculated for the terrestrial food community and for the diets of *L. rheocola*, juvenile *L. nannotis*, adult male *L. nannotis* and adult female *L. nannotis*. Spearman's rank correlations (Zar 1984) were used to investigate seasonal variations in the relationship between diet (*L. nannotis* and *L. rheocola*) and food availability. Again, seasonal comparisons were conducted using only data collected during the peak seasons (December–February) and (June–August).

To determine whether prey type changed through ontogeny, *L. nannotis* was divided by snout–vent length into eight size categories. For individual prey taxa (Coleoptera, Blattodea, Hymenoptera, Hemiptera, Araneae, etc.), correlations (Zar 1984) were conducted between the mean snout–vent lengths for the eight size groups and the volumetric proportion of each prey type represented within the diets of frogs of each size category. Proportions did not conform to normality and were therefore arcsin-transformed before analysis. Two-way MANOVAs were then conducted to test the effect of size (small, intermediate, large frogs) and season (wet, dry) on the numeric and volumetric prey composition within the diets of male and female *L. nannotis*. Data for males and females were analysed separately to avoid confounding the results with sex-specific prey preferences.

Simple linear correlations (Zar 1984) were used to test for associations between snout–vent length and the number of prey found in faeces, and the mean length of prey and the mean volume of prey. The number, length and volume of prey were multiplicative and therefore log-transformed. One-way ANOVAs (Zar 1984) were also used to test for differences in the number of prey, length of prey and volume of prey within the diets of juvenile, adult male and adult female *L. nannotis*.

Results

Food availability

During monthly surveys of availability of aquatic food 4390 individuals from 12 invertebrate taxa were collected. Trichopteran larvae accounted for 37.13% of items captured, followed by ephemeropteran larvae at 28.06%, hemipterans (including mesoveliids and notonectids) at 19.29% and decapods at 6.42%. Aquatic food availability did not vary seasonally (MANOVA: $F = 0.72$, d.f. = 8, $P = 0.68$) but did differ significantly between microhabitats (MANOVA: $F = 64.44$, d.f. = 16, $P = 0.0002$). Coleoptera, Decapoda and Hemiptera were significantly more abundant in open water than on rocks beside calm water ($P = 0.001$, $P = 0.0001$, $P = 0.0002$ respectively) or on rocks beside fast-flowing water ($P = 0.012$, $P = 0.0001$, $P = 0.0003$ respectively). Ephemeropteran larvae were significantly more abundant on

rocks beside fast-flowing sections than in open water ($P = 0.0001$).

During monthly surveys on availability of terrestrial food 2985 individuals from 16 invertebrate taxa were collected. Dipterans were the most abundant, accounting for 79.53% of those captured. Coleopterans, hemipterans, hymenopterans and Araneae were also common. Terrestrial food availability did not vary seasonally (MANOVA: $F = 1.30$, d.f. = 6, $P = 0.272$), but did differ significantly between night and day (MANOVA: $F = 33.65$, d.f. = 6, $P = 0.0002$) and among microhabitats in the stream, stream-side vegetation and forest (MANOVA: $F = 3.22$, d.f. = 12, $P = 0.0003$). Dipterans ($P = 0.0001$), hemipterans ($P = 0.003$) and hymenopterans ($P = 0.0003$) were significantly more abundant during the day than at night. Coleopterans were more abundant in the stream than in stream-side vegetation ($P = 0.003$). Dipterans were significantly more abundant in the stream than in stream-side vegetation ($P = 0.0002$). Mean invertebrate density ranged from 3.25 invertebrates per trap in August 1996 to 14.89 invertebrates per trap in October 1996 and was therefore too low to saturate the traps.

Diet

Faecal samples were collected from 241 *L. nannotis* (48 juvenile, 135 male, 58 female), 92 *L. rheocola* (85 male, 7 female) and 13 *N. dayi* (all male). The diets of all three species contained a range of terrestrial and aquatic prey, including dipterans, coleopterans, hemipterans, Formicidae, Araneae, dipteran larvae, trichopteran larvae and ephemeropteran larvae (Table 1). *L. nannotis*, *L. rheocola* and *N. dayi* were generally indiscriminate in their selection of prey, consuming most prey items in proportions similar to those found in the environment. Despite this, all three species selected for blattodeans and *L. nannotis* and *L. rheocola* selected for isopteran and odonates (adults and larvae) and discriminated against adult and larval trichopterans and lepidopterans (Table 1).

The diet of *L. nannotis* was significantly different in numeric (MANOVA: $F = 2.005$, d.f. = 42, $P = 0.0002$) and volumetric (MANOVA: $F = 3.465$, d.f. = 42, $P = 0.0003$) composition from those of *L. rheocola* and *N. dayi*. The diet of *L. nannotis* contained a substantially greater aquatic content than did those of *L. rheocola* and *N. dayi* (Table 1).

Seasonal diet shift

Litoria nannotis and *L. rheocola* experienced a seasonal shift in their selectivity for prey. During the dry season the diets of *L. nannotis* and *L. rheocola* were closely correlated with terrestrial food availability in most habitats, indicating a generalist diet. During the wet season, however, there were fewer correlations between diet and food availability, suggesting that the frogs were more discerning in their choice of prey (Table 2). Interestingly, despite the increase in prey selectivity, the diets of all three species were more

Table 1. Mean number and volume (mm³) of prey found in faeces of *L. nannotis*, *L. rheocola* and *N. dayi*

	<i>Litoria nannotis</i> (n = 241)				<i>Litoria rheocola</i> (n = 92)				<i>Nyctimystes dayi</i> (n = 13)			
	Mean no.	s.e.	Mean vol.	s.e.	Mean no.	s.e.	Mean vol.	s.e.	Mean no.	s.e.	Mean vol.	s.e.
Diptera	1.373	0.274	2.58	0.571	1.95	0.131	6.02	0.702	0.846	0.317	2.92	1.554
Trichoptera	0.017	0.009	0.116	0.096	0.022	0.015	0.207	0.169				
Ephemeroptera	0.008	0.004	0.108	0.115								
Odonata	0.05	0.017	5.66	1.727	0.011	0.011	0.022	0.022				
Coleoptera	0.71	0.098	8.31	2.191	0.326	0.063	1.68	0.529	0.538	0.183	4.5	2.177
Lepidoptera	0.008	0.006	1.24	0.973								
Orthoptera	0.116	0.022	1.79	0.434	0.163	0.045	3.402	1.208				
Mantodea	0.568	0.225	0.06	0.069								
Hemiptera	0.572	0.086	3.062	0.701	0.261	0.068	3.087	1.192	0.231	0.122	0.846	0.529
Blattodea	0.075	0.02	6.42	2.456	0.098	0.035	2.26	0.894	0.077	0.077	3.08	3.08
Dermaptera	0.008	0.006	0.166	0.145	0.011	0.011	0.163	0.164				
Opiliona	0.004	0.004	0.012	0.014								
Hymenoptera	0.884	0.058	3.88	0.397	0.391	0.133	1.986	0.681	0.538	0.914	0.938	0.449
Isoptera	0.249	0.166	0.301	0.239	0.109	0.057	0.109	0.057				
Araneae	0.295	0.032	2.22	0.723	0.402	0.066	1.33	0.274	0.692	0.175	4.38	1.96
Acarina	0.062	0.019	0.015	0.011	0.043	0.021	0.023	0.015	0.077	0.077	0.008	0.008
Scorpionida	0.008	0.006	0.008	0.005	0.011	0.011	0.022	0.022				
Diplopoda	0.282	0.037	4.15	1.501	0.011	0.011	0.272	0.273	0.077	0.077	0.154	0.154
Chilopoda	0.012	0.009	0.108	0.034								
Gastropoda	0.025	0.012	0.361	0.284	0.022	0.015	0.087	0.077				
Ostracoda	0.004	0.004	0.001	0.001	0.022	0.015	0.007	0.005	0.077	0.077	0.023	0.023
Dipteran larvae	0.963	0.359	0.461	0.172	0.359	0.361	0.108	0.108	0.077	0.077	0.023	0.023
Plecopteran larvae	0.104	0.025	1.07	0.596	0.043	0.021	0.228	0.124				
Trichopteran larvae	0.905	0.169	1.91	0.357	0.022	0.015	0.023	0.022	0.077	0.077	0.154	0.192
Odonate larvae	0.075	0.017	4.11	1.466	0.054	0.024	0.619	0.338	0.154	0.104	3.85	2.604
Ephemeropteran larvae	0.303	0.043	3.27	0.822	0.033	0.019	0.087	0.168	0.077	0.077	1.15	1.15
Lepidopteran larvae	0.228	0.043	0.749	0.171	0.076	0.026	0.066	0.027				
Coleopteran larvae	0.037	0.014	0.631	0.325	0.022	0.011	0.109	0.087				

diverse in the wet season than in the dry season (see Simpson's diversity values, Table 3).

The diet of *L. nannotis* displayed a significant seasonal shift in the numeric (MANOVA: $F = 2.65$, d.f. = 23, $P = 0.0004$) and volumetric prey composition (MANOVA: $F = 2.06$, d.f. = 23, $P = 0.004$). The wet-season diet of *L. nannotis* contained significantly greater numbers of Odonata ($P = 0.0002$) and Trichoptera ($P = 0.036$) and greater volume of Odonata ($P = 0.001$) than the dry-season diet. The wet-season diet also contained a significantly smaller number ($P = 0.0003$) and volume ($P = 0.001$) of Diplopoda than the dry-season diet.

Sex-specific diet shift

The diets of juvenile, adult male and adult female *L. nannotis* varied substantially with respect to the number, size and type of prey consumed. Females consumed significantly fewer prey (ANOVA: $F = 8.98$, d.f. = 2, $P = 0.0002$) than did juveniles. The prey consumed by females were of significantly greater length (ANOVA: $F = 12.66$, d.f. = 2, $P = 0.00003$) and volume (ANOVA: $F = 21.33$, d.f. = 2, $P = 0.00002$) than those consumed by juveniles and adult males. The diet of adult males contained a substantially greater number of aquatic prey than did the diets of juveniles and adult females.

The diets of juveniles, adult males and adult females differed significantly in numeric (MANOVA: $F = 2.29$,

d.f. = 46, $P = 0.0003$) and volumetric (MANOVA: $F = 12.11$, d.f. = 46, $P = 0.0001$) prey composition. The diet of juveniles differed from that of adult females in that it contained significantly greater numbers of coleopterans ($P = 0.002$), dipterans ($P = 0.0002$) and hemipterans ($P = 0.007$) and a significantly greater volume of dipterans ($P = 0.005$). Dipterans were also more common in the diet of juveniles than in that of adult males ($P = 0.006$).

The diet of adult males contained a greater proportion of aquatic invertebrates. Larval Ephemeroptera were found in significantly greater numbers in the diet of adult male than in the diet of adult female *L. nannotis* ($P = 0.003$). The diet of adult males also contained significantly greater volumes of larval Ephemeroptera ($P = 0.001$) and Trichoptera ($P = 0.005$) than did the diet of adult females.

Adult females consumed significantly greater numbers of Diplopoda ($P = 0.007$) and significantly greater volumes of Diplopoda ($P = 0.002$), Lepidoptera ($P = 0.0001$), and Odonata ($P = 0.002$) than did juveniles of *L. nannotis*. The diet of females also contained significantly greater numbers of Decapoda ($P = 0.007$) and significantly greater volumes of Lepidoptera ($P = 0.0004$) and Orthoptera ($P = 0.003$) than did that of adult males.

Ontogenetic shift in diet

In *L. nannotis*, prey dimensions were correlated with snout-vent length. As snout-vent length increased, the

Table 2. Spearman rank correlations between diet and availability of terrestrial and aquatic food
*, $P < 0.05$

Food availability	<i>Litoria nannotis</i> Juvenile		<i>Litoria nannotis</i> Male		<i>Litoria nannotis</i> Female		<i>Litoria rheocola</i> All frogs	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Forest during day	0.870*	0.584*	0.669*	0.516*	0.502	0.743*	0.584	0.877*
SS Vegetation during day	0.759*	0.739*	0.469	0.697*	0.476	0.772*	0.427	0.749*
Stream during day	0.675	0.831*	0.491	0.574*	0.325	0.750*	0.451	0.674*
Forest at night	0.712*	0.695*	0.405	0.641*	0.28	0.810*	0.529	0.923*
SS Vegetation at night	0.781*	0.591*	0.539*	0.552*	0.457	0.652*	0.618*	0.698*
Stream at night	0.636	0.634*	0.457	0.501*	0.347	0.620*	0.522	0.449
Aquatic	0.355	0.3	0.544	0.282	0.095	0.369	0.002	0.068

Table 3. Seasonal measures of Simpson's diversity index for arthropods in diet and food availability samples

	<i>n</i>	Wet season		<i>n</i>	Dry season	
		Index of abundance	Simpson's diversity		Index of abundance	Simpson's diversity
Food availability	1296 traps	1.1 arthropods per trap per hour	1.6	1728 traps	0.9 arthropods per trap per hour	1.6
<i>Litoria nannotis</i> – Juvenile	16 frogs	9.1 arthropods per frog	5.3	24 frogs	10.3 arthropods per frog	4.0
<i>Litoria nannotis</i> – Male	41 frogs	8.8 arthropods per frog	8.9	56 frogs	9.2 arthropods per frog	7.8
<i>Litoria nannotis</i> – Female	17 frogs	3.2 arthropods per frog	12.9	28 frogs	4.3 arthropods per frog	9.4
<i>Litoria nannotis</i>	74 frogs	7.6 arthropods per frog	10.0	108 frogs	8.1 arthropods per frog	8.2
<i>Litoria rheocola</i>	34 frogs	4.9 arthropods per frog	4.4	25 frogs	6.1 arthropods per frog	2.5
<i>Nyctimystes dayi</i>	10 frogs	4.2 arthropods per frog	7.9	3 frogs	1.3 arthropods per frog	2.0

number of prey decreased significantly (linear correlation: $P = 0.029$), whereas the length (linear correlation: $P = 0.0003$) and volume (linear correlation: $P = 0.00001$) (Fig. 1) of prey increased. In addition, correlations between the mean snout–vent lengths of frogs (grouped by size) and the volumetric proportion of individual prey in each size group revealed an ontogenetic shift in prey type. The proportion of the total volume of prey accounted for by dipterans (linear correlation: $P = 0.008$), dipteran larvae (linear correlation: $P = 0.025$) and hemipterans (linear correlation: $P = 0.032$) declined significantly as frog snout–vent length increased (Fig. 2). The MANOVA comparing numeric and volumetric proportions of prey among small, intermediate and large frogs (with sexes separated) illustrated an ontogenetic shift in prey type, independent of sexual dietary differences. Large males consumed significantly greater volumetric proportions of homopterans, isopterans and ostracods than did small males (MANOVA: $F = 1.45$, d.f. = 60, $P = 0.030$). However, this was true for the wet season only, there being a significant interaction between season and size (MANOVA: $F = 1.41$, d.f. = 60, $P = 0.043$). The diet of large females contained a significantly greater numeric proportion of odonatan and orthopterans than did the diet of small females (MANOVA: $F = 1.68$, d.f. = 52, $P = 0.030$).

Discussion

Litoria nannotis, *L. rheocola* and *N. dayi* feed relatively indiscriminately on a wide range of terrestrial and aquatic prey, including dipterans, coleopterans, hemipterans, hymenopterans, Araneae, trichopteran larvae, ephemeropteran larvae and plecopteran larvae. Most prey were solitary, mobile forms, with the exception of ephemeropteran larvae and Formicidae. The lack of strong selectivity in their choice of prey suggests that all three species are relatively opportunistic sit-and-wait predators. This is also supported by concurrent behavioural studies (Hodgkinson and Hero 2001, 2002). Indiscriminate or opportunistic diets are characteristically observed in sedentary predators (Toft 1980, 1981; Huey and Pianka 1981; Simon and Toft 1991). Predators with slow foraging velocity and limited foraging ranges contact prey less frequently and encounter fewer prey types. Sedentary predators can therefore less afford to discriminate among prey taxa. In contrast, actively foraging predators encounter more prey and can therefore specialise on optimal items.

Interspecific variations in diet

The diet of male *L. nannotis* was significantly different in numeric and volumetric composition from those of male

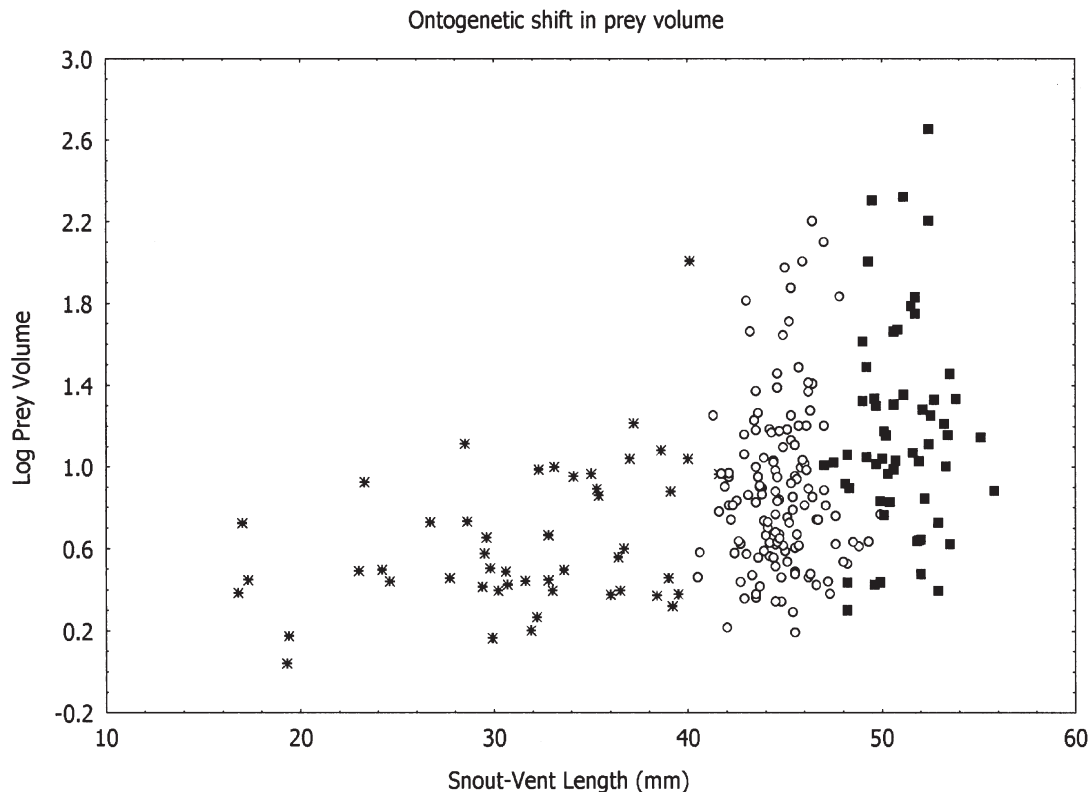


Fig. 1. Relationship between snout-vent length of *Litoria nannotis* and the (log) mean volume of prey found in each faecal sample (asterisks = juveniles, open circles = adult males, closed squares = adult females).

L. rheocola and *N. dayi*. The difference in diet may have been caused by interspecific variations in morphology and habitat use. Males of *L. nannotis* are considerably larger than males of *L. rheocola* and *N. dayi* and can therefore feed on larger prey items. The selection for larger prey may have created a shift in prey type, since mean arthropod sizes often differ among taxonomic groups (Schoener and Janzen 1968).

The variation in diet may also be partly caused by an interspecific difference in microhabitat preferences. *L. nannotis* is typically found adjacent to waterfalls in fast-flowing sections of the stream, whereas *L. rheocola* and *N. dayi* occur in more open, gently flowing stream sections (Hodgkison and Hero 2002). It was therefore not surprising that items such as ephemeropteran and odonatan larvae (which were more abundant in fast-flowing stream sections) were rarely found in the diet of *L. rheocola* and *N. dayi*.

Seasonal shift in diet

Litoria nannotis and *L. rheocola* displayed a seasonal shift in prey selectivity, feeding more indiscriminately during the dry season than in the wet season. Many seasonal shifts in prey selectivity simply reflect a change in food availability (Pianka 1970; Sexton *et al.* 1972; Vitt and Lacher 1981; Schoener *et al.* 1982; Burquez *et al.* 1986; Van Sluys 1995; Rocha 1996), particularly in tropical regions where

arthropod abundance is related to humidity levels (Wolda 1980; Stamps and Tanaka 1981). However, this was not the case at Tully Gorge, since food availability showed negligible variation among seasons. Instead, the seasonal shift in prey selectivity reflects a decline in the frogs' ability to access prey. The foraging activities of *L. nannotis* and *L. rheocola* were significantly restricted during the dry season because of the increased potential for dehydration (Hodgkison and Hero 2001, 2002). This reduction in activity would inevitably lead to a decline in the number of prey encounters, which, according to Optimal Foraging Theory, would account for the observed decline in prey selectivity (Pyke *et al.* 1977).

Sex-specific shift in diet

Differences between the diets of males and females have been related to shifts in behaviour (Pengilly 1971; Christian 1982; Woolbright 1985; Donnelly 1991; Parmelee and Guyer 1995), to morphology (Schoener *et al.* 1982) and to intraspecific competition (Schoener 1967). The diets of juvenile, adult male and adult female *L. nannotis* displayed significant differences in numeric and volumetric composition, differences in aquatic content (adult males consumed more aquatic prey than were consumed by juveniles and adult females) and differences in prey

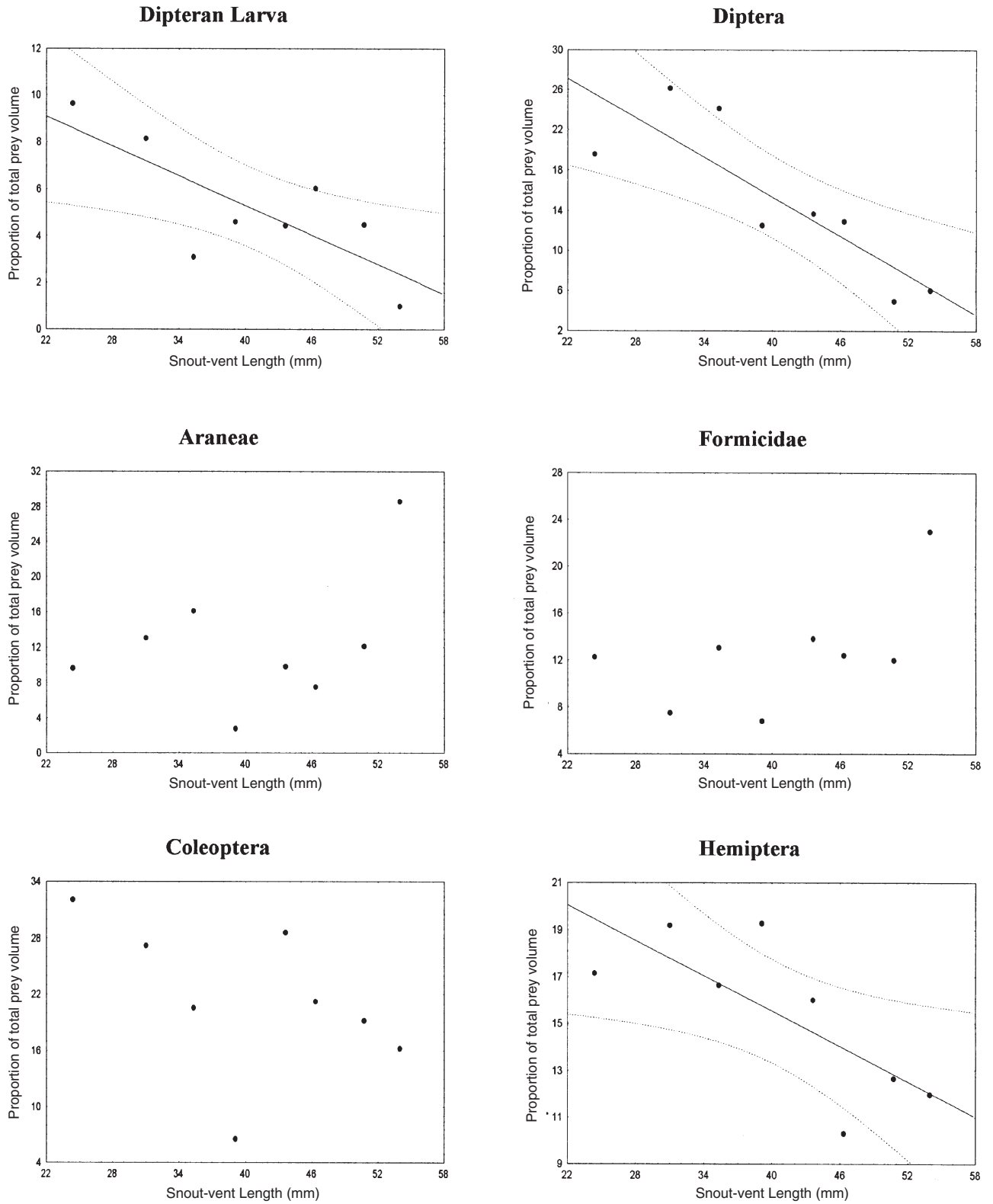


Fig. 2. The proportion (arcsin-transformed) of the total volume of prey in each snout-vent length group of *Litoria nannotis*, by each type of arthropod.

selectivity (females were the most selective and juveniles the most indiscriminate). These differences are believed to be caused by shifts in foraging behaviour and morphology.

Among many species of frogs and lizards, foraging activities by males are restricted by a commitment to territorial behaviour (Pengilley 1971; Christian 1982; Woolbright 1985; Donnelly 1991; Parmelee and Guyer 1995). This commitment often creates differences in the foraging behaviour and diet of males and females. Within this population of *L. nannotis*, while females and juveniles often venture into stream-side vegetation to forage at night, males display a degree of fidelity to the breeding site (Hodgkison and Hero 2002). This fidelity is a likely explanation for the increased aquatic content in the diet of male *L. nannotis* and may explain the reduction in prey selectivity. As a result of males remaining at the stream, their foraging activity is greatly reduced. Males are therefore likely to encounter a smaller number and variety of prey and would consequently be less likely to discriminate against those encountered.

Differences in morphology can also have a substantial impact on diet. *L. nannotis* is sexually dimorphic, adult females being considerably larger (SV = 49.1–54.7 mm) than adult males (SV = 40.1–47.9 mm) (Liem 1974). Consequently, the apparent increase in prey selectivity by females may simply reflect their ability to utilise a greater proportion of the available prey community.

Ontogenetic shift in diet

Many frogs and lizards display ontogenetic shifts in selection for prey size and type. These shifts can be caused by a change in morphology (Pengilley 1971; Labanick 1976; Donnelly 1991; Van Sluys 1993) or foraging behaviour (Toft 1981, 1985; Strussmann *et al.* 1984; Lima and Moreira 1993). *L. nannotis* displayed an ontogenetic shift in prey size: as snout–vent length increased, *L. nannotis* consumed fewer, but larger, prey. Similar shifts in prey dimensions have been reported in other predators that swallow their prey whole (Labanick 1976; Christian 1982; Donnelly 1991; Van Sluys 1993). Such predators are limited to eating prey that fit into their mouth. Small individuals are therefore constrained to eat smaller, less valuable prey and compensate for this by increasing the number of items consumed. As individuals become larger they can select from a wider range of prey sizes. In some species, larger individuals discriminate against small prey, which are considered less lucrative (Rocha 1989). However, this was not the case for *L. nannotis*, as large frogs selected a range of small and large prey.

Litoria nannotis also displayed an ontogenetic shift in prey type. As frog snout–vent length increased, dipterans, dipteran larvae and hemipterans accounted for a declining proportion of the total volume of prey. The diets of small and large males differed significantly in volumetric composition of prey and the diets of small and large females differed

significantly in numeric composition. The ontogenetic shift in prey type may be partly caused by the shift in selection for prey size since mean prey sizes often differ between arthropod orders (Schoener and Janzen 1968). Ontogenetic shifts driven by a change in prey size have been observed in reptiles (Rose 1976; Van Sluys 1993) and post-metamorphic amphibians (Pengilley 1971; Labanick 1976; Christian 1982; Donnelly 1991; Wiggins 1992).

Many ontogenetic shifts are also caused by a shift in foraging behaviour (Schoener and Gorman 1968; Clark and Gibbons 1969; Griffiths 1975; Grossman 1980; Toft 1981, 1985; Mushinsky *et al.* 1982; Stoner and Livingstone 1984; Strussmann *et al.* 1984; Pough *et al.* 1989; Lima and Moreira 1993; Adams 1995). In amphibians this is because individuals become larger through ontogeny, and therefore become more resilient to evaporative water loss and possess more effective defence and escape mechanisms. Such attributes allow greater foraging potential in larger frogs. Despite this, there is no evidence to suggest that the foraging behaviour of *L. nannotis* changes with frog size.

In summary, while *L. nannotis*, *L. rheocola* and *N. dayi* are generalist feeders, they display a degree of selectivity for specific prey when foraging conditions are optimal, discriminating against common prey (e.g. dipterans, coleopterans, trichopterans and hymenopterans) and selecting rare items (e.g. blattodeans, dermapterans and isopteran). Nevertheless, *L. nannotis*, *L. rheocola* and *N. dayi* are capable of feeding on a range of prey and demonstrate the capacity to compensate for disruptions in foraging activity (imposed by reproductive commitments and adverse environmental conditions). This capacity for dietary adaptation suggests that the populations of *L. nannotis*, *L. rheocola* and *N. dayi* investigated in this study may be resistant to periodic declines in feeding efficiency.

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