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Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake

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Summary

1. Sex-based differences in diets are widespread among animals, but may often reflect sex differences in body size or in the times and places that feeding occurs, rather than sex-specific prey-selection behaviour. We examined these hypotheses with detailed information on the types and sizes of fishes consumed by filesnakes, *Acrochordus arafurae* McDowell, 1979, based on a 4-year field study in the Wet–Dry tropics of northern Australia.

2. These aquatic snakes show extreme sexual dimorphism in body length, body shape, relative head size, head shape, foraging habitat and diet. The composition of the diet varied seasonally and with the size as well as the gender of the snakes. Both sexes ate more frequently during the Wet season, apparently because of higher prey availability at this time.

3. Both sexes showed significant selectivity of prey species, but differed profoundly in food habits. Female filesnakes generally consumed only a single large prey item at a time, whereas the stomachs of males typically contained many small prey items.

4. Males were relatively unselective foragers, with little evidence of ontogenetic shifts in prey size or prey type. In contrast, large females ate larger prey items, and showed an ontogenetic shift from a generalized (male-like) diet to 'sleepy cod' (eleotrids) and finally to plotosid catfish.

5. When comparison was restricted to snakes of the same head length, males and females differed significantly in dietary composition and in prey sizes, but not in feeding frequencies or the relative numbers of snakes containing single versus multiple prey items.

Key-words: acrochordid, *Acrochordus arafurae*, diets, foraging, sexual dimorphism, snake.

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Introduction

The types, sizes and amounts of prey consumed by a predator are influenced by many aspects of the animal's biology, including its morphology, physiology, behaviour, reproductive status and habitat choice (e.g. Pyke Pulliam & Charnov 1977; Ryan, Bartholomew & Rand 1983; Savitsky 1983). In many species, the composition of the diet varies considerably on a microgeographic basis (Kephart 1982). Even within a single individual, dietary composition may shift with time: ontogenetically, seasonally, or in relation to reproductive activities (e.g. Shine 1980, 1991b; Kephart & Arnold 1982; Mushinsky, Hebrard & Vodopich 1982). Detailed analyses of the sources of variance in dietary composition may clarify the determinants of prey selection and capture rates in nature.

One potential source of variation in dietary composition is the gender of the predator. Sex differences in feeding habits and in associated feeding structures (mouthparts, etc.) are widespread among animals, suggesting that selection for niche divergence may contribute substantially to the evolution of sexual dimorphism (Darwin 1871; Slatkin 1984). Even if sexual selection is responsible for the initial morphological divergence in secondary sexual characteristics, ecological factors may then act either to constrain or amplify this initial sexually selected difference (Slatkin 1984; Shine 1989). The role of ecological factors in the evolution of sexual dimorphism has been controversial not because of faulty logic or contradictory evidence, but because the hypothesis of 'niche divergence' is less amenable to testing than is the idea of sexual selection (Shine

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1989). In order to be able to distinguish ecologically based dimorphism from sexually selected dimorphism, data are needed on animals that satisfy two main criteria: (i) the feeding structures are not subject to sexual selection; and (ii) dietary divergence between the sexes requires morphological divergence in feeding structures. Snakes fulfil these two conditions, because male–male combat is rare (and even when it occurs, usually does not involve biting), and many snakes are gape-limited predators (so that any sex-based divergence in prey sizes will require divergence in jaw size) (Shine 1989).

Sexual dimorphism in relative head size is widespread among snakes (Shine 1991a), but interpretation of these data is hindered by the paucity of information on sex differences in diets. Most studies on snake diets report only on lists of prey items, with no attempt to investigate intraspecific dietary differences (Mushinsky 1987). The present paper provides a detailed description of dietary composition (in terms of prey type and prey size) of an aquatic snake species that displays extreme sexual dimorphism in several characteristics. Female filesnakes (*Acrochordus arafurae*) are larger and more heavy-bodied than males, have larger heads relative to body length, and larger jaws relative to head size (Shine 1986b, 1991a; Camilleri & Shine 1990). Indeed, this species is perhaps the most highly dimorphic snake species yet studied (Shine 1991a). The extreme dimorphism of *A. arafurae* provides an ideal opportunity to investigate the influences of three factors — gender, body size and fluctuations in prey availability — on the sizes and types of prey consumed by this species. A previous ecological study of *Acrochordus arafurae* showed that female filesnakes ate larger prey than did males, and that larger snakes (and hence, females) tended to be found in deeper water than did smaller animals (including males) (Shine 1986b). However, Shine's dietary data were insufficiently detailed to separate the influence of gender from any influence of body size, relative head size, or prey availability. In the present paper, we analyse a more extensive data set (gathered independently from that used in Shine's 1986b analysis) to clarify the determinants of sex-related differences in prey consumption in *A. arafurae*.

Methods

STUDY SPECIES AND STUDY AREA

Arafura filesnakes are large (males up to 1·5 m, females up to 2·0 m) piscivorous, entirely aquatic non-venomous snakes. They forage at night, mostly in shallow water in search of sleeping fishes (Shine 1986a,b). The metabolic rates of acrochordids are lower than those of most other snakes, and many aspects of their ecology (low rates of feeding, growing and reproducing, delayed maturation, and high population densities) have been interpreted as adaptations to (or consequences of) low rates of energy throughput (Shine 1986a; Houston 1992). We studied these animals in Magela Creek, approximately 10 km north of Jabiru in the Northern Territory. This area is in Kakadu National Park, and within the 'Wet–Dry' tropics of northern Australia. Temperatures are high throughout the year (mean annual temperature at Jabiru = 27 °C) but rainfall is strongly seasonal, with about 93% of the annual rainfall during the monsoonal ('Wet') season from December to March (Bishop *et al.* 1980). Magela Creek consists of a series of isolated billabongs during the Dry-season, but Wet-season flooding connects these billabongs over a large area. The study area and the general biology of Arafura filesnakes have been described elsewhere in more detail (Shine 1986a,b; Shine & Lambeck 1985; Houston 1992).

SAMPLING TECHNIQUES AND FISH TAXONOMY

Sampling was carried out over a total of seven trips (five Dry-season, two Wet-season) over a 4-year period, for a total of 330 days' fieldwork (3880 net-nights). Snakes and fishes were caught in fyke nets (4 m long, 0·75 diameter at mouth, with 10 m leader) set in shallow water, as described by Shine (1986a). The nets were checked and cleared daily, and the snakes processed, marked and released within a few hours of being removed from the nets (Houston 1992). We recorded the gender, mass, snout–vent length, head length and reproductive status (gravid or non-gravid) of the snakes, and palpated them to detect prey items. The flaccid bodies of filesnakes make it possible to detect incompletely digested bones in addition to entire prey items (Shine 1986a). Prey items were removed by forced regurgitation, and only taken from snakes at the time of their initial capture (i.e. prey items detected in recaptured snakes were not removed). We did not attempt to remove individual bones remaining from incomplete digestion, or large and spinous prey items (because of the risk of internal injury to the snakes) but recorded the presence of prey in such cases. Fish remain detectable by palpation for about 4 days after feeding in captive filesnakes maintained at 30 °C (Shine 1986a), so that only the initial record was used for analysis of feeding frequencies in cases where snakes, recaptured within a 7-day period, contained detectable prey items on both occasions. Prey items were identified and, if entire, weighed and measured (total length and maximum circumference, ±1 mm).

Although the fyke nets undoubtedly provide biased samples of total billabong fish faunas, the shallows sampled by these nets are the same areas used by foraging filesnakes (Shine & Lambeck 1985).

Hence, the fyke nets provided a convenient means of assessing relative availabilities of the various fish taxa to filesnakes. All of the fish species recorded as prey items were also collected in fyke nets, but not all of the fish taxa recorded from fyke nets were recovered from filesnake guts. Nonetheless, confining snakes in fyke nets with fishes could enable snakes to catch fish (both in quantity and taxa) which would otherwise not be available. Therefore, prey items that were estimated to be less than 25% digested (=eaten with 24 hours, based on regurgitated prey items from captive snakes) were recorded, but are not included in analyses unless otherwise stated. This decision may have eliminated some cases where snakes had caught prey shortly before being captured themselves.

Fish taxonomy follows that in Merrick & Schmida (1984), with most prey being identified to species except where precluded by unresolved taxonomic problems: (i) plotosid (eel-tail) catfish were simply identified to family; and (ii) two similar species of glass perch (F. Ambassidae) were not separated in our analyses. We also note that the correct specific designation of mullet (F. Mugilidae) and sleepy

Table 1. Summary of fish taxa caught in fyke nets in five different Magela Creek billabongs, (in bold)*; year, season and number of net-nights also given

	Fish per net-night											
	Djdj 1986 Dry	**Djdj** 1986–87 Wet	**Djdj** 1987 Dry	**Djdj** 1987–88 Wet	**Djdj** 1987 Dry	**Geig** 1986–87 Wet	**Geig** 1987 Dry	**Geig** 1987–88 Wet	**Maka.** 1987 Dry	**Maka.** 1987 Dry	**N-G** 1987 Dry	**Djab.** 1987 Dry
Prey taxa	(511)	(264)	(759)	(385)	(50)	(88)	(142)	(120)	(146)	(18)	(146)	(288)
'Mouth almighty' *Glossamia aprion*	0·25	23·82	0·35	14·64	0·18	3·85	0·49	0·59	1·50	5·50	2·07	0·71
Glass perch *Ambassis* spp.	2·09	4·00	0·64	0·51	0·38	34·52	0·28	36·88	0·45	1·72	0·92	5·69
Eel-tailed catfish Family Plotosidae	0·16	1·24	0·08	0·26	0	1·26	1·90	0·33	0·60	0·17	0·12	0·03
Fork-tail catfish *Arius leptaspis*	0·16	0·26	0·10	0·13	0·04	0·07	0·37	0·12	0·20	0·22	0·82	0·15
Chequered rainbow fish *Melanotaenia splendida*	0·12	2·39	0·01	0·43	0·20	0·65	0·08	1·53	0·01	0·22	0·03	0·03
Barramundi *Lates calcarifer*	0·14	0·02	0·16	0	0·02	0	0·02	0·01	0·19	0·28	0·02	0·05
Sleepy cod *Oxyeleotris lineolatus*	0·15	0·15	0·33	0·34	0·10	0·33	0·73	0·42	0·24	0·22	0·26	0·23
Penny fish *Denariusa bandata*	0·26	1·95	0·05	0·97	0·02	1·08	0·04	0·25	0	0·56	0·42	0·18
Empire fish *Hypseleotris compressa*	0·07	0·27	0·07	0·69	0·04	0·20	0·10	1·35	0·26	0·17	0·07	0·02
Archer fish *Toxotes chaetareus*	0·01	0	0	0	0	0	0	0	0	0	0	0
Black-banded rainbow fish *Melanotaenia nigrans*	0	0	0	0·04	0	0	0	0·01	0	0	0	0
Purple-spotted gudgeon *Mogurnda mogurnda*	0	0·01	0	0·06	0	0	0	0·03	0	0	0	0
Tarpon *Megalops cyprinoides*	0	0	0	0·01	0	0	0·02	0·01	0·01	0	0·01	0
Saratoga *Scleropages jardinii*	0	0·01	0	0	0	0	0·01	0	0·02	0	0·01	0
Hardyheads *Craterocephalus stercusmuscarum*	0	0·01	0	0	0·16	0	0	0	0	0	0	0
One-gilled eel *Ophisternon guttarale*	0	0	0·01	0·01	0	0	0	0	0·03	0	0	0
Spangled grunter *Leiopotherapon unicolor*	0	0	0	0	0	0	0	0·01	0	0	0	0
Striped grunter *Amniataba percoides*	0	0	0	0	0	0·02	0	0	0	0	0·01	0
Midgley's grunter *Pingalla midgleyi*	0	0	0	0	0	0	0	0	0	0	0	0
Bony bream *Nematolosa erebi*	0	0·03	0	0	0	0·02	0	0	0	0	0	0·01
Mullet *Liza diadema*	0	0	0	0	0	0	0·08	0	0	0	0	0·01

* Billabongs:
Djdj, Djarrdjarr; Geig, Geig; Maka., Makamala; N-G, Namankurl-Gaduduba complex; and Djab, Djabiluku.

cod (F. Eleotridae) in the study area is doubtful (C. Humphrey, D. Walden, M. Robinson, personal communication), and we simply adopt the names in common usage for these species (*Liza diadema* and *Oxyeleotris lineolatus* respectively: Merrick & Schmida 1984).

Results

PREY AVAILABILITY

Overall (all billabong and trip samples pooled), we captured 3627 filesnakes during the study (total of 3834 captures), with two-thirds of these animals coming from a single billabong (Djarrdjarr). We also recorded 21 fish taxa in our fyke net samples (Table 1). The highest mean capture rates of fishes per net-night were obtained during the two Wet-season field trips, and the mean capture rates of glass perch (*Ambassis* spp.) and 'mouth almighties' (*Glossamia aprion*) were an order of magnitude higher than for any other fish taxon, especially during the two Wet-season field trips. However, whereas high numbers of glass perch were caught in Geig Billabong, most of the 'mouth almighties' were caught in Djarrdjarr Billabong.

TAXONOMIC COMPOSITION OF FILESNAKE DIETS

Filesnakes were found to be exclusively piscivorous. Detectable prey items were located in 10% (381 out of 3834) of snakes, including multiple records for individuals recaptured at least 7 days apart. However, 124 of these records were excluded from further analysis. These consisted of freshly ingested (<25% digested) prey items obtained from 81 snakes (excluded from analysis because these fishes were probably captured while trapped in fyke nets), and prey items palped but not removed from a further 43 snakes. The following analyses are based on the remaining 267 snakes (7% of snakes captured) that contained prey items which were at least one-quarter digested. Twelve of the 21 fish taxa caught in fyke nets (57%) were recorded from filesnake guts, but 97% of the prey items recorded comprised only six fish taxa: Glass perch, 'mouth almighty', sleepy cod, plotosid catfish, chequered rainbow fish, and empire fish (Table 2). The remaining taxa were pooled in a 'minor taxa' category in further analyses in order to overcome the problem of empty data cells.

Overall, the composition of fish taxa recovered from both female and male filesnake guts differed significantly from the composition of fish taxa in the fyke net samples (pooled samples: ♀♀, $\chi^2_{20} = 475$, $P \leq 0{\cdot}001$; ♂♂, $\chi^2_{20} = 183{\cdot}6$, $P \leq 0{\cdot}001$; Table 2). Treating each of the six major prey taxa separately (together with the pooled minor taxa group), we used chi-square to test the null hypothesis that each fish type occurred in the same proportion in the guts of male and female filesnakes as in the corresponding fyke net sample. Each of the six major prey taxa differed significantly in relative frequency of occurrence between fyke net samples and filesnake gut contents in both male and female snakes (Table 3). Apart from glass perch and the pooled minor taxonomic group, each of the other five taxa occurred in significantly higher frequencies among stomach contents in both male and female filesnakes than in the fyke net samples (Table 3).

The numeric composition of gut contents differed significantly between male and female filesnakes ($\chi^2_{11} = 54{\cdot}6$, $P < 0{\cdot}001$). However, apart from the ambassid *D. bandata* (penny fish), the six most commonly eaten prey taxa corresponded with the most common fish taxa in the fyke net samples (Table 2). Although the glass perch (*Ambassis* spp.) was the most abundant fish in fyke net samples (Table 2), this taxon occurred significantly less often in the gut contents of both male and female filesnakes than in the fyke net samles (Table 3), and was even less important as a component of the filesnake diet in terms of prey mass (Fig. 1). Glass perch were found in significantly higher numbers in the stomachs of male filesnakes than female filesnakes ($\chi^2_1 = 15{\cdot}5$, $P \leq 0{\cdot}001$). Table 1 shows that glass perch were the most numerous fish in fyke net samples, particulary in Wet-season samples, as well as being one of the smallest fishes caught. Hence, the abundance of glass perch in filesnake gut contents may simply reflect their high availability to snakes. Electivity indices (*D*-values: Jacobs 1974) for this taxon suggest that both male and female filesnakes generally discriminated against glass perch (Fig. 2).

The 'mouth almighty', *G. aprion*, was the second most common taxon found in filesnake guts. 'Mouth almighties' were of similar importance numerically in the diets of male and female snakes ($\chi^2_1 = 0{\cdot}11$, NS, Table 2), and most *D*-values suggested that snakes were actively selecting this taxon (Fig. 2).

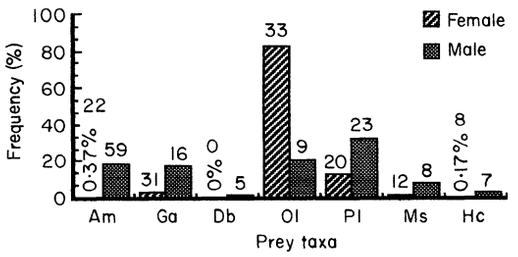

Fig. 1. Relative importance of fish taxa as percentages by mass in the diets of male (solid columns) and female (stippled columns) filesnakes in Magela Creek billabongs. Figures above columns denote the number of prey items. Key to fish taxa: Am, *Ambassis* spp.; Db, *Denariusa bandata*; Ga, *Glossamia aprion*; Ms, *Melanotaenia splendida*; Pl, plotosid catfish; Ol, *Oxyeleotris lineolatus*; and Hc, *Hypseleotris compressa*.

Table 2. Comparison of the numeric composition of fish taxa in fyke net samples with prey items recovered from filesnakes sampled in Magela Creek billabongs. Taxa are arranged in descending order of numeric importance as filesnake prey items

Fish taxa	Family	Composition of fyke net samples		Percentage of prey items		
		Total count	%	♀♀ ($n = 107$)	♂♂ ($n = 256$)	♀♀ + ♂♂ ($n = 363$)
Glass perch *Ambassis* spp.	Ambassidae	21656	68·6	17·8	43·0	35·4
'Mouth almighty' *Glossamia aprion*	Apogonidae	4010	12·7	23·4	25·0	24·3
Sleepy cod *Oxyeleotris lineolatus*	Eleotridae	816	2·6	24·3	5·0	10·9
Eel-tailed catfish	Plotosidae	1098	3·5	14·0	8·0	9·9
Chequered rainbow fish *Melanotaenia splendida*	Melanotaeniidae	1137	3·6	12·2	8·0	9·0
Empire fish *Hypseleotris compressa*	Eleotridae	670	2·1	5·6	8·0	7·6
Penny fish *Denariusa bandata*	Ambassidae	1297	4·1	0	2·0	1·4
One-gilled eel *Ophisternon guttarale*	Synbranchidae	11	0	0	1·0	0·6
Archer fish *Toxotes chaetareus*	Toxotidae	5	0	1·0	0	0·3
Tarpon *Megalops cyprinoides*	Megalopidae	10	0	1·0	0	0·3
Spangled grunter *Leiopotherapon unicolor*	Teraponidae	2	0	0·9	0	0·3
Bony bream *Nematolosa erebi*	Clupeidae	15	0·1	0	0·4	0·3
Fork-tail catfish *Arius leptaspis*	Ariidae	540	1·7	0	0	0
Barramundi *Lates calcarifer*	Centropomidae	244	0·8	0	0	0
Black-banded rainbow fish *Melanotaenia nigrans*	Melanotaeniidae	16	0·1	0	0	0
Purple-spotted gudgeon *Mogurnda mogurnda*	Eleotridae	29	0·1	0	0	0
Saratoga *Scleropages jardinii*	Osteoglossidae	8	0	0	0	0
Hardyheads *Craterocephalus stercusmuscarum*	Atherinidae	2	0	0	0	0
Striped grunter *Amniataba percoides*	Teraponidae	5	0	0	0	0
Midgley's grunter *Pingalla midgleyi*	Teraponidae	1	0	0	0	0
Mullet *Liza diadema*	Mugilidae	15	0·1	0	0	0

However, 'mouth almighties' formed a minor proportion of the total mass of prey items (Fig. 1). Both sleepy cod and plotosid catfish were recovered in significantly higher proportions from the stomachs of female rather than male snakes (sleepers: $\chi^2_1 = 73$, $P \leq 0{\cdot}001$; Plotosidae: $\chi^2_1 = 4{\cdot}4$, $P \leq 0{\cdot}001$), and more often in snake stomachs than in fyke net samples (Table 3). *D*-values indicated that snakes were actively selecting plotosids, while showing an ambivalent result with sleepers (Fig. 2), but almost 90% of the total mass of the stomach contents of female snakes consisted of sleepy cod (Fig. 1). Both empire ($\chi^2_1 = 0{\cdot}9$, NS), and chequered rainbow fish ($\chi^2_1 = 2{\cdot}6$, NS) occurred in similar proportions in the diets of male and female snakes.

The composition of fish taxa differed significantly between dry and wet seasons in fyke net samples ($\chi^2_6 = 5993{\cdot}9$, $P \leq 0{\cdot}001$, Fig. 3), and in the stomach contents of male ($\chi^2_6 = 35{\cdot}4$, $P \leq 0{\cdot}001$) and female ($\chi^2_6 = 32{\cdot}8$, $P \leq 0{\cdot}001$) filesnakes. The taxonomic composition of the prey items recovered from male filesnakes bore a close similarity to fyke net samples, with the main difference being the high proportion of plotosid catfish eaten by male snakes during the dry season. Indeed, the significant difference between the proportional occurrence of fish taxa in the gut contents of male filesnakes and the occurrence of these taxa in the fyke net samples ($\chi^2_6 = 48{\cdot}1$, $P \leq 0{\cdot}001$) disappeared if plotosid catfish were excluded from the analysis ($\chi^2_5 = 4{\cdot}8$, NS).

Table 3. Chi-square values and significance levels of the difference between the frequency of occurrences of fish taxa in fyke net samples, and their occurrence in the diets of male and female filesnakes. Sample size = number of prey items

	♀♀ ($n = 107$)		♂♂ ($n = 256$)	
Fish Taxa	χ^2_1	P	χ^2_1	P
Glass perch *Ambassis* spp.	40·3	<0·001	25·3	<0·001
Mouth almighty *Glossamia aprion*	9·6	<0·005	30·5	<0·001
Sleepy cod *Oxyeleotris lineolatus*	193·8	<0·001	6·0	<0·03
Eel-tailed catfish F: Plotosidae	33·8	<0·001	16·2	<0·001
Chequered rainbow fish *Melanotaenia splendida*	21·7	<0·001	12·6	<0·001
Empire fish *Hypseleotris compressa*	6·3	<0·03	45·4	<0·001
Minor taxa	2·7	NS	5·5	<0·03

Female filesnakes ate many sleepy cod during the Dry-season sample, and many chequered rainbow fish during the Wet-season sample (Fig. 3). This trend was present in billabongs in all years of the study, with *D*-values suggesting that chequered rainbow fish were avoided by snakes during the Dry-season, but actively preferred during the Wet season (Fig. 2).

ONTOGENETIC CHANGES AND SEXUAL DIFFERENCES IN FILESNAKE DIETS

The prey taxa eaten by filesnakes covered a wide range of sizes, with standard lengths from 35 mm (penny fish, *Denariusa bandata*) to 480 mm (sleepy cod, *Oxyeleotris lineolatus*). Four of the six major prey taxa consisted of relatively small fish, with mean circumferences of no more than 6 cm. However, two taxa (sleepy cod and plotosid catfish) were considerably larger than the others. Because relatively few captured snakes contained prey items that were more than one-quarter digested, data from all of the samples were pooled to test for ontogenetic shifts in diet. Snakes were divided into five size groups based on head length: 15·0–24·9 mm, 25·0–34·9 mm, 35·0–44·9 mm, 45·0–54·9 mm, and 55·0–64·9 mm. Because of the extreme difference in body sizes between male and female filesnakes, male snakes were only represented in the first two size groups. Data from seven male snakes with head lengths between 35 and 37 mm were included in the second size group, as these data were too few to warrant a separate size group of male snakes.

Figure 4 compares the taxonomic composition of diets among the five size-classes of female snakes, and shows that: (i) *Ambassis* spp. were not eaten by the two largest size-classes of female snakes (>50 mm head length); (ii) sleepy cod and plotosid catfish were common prey types for the second-largest size-class of female snakes; and (iii) plotosid catfish were the only prey recorded from the stomachs of the largest size-group of female snakes. The significant differences in taxonomic composition of prey among size-classes of female snakes (Fig. 4; $\chi^2_{24} = 94·2$, $P < 0·001$) are not due entirely to plotosid catfish ($\chi^2_{15} = 51·7$, $P < 0·001$ after exclusion of plotosids from the analysis). No such ontogenetic dietary shifts were found in male filesnakes ($\chi^2_6 = 9·66$, $P = 0·14$; Fig. 5), although the power of this test is reduced by

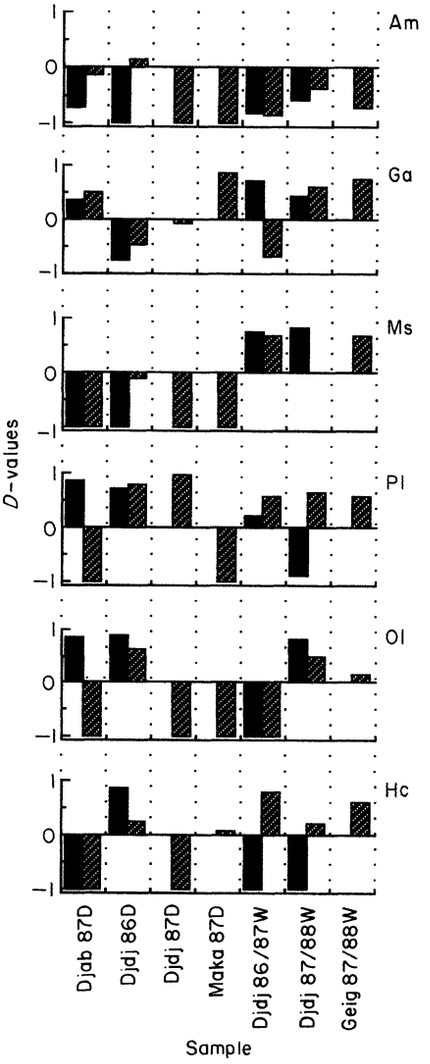

Fig. 2. Jacobs Electivity Indices (*D*-values) calculated for seven samples (each of which includes ≥10 prey items) of male (solid columns) and female (stippled columns) filesnakes. Key to sample codes: Djab, Djabiluku Billabong; Djdj, Djarrdjarr Billabong; Maka, Makamala Billabong. Year and season (D = Dry, W = Wet) follow billabong names. Key to fish taxa: Am, *Ambassis* spp.; Ga, *Glossamia aprion*; Ms, *Melanotaenia splendida*; Pl, plotosid catfish; Ol, *Oxyeleotris lineolatus*; and Hc, *Hypseleotris compressa*. Season (D = Dry, W = Wet) and year follow billabong names. *D*-values were calculated for females only for Djarrdjarr 1987 Dry, and males for Makamala 1987 Dry and Geig 1987–88 Wet.

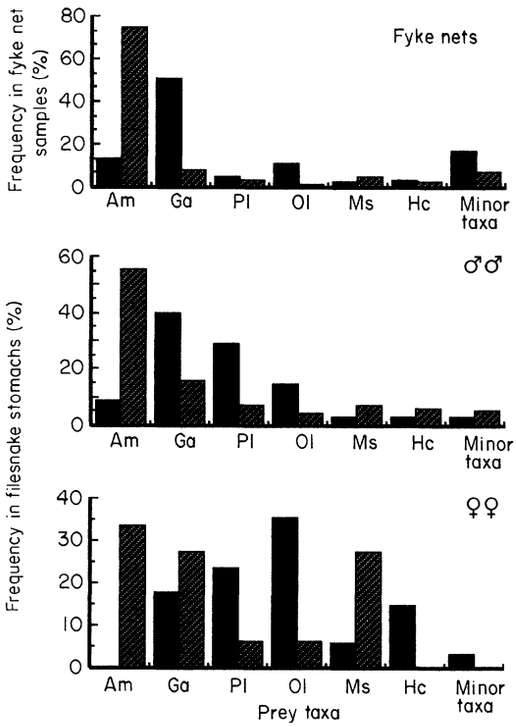

Fig. 3. Seasonal comparison of fish taxa in fyke net samples ($n_{Wet} = 15966$, $n_{Dry} = 3086$), and in the stomach contents of male ($n_{Wet} = 101$, $n_{Dry} = 35$) and female ($n_{Wet} = 33$, $n_{Dry} = 34$) filesnakes in Djarrdjarr Billabong. Data are from pooled Dry (solid columns: 1986 + 1987) and Wet (cross-hatched columns: 1986–87 + 1987–88) season samples.

the fact that males were only represented in the two smallest size-classes of snakes. Although glass perch and 'mouth almighties' were important components of the diets of both male and female filesnakes, the taxonomic composition of prey differed significantly between similar-sized males and females in the range of head-lengths over which both sexes were represented ($\chi^2_{18} = 42$, $P < 0{\cdot}001$; Fig. 5).

RELATIONSHIPS BETWEEN PREY SIZE AND PREDATOR SIZE

Because prey circumference and prey mass were highly correlated ($r^2 = 0{\cdot}82$, $F_{1,67} = 301{\cdot}21$, $P < 0{\cdot}001$), we used prey circumference as a general indicator of prey size. Larger snakes tended to consume larger prey items than did smaller snakes. Both male and female snakes tended to consume a wider range of prey sizes at larger body sizes. Prey circumference was significantly correlated with head length in female filesnakes ($r^2 = 0{\cdot}74$, $F_{1,55} = 156{\cdot}1$, $P < 0{\cdot}001$), but not in male snakes ($r^2 = 0{\cdot}10$, $F_{1,29} = 2{\cdot}98$, NS). The correlation between head length and prey circumference was thus significantly higher in female snakes than in males (Snedecor & Cochran 1987, p. 186: $z = 4{\cdot}07$, $P < 0{\cdot}01$). In female snakes the minimum size of prey items consumed (as well as mean prey size) increased with the size of the snake (Fig. 6). The minimum prey sizes (circumferences) of five size groups of female snakes (20·0–29·9, 30·0–39·9, 40·0–49·9, 50·0–59·9 and 60·0–69·9 mm head length) increased at larger head sizes (Spearman Rank Correlation, $r = 1{\cdot}00$, $P = 0{\cdot}01$). The size range of male snakes was too small for a similar analysis (Fig. 6).

The larger mean prey size of female snakes than of conspecific males is clearly due primarily to the larger size of females. The larger size of females, in turn, is a function of sexual dimorphism in three different traits: (i) female filesnakes grow much larger than males in terms of body length and (especially) mass; (ii) female filesnakes have significantly larger heads than males for any given SVL; and (iii) female filesnakes have larger jaws relative to overall head length (Shine 1986b; Camilleri & Shine 1990). However, although the dietary difference between the sexes is due partly to these kinds of dimorphism, the dietary difference remains significant even after the effects of these size differences are removed in our analyses. Even when prey sizes were compared

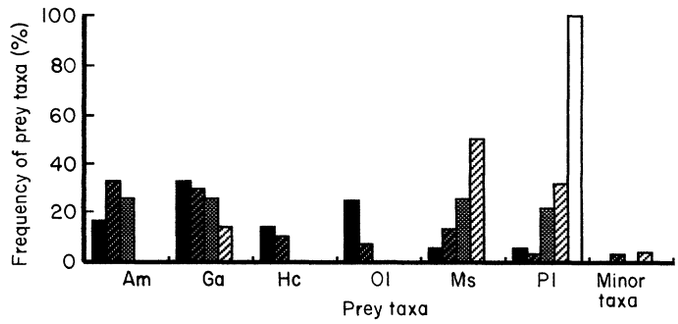

Fig. 4. Comparison of the taxonomic composition of fishes eaten by female filesnakes of five size classes (head lengths). Key to fish taxa: Am, *Ambassis* spp. ($n = 22$); Ga, *Glossamia aprion* ($n = 31$); Ms, *Melanotaenia splendida* ($n = 11$); Pl, plotosid catfish ($n = 17$); Ol, *Oxyeleotris lineolatus* ($n = 32$); Hc, *Hypseleotris compressa* ($n = 8$); minor taxa ($n = 2$). Size-classes; ■, 15·0–24·9 mm ($n = 36$); ▨, 25·0–34·9 mm ($n = 30$); ▩, 35·0–44·9 mm ($n = 23$); ▨, 45·0–54·9 mm ($n = 28$); □, 55·0–64·9 mm ($n = 10$).

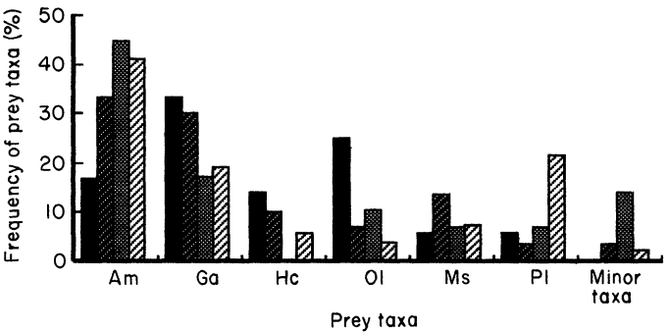

Fig. 5. Comparison of the taxonomic composition of gut contents between similar-sized male (n fishes = 143) and female (n fishes = 62) filesnakes in Magela Creek. Female size-classes: ■, 15·0–24·9 mm (n = 36); ▨, 25·0–34·9 mm (n = 30). Male size-classes; ▩, 15·0–24·9 mm (n = 29), ▨, 25·0–34·9 mm (n = 111). For names of fish taxa see caption to Fig. 4.

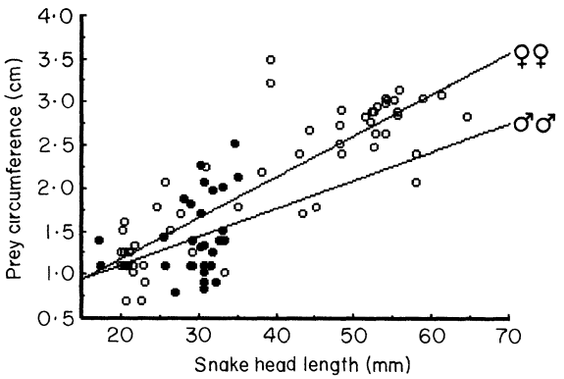

Fig. 6. Relationship of snake head length to prey circumference for 56 female filesnakes (○: $r^2 = 0{\cdot}74$, $F_{1,55} = 156{\cdot}1$, $P < 0{\cdot}001$), and 30 male filesnakes (●: $r^2 = 0{\cdot}10$, $F_{1,29} = 2{\cdot}98$, NS) in Magela Creek.

between males and females over the same range of head lengths (HL = 18·6–37·0 mm), the relationship between snake head length and mean prey circumference differed significantly between males and females (single-factor ANCOVA with HL as the covariate: slopes $F_{1,150} = 4{\cdot}46$, $P = 0{\cdot}036$). The difference in the snake size/prey size relationship between males and females was even more pronounced when SVL was used in the analysis instead of head length (restricting comparison to SVLs between 53·0 and 114·6 cm, using single-factor ANCOVA with SVL as the covariate: slopes $F_{1,165} = 10{\cdot}35$, $P = 0{\cdot}002$). Within this SVL range, females ate significantly larger prey (including freshly ingested prey items: n snakes = 57; mean prey circ. = 6·96 cm; SD = 7·76) than did males n snakes = 112; mean prey circ. = 4·2 cm; SD = 2·09: $t_{167} = 3{\cdot}58$, $P < 0{\cdot}001$).

NUMBER OF PREY ITEMS INGESTED

Thirty-two per cent (84 out of 266) of snakes with prey items more than one-quarter digested contained more than a single prey item. Multiple prey items were found in a higher proportion of male snakes (40%: 49 out of 122) than female snakes (24%: 35 out of 144: $\chi^2_1 = 7{\cdot}69$, $P < 0{\cdot}01$). However, over the same size range (head length = 18·6–37·0 mm) the frequency of multiple prey items did not differ between males (39%: 44 out of 114 snakes) and females (44%: 26 out of 59 snakes). Only 10% (8 out of 84 snakes) of large females (>37·0 mm HL) contained multiple prey items. Almost twice as many snakes with food contained multiple prey items in the Wet season (56·8%: 42 out of 74 snakes) compared with Dry-season samples (28·3%: 28 out of 99 snakes: $\chi^2_1 = 14{\cdot}25$, $P < 0{\cdot}001$). Hence, we compared the taxonomic composition of single *versus* multiple prey items separately in Dry and Wet-season samples. In male snakes, the taxonomic composition of single *vs.* multiple prey differed in both seasons (Dry, $\chi^2_6 = 19{\cdot}0$, $P < 0{\cdot}01$; Wet, $\chi^2_6 = 38{\cdot}9$, $P < 0{\cdot}01$) whereas in females this difference was significant in the Dry season ($\chi^2_6 = 15{\cdot}8$, $P < 0{\cdot}01$) but not in the Wet season ($\chi^2_6 = 5{\cdot}7$, NS). The most notable differences in taxonomic composition between single and multiple feeding states was a marked increase in the proportion of glass perch (*Ambassis* spp.) in multiple feeding states in filesnakes of both sexes, accompanied by a reduction in the proportions of the two largest prey taxa (*O. lineolatus* and Plotosidae) (Fig. 7). Elimination of *Ambassis* spp. from the chi-square analyses meant that the composition of prey did not differ significantly between single and multiple feeding states in male snakes ($\chi^2_5 = 4{\cdot}17$, $P = 0{\cdot}53$), but still differed significantly in females ($\chi^2_5 = 16{\cdot}1$, $P < 0{\cdot}001$).

FREQUENCY OF FEEDING

Recapture frequencies of individual snakes were too low to enable us to measure feeding frequencies directly, so we inferred feeding frequencies from the proportion of snakes containing detectable prey items. The numbers of male and female filesnakes containing prey items in nine Dry-season samples and four Wet-season samples are summarized in Table 4. To eliminate variability due to geographic differences, seasonal and annual variations in feeding frequency were examined using chi-square analyses on data obtained from Djarrdjarr Billabong during the 1986 and 1987 Dry seasons and the 1986–87 and

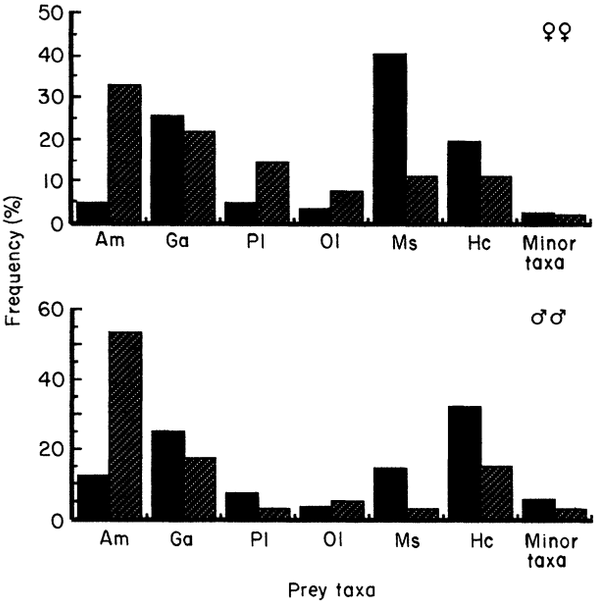

Fig. 7. Taxonomic composition of single ($n_{female} = 87$, and $n_{male} = 63$; solid columns) and multiple ($n_{female} = 55$, and $n_{male} = 99$; stippled columns) prey items recovered from 132 female (upper figure), and 92 male (lower figure) filesnakes. Am, *Ambassis* spp.; Ga, *G. aprion*; Hc, *H. compressa*; Ms, *M. splendida*; Ol, *O. lineolatus*; and Pl, plotosid catfish.

1987–88 Wet seasons. These comparisons revealed that the relative numbers of filesnakes containing prey did not differ significantly from year to year in either Dry-season samples ($\chi^2_1 = 0{\cdot}19$, $P > 0{\cdot}80$) or Wet-season samples ($\chi^2_1 = 0{\cdot}14$, $P > 0{\cdot}90$). However, prey items were detected in significantly higher proportions in Wet-season samples than in Dry-season samples both in male snakes ($\chi^2_1 = 112{\cdot}5$, $P < 0{\cdot}001$) and in female snakes ($\chi^2_1 = 48{\cdot}7$, $P < 0{\cdot}001$). An average of 4·4% of female snakes contained prey items in Dry-season samples, compared with 23·5% of females in Wet-season samples. Likewise, an average of 6·4% of male filesnakes contained prey in the Dry-season samples compared with 39% of male snakes in Wet-season samples. Contingency table analysis shows that males tended to feed more frequently than females overall ($\chi^2_1 = 6{\cdot}77$, $P < 0{\cdot}009$), although we could not detect significant sex differences in feeding frequency when data for each season were analysed separately (Dry, $\chi^2_1 = 0{\cdot}32$, $P = 0{\cdot}57$; Wet, $\chi^2_1 = 2{\cdot}62$, $P = 0{\cdot}11$). The latter analysis is a more powerful one, because it is not confounded by sex differences in season of capture. Nonetheless, it remains possible that same-sized males and females differ in feeding frequency, and that this difference is obscured by the different average body sizes of the two sexes. We assessed this possibility as follows. When 908 male and 614 female snakes of similar snout–vent lengths were compared, we found that each sex fed more frequently during the Wet season (males, $\chi^2_1 = 71{\cdot}0$, $P < 0{\cdot}001$; females, $\chi^2_1 = 21{\cdot}5$, $P < 0{\cdot}001$). However, the frequency of feeding did not differ significantly between males and females in either season (Dry, males 5·1%, females 5·1%, $\chi^2_1 = 0{\cdot}002$, $P > 0{\cdot}95$; Wet, males 24·8%, females 19·7%, $\chi^2_1 = 0{\cdot}69$, $P > 0{\cdot}50$). Thus, feeding rates differ between seasons but are relatively similar in male and female filesnakes, regardless of body-size differences between the sexes.

Assuming that approximately 4 days are required to digest prey (Shine 1986a), we estimate that female filesnakes eat, on average, once every 91 days during the Dry season, and male snakes feed once every 63 days. On the other hand, Wet-season feeding frequencies were much higher: female snakes were estimated to feed once every 17 days on average, and male snakes to eat once every 11 days. Billabong water temperatures peak in the early Wet season and remain slightly warmer until the early Dry season (Bishop *et al.* 1980). Hence, filesnakes may digest prey items more quickly during the Wet season so that real Wet-season feeding rates may be even higher than those estimated above.

We also used data from Djarrdjarr Billabong to examine whether differences in Wet and Dry-season feeding frequencies simply reflected differences in fish availability. The proportions of snakes containing *freshly* ingested prey differed significantly between seasons, as was the case in previous analyses which dealt with prey items consumed before the snakes were trapped ($\chi^2_1 = 10{\cdot}9$, $P < 0{\cdot}001$). Fresh prey items were found in 2% (31 of 1533) of snakes in Dry-season samples, compared with more than 5% (15 of 274) of snakes during the Wet season. To determine whether snakes were more likely to feed on trapped fish, these figures need to be corrected for differences in the numbers of fish caught per net-night in each season. Higher numbers of fish were caught in Wet-season samples (24·6 fish per net-night), than in Dry-season samples (2·4 fish per net-night), a ratio of approximately 10:1 Wet:Dry.

Table 4. Summary of feeding frequencies in filesnakes in Magela Creek Billabongs. Key to samples: Djabiluku Billabong (Djab); Djarrdjarr Billabong (Djdj); Geig Billabong (Geig), Makamala Billabong (Maka); Namankurl-Gadjuduba billabong complex (N-G). Except where otherwise indicated, the numbers in columns show the numbers of snakes in each category. Under 'sample' we show the abbreviated billabong name followed by the year and season

		Feeding state						
Sample	Gender	Number of snakes without prey	Prey (>25% digested)	Total	Proportion with >25% digested prey	Fresh (>25% digested) prey only	Grand total	Proportion with fresh prey only
Djab	F	227	14	241	0·06	0	241	0
1987 Dry	M	159	9	168	0·05	4	172	0·02
Djdj	F	433	20	453	0·04	4	457	0·01
1985 Dry	M	327	18	345	0·05	4	349	0·01
Djdj	F	364	20	384	0·05	5	389	0·01
1986 Dry	M	458	26	484	0·05	8	492	0·02
Djdj	F	360	13	373	0·04	11	384	0·03
1987 Dry	M	250	11	261	0·04	7	268	0·03
Geig	F	12	0	12	0	0	12	0
1986 Dry	M	18	4	22	0·18	0	22	0·18
Geig	F	59	3	62	0·05	4	66	0·06
1987 Dry	M	87	5	92	0·05	4	96	0·04
Maka	F	31	3	34	0·09	0	34	0
1986 Dry	M	22	1	23	0·04	0	23	0
Maka	F	137	6	143	0·04	9	152	0·06
1987 Dry	M	171	14	185	0·08	11	196	0·06
N-G	F	32	2	34	0·06	0	34	0
1987 Dry	M	82	2	84	0·02	0	84	0
Djdj	F	48	13	61	0·21	7	68	0·1
1986–87 Wet	M	43	14	57	0·25	3	60	0·05
Djdj	F	27	10	37	0·27	3	40	0·08
1987–88 Wet	M	65	39	104	0·38	2	106	0·02
Geig	F	8	3	11	0·27	3	14	0·21
1986–87 Wet	M	8	6	14	0·43	2	16	0·13
Geig	F	8	2	10	0·20	1	11	0·09
1987–88 Wet	M	24	23	47	0·49	5	52	0·1

Thus, filesnakes during the Wet season were exposed to approximately 10 times as many trapped fishes as when caught during the Dry season, but were only twice as likely to have fed while in the nets.

Discussion

Although the main focus of this paper is the sex difference in feeding biology, we first need to deal with the other factors affecting feeding rates and dietary composition in Arafura filesnakes. The frequency of feeding is of particular interest in this species, because *A. arafurae* has been claimed to feed less frequently than other species of snakes (Shine 1986a). Based on limited data, Shine estimated feeding frequencies of approximately once every 40 days. Our more extensive data show that the situation is more complex than this, but the mean values are probably close to Shine's estimate. Shine (1986a) found that only 5% of his filesnakes contained prey, a proportion that was far lower than those recorded for any other species of snake (see Table 5: Shine 1986a). In the present study, Dry-season feeding frequencies were similar to the 5% of snakes containing food reported by Shine. Although 24% of females and 38% of males contained prey during the Wet season, these proportions are still lower than the published records for most of the species listed by Shine (Table 5: Shine 1986a). Also, Dry season conditions normally prevail for most of the year, so that the 'average' feeding rate over the year will be closer to the Dry-season rate than to that recorded during the Wet season.

Why do filesnakes feed more frequently during the Wet season? Our analyses support the idea that the snakes are equally willing to feed in both seasons, but feeding opportunities are limited during Dry seasons by a lower availability of fish (perhaps because fish are in lower numbers or are less 'catchable'). When the proportions of snakes containing freshly ingested prey (probably eaten in the fyke nets) were compared between Wet and Dry seasons, fewer snakes contained fresh prey during the Wet season compared to the numbers of prey available at that time. Trapped filesnakes were exposed to approximately 10 times as many fishes during the Wet season as during the Dry season, but were only twice as likely to have fed while in the nets. Hence, these data support the hypothesis that the low feeding rates of filesnakes in the Dry season are due to lower availability of prey: (i) fish are indeed more common in the Wet season (as judged by their

numbers in fyke nets), and (ii) trapped snakes eat more fish, relative to the numbers available per net, during the Dry season.

The dietary habits of an acrochordid are also influenced by its body size. Ontogenetic shifts in both prey size and prey type have been reported in several species of snakes (e.g. Mushinsky *et al.* 1982; Slip & Shine 1988; Shine & Slip 1990; Miller & Mushinsky 1990), with maximum prey size generally increasing with increasing snake size (e.g. Voris & Moffett 1981; Shine 1991b; Wallace & Diller 1990). Minimum prey sizes also increase with increasing snake size in the beaked sea snake, *Enhydrina schistosa* (Voris & Moffett 1981) and in female *A. arafurae* but not in many other species of snakes (Shine 1991b). Some size-related dietary shifts may result from onotogenetic shifts in habitat use and, thus, the rates at which snakes of different sizes encounter prey of different sizes. Such a size-related habitat shift has been reported in *Acrochordus arafurae* with larger snakes (especially females) tending to be captured in deeper water (Shine 1986b). Within the billabongs inhabited by *A. arafurae*, the average size of fishes also tends to be larger in deeper water (Bishop *et al.* 1980). We did not sample deep water in the present study for logistical reasons (capture rates are generally low, and traps need to be checked frequently to avoid drowning trapped snakes). However, previous telemetric studies of *A. arafurae* have shown that even large snakes spend much of their time in the shallows, and all size-classes of the *A. arafurae* population are well-represented in our samples. Thus, our restriction of sampling to shallow waters should not introduce significant bias into our dietary data.

Filesnakes are specialist feeders in that they are exclusively piscivorous. However, despite the broad scope for generalized opportunistic feeding (we recorded 21 fish taxa from fyke net samples), only 12 of these taxa were recorded from the guts of snakes. Also, 97% of prey items comprised only six taxa. Although the six most frequently eaten prey items corresponded with the six most abundant fish taxa in the fyke net samples, our data suggest that the snakes were actively selecting most of these fish. Apart from glass perch, these fishes were mostly found in significantly higher frequencies in the guts of snakes, compared with their frequencies in fyke net samples. The Jacobs index indicated that snakes were actively avoiding glass perch, by far the most abundant fish taxon in the fyke net samples. We recognize, however, that these biases may reflect variance in the filesnakes' abilities to detect or capture different prey species, rather than active selection of particular prey items.

Despite the overall similarities in dietary composition and in the extent of the seasonal shift in feeding rates, male and females filesnakes different profoundly in many aspects of their diets.

Feeding rates. Although male filesnakes ate more often than did females overall, the sex difference in feeding rates, male and females filesnakes differ either season. Thus, the biological significance of this result remains questionable.

Frequency of multiple prey items. Males often contained multiple prey items, whereas females (especially large females) tended to eat single large prey items rather than multiple small prey items. This sex difference in the relative numbers of single versus multiple prey items disappeared when the comparison was restricted to animals of the same range of body sizes. Thus, large acrochordids tend to eat single rather than multiple prey, and the sex difference is simply a consequence of the sexual size dimorphism in this species.

Prey size. Females ate larger prey items than males, and this difference persisted even when the comparison was restricted to male and female snakes of the same range of body sizes or head lengths (Fig. 6). Hence, the sex with the relatively larger head takes disproportionately larger prey items, as predicted by the hypothesis that sex differences in the size and shape of the head have evolved to allow trophic divergence between the sexes (Camilleri & Shine 1990).

Relationship between predator size and prey size. There was no significant correlation between head size and prey size in male filesnakes, and little evidence of ontogenetic shifts in either prey size or prey species. In contrast, the correlation between head size and prey size was highly significant in female snakes, with both minimum and maximum prey sizes increasing with increasing snake head size.

Prey type. Male filesnakes tended to be relatively unselective, whereas the taxonomic composition of the diet of females became increasingly specialized with increasing snake size. For example, glass perch (Ambassidae) were eaten mostly by male snakes, whereas plotosid catfish were the only prey type recorded from the largest size-class of female snakes. We cannot determine if large female snakes were actively selecting sleepers and plotosids, or whether these were the taxa which females contacted most frequently (perhaps in deeper water), or were able to capture most easily. The sex difference in taxonomic composition of the diet is due largely to sex differences in body size and in relative jaw size, but remains significant even when comparison is restricted to males and females over the same range of head lengths (Fig. 5).

In summary, our data paint a complex picture of the determinants of dietary composition and feeding rates in filesnakes. Seasonal changes in prey availability exert a considerable influence, as does the

body size of the snake. However, even when both of these factors are taken into account, male and female filesnakes feed on different prey species and different prey sizes. In conjunction with the morphological divergence between males and females in this species — especially the divergence in relative head size and in jaw dimensions — these dietary data provide strong support for the hypothesis that sexual dimorphism in filesnakes has been influenced by natural selection for different ecological roles in males and females. We do not suggest that the extreme sexual dimorphism exhibited by this species results entirely from selection for niche divergence. Instead, it seems likely that body sizes in males and females initially diverged through selection for larger litter sizes (and thus body sizes) in females, in the absence of any equivalent sexual-selection advantage to larger body sizes in males. Given this divergence, independent adaptations of each sex to different prey types and sizes have exaggerated the degree of size dimorphism, and contributed to the evolution of sex differences in relative head size and head shape (Shine 1986b; Camilleri & Shine 1990). Such sex-based dietary differences might also reflect selection for higher energy or nutrient intake in the sex (females) which must devote more resources to reproductive output (e.g. Shine 1989). Additional data on other sexually dimorphic species will be needed before more detailed predictions from this hypothesis can be tested.

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References

Bishop, K., Allen, S., Pollard, D. & Cook, M. (1980) *Ecological studies on the fishes of the Alligator Rivers Region, Northern Territory (Final report in 3 parts)*. Supervising Scientist for the Alligator Rivers Region, Sydney, NSW.

Camilleri, C. & Shine, R. (1990) Sexual dimorphism and dietary divergence: differences in trophic morphology between male and female snakes. *Copeia*, **1990**, 649–658.

Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*. Murray, London.

Houston, D. (1992) *Ecology of the arafura filesnake*. Acrochordus arafurae, *in northern Australia*. PhD thesis, University of Sydney, NSW.

Jacobs, J. (1974) Quantitative measurement of food selection. Prey size and food selection of *Psammodromus algirus* (Lacertidae) in central Spain. *Oecologia*, **14**, 413–417.

Kephart, D.G. (1982) Microgeographic variation in the diets of garter snakes. *Oecologia*, **52**, 287–291.

Kephart, D.G. & Arnold, S.J. (1982) Garter snake diets in a fluctuating environment: a seven year study. *Ecology*, **63**, 1232–1236.

Merrick, J. & Schmida, G. (1984) *Australian Freshwater Fishes*. Griffin Press Ltd, South Australia.

Miller, D.E. & Mushinsky, H.R. (1990) Foraging ecology and prey size in the Mangrove Water Snake, *Nerodia fasciata compressicauda*. *Copeia*, **1990**, 1099–1106.

Mushinsky, H.R. (1987) Foraging ecology. *Snakes: Ecology and Evolutionary Biology* (eds R.A. Seigel, N.B. Ford & S.S. Novak), pp. 302–334. Macmillan, New York.

Mushinsky, H.R., Hebrard, J.J. & Vodopich, D.S. (1982) Ontogeny of water snake foraging ecology. *Ecology*, **63**, 1624–1629.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, **52**, 137–154.

Ryan, M., Bartholomew, G.A. & Rand, A.S. (1983) Energetics of reproduction in a neotropical frog, *Physalaemus pustulosus*. *Ecology*, **64**, 1456–1462.

Savitsky, A.H. (1983) Coadapted character complexes among snakes: fossoriality, piscivory and durophagy. *American Zoologist*, **23**, 397–409.

Shine, R. (1980) 'Costs' of reproduction in reptiles. *Oecologia*, **64**, 92–100.

Shine, R. (1986a) Ecology of a low-energy specialist: food habits and reproductive biology of the Arafura filesnake (Acrochordidae). *Copeia*, **1986**, 424–437.

Shine, R. (1986b) Sexual differences in morphology and niche utilisation in an aquatic snake. *Acrochordus arafarae*. *Oecologia*, **69**, 260–267.

Shine, R. (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology*, **64**, 419–464.

Shine, R. (1991a) Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist*, **138**, 103–122.

Shine, R. (1991b) Why do larger snakes eat larger prey? *Functional Ecology*, **5**, 493–502.

Shine, R. & Lambeck, R. (1985) A radiotelemetric study of movements, thermoregulation and habitat utilisation of Arafura filesnakes (Serpentes, Acrochordidae). *Herpetologica*, **41**, 351–361.

Shine, R. & Slip, D.J. (1990) Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae). *Herpetologica*, **46**, 283–290.

Slatkin, M. (1984) Ecological causes of sexual dimorphism. *Evolution*, **38**, 622–630.

Slip, D.J. & Shine, R. (1988) Feeding habits of the diamond python, *Morelia s. spilota*: ambush predation by a boid snake. *Journal of Herpetology*, **22**, 323–330.

Snedecor, G.W. & Cochran, W.G. (1987) *Statistical Methods*, 7th edn. Iowa State University Press, Ames, Iowa.

Voris, H. & Moffett, M. (1981) Size and proportion relationship between the Beaked Sea Snake and its prey. *Biotropica*, **13**, 15–19.

Wallace, R.L. & Diller, L.V. (1990) Feeding ecology of the rattlesnake *Crotalus viridus oreganus*, in northern Idaho. *Journal of Herpetology*, **24**, 246–253.

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