

## Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*

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**Abstract.** Filesnakes (*Acrochordus arafurae*) are large (to 2 m), heavy-bodied snakes of tropical Australia. Sexual dimorphism is evident in adult body sizes, weight/length ratios, and body proportions (relative head and tail lengths). Dimorphism is present even in neonates. Two hypotheses for the evolution of such dimorphism are (1) sexual selection or (2) adaptation of the sexes to different ecological niches. The hypothesis of sexual selection is consistent with general trends of sexually dimorphic body sizes in snakes, and accurately predicts, for *A. arafurae*, that the larger sex (female) is the one in which reproductive success increases most strongly with increasing body size. However, the sexual dimorphism in relative head sizes is not explicable by sexual selection.

The hypothesis of adaptation to sex-specific niches predicts differences in habitats and/or prey. I observed major differences between male and female *A. arafurae* in prey types, prey sizes and habitat utilization (shallow versus deep water). Hence, the sexual dimorphism in relative head sizes is attributed to ecological causes rather than sexual selection. Nonetheless, competition between the sexes need not be invoked as the selective advantage of this character divergence. It is more parsimonious to interpret these differences as independent adaptations of each sex to increase foraging success, given pre-existing sexually-selected differences in size, habitat or behavior. Data for three other aquatic snake species, from phylogenetically distant taxa, suggest that sexual dimorphism in food habits, foraging sites and feeding morphology, is widespread in snakes.

These two explanations for sexual dimorphism provide different predictions. The hypothesis of sexual selection predicts that the relationship between reproductive success and body size will differ between males and females in a sexually dimorphic species: the larger sex should be the one in which reproductive success increases most strongly with increasing body size. Any morphological differences between the sexes should be explicable as adaptations to increase reproductive success. Considerable support has been gained for the sexual selection model. For example, male superiority in body size and the development of sex-specific “weaponry” are greatest where male-male competition is intense, as in highly polygynous species (Gill 1871; Selander 1972; Crook 1972, 1973; Wiley 1974; Brown 1975; Gautier-Hion 1975; Clutton-Brock et al. 1977; Leutenegger and Kelly 1977; Harvey et al. 1978; Shine 1978, 1979; Spassov 1979; Alexander et al. 1979; Berry and Shine 1980). Similarly, information on body size and reproductive success in males and females also is consistent with the idea that sexual dimorphism evolves to adapt each sex to its reproductive role (Fitch 1956; Harris 1964; Trivers 1976; Stamps 1977; Ruby 1981; Dugan 1982; Werner 1982; Andren and Nilson 1981; Kelleway 1982; Davies and Halliday 1977; Howard 1979; Clutton-Brock et al. 1982).

The hypothesis of ecological causation of sexual dimorphism predicts that the sexes will differ in ecological traits such as prey types or habitat utilization. However, the usefulness of this prediction is reduced by the inability to specify which sex should be larger, and by the possibility that these ecological differences might simply be consequences of sexually-selected dimorphism. Hence, ecological differences may be consistent with either hypothesis. The only unambiguous evidence for the “ecological causation” hypothesis is sexual dimorphism in the size or morphology of the feeding apparatus (e.g. jaw size or bill shape), greater than that expected from body-size differences (Selander 1966). Such character divergence might enable differential niche utilization by the two sexes. It is not explicable by sexual selection unless the size or shape of the feeding apparatus also is significant in intrasexual or epigamic selection. For example, larger head sizes in males than females may evolve by sexual selection if male-male combat involves use of the jaws (e.g. lizards: Vitt 1983; Carothers 1984). Evidence for the “ecological causation” hypothesis is relatively meagre. Although there are many examples of ecological differences between the sexes (e.g. Clutton-Brock et al. 1982; Bowen 1984; Lamb 1984; Schoener 1977), and sex

In many animals, adult males and females differ substantially in body size and morphology. An extensive literature on the evolutionary causes for such differences (e.g. Darwin 1874; Ghiselin 1974; Clutton-Brock et al. 1982; Slatkin 1984), focuses on two possible mechanisms:

(i) *Sexual selection*, whereby large body size or some morphological feature confers a greater advantage to one sex than to the other, because of differences in the ways that reproductive success is determined in the two sexes.

(ii) *Ecological causes*, whereby differing sizes or morphologies adapt the two sexes to different ecological roles. For example, competition for food between males and females may lead to ecological character displacement, achieved by the evolution of differences in body size or morphology of the feeding apparatus (e.g. Selander 1972).

differences in trophic morphology (e.g. Baird 1965; Fedducia and Slaughter 1974; McEachran 1977; Schoener 1967, 1977; Harvey et al. 1978; Carothers 1984; Vitt 1983), most of these could be interpreted as consequences of sexual selection rather than as adaptations for differential niche utilization. The crucial evidence – character divergence in feeding morphology, in a degree or direction inconsistent with sexual selection – is rare. The only unambiguous examples are dimorphic bill shapes in a few species of birds (Darwin 1874; Selander 1966, 1972; Bell 1982), and dimorphic claw sizes in an insect (the ambushbug: Mason 1977).

The present study documents another example of this phenomenon, in an aquatic Australian snake (*Acrochordus arafurae*), and investigates the evolution of this dimorphism in the light of the hypotheses outlined above. Data are presented on sexual dimorphism in size and morphology, reproductive success as a function of body size in males and females, and ecological (dietary, habitat) differences between the sexes. Finally, limited data on three other snake species are presented to show that the situation in *A. arafurae* may be widespread among snakes.

## Materials and methods

Arafura filesnakes are large (up to 2 m long), heavy-bodied aquatic snakes. The skin is loose, flabby and covered with small conical scales, giving a file-like appearance. *Acrochordus arafurae* is one of only three species of the Arochordidae, a group which is so unusual in both morphology and physiology that they are believed to be only distantly related to other living snakes (McDowell 1975, 1979; Rieppel 1980; Seymour et al. 1981). Recent studies of *A. arafurae* describe reproductive biology, population densities, food habits, habitat utilization, movements and thermoregulation (Shine 1986; Shine and Lambeck 1985).

This study was carried out in the central northern section ("Alligator Rivers Region") of Australia's Northern Territory, 250 km east of Darwin. Apart from initial studies on the Mary River, most data were gathered on Magela Creek, a small stream flowing from the Arnhemland escarpment to the East Alligator River. The creek consists of discrete lagoons (billabongs) during the dry season (May–December) but torrential monsoon rains during the wet season (January–April) connect all the billabongs into a single watercourse. In the lower reaches of the Magela, an extensive floodplain (approximately 25 × 5 km) is inundated, often to a depth of 2 m, during the wet season. Hence, the billabongs have extensive shallowly-inundated fringes during this period.

Data were gathered in January–March 1982, July–August 1982; January–February 1983 and October–November 1983. Snakes were collected by four methods: (i) Shallow (<0.5 m) water areas were searched at night with flashlights. This was most effective in the wet season, when extensive shallow areas existed. (ii) Specimens were collected by groping under logs and among stilt roots of *Pandanus* (*Pandanus aquaticus*) and freshwater mangrove (*Barringtonia acutangula*). The snakes can be recognized by touch and are easily collected. This technique worked best when water levels were low, concentrating snakes in the few remaining inundated areas. (iii) Snakes were captured in drum nets, 60 cm diameter, with funnels at both ends and baited with freshly killed fish. This design was based on turtle traps (Legler 1960) but with smaller (10 cm) funnel open-

ings to prevent ingress of turtles or large fishes. These traps were productive in both shallow and deep water. (iv) Snakes were also taken in unbaited fyke nets, 60 cm diameter, with leaders 30 cm high and 2 to 4 m long. These were most effective set perpendicular to the bank in shallow water, with the leader running from the bank to the funnel.

The data taken from captured snakes were: snout-vent length (henceforth, SVL), tail length, head length (from the tip of the snout to the back of the articular, with vernier calipers), weight, sex (determined by tail shape and size – see below), presence and identity of prey items in the stomach (determined by palpation and forced regurgitation), and reproductive condition in adult females (oviducal eggs could be detected by palpation). Most snakes were released after capture, but 120 were dissected for determination of reproductive cycles and body sizes at maturity. Gravid females captured in August 1982 and November 1983 were maintained in the laboratory at 30° C until parturition. Neonates were killed by freezing, and then measured (SVL, tail length, head length, weight), and sexed by eversion of hemipenes using injection of water into the tail. For detailed methodology and results on general ecology, see Shine (1986) and Shine and Lambeck (1985).

## Results

### *Sexual dimorphism in body size and morphology*

(i) *Size at sexual maturity.* All males (n=39) over 90 cm SVL were reproductively mature (enlarged testes and/or thickened vasa efferentia), as were single specimens of 86 cm and 82 cm. Another 82-cm male was immature, as were single animals at 86 cm and 89 cm SVL. Hence, most male *A. arafurae* mature at 82 to 90 cm SVL.

The exact size at maturity in females is difficult to determine because of the low proportion of reproductive females in all size classes. The four smallest reproductive females (i.e. with enlarged oviducts, or ovarian follicles >10 mm diameter) measured 113, 116, 120 and 125 cm SVL. This suggests that females mature at about 115 cm SVL, although the low proportion of reproductive females means that some individuals may not mature until they attain much larger sizes.

(ii) *Average adult sizes, and morphology.* The average size of adult females (135 cm SVL, 1400 gm) was much greater than that of adult males (105 cm, 660 gm) (Table 1). Average adult sizes for both males and females were very consistent in samples taken at different localities and dates (Table 1).

Sexual dimorphism is shown not only in absolute body size, but also in the allometric relationship of head length, tail length, and body mass *versus* SVL. At any given body length, females have significantly (analysis of covariance,  $P < 0.001$  in all cases) heavier bodies, shorter tails and larger heads than do males (Figs. 1, 2). The relationship between body length and mass in the two sexes was examined in detail, because of the possibility that it could be influenced by seasonal variations in condition. The data base was restricted to snakes less than 120 cm snout-vent length, to ensure that males and females of equivalent SVLs were compared. All specimens used were from Leichhardt Billabong, and comprised samples from both the wet-season (53 males, 33 females) and dry-season (52 males, 34 fema-

**Table 1.** Sample sizes, body sizes and adult sex ratio among major samples of the filesnake *Acrochordus arafurae* from Alligator Rivers region, Northern Territory, Australia. All SVL measurements in cm. Unsexed juveniles are included with juvenile males

Location	Buffalo Billabong	Mary River	Leichhardt Billabong	Leichhardt Billabong	Hidden Billabong	Hidden Billabong
Date	Feb 1982	Aug 1982	Feb 1983	Nov 1983	Nov 1983	Nov 1983
Capture method	Spot-lighting	Groping	Nets	Nets	Nets	Groping
Total sample size	42	85	129	206	164	45
<i>Females</i>						
(i) Juveniles						
<i>N</i>	7	15	25	27	16	5
SVL ( $\bar{x}$ , & s.d.)	89.3 (13.7)	80.6 (23.8)	98.0 (12.4)	99.4 (15.2)	96.4 (18.9)	104.6 (3.7)
extremes	70–112	49–113	58–113	64–114	60–113	101–109
(ii) Adults						
<i>N</i>	8	36	51	125	79	32
SVL ( $\bar{x}$ , & s.d.)	134.9 (13.0)	130.3 (11.0)	128.8 (7.7)	132.1 (8.3)	135.2 (10.8)	137.2 (10.3)
extremes	119–150	117–156	115–148	115–153	115–164	116–164
<i>Males</i>						
(i) Juveniles						
<i>N</i>	5	16	1	2	4	0
SVL ( $\bar{x}$ , & s.d.)	41.0 (8.0)	58.3 (11.8)	64.0	71.0	79.5 (1.3)	–
extremes	35–55	44–79	–	69–73	78–81	–
(ii) Adults						
<i>N</i>	22	18	52	52	65	8
SVL ( $\bar{x}$ , & s.d.)	102.1 (8.7)	104.5 (6.8)	105.4 (6.7)	104.0 (5.9)	106.5 (6.5)	108.9 (5.9)
extremes	90–120	91–114	88–118	89–118	88–120	101–116
Adult sex ratio ( $\text{♂}/\text{♀}$ )	2.75	0.50	1.02	0.42	0.82	0.25

les). Linear regression analysis (Zar 1974) was used to determine the most appropriate regression relationships between snake SVL and mass, taking into account the effects of sex and season. Four models, of different levels of complexity, were tested:

Model I: 1 slope, 1 intercept (a single regression including data for both sexes and both seasons).

Model II: 2 slopes, 2 intercepts (fitting data for males and females separately, but combining data from wet- and dry-seasons within each sex).

Model III: 2 slopes, 4 intercepts (fitting all four data sets separately, but maintaining equal slopes for wet- and dry-season samples within each sex).

Model IV: 4 slopes, 4 intercepts (fitting all four data sets separately).

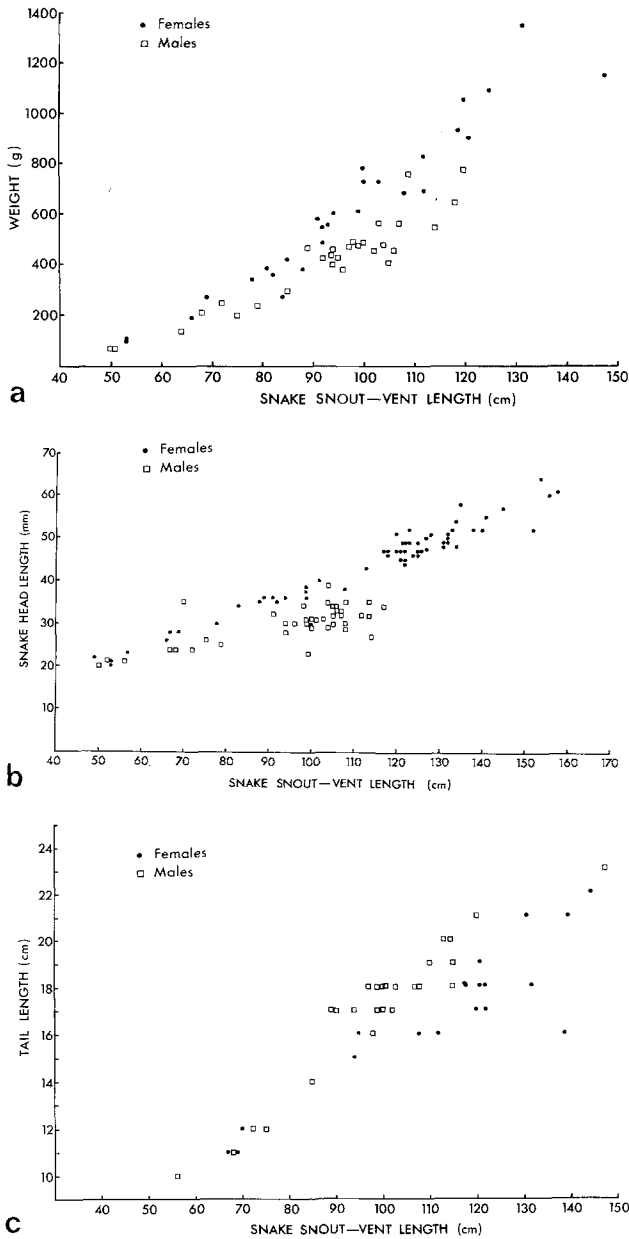
Model II was found to be more appropriate than Model I ( $F = 55.87$  on 2, 168 d.f.,  $P < 0.001$ ), indicating a significant difference between the sexes in the relationship between SVL and mass. However, allowing for seasonal differences within sexes (Model III) did not explain significantly more variance ( $F = 1.43$  on 1, 166 d.f., n.s.). Neither was there a significant reduction in variance by using the most complex model (IV:  $F = 1.39$  on 4, 164 d.f., n.s.). Hence, there are clear differences between sexes, but not between seasons, in the relationship between mass and body length. Data on two captive-born litters showed that sexual dimorphism in head length, tail length and body mass is already present at birth (analysis of covariance, male *versus* female,

$n = 23$ , 14: head length/SVL – slopes  $F = 0.07$ , intercepts  $F = 29.4$ ,  $P < 0.01$ ; mass/SVL – slopes  $F = 1.8$ , intercepts  $F = 1066.3$ ,  $P < 0.01$ ; tail length/SVL – slopes  $F = 2.5$ , intercepts  $F = 6838.9$ ,  $P < 0.01$ ).

#### *Reproductive success as a function of body size*

For full details on reproductive biology, see Shine (1986): here, I summarize information relevant to the relationship between reproductive success (RS) and body size in each sex. Mating occurs in the dry season, in mating “balls” consisting of one female together with one to eight males. No aggression between males was noted, either in the field or in captivity. Hence, the mating system resembles that of natricine colubrids (e.g. Aleksuk and Gregory 1974), where male RS presumably is relatively independent of body size. This conclusion is supported by data on the body lengths of three copulating males (98, 104, 105 cm SVL), compared to eleven unsuccessful males in the same mating aggregations ( $\bar{x} = 101.4$  cm, s.d. = 5.1), and to males overall ( $\bar{x} = 105.1$  cm,  $n = 217$ ).

Females ovulate late in the dry-season and give birth late in the wet-season (February to April). Neonates averaged 37 cm SVL, and 32 gm. Fecundity of *A. arafurae* averaged 16.9 (S.D. = 4.7, range = 11 to 25) and was highly correlated with female body size ( $r = 0.83$ ,  $P < 0.01$ : Fig. 3). The proportion of reproductive animals also varied with SVL, being higher in larger animals (Fig. 3:  $n = 12$  divisions of

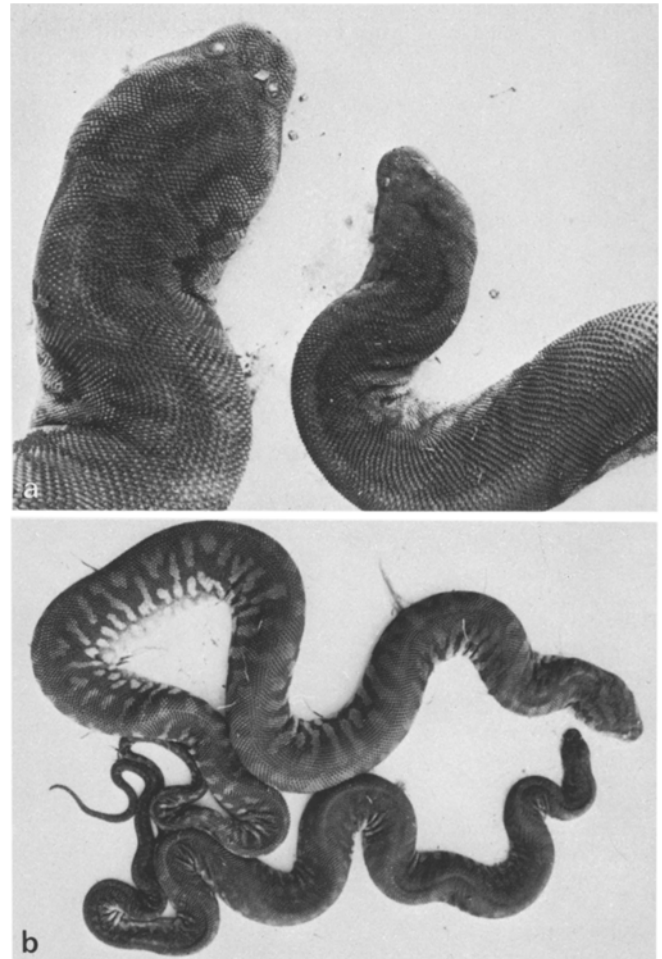


**Fig. 1 a-c.** Sexual dimorphism in body proportions of Arafura filesnakes from Magela Creek, Northern Territory, Australia. At any given body length, females are significantly heavier, with larger heads and shorter tails

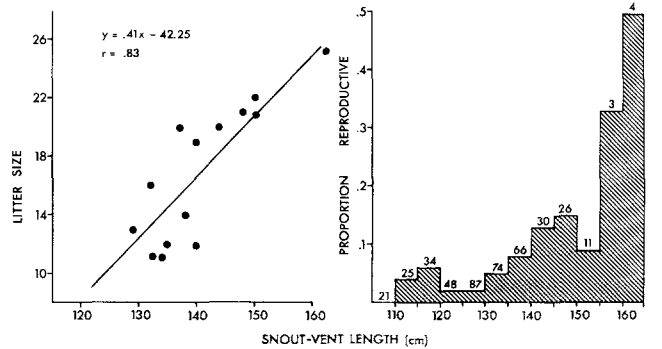
SVL,  $R = 0.72$ ,  $P < 0.01$ ). Because both determinants of female RS (fecundity and reproductive frequency) increase with body size, larger females have much higher mean annual fecundity. For example, a female of 123 cm SVL averages 0.4 offspring per year, whereas a 167-cm female averages 13.0 offspring. Clearly, female RS increases rapidly with body size (using 5-cm SVL increments:  $n = 11$ ,  $r = 0.84$ ,  $P < 0.01$ ; slope = 0.20).

*Ecological differences between the sexes*

**Food habits.** Filesnakes are exclusively piscivorous, but consume a variety of species (Table 2). Significant differences in prey type exist between the diets of adult males and females (contingency  $\chi^2 = 21.6$ ,  $P < 0.003$ ) and between ju-



**Fig. 2 a, b.** Sexual dimorphism in Arafura filesnakes from Leichhardt Billabong, Magela Creek. These photographs compare average-sized adult male and female filesnakes. The male is smaller and has a much smaller head



**Fig. 3.** Fecundity of adult female Arafura filesnakes from the Alligator Rivers Region, and the proportion of adult-sized females in reproductive condition

venile and adult females ( $\chi^2 = 20.6$ ,  $P < 0.02$ ). However, diets of adult males and juvenile females are similar with respect to prey type (contingency  $\chi^2 = 7.71$ ,  $P = 0.46$ ). Most prey items for males were eeltail catfish (*Neosilurus*) and *Glossamia* (67% of diet in males, 9% in females), whereas females ate mainly “sleepy cod” (*Oxyeolotris*) and barramundi (*Lates*: 7% in males, 57% in females).

**Table 2.** Prey items recorded from stomachs of male and female filesnakes collected in Alligator Rivers region, Northern Territory, Australia

Prey type	Prey in adult ♂ <i>Acrochordus</i>		Prey in juvenile female <i>Acrochordus</i>		Prey in adult ♀ <i>Acrochordus</i>	
	<i>N</i>	masses (g)	<i>N</i>	masses (g)	<i>N</i>	masses (g)
	Eeltail catfish, ssp. unknown	5	4–10	5	7–10	1
Eeltail catfish, <i>Neosilurus hyrtilii</i>	1	9	0	–	0	–
Mouth Almighty, <i>Glossamia aprion</i>	4	5–20	4	3–9	1	20
Barramundi, <i>Lates calcarifer</i>	0	–	1	600	5	200–300
Sleepy cod, <i>Oxyeleotris lineolatus</i>	1	100	2	40–270	8	25–882
Checked Rainbow, <i>Melototaenia maculata</i>	2	4–5	1	4	0	1
Bony Bream, <i>Nematalosa</i> sp.	0	–	2	3–200	0	–
Tarpon, <i>Megalops cyprinoides</i>	0	–	0	–	2	200–260
Forktail catfish, <i>Hexanematichthys leptaspis</i>	0	–	0	–	2	20–300
Banded Grunter, <i>Amniataba percoides</i>	0	–	2	41–50	0	–
Long Tom, <i>Strongylura krefftii</i>	1	163	0	–	2	100–130
Fish, spp. unknown	1	1	0	–	2	16
Catfish spines	3	–	0	–	1	–
<b>Totals</b>	<b>18</b>	<b>1–163</b>	<b>17</b>	<b>3–600</b>	<b>24</b>	<b>16–882</b>

Similar results obtain with the size (reconstituted mass) of prey items consumed. Prey of adult males ( $n=15$ ,  $\bar{x}=24.0$  g,  $s.d.=45.4$ ) are much smaller than those of adult females ( $n=21$ ,  $\bar{x}=290.7$  g,  $s.d.=265.5$ : Mann-Whitney  $U=90$ ,  $P<0.02$ ) but similar to those of juvenile females ( $n=16$ ,  $\bar{x}=79.6$  g,  $s.d.=158.7$ :  $U=96.5$ ,  $P>0.05$ ). The comparison between prey of adult males and juvenile females is important because the two groups of snakes are similar in SVLs (mean of 106, 103 cm), whereas females have much larger heads (mean head lengths 30.7, 40.4 cm, no overlap between the sexes). Both groups ate many small prey (<10 g), but the females also ate a few large items (maximum prey mass 800 versus 163 g), resulting in a higher variance in prey size among juvenile females than males ( $F=12.2$ ,  $P<0.01$ ). This difference must be due at least in part to head-size differences between the sexes, because a male would be physically unable to ingest the largest prey. Prey larger than 100 g were difficult to palp from male snakes, because of the enormous distension of the jaws required. Prey of up to 500 g were easily palpated from female snakes of similar SVLs.

**Habitats.** Filesnakes are entirely aquatic, living in billabongs during the dry season and spreading out into inundated grassland with the onset of wet-season flooding. Telemetered filesnakes were virtually sedentary during daylight

hours but moved extensively at night (Shine and Lambeck 1985). Sex differences in habitat utilization were evident in drum-net catches from Leichhardt Billabong during the wet season: females were collected most often in deep-water (>1 m) nets, and males in shallow-water (1 < m) nets ( $2 \times 2$  contingency  $\chi^2=14.5$ ,  $P<0.001$ ). At this time, most of the females from deep water were adults (88%) whereas many of those from shallow water were juveniles (47%:  $2 \times 2$  contingency  $\chi^2=8.25$ ,  $P<0.01$ ). That is, most males (87%) and immature females (69%) were in shallow water, whereas adult females were found in both habitat types (54% in deep water). However, a sample in the dry season showed no bias with water depth in relation to sex ratio (contingency  $\chi^2=0.02$ , n.s.) or mature versus immature females ( $\chi^2=0.22$ , n.s.). The proportions of juvenile to adult males did not differ between deep and shallow water in either comparison. The bias towards males in shallow water during the wet season is also evident in the sample collected by aid of a flashlight in shallow (<0.5 m) water: males outnumber females by almost 3:1, whereas females predominate in samples collected in deeper water (Table 1:  $2 \times 2$  contingency  $\chi^2=13.6$ ,  $P<0.001$ ).

## Discussion

Sexual dimorphism in adult body sizes is widespread in reptiles. Data on anoline lizards have been used to support the hypothesis that sexual dimorphism evolves to reduce intersexual competition for food (e.g. Schoener 1967, 1977). However, most authors have concluded that sexual size dimorphism is best explained by sexual selection (e.g. Darwin 1874; Trivers 1976; Shine 1978; Berry and Shine 1980; Stamps 1983; Fitch 1976, 1978, 1981; Schoener et al. 1982). Sexual dimorphism in body sizes is common in snakes, the female usually (>60% of species) being larger than the male (Shine 1978; Fitch 1981). In many snakes, the mating system seems not to involve any aggressive male behavior (Aleksiuk and Gregory 1974; Blanchard and Blanchard 1941; Finneran 1949). The greater size of the female thus has been attributed to sexual selection for increased fecundity, and the absence of any reproductive advantage to large body size in males (e.g. Shine 1978; Semlitsch and Gibbons 1982; Fitch 1981). This interpretation is supported by a trend for males to be larger than females in species where male-male combat occurs (Shine 1978). There is a problem with terminology here. Assuming that large body size in females evolves to allow higher fecundity, should it be attributed to “sexual selection” or “natural selection”? It is a trait which evolves purely because of an advantage in reproduction rather than survivorship, but (unlike other sexually-selected traits) does not relate directly to interactions between the sexes. In this paper I use the term “sexual selection” for this phenomenon, because of the similarity of this process to that acting in males, where large body size is favoured because it increases success in male–male interactions. The degree of SVL dimorphism in *A. arafurae* is higher than in most, but not all, other snakes (Fitch 1981), possibly because of aquatic habits. Extreme dimorphism is common in diverse aquatic snakes (Laticaudidae, Hydrophiidae, natricine, hydropsine, homalopsine, and colubrine Colubridae: Fitch 1981).

My data on *Acrochordus arafurae* are consistent with the hypothesis that sexual selection is responsible for sexual dimorphism in body length. Reproductive success of fema-

les is strongly dependent on body size, with larger females producing larger, more frequent litters (Fig. 4). In contrast, reproductive success of males probably does not depend so much on body size. The observations of several males entwined around one female suggest that male-male aggression does not occur. Also, the body lengths of copulating males were no larger than those of "unsuccessful" males. Hence, males seem to maximize their individual fitness by maturing at relatively small size, and allocating their available energy to mate-searching behavior rather than to body growth. This explanation was proposed by Semlitsch and Gibbons (1982) for dimorphism in *Nerodia*, and by Shine (1978) for dimorphism in all snake species lacking male combat.

However, sexual dimorphism in *A. arafuræ* involves more than body length. The longer tails of males (Fig. 2) presumably reflect the need to fit the hemipenes into the base of the tail: this tail-length dimorphism is widespread in reptiles (e.g. Klauber 1943). The other allometric differences, in body mass and head length, are less easy to explain, and are not predicted by sexual selection theory. The heavier build of females could be attributed to selection for ability to carry developing embryos (to increase space in the body cavity for the litter?) but the extreme dimorphism in head sizes of females and males cannot be explained in this way. If males were the sex with the larger heads, and if male-male combat or sequestering were important in the mating system (as in many lizards), one might imagine that males evolved larger heads to aid success in combats (e.g. Vitt 1983; Carothers 1984). However, this hypothesis is inconsistent with the larger head size of females.

I suggest that these differences in head size have evolved as adaptations to different prey sizes. The large size of prey relative to snake head lengths means that head size must limit maximum prey size, as seems to be true in many snakes (e.g. Shine 1977; Voris and Voris 1981). Adult female filesnakes ate much larger prey than did adult males (mean prey masses 291 g vs 24 g respectively). Prey-size differences were evident even in males and females at the same body size. The sexes also differed significantly in habitat in the wet-season, when males were found in shallower water. Data from Magela Creek show that fishes from deep water are consistently larger than shallow-water fishes (Bishop and Harland 1986). Thus, habitat differences expose male and female filesnakes to different prey sizes. This may explain why average prey mass of adult females was 12 times that of males, despite the differences between the sexes of only 26% in SVLs and 67% in head lengths.

Given that the observed head-size dimorphism of *A. arafuræ* is consistent with the hypothesis of dietary specialization by each sex, what is the selective advantage of such specialization? A recent review (Slatkin 1984) suggests three possible mechanisms: (i) competition between the sexes for a limiting resource may lead to character displacement (e.g. Selander 1972; Schoener 1967, 1977); (ii) intrinsic differences between males and females in reproductive roles may favour independent adaptations in each sex to increase foraging efficiency; (iii) certain models of optimal foraging suggest that there may be two body sizes at which foraging efficiency is maximized: these optima may be occupied by different morphs, different age-groups, or different sexes (Schoener 1969).

The third hypothesis is least likely on the grounds of population genetics (Slatkin 1984) and depends upon a

number of assumptions about foraging strategies, costs of time and energy, and prey availability (Schoener 1969). In particular, bimodal niches would not be expected in "searching" foragers (Schoener 1969), like *A. arafuræ* (Shine and Lambeck 1985). The other two hypotheses are more difficult to dismiss, but may be evaluated on the basis of parsimony. The "competitive displacement" model requires that the sexes compete for a limiting resource, and that character displacement of feeding morphology is sufficient to reduce such competition. In contrast, the "dimorphic niche" hypothesis merely requires that pre-existing differences from the action of sexual selection (e.g. dimorphic body sizes, activity times seasonally or diurnally, habitat utilization, feeding rates) are sufficiently major that subsequent morphological adaptations to these differences will evolve. The selective pressures for these adaptations need not involve competition, either within a sex or between sexes. All that is required is that a change in feeding morphology enables an animal to feed more efficiently: perhaps on a wider range of prey, or at a higher rate, or with less risk to itself. If the sexes already differ substantially because of sexual selection, there is no reason to expect that their subsequent independent adaptations for foraging will be similar.

Sexual selection often may produce sex differences in foraging biology. For example, mate-searching behavior in males may result in their being more mobile, their occupying different habitats, and in their being active at different times and (therefore) at different body temperatures than females. These factors should influence encounter rates with different prey, as well as their ability to capture and handle prey. Similarly, a reduction in food intake during gestation in females (e.g. Keenlyne 1972; Keenlyne and Beer 1973; Shine 1980) and during the mating season in males (e.g. Aleksuk and Gregory 1974) might result in the sexes foraging at different seasons. Reinert (1984) reviews several studies showing extensive sex differences in habitats, temperatures and feeding habits in snakes. There was no evidence for seasonal or sexual variations in feeding rate in *A. arafuræ*: the proportions of fyke-netted snakes with food were not significantly different between sexes and seasons ( $4 \times 2$  contingency  $\chi^2 = 1.45$ , 3 d.f., n.s.). A more important factor might be the sexually-selected difference in body size; in *A. arafuræ*, the smaller body size of males may suit them to shallow-water foraging. Lastly, energy requirements for reproduction often may be higher in females than in males (e.g. Smith 1976; Andrews and Asato 1977), perhaps favoring different adaptations for foraging.

The nature of advantages and disadvantages of different head sizes remains unknown, but might be related to efficiency of feeding (e.g. Catling and Freedman 1980). Snakes appear to be "gape-limited" predators (e.g. Schmidt and Holbrook 1984): maximum prey size increases with predator head size in all species studied to date (Shine 1977; Greene 1984; Reynolds and Scott 1982; Pough and Groves 1983; Voris and Voris 1983, Sieb 1981). Hence, any selection for an increase in prey size would be reflected in an evolutionary increase in head size. If this selective pressure applied to only one sex, divergence in relative head sizes would evolve. Thus, snakes may be an excellent group in which to examine the evolution of sex-based ecological differences. Data on two other groups of aquatic snakes are consistent with this suggestion. In the Fijian seasnake *Laticauda colubrina* (Laticaudidae) and in two North American

freshwater colubrids *Nerodia cyclopion* and *N. rhombifera* (Colubridae), females grow larger than males and eat larger (deeper-water) species of fishes (Pernetta 1977; Mushinsky et al. 1982). I measured preserved specimens of all three species at the Carnegie Institute (Pittsburgh, Pa.), and found that females had larger heads relative to body length in each case (analysis of covariance: *L. colubrina* –  $n=32$ , 30, slopes  $F=20.4$ ,  $p<0.01$ ; *N. cyclopion* –  $n=18$ , 36, slopes  $F=3.2$ ,  $p=0.08$ , intercepts  $F=15.3$ ,  $p<0.01$ ; *N. rhombifera* –  $n=25$ , 26, slopes  $F=5.5$ ,  $p<0.03$ ). These data, although preliminary, suggest that *A. arafurae* is not unique: sexual dimorphism in body sizes, head sizes, foraging habitats and prey sizes may be widespread in snakes. Because specialization on different prey sizes is likely to be reflected in character divergence of feeding morphology, snakes may prove to be ideally suited for analyses of the ecological significance of sexual dimorphism.

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