Population Demography of Arafura Filesnakes (Serpentes: Acrochordidae) in Tropical Australia

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ABSTRACT.—A mark-recapture study of filesnakes (Acrochordus arafurae) in freshwater billabongs of northern Australia provided data on >3400 snakes over a four-year period. Population densities were estimated by a modified jackknife technique, and were much higher than in most previously-studied species of snakes, with >400 snakes per hectare surface area (>100 kg ha⁻¹) in the main study billabong. This high biomass can be maintained because of the high abundance of prey (fishes), coupled with the low metabolic requirements (and hence, low feeding rates) of acrochordid snakes. Comparisons of sex ratios in trapped samples and in population estimates showed that male filesnakes were less "catchable" in our fyke-nets than were females. Sex ratios differed among billabongs, with a trend for more males in broad shallow back-flow billabongs and more females in narrow deep main-channel billabongs. This sex difference mirrors a size-related difference in habitat selection documented in earlier studies of this species. Filesnake populations contain a high proportion of immature snakes, because of delayed maturation in this species, but mortality rates among adult animals (especially, adult females) seem to be low. The size structure (and hence, we infer, age structure) of the population varied considerably from year to year, depending on levels of reproduction and thus, juvenile recruitment. This episodic recruitment means that populations are dominated by particular age classes, and are unlikely to attain stable age distributions.

If the ecological processes occurring within a population are to be understood, and particularly if that population is to be harvested, demographic information is of great value. The first aim of any demographic study is to determine how many animals are present in the population, and then to estimate variables such as the age structure, sex ratio, and rates of birth, death, and migration. However, there is a dearth of detailed demographic information for most species of squamate reptiles, especially snakes (Turner, 1977; Parker and Plummer, 1987). Despite the difficulty of obtaining such data, intensive mark-recapture studies—and especially, the pioneering studies of Henry S. Fitch (e.g., 1949, 1960, 1963)—have demonstrated the feasibility and value of work of this kind.

The present paper presents basic demographic information from a four-year mark-recapture study of a population of Arafura filesnakes (Acrochordus arafurae) living in the highly seasonal "Wet-Dry" tropics of northern Australia. Our study was stimulated by two issues. Firstly, acrochordid snakes offer an ideal opportunity to test the prediction that ectothermic predators, because of their low maintenance metabolic requirements, are able to sustain a high standing crop biomass (Pough, 1980). Acrochordids have much lower metabolic rates than other snakes (Seymour et al., 1981) and thus could be expected to achieve unusually high population densities under favorable conditions. Shine's (1986a) preliminary study of A. arafurae suggested that this prediction was supported, but sample sizes of that study were small (N = 244 snakes marked, 11 recaptured). Secondly, acrochordids are important traditional food items for Aboriginal people in many areas, and our population of Acrochordus arafurae is harvested regularly (Shine, 1986b). Whether or not this harvest is sustainable in the long term is a question of some interest in view of the low reproductive rates and delayed maturation of this species (Shine, 1986a; Houston and Shine, 1993b) allied with the tendency of Aboriginal hunters to selectively harvest the (relatively rare) reproductive female snakes (Shine, 1986b). In order to evaluate the capacity of A. arafurae to withstand exploitation by humans, data are needed on the total numbers of snakes in each waterbody, the degree to which billabong populations are isolated, and the possibility that male and female filesnakes may tend to occupy different billabongs.

MATERIALS AND METHODS

Study Species and Study Area.—Arafura filesnakes are large (males to 1.5 m total length, females to 2.0 m), piscivorous, entirely aquatic venomous snakes. 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. Tem-
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 through 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. We trapped 3627 snakes in nine billabongs, but most of the data in this paper come from a single waterbody (Djarrdjarl Billabong). Included in the 3627 snakes were 73 collected using methods other than fyke-nets (e.g., grappling in shallow water). Ninety-five percent of all snakes (3451) were marked and released. The study area and the general biology of Arafura filesnakes have been described elsewhere in more detail (Shine and Lambeck, 1985; Shine, 1986a, c; Houston, 1992; Houston and Shine, 1993a, b).

Data were gathered during seven field trips lasting 29 to 116 d. Because capture rates were higher during the Dry-season, we concentrated trapping at this time (17 August–15 September 1985 and 24 November 1985–21 January 1986; 24 October–10 December 1986; 29 August–22 December 1987; 18–30 October 1988), although two Wet-season trips were carried out also (22 March–19 April 1987; 25 March–28 April 1988). The snakes were captured at night in fyke-nets in shallow water, and removed from the nets the following morning for processing before being released at the site of capture later in the day. All snakes were measured, sexed (by relative tail length and head length—see Shine, 1986a for criteria), and individually marked by heat-branding with a modified soldering iron (Houston and Shine, 1993a, b). All recaptured snakes showed excellent healing, with the mark showing clearly as an unpigmented area against the grey-brown surrounding skin. Obtaining a valid and repeatable measure of snake body size is difficult because of the highly elastic bodies of filesnakes. Head-length (measured along the length of the dentary bone from the posterior edge of the quadrate to the snout) proved to be a more highly repeatable measure of an animal’s size than was snout-vent length (Houston and Shine, 1993a, b), and thus was used as the index of body size for our statistical analyses.

Definition of Populations.—Any study of mobile animals faces the problem of population delineation. Fortunately, floodplain billabongs of Kakadu National Park are isolated from each other during the Dry-Season, so that filesnakes (which are entirely aquatic) occur in discrete closed populations in each of the floodplain billabongs at this time. As recruitment of neonates only occurs during the Wet-season (Shine, 1986a) these populations are not subject to any gains during the Dry-season, and the only losses are through mortality. However, monsoonal flooding during the Wet-season links the billabongs in a huge shallowly-inundated floodplain. Radiotelemetric and mark-recapture studies reveal that filesnakes travel between billabongs at this time (Shine and Lambeck, 1985; Houston, 1992).

Estimates of Population Size.—Equal catchability is assumed in most methods for estimating population sizes, but is often violated by the data (Pollock et al., 1990). The heterogeneity model of Burnham and Overton (1978, 1979) partially overcomes this problem by assuming that capture probabilities are constant over time but variable among individuals, with the individual capture probabilities forming a random distribution on an arbitrary time interval. These authors used the jackknife technique to derive a series of estimators of capture probabilities, each of which is a linear combination of capture frequencies. We used Chao’s (1987) method because it is robust to low (mean ≤2) frequencies of recapture. We then estimated population size using the method of Pollock (1982), with two tiers of sampling: primary periods (annual dry-season samples), and secondary periods (consecutive days of sampling contained within each dry-season trip). Biases in population estimates can be reduced by treating sex and/or age categories separately (Pollock et al., 1990). Because of the extreme sexual size dimorphism in filesnakes, population sizes were estimated separately for males and females.

Trapping data here are not suitable for pooled trapping data from the first two field trips (both within the 1985 Dry-season, an overall sampling period covered 157 d). The population was closed to migration and neonatal recruitment throughout this time. The proportions of previously marked animals were similar in the samples obtained during the last five days of the first trip and during the first five days of the second trip, confirming that there was no significant emigration or immigration among billabongs during the intervening period (2.2% of 93 snakes vs. 5.3% of 152 snakes, x² = 1.43, P > 0.05).

Sex Ratio.—Sex ratios, expressed as the proportion of females (Caughley, 1977) were calculated in two separate (but non-independent) ways: based either on the actual numbers of snakes that we captured, or on our population estimates for each sex. We compared Dry-season sex ratios derived in both of these ways among billabongs for the 1987 Dry-season sample, and within Djarrdjarl Billabong among years. The
standard errors of sex ratios were calculated as suggested by Caughley (1977, p. 150), and any apparent departures from a 1:1 sex ratio were tested using chi-square. If males and females are equally catchable, sex ratios based on the numbers of captured snakes should be similar to sex ratios based upon the Chao estimates.

**Size and Age Structure of the Population.**—We examined population structure in terms of body sizes of the snakes. Size-based analysis avoids the inaccuracies inherent in age assignment, and may be valuable in its own right because reproductive maturity and fecundity are probably related to size rather than age in many reptile species (Andrews, 1982). Although age is a crucial life-history variable, great variability in growth rates makes it difficult to infer the ages of snakes from their body sizes. Our only age-based analysis was to calculate the proportions of animals >4 yrs of age, for comparison with studies on other snake species (Parker and Plummer, 1987). The relationship between age and size was determined from general growth patterns in *A. arnfras*, which in turn were derived from recaptures of marked snakes (Houston and Shine, 1993b). Any errors due to unusually fast-growing or unusually slow-growing animals should tend to cancel each other out, and thus the overall estimate may provide useful information on this aspect of age structure in our *A. arnfras* population.

**RESULTS**

**Estimates of Population Size.**—The proportion of marked snakes among all snakes that we captured during the last five days’ trapping each Dry-season gives an index of our ability to mark the population. For Djarrdjar Billabong, this proportion was 13% (11 of 82 snakes) in 1985, 35% (21 of 60) in 1986 and 30% (18 of 61) in 1987. Thus, we succeeded in marking a significant proportion of the population.

Our estimates of the Dry-season population suggested that males outnumbered females. The population contained between 1321 and 2445 females, and 1764 to 3160 males (Fig. 1). Based on overlapping confidence limits, population estimates did not differ significantly among years. Population estimates obtained by summing separate adult and immature estimates for each sex differed slightly from the total of over-

<table>
<thead>
<tr>
<th>Billabong</th>
<th>Surface area (ha)</th>
<th>Population estimate</th>
<th>Snake ha⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Females</td>
<td>Males</td>
<td>Total</td>
</tr>
<tr>
<td></td>
<td>(as % of total)</td>
<td>(as % of total)</td>
<td>(as % of total)</td>
</tr>
<tr>
<td>Djibiliku</td>
<td>34.3</td>
<td>2436</td>
<td>3223</td>
</tr>
<tr>
<td></td>
<td>(722, 30%)</td>
<td>(1659, 50%)</td>
<td>(881, 19%)</td>
</tr>
<tr>
<td>Djarrdjar</td>
<td>17.2</td>
<td>2445</td>
<td>4541</td>
</tr>
<tr>
<td></td>
<td>(498, 20%)</td>
<td>(881, 19%)</td>
<td>(881, 19%)</td>
</tr>
<tr>
<td>Makamala</td>
<td>10.8</td>
<td>1590</td>
<td>1267</td>
</tr>
<tr>
<td></td>
<td>(646, 41%)</td>
<td>(346, 27%)</td>
<td>(346, 27%)</td>
</tr>
<tr>
<td>Geig</td>
<td>9.6</td>
<td>1027</td>
<td>436</td>
</tr>
<tr>
<td></td>
<td>(320, 31%)</td>
<td>(157, 34%)</td>
<td>(157, 34%)</td>
</tr>
</tbody>
</table>
TABLE 2. Comparison of file snake sex ratios (proportion female), calculated by two different methods for four Magela Creek billabongs during the Dry-season of 1987: (i) Chao population estimates, and (ii) direct enumeration in collected samples. $x^2$ tests compare the observed sex ratio to a null hypothesis of equal numbers of males and females.

<table>
<thead>
<tr>
<th>Billabong</th>
<th>Sample counts</th>
<th>Sample</th>
<th>Chao estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Females</td>
<td>Males</td>
<td>Sex ratio</td>
</tr>
<tr>
<td>Djabiluku</td>
<td>219</td>
<td>159</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>(P &lt; 0.005)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Djarrdjar</td>
<td>310</td>
<td>243</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>(P &lt; 0.005)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Makamala</td>
<td>132</td>
<td>168</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>(P &lt; 0.001)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gei g</td>
<td>133</td>
<td>77</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>(P &lt; 0.001)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

All male and female estimates for the 1987 Djarrdjarl sample. The overall number of female snakes was estimated as 2445 (SE = 20.3), whereas the sum of separate estimates for immature and adult snakes was slightly higher (2800, with SE = 33.1 for immatures, 27.9 for adults). For males, in contrast, the sum of separate estimates for immature and adult snakes (4055, with SE = 49.9 for juveniles, 40.5 for adults) was slightly lower than the overall estimate (4541 ± 37.7).

When population sizes were compared among billabongs during the 1987 Dry-season (when the largest samples were available), the highest estimate was obtained for Djarrdjarl Billabong, while the smallest estimate was for Geig (Table 1). Population densities were calculated by dividing these estimates of total numbers per billabong by the Dry-season surface area of each billabong (determined from outline maps—Pancontinental, 1981). File snake population densities (snakes per hectare of billabong surface area) differed significantly among billabongs ($x^2_{SE} = 161.1, P < 0.001$), with the highest population density being estimated for Djarrdjarl Billabong (406 snakes ha$^{-1}$). How-
ever, densities were very high (>150 snakes ha⁻¹) in all four of the billabongs studied (Table 1).

Sex Ratio.—Overall sex ratios (proportions of female snakes in the population, based on the Chao population estimates) showed a strong male bias in Djaradjarr Billabong in each year (0.39, SE = 0.007 in 1985; 0.43, SE = 0.009 in 1986; 0.35, SE = 0.006 in 1987). Chi-square analysis confirmed that each of these values differs significantly from 0.5 (P < 0.001 in each case). Sex ratios in each of the other three billabongs sampled during the 1987 Dry-season also differed significantly from 1:1. Populations in Djabiluku Billabong consisted predominantly of male snakes (sex ratio = 0.42 ± 0.007), whereas those of Makamala (0.56 ± 0.006) and Geig (0.69 ± 0.001) consisted predominantly of females. There was poor agreement between sample sex ratios, and sex ratios based on the Chao population estimates (Table 2), suggesting that males and females differed in "catchability".

Size and Age Structure of the Population.—Fig. 2 compares the relative proportions of immature and adult filesnakes in Dry-season populations (based on the Chao population estimates) among Djaradjarr, Makamala and Geig billabongs over a three-year period. A three-dimensional contingency table test of partial independence (Zar, 1984) revealed that these proportions varied among billabongs and years ($\chi^2 = 189.2, P < 0.001$). Population size-struc-
ture histograms for Djurrjarr Billabong, based on the Chao estimates of population size for the three Dry-seasons, were constructed separately for each sex using arbitrary 5 mm head length categories. Changes in the size structure of the population over successive Dry-seasons are shown in Fig. 3. A notable feature is the high proportions of immature animals, mostly neonates of both sexes, present in the 1986 and 1987 Dry-season samples.

**Discussion**

Recapture data suggest that we had managed to capture and mark up to one-third of the total billabong population by the end of each Dry-season, so that our estimates of population parameters should be relatively accurate. One way of assessing the reliability of population estimates derived from mark-recapture data is to calculate error values (standard errors of the mean). Many error values for published estimates of snake population densities are so high as to render the figures meaningless (Parker and Plummer, 1987), but standard errors of our Dry-season population estimates were relatively low (19 to 50% of associated population estimates: Table 1).

**Population Density.**—Dry-season population densities of A. arafurae were $\geq 150$ snakes ha$^{-1}$. Population densities of $> 50$ snakes per ha were reported for only nine of 51 species reviewed by Parker and Plummer (1987), and one of these records came from an earlier study of A. arafurae (Shine, 1986a). Each of the eight unusually abundant species were colubrids with much smaller mean body sizes than A. arafurae. Hence, the biomass of A. arafurae present in Djurrjarr Billabong during the Dry-season is much higher than has been reported for any other snake species. For example, the highest biomass figures identified by Parker and Plummer (1987) were for the American colubrids Regina alleni (30.8 kg/ha) and Ophiondrus aschias (7.1 kg/ha). Our filesnakes averaged 725 g body mass (based on 4184 snakes), so the mean biomass per hectare surface area at Djurrjarr was certainly greater than 100 kg/ha. Thus the high population densities of filesnakes, at least during the Dry-season, are consistent with the prediction that ectothermic predators with low metabolic rates will be able to attain very high standing-crop biomass under favorable conditions (e.g., Pough, 1980).

The Dry-season concentrations of filesnakes may seem analogous to the aggregations of some temperate-zone species of snakes at hibernacula (Turner, 1977; Parker and Plummer, 1987), and thus not representative of 'normal' conditions experienced by filesnakes. However, there are two important differences: the Dry-season occupancies about nine months of the year, and filesnakes are active and continue to feed during this time (Houston and Shine, 1993a). The high densities of snakes at this time nevertheless may not be sustainable over a longer period: during Wet-season flooding the snakes move out of the billabongs so that the population density at this time will be much lower: approximately nine snakes ha$^{-1}$ based on the sum of the population estimates for all billabongs divided by the floodplain area encompassing them.

**Sex Ratio.**—Before attempting to interpret the variability in sex ratios among billabongs, we consider the discrepancy between sex ratios in our catch, and sex ratios based on the Chao population estimates. In three out of four instances the population ratios were very different from the sample ratios (Table 2). This discrepancy would be expected if there was unequal catchability between the sexes, such as could result from sex differences in body size, habitat selection, or activity patterns (Gibbons and Semlitsch, 1987). Methods of capture affect the sex ratio of filesnake samples, as the sex that is more difficult to capture is under-represented (Shine, 1986c). The Chao procedure eliminates this bias. Because the sexes are not equally catchable, the Chao estimates of sex ratio are more reliable than the actual numbers of snakes captured.

During the 1987 Dry-season, two billabongs had significantly more male snakes than female snakes, whereas the reverse was true in two others (Table 2). Sex ratios remained male-biased over three consecutive Dry-seasons in Djurrjarr Billabong, suggesting consistency in this respect over time. Similarly extreme biases in population sex ratios have been reported in other species of snakes (Parker and Plummer, 1987). Although biased primary sex ratios have been reported in both oviparous (Pituophis melanoleucus, Burger and Zappoliti, 1988) and viviparous (Noma scutatus, Shine and Bull, 1977; Vipera berus, Madsen and Shine, 1992) snakes, filesnakes appear to produce approximately equal numbers of sons and daughters (Shine, 1986c; and 12 males and 17 females were born to captive filesnakes during the present study). Thus, biased sex ratios among filesnake populations in the field are probably due to sex differences in survival rates or in behavior.

We speculate that sex ratios in filesnake populations may be affected by differential habitat selection by male and female snakes, and particularly by sex-specific preferences based on the physiography of billabongs. Floodplain billabongs can be separated into: (i) main-channel billabongs like Makamaka and Geig, which are deep and narrow with steeply sloping and well-vegetated banks; and (ii) back-flow billabongs...
like Djarri and Djabaluka, which are broad and relatively uniform in depth and have extensive shallow areas covered in floating vegetation (Bishop et al., 1980). Telemetry studies have shown that large adult female file snakes tend to be found in deeper water than the much smaller males and immature females (Shine, 1986c). This bias is consistent with our data on billabong sex ratios, in that the large female snakes are more common in the deep-water billabongs whereas the smaller male snakes are found mostly in the shallower back-flow waterbodies. Water depth could influence the distribution of snakes of different body sizes through its effects on either the availability of prey, or of diurnal refuge sites (and hence, on vulnerability of the snakes to predation). Shine and Lambeck (1985) suggested that predation by sea eagles may influence habitat selection by file snakes. Captive file snakes are very timid when coming to the surface to breathe, and tend to choose resting sites where they do not have to extend much of their bodies away from shelter to reach the surface (pers. obs.). Smaller snakes (and thus, males rather than females) may achieve this situation mostly in billabongs with extensive shallow areas. Also, large fish, the main prey of large (female) snakes in Magela Creek (Houston and Shine, 1993a), are encountered more frequently in deeper water (Bishop et al., 1980).

**Size and Age Structure of the Population.** The population structure of file snakes may differ from that of most previously-studied snakes. In most large, late-maturing snake species, populations consist mainly of adult animals (Parker and Plummer, 1987). For example, these authors calculated that the proportion of adult animals averaged 0.81 in 11 populations of late-maturing colubrid snakes, and 0.70 in 14 populations of early-maturing colubrids. The proportion of mature file snakes is lower (usually <0.50; see Fig. 2). However, late maturation (5 yr in males, 7+ yr in females; Houston and Shine, 1993b) means that many immature *A. arafurae* are quite old. Using the relationship between growth rate and body size in recaptured snakes to assess approximate ages of all animals in the population, we estimate the proportion of snakes >4 years old to be slightly higher in our file snakes (0.52 to 0.66 in females, 0.30 to 0.52 in males: Fig. 3) than in most other species studied to date (means of 0.09 in early-maturing colubrids, 0.42 in late-maturing colubrids, 0.35 in late-maturing vipers; Parker and Plummer, 1987).

High proportions of large adult file snakes, especially females, suggest that mortality rates may be low during adult life. Nonetheless, this comparison must be made cautiously, because the file snake population structure may vary considerably from year-to-year. We observed strong annual variation in recruitment of neonatal file snakes: very few juvenile snakes were caught in Djarri Billabong during the 1985 Dry-season, but neonatal snakes comprised a large proportion of the population one year later, and the same cohort was significant two years later (Fig. 3). The sudden increase in immature animals reflects a high reproductive output in early 1986, as evidenced by a large proportion of gravid females in 1985 (Houston and Shine, in prep.). Although the proportions of immature snakes differed significantly among the three different billabongs which we examined, the overall trends were similar (Houston and Shine, in prep.). However, we note that this tendency for episodic recruitment has the important result that file snake populations tend to be dominated by cohorts from years of unusually high reproductive output. Thus, 'stable age distributions' are unlikely to be reached in file snake populations.

Lastly, what do these data tell us about the likely impact of harvesting of file snakes by Aboriginal hunters? This hunting occurs throughout the year, but is most intense late in the Dry-season (usually, November-December), when water levels are at their lowest and the snakes can be captured by people wading through shallow water and groping under logs and floating grass-mats (Shine, 1986b). Our data show that file snakes occur in huge numbers in Magela Creek, so that despite their low and variable recruitment rates, the snakes can probably withstand considerable harvesting. Our radio-telemetric and mark-recapture studies document significant migration of file snakes among billabongs during the Wet-season (Shine and Lambeck, 1985; Houston and Shine, 1993c), so that local extinctions in specific billabongs would probably have little long-term effect. Reproductive females constitute only a small proportion of the file snake population, and are over-represented in catches by Aboriginal hunters because they are preferred food items, and are easier to catch (Shine, 1986b). The concentration of these relatively rare reproductive females in a few billabongs suggests that harvesting these areas might disproportionately reduce file snake populations in the long term. However, in practice these areas are exposed to relatively little harvesting pressure because these deep main-channel billabongs are also the favored habitat of large saltwater crocodiles (*Crocodylus porosus*). Crocodiles pose a significant danger to humans wading in the shallows and tend to reduce but not eliminate Aboriginal harvesting in these areas. Given the low numbers of Aboriginal hunters in the region at present, there seems little reason for concern about this...
potential threat to the conservation status of Acrochordus arafurae.

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