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April 1981

# A Comparison of Reproductive Strategies among Marine Snakes

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### SUMMARY

(1) Gravid females representing fourteen species of marine snakes were collected from four localities along the coast of Malaysia in 1975. The average clutch size ranged from 2.9 to 17.8 but most species had between three and seven young. The number of young produced and the size of gravid *Lapemis hardwickii* differed significantly at two sites in the Straits of Malacca. Eight species showed a significantly positive relationship between the number of oviducal eggs and female weight. The rate of infertility among ten species ranged from 4.5 to 20%.

(2) Sex ratios in the collections varied significantly through time and between localities. *Enhydrina schistosa* and other species collected at Muar showed tightly synchronized annual reproductive cycles. Species at other localities appeared to have more loosely synchronized cycles.

(3) A comparison of species in terms of clutch size, female weight and estimated birth weight revealed several distinct reproductive patterns that are considered in the context of *r* and *K*-selection. *Hydrophis fasciatus* is a small species that produced small clutches of medium sized young and it puts out the highest relative effort per embryo of any marine snake, 11 %. *Lapemis hardwickii* and *Thalassophina viperina* are large snakes which have three or four very large young. Their relative effort per embryo is high, too. *Enhydrina schistosa* is the largest species studied and has many medium sized offspring. Its relative effort per embryo is the lowest of any marine snakes studied (2%). The remaining species make up a loose group that falls between the group *T. viperina* and *L. hardwickii* and *E. schistosa* in terms of effort per embryo. In general, these species have modest sized clutches and small female weights.

### INTRODUCTION

The great majority of reptiles are oviparous but certain squamates have become ovoviviparous or viviparous. Among the lizards, eleven of seventeen families have one or more species which bear live young and among snakes, nine of ten families contain live-bearing species (Fitch 1970). Extensive evidence supporting the multiple origin of viviparity in snakes and lizards and a review of the ecological correlates have been presented by Tinkle & Gibbons (1977). Among the sea snakes there are three major lineages (Voris 1977). One is the genus *Laticauda* and it is oviparous and probably also ovoviviparous (Smith 1930; Smedley 1931). The other two lineages (the *Aipysurus* and *Emydocehalus* groups and Hydrophiinae of Smith (1926)) consist entirely of viviparous species (Kasturirangan 1950, 1952; Smith 1926; Wall 1921). The only nonhydrophid marine snake is *Acrochordus granulatus* (Sch-

neider) (Acrochordidae) and it too is viviparous. In these groups the major advantage of giving birth to live young would seem to be the emancipation of the adult female from terrestrial habitats for which she is so poorly adapted (Neill 1964). In this paper we compare the reproductive biology of marine species which have already made the shift to viviparity and may now be making other adjustments within the viviparous mode.

One purpose of this paper is to present new information on the reproductive biology of several species of marine snakes. A second purpose is to integrate the above information in order to define reproductive plans and then compare marine species to one another and to some terrestrial snakes.

## MATERIALS AND METHODS

From December 1974 to September 1975, marine snakes were collected from four sites along the coast of the Malay Peninsula. Three localities were sampled in the Straits of Malacca (Sungai Buloh, 3°14'45"N, 101°18'10"E; Muar, 2°3'20"N, 102°34'20"E; Parit Botak, 1°41'45"N, 103°6'15"E) and one locality in the South China Sea (Endau, 2°40'0"N, 103°38'0"E). A total of 259 gravid females representing fourteen species was present in the samples from these localities. Table 1 gives the collection periods for each locality and the sample sizes for the fourteen species for which there was one or more gravid females. The species represent two families of snakes, Acrochordidae (*Acrochordus granulatus*) and Hydrophiidae (other species). Details on collecting and preservation techniques can be found elsewhere (Jeffries & Voris 1979).

Each preserved female was dissected and her reproductive condition noted. When enlarged ovarian or oviducal eggs were present, they were counted and measured. In cases where embryos were detectable, the state and the number of developing (fertile) eggs were noted. Each female was drained of any excess alcohol and weighed. Next the oviducts were removed and the female was then reweighed. Each embryo and yolk were weighed separately.

The species under study here are viviparous (Kasturirangan 1950, 1952) and nutrients are added to the developing egg after ovulation. One consequence of this is that developing eggs of different ages cannot be directly compared in terms of weight or volume. The samples we have are highly variable with respect to embryonic developmental stage. Full term embryos are comparable, but these were present in only a small fraction of the females collected. We have devised a method for estimating the weight of full term embryos to facilitate making between-species comparisons. For each species, a plot of the average embryo weight *v* the average yolk weight for all gravid females was prepared. These plots show the relationship between the decrease in yolk weight and the increase in embryo weight that occurs in each species. Using the major axis (Slade 1977) we have drawn a line through these points. This line estimates birth weight where it intersects the embryo weight axis and where yolk weight equals zero.

## RESULTS

### Intraspecific relationships

The number of offspring produced varies within and between populations of a species according to female size. Figure 1 shows the relationship between the log of the female empty weight and the number of oviducal eggs produced for nine species. The sample sizes for *A. peronii, H. cyancinctus, H. melanosoma, H. ornatus,* and *M. gracilis* were small and thus
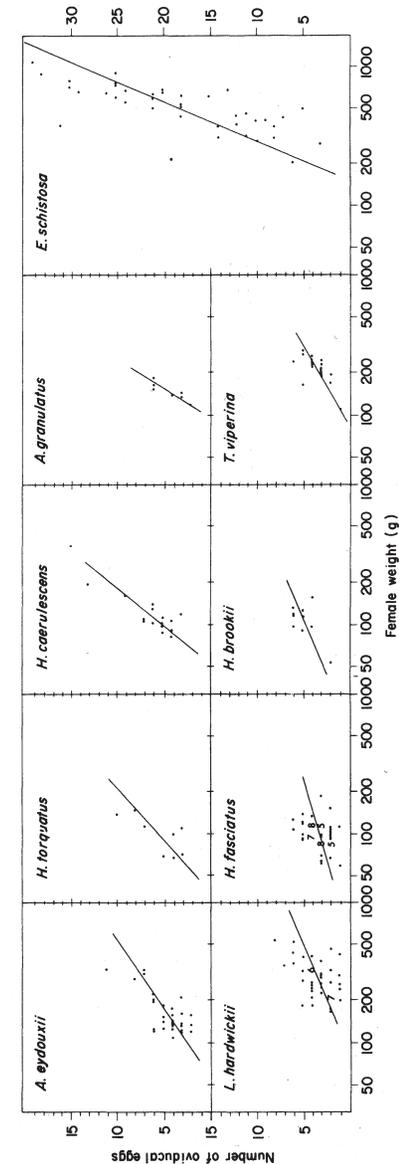


Fig. 1. Number of oviducal eggs plotted against the log of the weight of the females for nine species. All regression lines are significant ($P < 0.05$) with the exception of *H. brookii*. Sample size, linear regression and correlation data are given in Table 2.

TABLE 1. Sample size data by locality for those species which were captured in significant numbers. The sex ratio, number of gravid females, and number of newborn snakes is given for each sampling period. The number of subadults captured is not given. The size range for newborn snakes was estimated as up to 10 cm larger than the average for full-term embryos

**Muar**

| | 8 Jan.–4 Feb. | | | 25 Feb.–13 March | | | 26 March–21 April† | | | 10–14 May | | | 5–8 Sept. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born |
| *Acalyptophis peronii* (Dumeril) | | | | | | | | | | | | | | | |
| *Aipysurus eydouxii* (Gray) | 1/1 | 1 | 0 | | | | | | | | | | | | |
| *Acrochordus granulatus* | 24/29 | 24 | 0 | 61/40 | 6 | 198 | | | | | | | 15/9 | 0 | 0 |
| *Enhydrina schistosa* (Daudin) | 5/4 | 0 | 0 | 10/6 | 3 | 0 | 0/3 | 0 | 95 | 16/6 | 0 | 27 | 3/0 | 0 | 0 |
| *Hydrophis brookii* Gunther | 0/1 | 1 | 0 | 1/0 | 0 | 0 | 3/0 | 0 | 8 | 3/2 | 0 | 8 | 1/0 | 0 | 0 |
| *Hydrophis caerulescens* (Shaw) | | | | | | | 12/11 | 6 | 10 | | | | | | |
| *Hydrophis cyanocinctus* (Daudin) | | | | | | | 0/3 | 0 | | | | | | | |
| *Hydrophis fasciatus* (Schneider) | | | | | | | | | | | | | | | |
| *Hydrophis melanosoma* Gunther | 10/5 | 3 | 0 | 7/10 | 3 | 2 | 13/11 | 1 | 76 | 6/1 | 0 | 26 | 3/1 | 0 | 1 |
| *Hydrophis ornatus* (Gray) | | | | | | | | | | | | | | | |
| *Hydrophis torquatus* (Cantor) | 5/1 | 1 | 0 | 5/7 | 3 | 0 | 3/5 | 0 | 3 | 1/4 | 2 | 4 | 1/2 | 0 | 0 |
| *Lapemis hardwickii* Gray | | | | | | | | | | | | | | | |
| *Microcephalophis gracilis* (Shaw) | | | | | | | | | | | | | | | |
| *Thalassophina viperina* (Schmidt) | | | | | | | | | | | | | | | |

**Sungai Buloh**

| | 18 Dec.–4 Feb. | | | 15–23 Feb.* | | | 18–23 March | | | 25–28 April | | | 22–27 Aug. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born |
| *Acalyptophis peronii* | | | | | | | | | | | | | | | |
| *Aipysurus eydouxii* | | | | | | | | | | | | | | | |
| *Acrochordus granulatus* | 10/10 | 0 | 0 | 1/3 | 1 | 0 | 2/1 | 0 | 0 | 1/2 | 2 | 0 | 5/4 | 1 | 0 |
| *Enhydrina schistosa* | | | | | | | | | | | | | | | |
| *Hydrophis brookii* | | | | | | | | | | | | | | | |
| *Hydrophis caerulescens* | 4/11 | 1 | 0 | 2/2 | 1 | 0 | 10/1 | 0 | 0 | 3/2 | 0 | 0 | 1/2 | 2 | 0 |
| *Hydrophis cyanocinctus* | 0/1 | 0 | 1 | | | | 1/1 | 0 | 0 | 0/1 | 0 | 0 | | | |
| *Hydrophis fasciatus* | | | | | | | | | | | | | | | |
| *Hydrophis melanosoma* | | | | | | | | | | | | | | | |
| *Hydrophis ornatus* | | | | | | | | | | | | | | | |
| *Hydrophis torquatus* | | | | | | | | | | | | | | | |
| *Lapemis hardwickii* | 32/34 | 1 | 0 | 35/37 | 3 | 1 | 16/19 | 5 | 12 | 4/19 | 5 | 164 | 3/1 | 0 | 22 |
| *Microcephalophis gracilis* | | | | | | | | | | | | | | | |
| *Thalassophina viperina* | | | | | | | | | | | | | | | |

**Parit Botak**

| | 15 Jan.–4 Feb. | | | 7–11 March | | | 1–21 April | | | Endau 14 April | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born | ♂♂/♀♀ | gravid ♀♀ | new-born |
| *Acalyptophis peronii* | 5/17 | 13 | 0 | 16/18 | 12 | 0 | 9/10 | 5 | 0 | 7/1 | 1 | 0 |
| *Aipysurus eydouxii* | 2/4 | 2 | 0 | 2/2 | 0 | 0 | 5/3 | 1 | 0 | 7/7 | 0 | 0 |
| *Acrochordus granulatus* | | | | | | | | | | | | |
| *Enhydrina schistosa* | | | | | | | | | | | | |
| *Hydrophis brookii* | 14/10 | 8 | 0 | 7/1 | 1 | 0 | 8/8 | 2 | 0 | | | |
| *Hydrophis caerulescens* | 0/3 | 1 | 0 | 1/6 | 1 | 0 | 1/2 | 0 | 0 | 5/4 | 3 | 0 |
| *Hydrophis cyanocinctus* | 11/31 | 26 | 0 | 13/38 | 33 | 0 | 16/33 | 9 | 0 | 2/3 | 0 | 0 |
| *Hydrophis fasciatus* | | | | | | | | | | | | |
| *Hydrophis melanosoma* | | | | | | | | | | | | |
| *Hydrophis ornatus* | | | | | | | | | | 3/5 | 1 | 0 |
| *Hydrophis torquatus* | | | | | | | | | | | | |
| *Lapemis hardwickii* | 17/17 | 12 | 0 | 8/30 | 14 | 3 | /23 | 3 | 20 | 31/30 | 3 | 0 |
| *Microcephalophis gracilis* | | | | | | | | | | 2/1 | 1 | 0 |
| *Thalassophina viperina* | | | | | | | | | | 26/29 | 22 | 0 |

* Specimens collected at Sekinchang are included here. Sekinchang trawlers serve the same trawling grounds as do boats from Sungai Buloh.
† This sample is known to be biased. Some age classes of some species were released without records.

Table 2. Data for ten species on the linear regressions of oviducal egg number v the log of the female weight (Fig. 1). The slopes and intercepts from these regression analyses are shown with their 95% confidence limits.

| Species | n | r² | P | slope | intercept |
|---|---|---|---|---|---|
| A. eydouxii | 31 | 0·52 | 0·001 | 10·16 ± 3·75 | −17·70 ± 8·26 |
| A. granulatus | 7 | 0·76 | 0·01 | 24·17 ± 15·73 | −47·74 ± 33·91 |
| E. schistosa | 39 | 0·49 | 0·001 | 35·37 ± 11·78 | −77·21 ± 30·90 |
| H. brookii | 10 | 0·38 | – | 6·31 ± 6·35 | −7·82 ± 12·82 |
| H. caerulescens | 16 | 0·62 | 0·01 | 18·64 ± 8·39 | −32·05 ± 17·07 |
| H. fasciatus | 69 | 0·12 | 0·01 | 4·28 ± 2·9 | −5·18 ± 5·99 |
| H. melanosoma | 7 | 0·42 | – | 13·67 ± 18·33 | −25·50 ± 42·27 |
| H. torquatus | 8 | 0·05 | 0·05 | 13·41 ± 13·11 | −20·98 ± 25·93 |
| L. hardwickii | 47 | 0·26 | 0·001 | 6·38 ± 3·24 | −12·19 ± 7·90 |
| T. viperina | 22 | 0·45 | 0·001 | 8·55 − 4·46 | −16·34 ± 10·39 |

they were omitted from the figure. Eight of the nine species depicted in Fig. 1 show a significant relationship ($P < 0.05$) between clutch size and female empty weight (Table 2). In one species, *Lapemis hardwickii*, we have samples from both Sungai Buloh ($n = 29$ and Parit Botak ($n = 14$), and there was a significant difference ($P < 0.05$) in mean number of eggs between these two populations (Fig. 2). Although egg production in the two populations of *Hydrophis caerulescens* also appears different, this difference was not significant ($P > 0.05$), probably because of the high variation of the Sungai Buloh population.

As there was a significant difference in the number of oviducal eggs produced by *L. hardwickii* from Parit Botak and Sungai Buloh (Fig. 2), and given strong correlation between number of oviducal eggs and female weight (Table 2), a difference in size was expected. The mean empty weight of Parit Botak gravid females (248.7 g, n = 7) was significantly less ($P < 0.001$) than the mean of Sungai Buloh gravid females (361.1 g, $n = 12$). Therefore, gravid females collected at Sungai Buloh were larger and produced more oviducal eggs than the gravid females collected at Parit Botak.
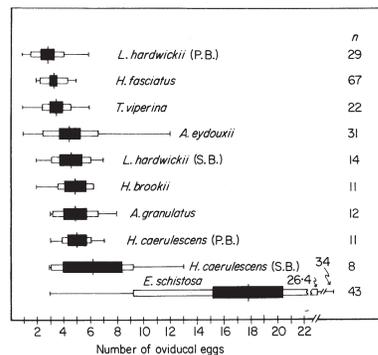


Fig. 2. Statistics on oviducal egg number for eight species. Each species is represented by specimens from one locality except for *H. caerulescens* and *L. hardwickii*. Each of these are represented separately by a Parit Botak (P.B.) and a Sungai Buloh (S.B.) population. The mean, two standard errors (filled area), one standard deviation (unfilled area) and range are given.
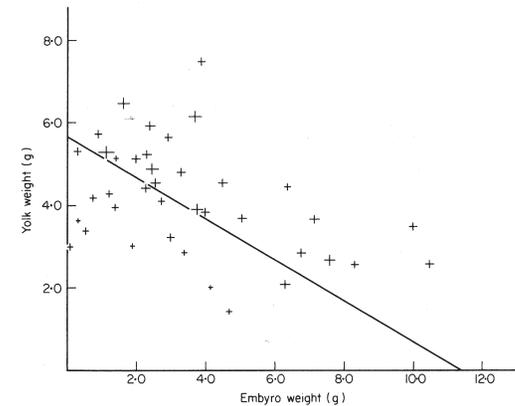


Fig. 3. For each clutch of thirty-nine *E. schistosa* gravid females the average yolk weight is plotted against the average embryo weight. The symbol size varies in proportion to the empty weight of the female. The line through the points is the major axis.

The relationship between mean embryo weights and mean yolk weights for *E. schistosa* was used to estimate birth weight (Fig. 3). The symbol size is set in proportion to the size of the female snake and it is clear that in this species large females tend to have larger embryos and yolks than small females. This relationship also hold in *L. hardwickii*, but is less pronounced. The remaining species do not show an increase in the size of the embryos with an increase in female size.

Within a species, the effort per full term embryo varies greatly among females (Table 3). The ranges in reproductive effort per embryo show a two- to seven-fold difference among females of a species. Much of this variation is directly attributable to the presence of infertile eggs. Estimates of effort per clutch are based on the product of the number of embryos and the effort per embryo. Thus the variation observed for effort per clutch is similar to that observed for effort per embryo (Table 3).

### Interspecific relationships

A comparison of oviducal egg production in populations of eight species showed that *Enhydrina schistosa* produced by far the largest clutches with a mean of 17.8 oviducal eggs (Fig.

Table 3. Data on the intraspecific variation in relative reproductive effort expressed as a percentage of female weight for species with twenty or more gravid females

| Species | n | Relative effort per embryo Range | CV | n | Relative effort per clutch Range | CV |
|---|---|---|---|---|---|---|
| A. eydouxii | 28 | 4·4–10·2 | 24·2 | 29 | 1·4–51·6 | 34·3 |
| E. schistosa | 39 | 1·0– 4·0 | 33·3 | 39 | 8·4–66·8 | 35·5 |
| H. fasciatus | 69 | 3·1–22·2 | 30·3 | 69 | 3·1–55·9 | 27·6 |
| L. hardwickii | 43 | 1·7–12·4 | 38·6 | 43 | 1·8–46·2 | 35·6 |
| T. viperina | 20 | 5·8–13·5 | 23·1 | 20 | 22·3–52·5 | 23·6 |

2). It had significantly more oviducal eggs than all other species studied ($P < 0.01$, *t*-test). Differences among the other populations were tested using a one-way analysis of variance and a Newman-Keuls multiple range test. The results of these tests indicate that the populations can be separated into two groups ($P < 0.05$). *Lapemis hardwickii* from Parit Botak, *Hydrophis fasciatus* and *Thalassophina viperina* formed a group that produced small clutches. The remaining populations formed a group with clutch sizes intermediate between the low group and *E. schistosa* (Fig. 2). Table 4 gives the mean number of oviducal eggs for ten species using pooled populations. Excepting *E. schistosa*, the range of means for the number of oviducal eggs for the remaining nine species is from 3.3 to 6.0.

A multiple range test was applied to the slopes of the four species that had both significant regressions and the largest sample sizes for the relationship between number of oviducal eggs and the log of female empty weight: *A. eydouxii*, *E. schistosa*, *H. fasciatus* and *L. hardwickii* (Fig. 1, Table 2). These four species form a continuum with *E. schistosa* having the steepest slope and a slope significantly different ($P < 0.01$) from the other three. *A. eydouxii* has the next steepest slope and then *L. hardwickii* and *H. fasciatus* have the flattest slopes. There were no significant differences ($P > 0.05$) between slopes for *E. eydo*uxii and *L. hardwickii* and for *L. hardwickii* and *H. fasciatus*, but the slope for *A. eydouxii* and *H. fasciatus* were significantly different ($P < 0.05$).

Estimated birth weights for ten species varied from 5.9 g for *H. caerulescens* to 23.5 g for *L. hardwickii* (Table 4). For each species the mean effort per embryo is a percent based on the average weight of the female and the mean birth weight (Table 4). The extremes here are striking with female *H. fasciatus* contributing an average of almost 11% of her body weight to each embryo while female *E. schistosa* contribute only about 2% to each offspring. The average total effort per clutch for ten species varies from about 24 to 39%. All the oviducal eggs of each species were classed as either fertile or infertile and a $\chi^2$ test was used to detect differences in fertility between species (Table 5). *Aipysurus eydouxii* showed a significantly higher infertility rate than the other species and *L. hardwickii* had significantly lower infertility. Small samples make conclusions on *H. brookii*, *H. torquatus*, *H. melanosoma* and *A. granulatus* speculative.

The ratio of male to female snakes captured varied. At Parit Botak, *A. eydouxii*, *H. caerulescens*, *H. fasciatus* and *L. hardwickii* had significantly skewed sex ratios in one or more

Table 4. Reproductive data for ten species of marine snakes.

| Species | *n* | Mean weight (g) | Birth weight* (g) | Mean number of oviducal eggs | Effort per clutch | Mean effort per embryo |
|---|---|---|---|---|---|---|
| *A. eydouxii* | 31 | 164·8 | 10·8 | 4·4 | 28·9 | 6·6 |
| *A. granulatus* | 7 | 143·3 | 7·9 | 4·3 | 23·6 | 5·5 |
| *E. schistosa* | 39 | 536·1 | 11·4 | 18·3 | 38·9 | 2·1 |
| *L. hardwickii* | 47 | 282·1 | 23·5 | 3·3 | 27·8 | 8·3 |
| *T. viperina* | 22 | 218·9 | 19·9 | 3·5 | 31·8 | 9·1 |
| *H. brookii* | 10 | 114·0 | 8·9 | 4·9 | 38·3 | 8·7 |
| *H. caerulescens* | 16 | 106·2 | 5·9 | 5·9 | 32·7 | 5·6 |
| *H. fasciatus* | 69 | 97·2 | 10·6 | 3·3 | 35·8 | 10·9 |
| *H. melanosoma* | 7 | 207·2 | 9·7 | 6·0 | 28·1 | 4·6 |
| *H. torquatus* | 8 | 98·2 | 6·2 | 5·5 | 34·9 | 6·3 |

* These figures are estimates. See the Materials and Methods section for the method.

Table 5. Data on fertility rates in ten species of marine snakes.

| Species | ♀♀*n* | Oviducal eggs *N* | % infertile | % snakes with ≥ 1 infertile egg |
|---|---|---|---|---|
| *A. eydouxi* | 31 | 141 | 20·0 | 32·3 |
| *A. granulatus* | 8 | 32 | 9·3 | 25·0 |
| *E. schistosa* | 43 | 754 | 10·7 | 59·5 |
| *H. brookii* | 11 | 52 | 5·8 | 27·2 |
| *H. caerulescens* | 17 | 100 | 13·0 | 5·9 |
| *H. fasciatus* | 71 | 237 | 11·4 | 22·5 |
| *H. melanosoma* | 7 | 42 | 14·2 | 28·6 |
| *H. torquatus* | 8 | 45 | 13·3 | 37·5 |
| *L. hardwickii* | 48 | 156 | 4·5 | 12·5 |
| *T. viperina* | 22 | 78 | 12·8 | 31·8 |

collection period (Table 1). The total collections from Parit Botak of *H. fasciatus*, *L. hardwickii* and *H. cyanocinctus* deviated significantly ($P < 0.05$, $\chi^2$ test) from an equal sex ratio with values of 0.28, 0.26 and 0.15 respectively (ratio is males divided by total sample). In each of the above cases there was a preponderance of females captured. Sex ratios deviating from equality were also observed in collections from other localities. For example, *E. schistosa* collected in February at Muar had a sex ratio of 0.60 and at Sungai Buloh *H. caerulescens* collected in March and *L. hardwickii* collected over all periods had ratios of 0.91 and 0.42 respectively. These values all differ significantly from one to one ($P < 0.05$) and in two cases there were more males than females. There is no consistent pattern of deviation from an equal sex ratio among or within species and, in fact, the sex ratios for *L. hardwickii* at Parit Botak (0.62), Sungai Buloh (0.42) and Endau (0.51) are all different from each other ($P < 0.05$). Sex ratios also varied temporally in our collections. For example, collections of *L. hardwickii* from Parit Botak in February, March and April had sex ratios of 0.5, 0.21, and 0.0 respectively. The latter two ratios are significantly different from 0.5 ($P < 0.001$).

The dynamic nature of the sex ratios lead us to suspect that many of the deviations from equality are a function of sexual differences in habitat selection and/or activity patterns rather than real differences between the number of males and females in the populations. Further support of this interpretation comes from sex ratios observed among *E. schistosa* embryos. A sex ratio of 0.51 came from data on 622 *E. schistosa* embryos from thirty-eight gravid females. This ratio is not significantly different from 0.50 ($P > 0.05$).

Muar is the best sampled locality (Table 1) and here male and female *E. schistosa* have a synchronized annual reproductive cycle with births in February and March (Voris & Jayne 1979). Nearly all the *Hydrophis brookii*, *H. melanosoma* and *H. torquatus* in this study were collected at Muar and gravid females ($n = 10$, 10, and 8 respectively) were captured only between January and April. These data suggest that these species have a synchronized reproductive cycle similar to that documented for *E. schistosa*.

At Sungai Buloh the distribution of gravid female *A. granulatus* and *H. caerulescens* suggest either loosely seasonal reproduction or possibly aseasonal reproduction (Table 1). *Lapemis hardwickii* shows a clear tendency for synchronous reproduction from February to April. The distribution of newborn snakes in our samples (0, 1, 12, 164, and 22) from December to August supports this assertion.

## DISCUSSION

An important component of the reproductive ecology of marine snakes involves the relationships among female weight, clutch size, birth weight, and reproductive effort. Relative reproductive effort (total clutch weight/female weight) varied little interspecifically (Table 4, coefficient of variation = 14.7%) compared to female weight ($CV$ = 68..1%), birth weight ($CV$ = 50.2%) clutch size ($CV$ = 74.9%). Since all species have approximately equal relative reproductive efforts, differences in reproductive strategies revolve around packaging: many, small young or few, large young.

The relationship between relative effort per embryo (birth weight/female weight) and mean clutch size (Fig. 4) demonstrates some of the important variation in the reproductive strategies of marine snakes. The two curves in Fig. 4 are the 20% and 45% relative reproductive effort isoclines; all snakes with efforts within these limits must be located within this isocline envelope. All but one marine species (a–i) are clustered at the upper left of the graph. This side of the envelope is associated with the *K*-strategy of the packaging spectrum (MacArthur & Wilson 1967). These snakes produce few relatively large young. *Enhydrina schistosa* (j) does not fall into this cluster; rather it is found in the lower right section of the graph as an *r*-strategist, producing many, relatively small young. The data from several terrestrial snakes are also plotted in Fig. 4 for comparison. The terrestrial snakes selected were of similar weights to the marine snakes studied (100–600 g). In spite of small sample size, one comment seems justified: marine snakes tend to have smaller clutches and larger relative birth weights than similar-sized terrestrial snakes. The exception to this observation is *E. schistosa*, whose clutch size and relative birth weights are similar to the terrestrial forms. As expected, small terrestrial snakes such as *Unechis goldii* (female weight = 18.7 g, clutch size = 4.3, Shine 1977) have small clutch sizes, perhaps reflecting a minimum size limit to birth weight.

Another view of the reproductive patterns of marine snakes is illustrated by the three-dimensional plot in Fig. 4. Comparison of the four extreme species reveals both the differences among species and the tradeoffs in adult weight, clutch size and birth weight which occur within this group of snakes. *Hydrophis fasciatus* (a), the smallest snake in this study, also has the smallest clutch size but its birth weight is about average (Table 4). *Hydrophis torquatus* (g) adults are similar to *H. fasciatus* in size but *H. torquatus* produces 40% more eggs per clutch; the newborn young, however, weigh 42% less than those of *H. fasciatus*. *L. hardwickii* (c) produces the same number of eggs per clutch as *H. fasciatus*, but adult size is 66% greater and birth weight is 55% larger. *Enhydrina schistosa* (i) has a newborn weight similar to *H. fasciatus* but adults weigh 82% more and the average clutch size is 85% larger than *H. fasciatus*.

When the factors involved in reproductive strategy are expressed in the equation :

$$\text{birth weight} = \frac{(\text{female weight})(\text{relative reproductive effort})}{\text{clutch size}},$$

it can be seen that the predictability of the tradeoffs described above are a function of the similarity of relative reproductive effort among different species of marine snakes.

The differences in packaging of reproductive effort represent important changes in the reproductive biology of marine snakes. The ecological significance of these differences has yet to be determined.

Although geographic variation in clutch size among snakes may be widespread, adequate supporting data are scarce. Fitch (1970) cites interpopulational differences in nine snake species. In each of these cases, comparisons have been made between populations which were sampled at different times and separated geographically by hundreds of miles.
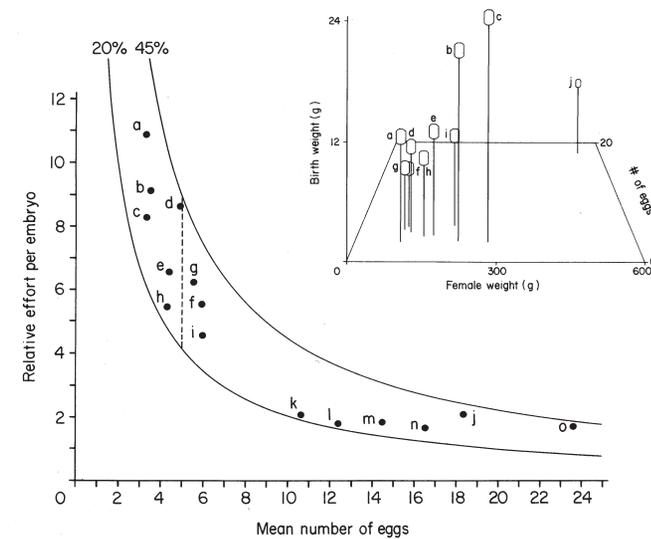


FIG. 4. The mean number of oviducal eggs is plotted against the relative effort per embryo for several snake species. The curved lines represent the 20 and 45% contours for the relative effort per clutch. (See text). Marine species identities are as follows: a *H . fasciatus*; b *T. viperina*; c *L. hardwickii*; d *H. brookii*; e *A. eydouxii*; f *H. caerulescens*; 9 *H. torquatus*; h *A. granulatus*; i *H. melanosoma*; j *E. schistoda*. The data on the terrestrial species are from the literature. The species are as follows: k *Coluber constrictor* (Fitch 1963); l *Pseudechis porphyriacus* (Shine 1977, 1978); m *Thamnophis sirtalis* (Fitch 1965); n *Austrelaps super* (Shine 1977,1978); o *Notechis scutatus* (Shine 1977, 1978). The insert is a three dimensional plot of the marine species and it uses the same letters as identifiers. For each species the average female weight is plotted with the estimated birth weight and the average number of oviducal eggs.

Six of the nine comparisons involve nominal subspecies. Where the authors have tried to interpret these findings, they have related their observations to both genetic (subspecific designations) and ecological (climatic) factors.

*Lapemis hardwickii* has a geographic range which includes the Philippines, Borneo, New Guinea, the Gulf of Siam and Australian waters. Our single comparison here is of samples taken at similar times from two localities 270 km apart in the Straits of Malacca. No dispersal barriers along the coast of Malaysia between these localities are known and the 1 to 2 knot currents in the Straits could move a floating snake this distance in about 4.5 days. In addition, *L. hardwickii* has been collected at several locations between these two sites. Qualitative traits (such as vertebrae counts) do not vary between these two populations as do average snout-vent lengths. Thus, given the short geographic distance and the lack of morphological differences between the two populations, we suspect that ecological constraints may be solely responsible for the differences in size and reproductive output of gravid females at these localities. At present we are testing this idea.

### Seasonality in reproduction

Numerous records on the reproductive conditions of specimens from small scattered collections appear in the literature but reveal virtually nothing about the timing of the various phases of the reproductive cycle of a species at one locality. However, Bergman (1943) has reported on six species of marine snakes (*Thalassophis anomalus, L. hardwickii, E. schistosa, H. fasciatus, H. brookii* and *H. cyanocinctus*) which were collected over several years at Surabaia, Java. At this locality, he collected pregnant females from May through October. He published extensive data for *L. hardwickii* (Bergman 1949) and *Thalassophis anomalus* (Bergman 1954) and reports births from October through December for both species. The breeding cycles of populations from Surabaia, Java, sampled from 1937 to 1941 and from the Straits of Malacca sampled in 1971 and 1975 are clearly out of phase. Kropach (1975) reported that *Pelamis platurus* exhibited a seasonal reproduction in the highly seasonal environment of the Bay of Panama. These observations and the difference observed between the highly synchronous *E. schistosa* from Muar and the loosely seasonal or a seasonal reproduction of *A. granulatus* and *H. caerul*escens from Sungai Buloh suggest a high degree of plasticity in the reproductive cycle. Apparently the degree and nature of seasonality in the environment affects marine snake species differentially resulting in breeding cycle variations within and between local regions.

### Intra-clutch sex ratios

Fisher ( 1930) showed that if male and female young are equally expensive to produce, then natural selection will favor the production of equal numbers of male and female offspring in the population. Trivers & Willard (1973) modified this idea slightly to note that while the populational production of males and females is equal, the optimal strategy of individual females might favor the production of one sex or the other. The situation where a skewed sex ratio is predicted has two conditions: when the size of newborns is correlated with the size of the mother, and when the birth size is differentially important to the sexes. Here small females should produce the sex that is least affected by small birth size.

*Enhydrina schistosa* certainly conforms to the first condition. There is a significant correlation between the mother's size and the weight of its offspring (Fig. 3). The second condition, that size is differentially important to offspring depending on their sex, seems to be met also. We know that large size is directly related to reproductive potential in *E. schistosa* because both the number of offspring produced and offspring size are significantly correlated with female size (Figs 1, 3). The relative importance of size to males is not known. Interestingly, female snakes grow about 10% larger than male snakes (Voris & Jayne 1979), an indication that large size is more important to the female. If this is true small females should produce clutches containing more males than females and our data on *E. schistosa* support this prediction. The sex of each embryo of thirty-eight clutches was determined by dissection and then the within clutch sex ratios were analyzed. We found the correlation between sex ratio and female weight to be statistically significant (Spearman's Rank Correlation Coefficient = –0.337, d.f. = 36, $P < 0.05$). Thus, for *E. schistosa* small females do tend to produce more male offspring. Unfortunately other species could not be analyzed due to either small samples or technical difficulties in determining the sex of the embryos.

### ACKNOWLEDGMENTS

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