SKEWED SEX RATIO IN SNAKES.

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INTRODUCTION

Fisher (1930) postulated his theory about the relative distribution of individuals as male and female. He stated that natural selection will favour equal production of each sex. This should be true if male and female young are equally expensive to produce. To express this effect sex ratio is defined as the number of males divided by the total number of individuals in a population. This ratio should be 1/2 in the Fisher theory. For a number of snakes it is known that the sex ratio deviates significantly from 1/2. However, males are favoured in about the same number of species as females are (see Appendix). There are several possibilities to cause dispersion of the sex ratio. We have to distinguish two different kinds of sex ratios called primary and secondary sex ratio.

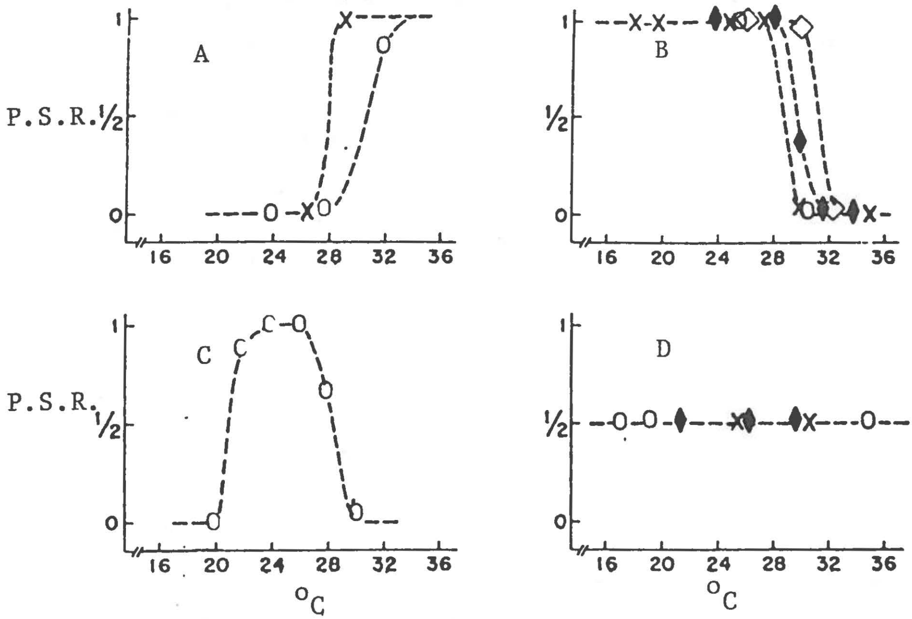
PRIMARY SEX RATIO

Sex ratio at birth (primary sex ratio) generally is not statistically different from 1/2. In a few cases dispersion is reported. Some are in favour of males (*Agkistrodon contortrix*, Fitch, 1960; *Elaphe quadrivirgata*, Fukada, 1960; *Notechis scutatus*, Shine & Bull, 1977; *Pituophis melanoleucus*, Gutzke et al., 1985). One is in favour for females

(*Elaphe climacophora*, Fukada, 1956). Several additions to the Fisher theory are proposed (Shine & Bull, 1977) but there are still a lot of questions about a number of uncertainties that can introduce experimental errors. Gutzke et al. (1985) and Shine & Bull (1977) collected eggs, incubated them at temperatures between 22^0 and 32^{0}C. Those eggs that had yet to hatch were opened and the embryos were sexed. They found respectively 66% and 60% were male in *Pituophis melanoleucus* and *Notechis scutatus*.
The temperature at which the eggs were incubated could influence the sex of the new born. This effect is studied mainly in turtles and lizards (Bull, 1980) and only in one snake species (*Nerodia fasciata*, Osgood, 1978). While this snake is live bearing, the adult females were placed in different temperature controlled environments until birth of their young. Figure 1 shows the effect of temperature for different reptiles (modified from Bull, 1980).
It is evident that this temperature effect is absent in the case of heteromorphic sex chromosomes, which is the case in snakes (Jones & Singh, 1985). This means that after conception the sex of an embryo is fixed and temperature only influences the period of prenatal development. Whether or not the skewed sex ratios mentioned above were indeed a deviation of the Fisher theory is questionable. Although a reasonable number of eggs was determined, collected over a reasonable, but still distinct area, the question of whether local influences of biological and seasonal origin also have their impact is unanswered.

SECONDARY SEX RATIO

Sex ratios observed in later age groups (secondary sex ratio) often deviates from equality. The



question is whether this deviation is real, reflecting actual population structure, or is apparent, reflecting different behavioural traits of males and females.
Seasonal influences can affect this sex ratio. Males often predominate in spring, because of their high sexual activity, while females leave the communal dens later (Gregory, 1974). While males stay near the den, females migrate soon after mating. This behavioural difference enhances sex ratios at the den and decreases it in the field.
The physiological aspect of the seasonal differences is the effect of the reproduction status of the snakes. It is well known that the behaviour of the pregnant female is quite different from that of the male, for instance, in foraging. If collect-

ing in a foraging area a skewed sex ratio is to be expected.
Another biological aspect is that mortality can also be sex dependent. While over a year's period no difference in mortality is found in *Nerodia sipedon*, Feaver (1977) showed that 47% of the total male mortality occurred during the spring mating season, whereas 50% of the female deaths occurred in summer, during periods of increased feeding.
So far from 19 colubrid and viperid species unequal secondary sex ratios are published (see Appendix). In 9 species males are favoured (a-i) and in 9 females are favoured (k-s). In one (j and t) males as well as females are favoured, giving rise to the arguments mentioned above.
One of the theories about structural deviation of the sex ratio deals with the size of the snake and its chance to survive. Feaver (1977) argued that the faster growing sex would feed more, which would expose it to greater risk of predation. So the large sex should have a greater mortality and therefore the secondary sex ratio should favour for the smallest sex. In 8 of the 9 species in which the females were favoured the females were larger, and in 5 of the 9 species favouring males, males were larger. Thus greater mortality in the larger sex is not supported by the data. It appears that the opposite is true. Perhaps being larger, although possibly increasing exposure to predation, also increases survivorship.

PARTHENOGENESIS

Whereas unisexual or parthenogenetic reproduction has been documented in a few lizard families, evidence shows that only one snake reproduces clonally. McDowell (1974) reported that the more than hundred animals of *Typlina braminus* he searched, no male specimen was found. They were collected over a wide range: Mexico, Madagascar, India, China, Bali, Australia. Nussbaum (1980) and Darevsky et al. (1985) observed the same snake (now named *Ramphotyphlops braminus*) on several islands of the Seychelles and collected only female snakes. Not any male specimen was found. From these observations it is concluded that *Ramphotyphlops braminus* can reproduce via parthenogenesis. An advantage of parthenogenesis is that distribution of the species even over small and isolated islands is much easier. Magnussen (1979) reported the fact that in *Acrochordus javanicus*, died after living seven years separated, one egg was found with a fully developed animal in it. The (also dead) young had the same scale and colour pattern as the adult.

So observed sex ratios can be misleading without a thorough knowledge of a species' biology and the conditions under which the samples were taken.

APPENDIX

Skewed secondary sex ratios favouring males:
a) *Coluber constrictor*; Brown & Parker, 1984.
b) *Diadophis punctatus*; Fitch, 1975.
c) *Heterodon platyrhinos*; Platt, 1969.
d) *Phyllorhynchus decurtatus*; Brattstrom, 1953.
e) *Pituophis melanoleucus*; Gutzke et al., 1985.
f) *Tantilla coronata*; Semlitch et al., 1981.
g) *Agkistrodon contortrix*; Fitch, 1960.
h) *Crotalus viridis*; Klauber, 1972.
i) *Vipera berus*; Viitanen, 1967.
j) *Masticophis taeniatus*; Julian, 1951.

favouring females
k) *Lycodonomorphus bicolor*; Madsen & Oosterkamp, 1982.
l) *Nerodia cyclopion*; Mushinsky et al., 1980.

m) *Nerodia fasciata*; Mushinsky et al., 1980.
n) *Nerodia sipedon*; Fitch, 1982.
o) *Opheodrys aestivus*; Plummer, 1985.
p) *Storeria dekayi*; Freedman & Catling, 1978.
q) *Thamnophis elegans*; Fleharty, 1967.
r) *Thamnophis radix*; Seibert & Hagen, 1947.
s) *Thamnophis sauritus*; Carpenter, 1952.
t) *Masticophis taeniatus*; Hirth & King, 1968.

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ERRATUM

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Legends of figure 1 at page 200.

Figure 1: Primary sex ratio's of different species of reptiles as function of incubation temperature.
A): Lizards: X: *Agama agama*, O: *Eublepharis macularius*.
B): Turtles: X: *Emys orbicularis*, ◇ : *Testudo graeca*, ◆ : *Caretta caretta*, O: *Chrysemys picta* and 3 spp of *Graptemys*.
C): Turtles: O: *Chelydra serpentina*
D): Snake: ◇ : *Natrix fasciata*, lizards: O: *Lacerta viridis*, turtle: X: *Trionyx spiniferus*.