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Are Crocodilian Sex Ratios Female Biased? The Data Are Equivocal

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Charnov and Bull (1977) propose that the evolution of environmental sex determinations (ESD) is favored when the individual fitness of males and females is strongly influenced by environmental factors and when the parent or offspring have relatively little control over the nature of the environment experienced. Living crocodilians lack heteromorphic sex chromosomes. For all species (11 of 23) examined to date, sex is determined by nest temperature during incubation of the eggs (TSD; Lang and Andrews, 1994). A benefit of TSD for crocodilians may be the assignation of "maleness" to those hatchlings that have the greatest potential for growth (Deeming and Ferguson, 1989; Webb and Cooper-Preston, 1989). Another consequence of the covariance of progeny sex and fitness is the supposition that population sex ratios may vary from 1:1 (Bull, 1980). Consequently, information on sex ratios of natural populations are of considerable interest for understanding the role of TSD in life-history strategies of crocodilians. Deeming and Ferguson (1989) suggested that sex ratios of wild crocodilian populations are skewed toward females, and Woodward and Murray (1993) constructed a life-history model that incorporates this unusual predominance of females. Although Deeming and Ferguson (1989) cite a few studies that report female-skewed sex ratios, they failed to conduct a broad survey of crocodilian populations to substantiate the claim.

I collected data from wild-produced animals for as many species of crocodilians as possible. Although considerable information on sex ratio from commercially hunted populations was available, samples based solely on harvests were excluded from the analyses because of a recognized male bias (Palmisano et al., 1973). Following Nichols and Chabreck (1980), I tested the hypothesis of a 1:1 sample population using the z test statistic (one-tailed test) and compared the male and female sex ratios using a χ^2 goodness-of-fit test. Statistical analyses were only conducted on data sets with $n \geq 40$.

Hatchling sex ratio.—Data for skewed primary sex ratios among crocodilians are equivocal. The female-biased *Alligator mississippiensis* sample (55 males:111 females; $z = -4.27$, $\chi^2 = 18.89$, $P < 0.001$) of Forbes (1940) was the first report of an unequal crocodilian sex ratio. Ferguson and Joanen (1983) reported a ratio of five females per male for a large sample of *A. mississippiensis* from Louisiana coastal marshes but did not present the numbers of males or females in the study. However, recent information suggests that sampling methodology may have biased these results (Mrosovsky and Provanca, 1992; Lang and Andrews, 1994). Campos (1993) presented detailed information on environmental factors affecting hatchling sex ratio for *Caiman yacare* but gave no overall sex ratio for a sample of more than 410 hatchlings. Nevertheless, during the two-year study, forest nests produced an equal mixture of males and females and nests on floating grass mats resulted in greater numbers of males (year 1) or females (year 2) (Campos, 1993). Asanza (1985) reported a significantly male-skewed ratio (301 males:157 females, $z = -6.68$, $\chi^2 = 45.28$; $P < 0.001$) from 13 *Caiman crocodilus* nests in Ecuador. In a sample of 4569 hatchlings from 15 river systems in Northern Australia, Webb and Smith (1984) found female *Crocodylus johnsoni* (65%) significantly outnumbered males ($z = -20.34$, $\chi^2 = 414.45$, $P < 0.001$).

Juvenile-adult sex ratios.—Of 33 data sets for juveniles, subadults, and adults with samples sizes greater than 40, 18 had significant differences in the number of males and females (Appendix). Fifteen (45.4%) were not significantly different from 1:1, 12 (36.4%) studies had male-skewed populations, and six (18.2%) were female skewed. Data were dominated by samples from the well-studied *A. mississippiensis*, based largely on captures of live animals. Seven of nine studies of *A. mississippiensis* found significantly greater numbers of males than females. Overall, 11 of 17 (64.7%) data sets for Alligatoridae were male skewed. Among 16 studies of other crocodilians, nine (56.3%) were neutral (no skew), six data sets (37.5%) reported female-skewed sex ratios, and one (6.3%) was male biased.

Discussion.—Biased sampling of populations represents a major impediment to analyses of sex-ratio information among reptiles (Gibbons, 1990; Mrosovsky, 1994), including crocodilians. Three potential sources of bias in determining crocodilian sex ratios are differential mortality, sexually dimorphic patterns of habitat selection, and inability to accurately determine the sex of juvenile animals. Differential mortality masks the hatchling sex ratio, whereas differences in habitat selection may skew the probability of capture to one sex or the other. The difficulty of correctly sexing neonate crocodilians without killing them has been reported by Joanen and McNease (1978) and Allsteadt and Lang (1995). Also, because of effects of habitat on nest conditions, the potential for biased sampling of hatchling sex-ratio may even be greater than for juveniles and adults (Ferguson and Joanen, 1983; Webb and Smith, 1984; Campos, 1993). In *C. yacare*, hatchling sex ratios on floating nests varied between years, whereas sex ratios of hatchlings from forest nests did not (Campos, 1993). Webb and Smith (1984) reported that the sex ratio of hatchling *C. johnsoni* depended on week of hatching, varied among locations on one river, and between years was related to water levels at the time of nesting. It is clear that, to reduce biased sampling, studies of hatchling sex ratios should be done over a variety of habitat types and preferably over a multiyear period.

No studies have specifically addressed the question of differential mortality of hatchling male and female crocodilians in the wild. Among immature *C. johnsoni*, Webb et al. (1983) reported no sex-specific mortality. Webb and Smith (1984) found differential embryonic mortality, with eggs incubated under female producing conditions more likely to die, but no postnatal pattern of sex-specific mortality was encountered for the same species (Webb et al., 1983). Rootes and Chabreck (1993) reported cannibalism to be a major source of mortality among juvenile *A. mississippiensis*, but males and females were eaten in proportion to their representation in the population.

Differences in habitat use by males and females are well known for adult (Joanen and McNease, 1970, 1972; Goodwin and Marion, 1979) and juvenile (McNease and Joanen, 1974) American alligators. Biased sampling resulting from sex-related habitat preferences has been suggested as a factor explaining the prevalence of male-skewed ratios among *A. mississippiensis*, but the extent to which it affects estimates of population sex ratio remain unquantified. Similar arguments could be made for other species with similar habitat requirements (e.g., *Crocodylus novaeguineae, Crocodylus porosus, Crocodylus rhombifer, M. niger*). Hines et al. (1968) acknowledged that their sample was biased from incorrectly assigning sex to small juveniles and by capturing animals principally in canals preferred by males. However, some of the studies summarized here appear to have sampled populations in an relatively unbiased fashion insofar as considerable effort was invested in sampling marsh habitats (Deitz, 1979; P. Wilkinson, 1985, unpubl.). Murphy (1977) stated that the male bias in his study was not habitat related because all areas of the pond were accessible, and Brandt's (1991) data were from the same site. Nichols and Chabreck (1980) considered their sample of *A. mississippiensis* to be representative of the population, but Ferguson and Joanen (1983) claimed that the Nichols and Chabreck study was biased toward males because captures were done by boat, limiting them to more open, deepwater habitats. In a later study, Rootes and Chabreck (1992) captured alligators in marsh habitats and still found male-skewed sex ratios and a sex ratio for live captures (63% males) similar to that of animals captured on baited hooks (60%).

In all likelihood, the extent to which mark-recapture studies are biased varies between species and among habitat types. In highly seasonal habitats, samples collected from dry-season ponds are most likely to be bias free. Under these conditions, savanna populations of *C. crocodilus* and *C. yacare* (Gorzula, 1978; Schaller and Crawshaw, 1982; Thorbjarnarson, 1991) have equal proportions of males and females. There are no data for female-skewed secondary sex ratios for any member of the Alligatoridae.

Crocodylids have a greater tendency toward female-skewed sex ratios than the Alligatoridae. Nevertheless, for the species with the largest data sets (*Crocodilus niloticus, C. novaeguineae,* and *C. porosus*) strong support for the prevalence of female-biased populations is lacking. Among Nile crocodiles, the largest data sets (Cott, 1961; Graham, unpubl.) have unskewed sex ratios. Female-skewed sex ratios from other studies are due to unusually low temperatures at a high-altitude site (Hutton, 1987) or potential bias from trapping technique (Kofron, 1990). Hall and Portier (1994) report a male-skewed sample of harvested and live-captured *C. novaeguineae*. Montague (1984) reports an equal sex ratio, and Hall (1990) found individual populations are either male skewed, female skewed, or unskewed. The overall sex ratio for the Lake Murray district is not significantly different from 1:1, although samples from the lower rainfall subdistrict (n = 538) were strongly female biased, whereas samples from a subdistrict that received about 20% greater annual precipitation (n = 948) were slightly male biased (Hall, 1990).

Among the Crocodylidae, only *C. johnsoni* (Webb and Smith, 1984) and *C. rhombifer* (Ramos et al., 1994) have a clearly female-skewed populations. Different patterns of TSD may influence primary and secondary sex ratios. Lang and Andrews (1994) noted that *A. mississippiensis* produces males over a wider range of temperatures than other species. The clear predominance of females for *C. johnsoni* may be a result of its unusual TSD pattern (Webb and Smith, 1984; Lang and Andrews 1994), with no constant temperature producing a predominance of males in artificial incubation experiments.

The data from the literature do not support blanket claims that crocodilian sex ratios are generally female. In fact, among the Alligatoridae a much stronger argument can be made for male-biased sex ratios. Among the Crocodylidae, both male- and female-biased population sex ratios are evident, including at the intraspecific level, a fact which urges caution when making statements concerning the significance of sex ratios above the level of the population.

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APPENDIX. CROCODILIAN SEX RATIO DATA FOR SAMPLES OF JUVENILES (j), SUBADULTS (s), AND ADULTS (a) WITH n ≥ 40 TAKEN FROM THE LITERATURE. Statistical significance was tested using the *z*-statistic and χ^2. Populations are either male biased (♂), female biased (♀), or neutral (N).

Species	Sample		Males	Females	z	χ^2	Bias	Source
Alligator mississippiensis	4631	j,s,a	2950	1681	−18.63***	347.74***	♂	Rootes and Chabreck, 1992
A. mississippiensis	1644	j,s,a	992	652	−8.36***	70.32***	♂	Nichols and Chabreck, 1980
A. mississippiensis	1549	j,s,a	918	613	−8.18***	60.26***	♂	P. Wilkinson, unpubl.
A. mississippiensis	727	j	446	281	−6.08***	37.45***	♂	Deitz, 1979
A. mississippiensis	325	j,s,a	207	118	−4.88***	24.37***	♂	O'Neill, 1949[a]
A. mississippiensis	186	j,s,a	134	52	−5.94***	36.15***	♂	Brandt, 1991
A. mississippiensis	112	j,s,a	85	27	−5.39***	30.04***	♂	Murphy, 1977
A. mississippiensis	85	j,s,a	39	46	−0.65	0.58	N	Taylor and Neal, 1984
A. mississippiensis	55	j,s,a	33	22	−1.35	2.20	N	Fuller, 1981
Caiman crocodilus	634	j,s,a	327	307	−0.76	0.63	N	Thorbjarnarson, 1991
C. crocodilus	458	j,s,a	301	157	−6.68***	45.28***	♂	Asanza, 1985
C. crocodilus	164	j,s,a	86	78	−0.55	0.39	N	Staton and Dixon, 1975
C. crocodilus	88	j,s,a	49	39	−0.96	1.14	N	Gorzula, 1978
Caiman yacare	84	a	39	45	−0.54	0.43	N	Schaller and Crawshaw, 1982
Melanoschus niger	53	j,s,a	47	6	−5.49***	31.72***	♂	Asanza, 1985
Paleosuchus palpebrosus	41	j,s,a	31	10	−3.12***	10.76**	♂	Asanza, 1985
P. trigonatus	112	j,s,a	92	20	−6.71***	46.29***	♂	Asanza, 1985
Crocodylus acutus	92	j,s	37	55	−1.77*	3.52	♀	W. King, K. Vliet, and J. B. Thorbjarnarson, unpubl.
C. acutus	54	j,s,a	32	22	−1.23	1.85	N	Thorbjarnarson, 1988
C. acutus	46	j,s	17	29	−1.62	3.13	N	Brandt et al., 1995
Crocodylus johnsoni	697	j,s,a	230	467	−8.94***	80.59***	♀	Webb and Smith, 1984
Crocidylus niloticus	651	j,s,a	324	327	−0.08	0.01	N	Cott, 1961
C. niloticus	480	s,a	159	179	−1.56	2.23	N	A. Graham, unpubl.
C. niloticus	100	j,s,a	33	67	−3.30***	11.56***	♀	Hutton, 1987
C. niloticus	98	s,a	35	63	−2.73**	8.00**	♀	Kofron, 1990
Crocodylus novaeguineae	2031	j,s	1042	989	−1.15	1.38	N	Montague, 1984
C. novaeguineae	1777	j,s	879	898	−0.42	0.20	N	Hall, 1990
C. novaeguineae	245	j,s,a	162	83	−4.98***	25.47***	♂	Hall and Portier, 1994
Crocodylus porosus	626	j	305	321	−0.60	0.41	N	Webb and Messel, 1978b
C. porosus	302	j,s,a	153	149	−0.17	0.05	N	Webb and Messel, 1978a
C. porosus	53	j,s	14	39	−3.30***	11.79***	♀	Hall, 1990
Crocodylus rhombifer	168	j,s,a	42	126	−6.40***	42.00***	♀	Ramos et al., 1994
Garialis gangeticus	472	j,s	239	233	−0.23	0.08	N	Lal and Basu, 1982

[a] Cited in Nichols and Chabreck, 1980.
* $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$.