

Sex ratios of American alligators (*Crocodylidae*): male or female biased?

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(Accepted 6 October 1999)

Abstract

Recent theoretical papers on temperature-dependent sex determination in reptiles are based on the assumption that crocodylian populations, particularly adults, are markedly female biased. While there is evidence that some crocodile populations may conform to this expectation, there is no compelling evidence that American alligator populations are female biased anywhere in the species' range. Previous data had indicated that some populations of juvenile and/or adult alligators were significantly male biased. However, these studies were criticized for sampling errors. Adult males typically occupy a different habitat from that of females, and males frequent areas where they are more likely to be caught. In contrast, in juveniles, both sexes occupy the same habitat. We determined the sex ratios of *c.* 3000 juvenile alligators collected from 11 sites over 6 years in south Louisiana. Our results indicate a significant sex bias (58% male), but variation was evident among samples. Sex ratios varied by year and site, and the interaction of these factors was significant. At one site in one year, there was a female bias (71%), but in no year was there an overall female bias across sites. From this study and earlier reports, we conclude that there is no evidence at present of female-biased sex ratios in the juvenile and/or adult alligator populations, and consequently, that certain models of temperature-dependent sex determination in reptiles require re-evaluation. Furthermore, our data suggest a pattern of differential mortality of females *vs* males during the first years of life, a pattern consistent with a key prediction of several differential fitness models for the adaptive significance of temperature-dependent sex determination in reptiles.

Key words: alligator, sex ratio, reptile, sex determination, crocodylian

INTRODUCTION

Skewed sex ratios in crocodile populations have been remarked on since Plumier in the 18th century reported that there were far more female than male American crocodiles *Crocodylus acutus* (cited by Rathke, 1866). Descourtilz (1809) assumed that crocodiles *Crocodylus acutus* in Santo Domingo must be polygamous because there was a 'rarity of males and a profusion of females'. Rathke (1866) noted that the ratio of five females to each male crocodile specimen in European museum collections was unlikely to be the result of chance alone, but offered no further explanation. Some recent population studies on juvenile and adult crocodiles have also indicated a female bias (Webb & Smith, 1984; Hutton, 1987), but the very large sample of adult Nile crocodiles taken by Cott (1961) exhibited a 1:1 sex ratio.

We now know that the sex of all crocodylian species examined to date is determined by egg incubation temperature (Ferguson & Joanen, 1983; Lang &

Andrews, 1994), a phenomenon known as temperature-dependent sex determination (TSD). Using artificial incubation, it is far easier to produce female crocodylians than males. In fact, it has been impossible to produce 100% male hatchlings using artificial incubation in several *Crocodylus* species (Lang & Andrews, 1994). Only with alligators can one guarantee producing 100% males at a constant incubation temperature. Constant incubation temperatures between 29 and 31 °C will produce all female hatchlings. At a constant incubation temperature of 32 °C a mixture of males and females is produced. The ratio of males to females at 32 °C varies according to the clutch. Incubation at 33 °C will produce all males, and at 34 °C will produce mixed-sex hatchlings, the exact ratio being clutch-dependent. Incubation at 35 °C is close to the upper lethal limit, but will result in all females (Lang & Andrews, 1994). Given this information, an alligator hatchling sex ratio in favour of females would be predicted as only a narrow range of temperatures will produce males, and a much

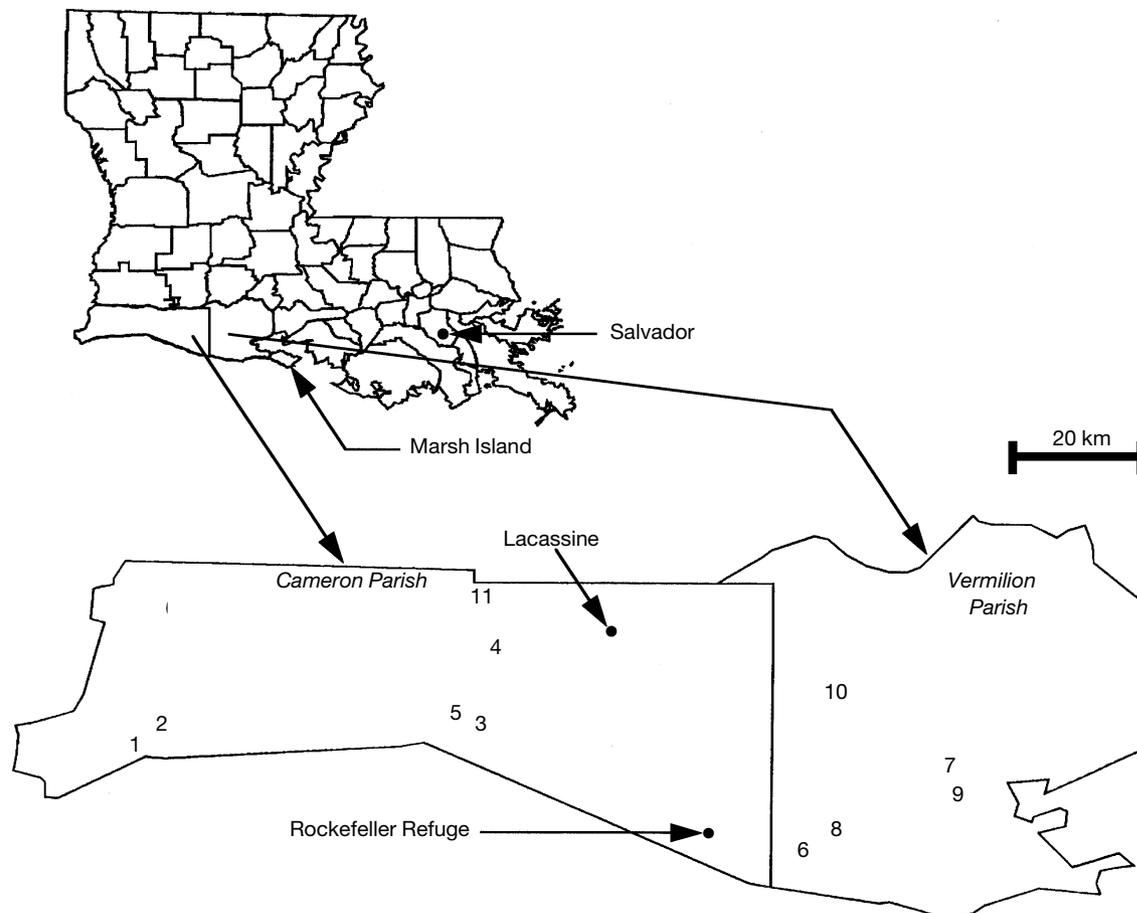


Fig. 1. Coastal area of south-west Louisiana. Numbers indice sampling locations.

wider range of temperatures will produce females. However, temperatures in natural nests are not constant and exhibit daily as well as seasonal variations (Rhodes & Lang, 1995, 1996). Thus, at present, there is no basis for predicting whether the hatchling sex ratio would be either male or female biased.

Recent theoretical papers on sex ratio, temperature-dependent sex determination (TSD) and survivorship in crocodylians (Deeming & Ferguson, 1991; Phelps, 1992; D. E. Woodward & Murray, 1993) base models on the assumption that all crocodylians, including alligators, have strongly skewed female-biased adult populations. While there is good evidence that some species of crocodiles may have female-biased populations, there are no data to support the assumption that alligator populations are similarly skewed. Earlier published reports suggested that, on the contrary, alligator populations may actually be male biased (Nichols & Chabreck, 1980), and a recent review of crocodylian sex ratios has also suggested that some alligator populations show evidence of a male bias (Thorbjarnarson, 1997).

We had the opportunity to examine the sex ratios of multiple samples of juvenile alligators collected over 6 years at 11 different locations in southern Louisiana. Our results, together with a review of the literature, indicate that contrary to theoretical assumptions, populations of

juvenile and adult alligators are not female biased, and in most instances show a significant male bias.

MATERIALS AND METHODS

Study sites

A map of the coastal area of south-west Louisiana is shown in Fig. 1. Marsh habitats are defined as fresh, intermediate and brackish based on salinity measurements and predominant vegetation according to Chabreck (1970). Each of the 11 sites where samples were taken are indicated in Fig. 1, and the approximate area and predominant vegetation at each site are presented in Table 1.

Animals

The alligators sampled in this study were part of a larger ongoing research project in which a large sample of wild juvenile alligators was caught to compare growth rates and survival with those of released farm-raised animals (Elsey *et al.*, 1992). Alligators were collected by hand from airboats at night, total body

Table 1. Marsh habitat types and sampling sites in south-west Louisiana

Location	Hectares ^a	Marsh type	Predominant vegetation
1	1550	Intermediate	<i>Spartina patens</i> , <i>Paspalum</i> sp., <i>Scirpus californicus</i>
2	1300	Intermediate	<i>Spartina patens</i> , <i>Paspalum</i> sp., <i>Scirpus californicus</i>
3	800	Intermediate	<i>Spartina patens</i> , <i>Vigna</i> sp., <i>Scirpus californicus</i> , <i>Sagittaria</i> sp., <i>Phragmites</i> sp.
4	2100	Fresh–intermediate	<i>Sagittaria</i> sp., <i>Spartina patens</i> , <i>Scirpus californicus</i>
5	1800	Fresh	<i>Sagittaria</i> sp., <i>Spartina patens</i> , <i>Scirpus californicus</i> , <i>Alternanthera</i> sp., <i>Phloxeroides</i> sp.
6	1000	Brackish	<i>Spartina patens</i> , <i>Paspalum</i> sp.
7	2000	Fresh–intermediate	<i>Sagittaria</i> sp., <i>Spartina patens</i> , <i>Typha</i> sp., <i>Paspalum</i> sp.
8	1100	Fresh–intermediate	<i>Sagittaria</i> sp., <i>Panicum hemitomon</i> , <i>Spartina patens</i>
9	400	Fresh	<i>Panicum hemitomon</i> , <i>Sagittaria</i> sp.
10	1000	Fresh	<i>Panicum hemitomon</i>
11	1200	Fresh	<i>Panicum hemitomon</i> , <i>Sagittaria</i> sp.

^a Values in hectares are approximations.

length measured to the nearest cm, sexed, tagged and released. Animals > 1.52 m total length were excluded from the analysis to avoid any bias resulting from habitat selection by sexually mature individuals (Joanen & McNease, 1975, 1989), but are included in Table 4. In Table 4, alligators < 76 cm were excluded because of the difficulty in identifying the sex of animals this size (Joanen & McNease, 1978). The method used to identify sex, based on clitero-penis size, gave earlier field researchers some difficulty in animals < 30 cm in total length, but careful measurements of this organ show a distinct sexual dimorphism at hatching (Allsteadt & Lang, 1995).

Statistical analyses

Sex ratios were analysed in 2 ways. Each sex ratio shown in Table 2 was tested for a significant departure from the expected ratio of 1 male to 1 female, using a 1-way χ^2 test (1 d.f., $P < 0.05$). In addition, sex ratio was analysed with a log-linear model (Sokal & Rohlf, 1994) in which location, year and their interaction were specified as possible sources of variation and tested at a significance level of $P < 0.05$. Version 3 of JMP[®] for Apple Macintosh was used for all statistical procedures (SAS Institute Inc., 1994).

RESULTS

A total of 2936 juvenile alligators (0.76–1.52 m in total length) was sampled at 11 localities over 6 years from 1990 to 1995. During this period the overall sex-ratio was 58% males and represented a significant departure from an expected one male to one female ($\chi^2 = 75.13$, 1 d.f., $P < 0.0001$). On a yearly basis overall sex ratios were male biased, ranging from 54 to 74% male (Table 2). Of the 29 separate sex-ratio determinations, 14 were male-biased (58–74% male; Table 2) and 14 did not show a bias, but only one was female biased (29% male; Table 2). When these determinations are contrasted across all locations in the years sampled, significant

sources of variation were location, year and the interaction of year by location, explaining 31%, 31%, and 38% of the total variation, respectively.

Overall, the year by location interaction was a significant source of variation (likelihood ratio (LR $\chi^2 = 47.4$, d.f. = 9, $P < 0.001$). This effect was evident in contrasts between localities 1 and 2 across years and was also evident in contrasts between localities 7 and 9 in all years sampled (Table 2). The interaction effect indicated that the year-specific response was location-dependent, and vice versa.

Taken separately, the effect of year was significant (LR $\chi^2 = 125.9$, d.f. = 17, $P < 0.001$). This effect was evident by comparing the sex ratios recorded at locations 1, 2 and 7 for 5 years, from 1991 to 1994 (Table 2). For example, at location 1, sex ratios were not male biased in 1991 and 1992, but were strongly male biased in 1993, 1994, and 1995. At location 9, yearly differences were even more striking. In 1990, the sex ratio was male biased; whereas in 1994, the sex ratio at this location was female biased (29% male). When locations are grouped, these year-to-year differences were less evident. Thus the combined values were mostly male biased, and similar with respect to per cent male.

When considered alone, the effect of location was also significant (LR $\chi^2 = 87.0$, d.f. = 12, $P < 0.001$). This effect was evident in comparisons at various locations within the same years. For example, at locations 1–7, yearly contrasts in 1991–94 indicated a male-biased sex ratio at locations 2 and 7 in 1991, but not at locations 1 and 4. In 1992, the sex ratio at location 7 was male biased, but not at locations 1 and 2. In 1993, the sex ratio only at location 1 was male biased; whereas in 1994, those at locations 1, 2 and 7 were male biased (Table 2). The combined yearly sex ratios for these locations (1, 2 and 7; see Table 2) showed a male bias at locations 1 and 7 for 1993–95, and an overall male bias at all three localities for 1990–95 (Table 2). Likewise, contrasts of locations 1–6 in 1993 and in 1994 revealed differences in sex ratios within each year. In 1994, location 9 was female biased, in contrast to locations 1, 2, 3, 5 and 7 where sex ratios were male biased. In contrast, only location 1 was male biased in 1993. Such

Table 2. Sex ratios of juvenile alligators in Louisiana. Values represent per cent males. Numbers in parentheses indicate sample size. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Values without asterisks are not significant

Location	1990	1991	1992	1993	1994	1995	1990–95
1		46 (305)	48 (67)	***67 (277)	*60 (126)	*62 (98)	***56 (873)
2		***63 (282)	47 (45)	54 (157)	*58 (242)		***59 (726)
3					*69 (32)		*69 (32)
4		46 (48)				63 (19)	51 (67)
5					*67 (182)	43 (77)	**60 (259)
6				49 (39)	53 (15)		50 (54)
7	***76 (78)	***63 (52)	***83 (46)	59 (61)	*56 (167)	***73 (60)	***65 (464)
8				39 (38)	35 (31)		38* (69)
9	***73 (90)			37 (59)	***29 (68)		50 (217)
10						*66 (67)	*66 (67)
11						57 (108)	*57 (108)
Overall	***74 (168)	54 (687)	58 (158)	***57 (631)	***57 (863)	***60 (429)	***58 (2936)

differences tend to be obscured when values for each locality were combined within a given year.

DISCUSSION

Almost 3000 alligators were collected during this survey over 6 years. Our data reveal that there were year-to-year and site-specific effects on sex ratio. In 1991 and 1992, the summed data did not differ significantly from a 1:1 sex ratio, but in all other years there was a highly significant male bias. At three sites there was no significant deviation from a 1:1 sex ratio when the samples from all years were summed, but at two of these sites the total sample size was small (67 and 54, respectively). Only at site 8 was there a significant female bias when the data were summed, and at only one site in 1994 with a relatively small sample size was there a significant female bias (Table 2). Overall juvenile alligator sex ratios in this data set showed no evidence of a female bias.

No effect of habitat could be detected. Similar male biases were seen in samples from fresh water and intermediate marshes. There was only one small sample from a brackish marsh (location 6) that was not significant. Juvenile alligators are less common in brackish habitat as they generally avoid salt water. Alligators lack the lingual salt glands that enable crocodiles to survive in sea water (Taplin *et al.*, 1982) and hatchling alligators will die within 24 h of exposure to full-strength sea water (T. Joanen, pers. comm.). Nesting females

therefore generally select nest sites in fresh water or intermediate habitat (Joanen & McNease, 1989; Wilkinson & Rhodes, 1992) and the hatchling alligators remain in these areas for the first 3 years of life (Giles & Childs, 1949; McNease & Joanen, 1974).

The juvenile animals in our data set represented several sequential years of hatchlings. It has been estimated that alligators in the size range 76–175 cm are from 3 to 5 years old (Chabreck & Joanen, 1979; Jacobsen & Kushlan, 1989; Dalrymple, 1996). The sample included those hatchlings that survived the 3–5 years before the start of this study and those that attained 76 cm in length during the 6 years of the study. Overall this sub-adult population in coastal Louisiana showed a highly significant male bias ($\chi^2 = 75.13$, 1 d.f., $P < 0.0001$).

Rhodes & Lang (1996) have reported that the sex ratio of hatchlings from natural nests in South Carolina varied from year-to-year depending on local climatic conditions. They noted that in years characterized by higher than average rainfall during the incubation period, nest temperatures were cooler, and consequently, more females were produced. In dry years, nest temperatures were warmer, and a higher proportion of males resulted. Nevertheless, the overall hatchling sex ratio in South Carolina was strongly skewed towards females.

Year-to-year variation in summer weather may account for some of the variability observed in this study. In Louisiana, alligators lay a single clutch of eggs in mid to late June. The period of sex determination in

alligators occurs between days 30 and 50, or for *c.* 3 weeks during the last half of July and the first week of August, based on the detailed studies of egg incubation at constant temperatures (Lang & Andrews, 1994). Hatching occurs in late August to early September (Joanen & McNease, 1989; Lance, 1989). In south Louisiana, rainfall is extremely patchy. Precipitation can vary significantly over small areas. If we look at rainfall totals at Rockefeller Refuge (see Fig. 1) during July and August from 1986 to 1995 (Table 3), it is clear that there is considerable year-to-year variation that could account for some of the variation seen in the sex ratio of the juveniles in our data. However, it was not possible in our study to assign individual alligators to hatchling cohorts from a particular year because the juveniles we sampled ranged in age from 3 to 5 years. Note that in 1991 at locations that are close together there was no sex bias at location 1 but a highly significant male bias at location 2, whereas in 1993 this trend is reversed with a strong male bias at location 1 and no bias at location 2 (Table 2; Fig. 1).

Field research on crocodylians is extremely difficult. The animals are secretive, dangerous and usually live in inaccessible areas, and hence studies on crocodylian ecology tend to be fragmentary. Data on the sex ratios of crocodylian populations are therefore potentially fraught with error. Cott (1961) for example was unable to find a single juvenile Nile crocodile in his extensive surveys in East Africa. Mrosovsky (1994) has pointed out sources of error in several publications on reptile sex ratios. It has been asserted that most surveys on sex ratios in alligator populations are biased towards males as a result of sampling error (D. E. Woodward & Murray, 1993).

In Table 4 we have assembled all the published data available on alligator sex ratios. In several studies, only adult alligators were sampled, and in some of these, animals were collected during the annual legal hunt of alligators (Palmisano, Joanen & McNease, 1973; Joanen, McNease & Linscombe, 1974). These studies, in particular, were selectively biased toward males because of the methods employed to hunt wild alligators. Adult male alligators occupy deep open water, whereas adult female alligators tend to occupy shallow secluded areas in the marsh (Joanen & McNease, 1987; Rootes & Chabreck, 1993). The hunting season has been designed to exclude killing reproductive females, by discouraging hunting in the marsh *vs* open water, and thus more adult males than females are killed (Joanen & McNease, 1987).

Juvenile alligators in south Louisiana show some habitat preference by sex, but in general both sexes favour the same habitat as nesting females, namely open marshland with small isolated ponds (McNease & Joanen, 1974; Rootes & Chabreck, 1993). Our samples were collected over large areas of wetlands from several sites along the Louisiana coast that were predominantly open marsh and thus avoided any artifact resulting from sex differences in habitat preference (see Fig. 1). Similar data collected during field research in South

Table 3. July and August rainfall totals (cm) at Rockefeller Refuge, Louisiana

Year	July	August	July + August
1986	17.04	5.87	22.90
1987	19.20	14.42	33.63
1988	26.64	25.29	51.94
1989	16.46	11.38	27.85
1990	10.18	5.92	16.10
1991	17.42	27.00	44.42
1992	18.03	12.19	30.22
1993	6.70	21.05	27.75
1994	12.65	7.82	20.47
1995	23.87	13.71	37.59

Carolina, Florida and Louisiana (Table 4) included both adults and juveniles and is less likely to have sampling errors (Bara, 1975; Nichols & Chabreck, 1980; Kinler & Taylor, 1992; Rootes & Chabreck, 1992; A. R. Woodward, Moore & Delany, 1992). All these relatively unbiased samples (that included a large proportion of juveniles) showed a strong male bias. None reported a female-biased sex ratio. The only obvious conclusion is that alligator populations have not been skewed towards females and have probably been male biased over much, if not all, of their entire range.

Rhodes & Lang (1995) suggested that alligator sex ratios in areas that have been intensively hunted may differ from undisturbed areas. If hunting of adult alligators selects males (Palmisano *et al.*, 1973; Joanen & McNease, 1987), we might expect female-biased, or 1:1 sex ratios in areas where hunting has been frequent. Our results in south Louisiana suggest that intensive hunting does not seem to have had this effect on the alligator population in Louisiana. In fact, there has been a highly significant male bias throughout the range of *Alligator mississippiensis* (Table 4), including many areas where adults are hunted.

In contrast, hatchling sex ratios may not show a male bias, but instead may be female biased. Earlier studies by Ferguson & Joanen (1983) in which large female biases in hatchlings were reported, have been criticized for a flawed methodology that involved collecting the eggs from natural nests before the period when sex had been irreversibly determined and then incubating the eggs at temperatures which produce females (Mrosovsky & Provancha, 1992; Lang & Andrews, 1994). Using field techniques that avoid this difficulty, recent studies in which thousands of hatchlings have been sexed have revealed female-biased sex ratios from natural nests in South Carolina and Louisiana. In South Carolina, the proportion of male hatchlings from natural nests in each of 6 years (1994–99) was 21, 42, 25, 0, 24 and 39% (Rhodes & Lang, 1995, 1996). Some individual nests did produce >80% males, but a much larger number of nests produced 100% females (Rhodes & Lang, 1996). Five years (1995–99) of data from natural nests in Louisiana showed a similarly skewed sex ratio: 11, 31, 26, 38 and 28% male hatchlings. Thus, there is evidence for a strong female bias in two widely

Table 4. Published data on sex ratios of the alligator^a

Location	Sample	Size class	% male	Reference
N. Carolina	25	<1.8 m	66.7	Fuller, 1981
	30	>1.8 m	66.7	
S. Carolina	482	<0.9 m	57.3	Bara, 1975
	255	0.91–1.8 m	54.9	
	51	>1.8 m	60.8	
S. Carolina	90	>1.8 m	78.9	Murphy, 1977
S. Carolina	337	1.8–3.66 m	55.3	Murphy & Coker, 1983
S. Carolina	1549	>0.46 m	59.3	Wilkinson, 1984
S. Carolina	41	1.8–3.85 m	73.0	Brandt, 1991
	145	>1.8 m	78.0	
Florida	~1000	not given	65.0	Hines, Fogarty & Chappell, 1968
Florida	727	0.41–1.08 m	61.3	Dietz, 1979
Florida	1950	<0.61 m	66.0	Woodward <i>et al.</i> , 1992
	1700	0.61–1.21 m	60.7	
	300	1.22–1.82 m	54.3	
	123	1.83–2.74 m	47.2	
Louisiana	325	~1.8 m	63.7	O'Neil, 1949
Louisiana	234	>1.8 m	60.4	Chabreck, 1966
Louisiana	108	1.2–1.8 m	70.4	Palmisano <i>et al.</i> , 1973
	195	>1.8 m	83.0	
Louisiana	248	1.2–1.8 m	62.5	Joanen, McNease & Linscombe, 1974
	595	>1.8 m	67.9	
Louisiana	1571	0.6–1.8 m	59.8	Nichols & Chabreck, 1980
	57	>1.8 m	68.4	
Louisiana	5206	>1.8 m	56.0	Taylor, Kinler & Linscombe, 1991
Louisiana	4151	0.45–1.2 m	63.8	Rootes & Chabreck, 1992
	480	>1.2 m	63.3	
Louisiana	2337	<1.8 m	58.0	Kinler & Taylor, 1992
	1836	>1.8 m	72.0	
Louisiana	2936	0.76–1.52 m	58.0	This study
	67	>1.52 m	60.0	

^a Data on sex ratios for hatchlings not included.

separated populations of hatchlings over multiple years.

1998, which produced the highest percentage of males in Louisiana (38%), was unusually dry during the nesting season. Only 0.28 cm of rain fell in May as opposed to an average of 10 cm for this month. As a result, nesting material was extremely dry and likely to produce 'hot' dry nests. Even under these conditions the percentage of male hatchlings was only 38%. Rhodes & Lang (1996) did note that rainfall was a good predictor of cooler nests and a higher percentage of females, and that in dry conditions a higher percentage of males would be produced. Similar results were reported for *Caiman crocodilus yacare* in Brazil in which the sex ratio of hatchlings from floating nests in the open unshaded areas varied from year-to-year, whereas hatchling sex ratio from forest nests was similar over the 2-year study (Campos, 1993). These data indicate that the sex ratios of alligator hatchlings can vary from site-to-site and year-to-year depending on local climatic conditions, but overall there seem to be more female than male hatchlings entering the population. On the other hand, the juvenile and adult alligator populations are clearly not female biased.

There are at least two possible explanations for male-biased sex ratios in juvenile alligators:

(1) *Male-biased hatchling production.* As discussed earlier, the available data on the sex ratios of alligator hatchlings from natural nests indicates a strong female bias over the last 5 years at two widely separated areas. Furthermore, there have been no major changes in rainfall patterns over the past 20 years that would suggest unusually dry nesting seasons and potential male-biased sex ratios. We must assume therefore that natural nests throughout the range of *A. mississippiensis* are probably producing mainly female hatchlings in most years.

(2) *Sex-specific, differential mortality of hatchlings.* It has been estimated that c. 84% of hatchling alligators are lost to predators during their first year of life (Carbonneau, 1987), but there are no data on differential mortality by sex of juvenile alligators (Rootes & Chabreck, 1992). Mortality rates for animals in this size class have been estimated as high, but few data exist (Taylor & Neal, 1984).

A somewhat similar situation occurs in a population of the European pond turtle *Emys orbicularis* in Brenne, central France. The adult population is skewed towards females with two females to every male, but the hatchling sex ratio is not biased (Pieau, 1998). Girondot & Pieau (1993) have shown that in long-lived species such as turtles, a slight difference in survival of one sex

vs the other can have marked consequences for the adult sex ratio. For example, it would take only a small per cent difference in the annual mortality rates between the sexes during the first few years of life to result in an adult sex ratio of 2:1.

In other reptiles with temperature-dependent sex determination, developmental temperatures experienced in the egg are known to influence hatchling size (Rhen & Lang, 1999a) and growth (Rhen & Lang, 1995) as well as certain aspects of physiology and behaviour (O'Steen, 1998; Rhen & Lang, 1999b). The temperature of egg incubation has been shown to affect post-hatching size, growth and survivorship under captive conditions for alligators and crocodiles, e.g. hatchlings from eggs incubated at a constant temperature of 31–32 °C were larger, grew faster and were generally healthier than hatchlings from eggs incubated at either temperature extreme (Joanen, McNease & Ferguson, 1987; Webb & Cooper-Preston, 1989; Allsteadt & Lang, 1994). If similar effects apply to eggs and hatchlings in nature, then such a sex-specific bias (i.e. conditions favouring male vs female size, growth and survivorship when eggs are incubated at mid-range, mostly male-producing temperatures) would be compatible with a pattern of differential mortality affecting females vs males during the first 2 years of life. As noted earlier, mortality of young alligators is high during this period, relative to the improved survivorship of older, larger juveniles. However, it remains to be seen if there is sex-specific differential mortality in young alligators under natural conditions. If so, this hypothesis may explain the observed patterns of male-biased sex ratios in alligators we have documented in this study. Such a result in alligators is consistent with predictions based on theoretical models of differential fitness to explain the adaptive significance of temperature-dependent sex determination in reptiles (Shine, 1999).

Acknowledgements

We thank Larry McNease, Darren Richard, Eric Richard, Tom Hess, Scott Schales and Steve Jenkins for help in catching the alligators, and Rob Kleiforth and Barry Wilson for help with Fig. 1. We also acknowledge the administrative support of James Manning and Lee Caubarreaux of the Louisiana Department of Wildlife and Fisheries.

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