

Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*

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Numerous explanations have been offered for biased sex ratios including sampling bias, skewed primary sex ratios, differential mortality, differential immigration and emigration, and differential maturity of the sexes. We observed a strongly male-biased population of the turtle *Malaclemys terrapin* in South Carolina, USA. The overall adult male:female sex ratio was 1.78:1. Although males predominated numerically, the probability of recapturing individuals of either sex was the same (0.44 for males, 0.38 for females). Sex ratios were consistently male biased when based on monthly and yearly samples. This bias was not altered by the use of different collecting techniques or restriction of the sample to major habitats within the study area. Previously reported adult sex ratios for other populations range from strongly male biased to strongly female biased. Reports of female-biased samples appear to be a result of sampling bias or the artificial conditions under which terrapins have been cultivated in the past. The excess of males in our population appears to be a result of differences in the timing of maturity between the sexes. Male *Malaclemys* mature after their third year and females after their sixth year. Assuming a minimal effect from the other potential factors and regular juvenile recruitment, we expect that male *Malaclemys* will maintain numerical superiority in most populations. We propose that adult sex ratio variation in turtles, and other organisms with sexual differences in the timing of maturity, can be explained with a simple model: the earlier maturing sex will predominate numerically.

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Introduction

Imbalanced adult sex ratios in turtle populations have been reported for decades (Hildebrand 1929, Cagle 1952, Bury 1979), although sampling bias has often been indicted as the explanation for these deviations from 1:1 (Ream and Ream 1966, Gibbons 1970). In this paper, we present evidence for a significant male-biased sex ratio in a population of the diamondback terrapin (*Malaclemys terrapin*). This bias is not a result of sampling error but instead results from a biological cause.

Sex ratios that differ from the 1:1 ratio predicted by Fisher (1930) have been of great interest to biologists and numerous explanations have been offered for their existence (see reviews in Hamilton 1967, Maynard Smith 1978, Armitage 1987, Chapman et al. 1989a).

Fisher (1930) originally envisioned a 1:1 sex ratio as evolutionarily stable, predicting that parental investment should be equally divided between male and female offspring. He argued that if a majority of offspring being produced were female, then a parent who produces mostly males will, on average, have more grandchildren than one that does not produce mostly males. Under these circumstances the sex ratio in a population will be restored to unity. The same argument would apply should an excess of males be produced. Hamilton (1967) later pointed out that Fisher's argument did not apply in extreme situations where there was local mate competition. Hamilton listed 26 species of insects and mites with habitual sib mating and an arrhenotokous breeding system that exhibited strongly female-biased offspring sex ratios. This strong female bias would be

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expected if a single male offspring can mate with all his sisters. Under these circumstances a parent that produces only one male per clutch will produce more grandchildren than one that produces more than one male. More recently, Trivers and Willard (1973) suggested that natural selection favors deviations away from 1:1 investment in the sexes rather than deviations in sex ratios per se. Their model, validated by data for several polygynous species of mammals, states that if there is greater variance in the future fitness of offspring of one sex relative to the other, then a parent in good physical condition will benefit by producing more of the high variance sex. All of these models fail to explain the enigmatic sex ratios exhibited by reptiles with environmental sex determination (Bull and Charnov 1989).

In a recent review of sex ratios in turtles, Gibbons (1990) identified four demographic factors that can influence the sex ratio of a natural population. The first factor is the sex ratio at hatching (hereafter referred to as the primary sex ratio). Evidence in support of skewed primary sex ratios has been reported for taxa as diverse as insects (King 1989) and birds (Howe 1977). Skewed primary sex ratios are especially possible in animals with environmental sex determination such as some turtles and a variety of other poikilotherms (Bull and Vogt 1979, Bull 1980, Morreale et al. 1984, Ferguson and Joanen 1982, Vogt and Bull 1982a, 1984, Conover 1984, Middaugh and Hemmer 1987, Deeming and Ferguson 1989, Lang et al. 1989). The second factor, differential mortality of the sexes, has also been suggested as a cause of skewed sex ratios by Selander (1965), Howe (1977), Hurly (1987) and Elmqvist et al. (1988). The third factor that may cause skewed sex ratios is differential emigration and immigration between the sexes (Morreale et al. 1984). The fourth factor is differential age at maturity between the sexes (Kozlowski 1989, Gibbons 1990, Lovich et al. 1990). Resource competition has been suggested as a cause of sex ratio variation in some organisms (Silk 1984, Chapman et al. 1989a, King 1989). However, the "local resource competition hypothesis" is based on the assumption that the sexes exhibit differential patterns of dispersal (Chapman et al. 1989b). Because of this relationship, the resource competition model is subordinate to the differential emigration and immigration model mentioned above.

A fundamental assumption in studies concerning sex ratios is that sampling is not biased (Gibbons 1970). Reports of unbalanced sex ratios can be caused by biased collecting techniques (Ream and Ream 1966) or by different capture probabilities between the sexes (Hurly 1987). Minimization of these biases is essential for meaningful interpretation of sex ratios.

In this paper, we discuss the male-biased sex ratio in a population of the diamondback terrapin (*Malaclemys terrapin*) and evaluate the applicability of the biased sample hypothesis and each of the four hypotheses proposed by Gibbons (1990) to our data. We use the "strong inference" procedure of Platt (1964, see also

Cousens 1985) to formulate our conclusions. Each explanation was tested as an alternative hypothesis to determine its utility. Our final conclusion is based on elimination of competing hypotheses.

Materials and methods

Defining sex ratio

As Ehrlich et al. (1984) noted, defining sex ratio as the relative proportion of males and females in a population conceals substantial difficulties of definition and computation. We consider it imperative that only sexually mature individuals be included in calculations of sex ratio. The adult sex ratio is important demographically because of the potential influence that the relative proportion of the sexes can have on time spent searching for mates, intrasexual competition, and annual propagule production.

Emlen and Oring (1977) advanced the concept of an operational sex ratio that they defined as the "average ratio of fertilizable females to sexually active males at any given time." This definition was criticized by Kluge (1981) because it did not define the duration of the sampling period, or the problems associated with determining sexual activity. Another definition was proposed by Ehrlich et al. (1984) in their work with butterflies. They defined realized sex ratio as the ratio of males in a demographic unit participating in the adult flight of a single generation to females in the same unit and generation.

In *Malaclemys*, strict adherence to the definitions proposed by Emlen and Oring (1977) and Ehrlich et al. (1984) is complicated by sperm storage (Hildebrand 1929) and overlapping generations, respectively. Thus, in this paper we define functional sex ratio as the relative proportion of sexually mature males to sexually mature females.

The study animal

The diamondback terrapin is the only species of turtle in North America that inhabits brackish coastal habitats exclusively. It is widely distributed along the coast of the United States from Cape Cod, Massachusetts to Corpus Christi, Texas. This species exhibits dramatic female dominated sexual size dimorphism (Gibbons and Lovich 1990). In our population, adult males have a mean straightline plastron length of 102 mm and females have a mean of 148 mm for a female to male body size ratio of 1.45. Mean male and female mass is 242 g and 705 g, respectively, for a female to male mass ratio of 2.91. Adults are easily sexed due to differences in body size and other secondary sexual characteristics. Females have proportionally wider heads than males, and males have long tails with the cloacal opening sit-

Table 1. Yearly variation in sex ratios (M:F) of diamondback terrapins from Kiawah Island, South Carolina. Ratios designated with an asterisk differ significantly from 1:1 at $P \leq 0.05$.

Year/sample	Males	Females	Ratio
1983			
First capture	24	4	6.00*
1984			
First capture	39	12	3.25*
All captures	49	13	3.77*
1985			
First capture	4	5	0.80
All captures	5	6	0.83
1986			
First capture	37	36	1.03
All captures	69	43	1.60
1987			
First capture	26	17	1.53
All captures	38	26	1.46
1988			
First capture	99	62	1.60*
All captures	127	85	1.49*
1989			
First capture	36	13	2.77*
All captures	70	29	2.41*
Combined			
First capture	265	149	1.78*
All captures	382	206	1.85*

uated posterior of the shell margin. Aspects of the natural history of this species are reviewed in Ernst and Barbour (1972) and Palmer and Cordes (1988).

The study site

Turtles were collected from 1983 to 1989 in salt marshes around Kiawah Island, South Carolina, USA. Kiawah Island is an Atlantic coast barrier island located about 25 km southwest of Charleston, South Carolina. The island comprises approximately 3200 ha, half of which is

Table 2. Monthly variation in sex ratios of diamondback terrapins from Kiawah Island, South Carolina. Ratios designated with an asterisk differ from 1:1 at $P \leq 0.05$.

Month	First capture			All captures		
	Sex			Sex		
	M	F	Ratio	M	F	Ratio
Apr	117	58	2.02*	167	86	1.94*
May	46	47	0.98	73	57	1.28
Jun	45	14	3.21*	58	17	3.41*
Jul	30	23	1.30	50	35	1.43
Aug	22	6	3.67*	24	9	2.67*

Table 3. Variation in sex ratio (M:F) of diamondback terrapins from Kiawah Island, South Carolina as a result of sampling technique. Ratios designated with an asterisk differ significantly from 1:1 at $P \leq 0.05$.

Technique/sample	Males	Females	Ratio
Trammel net			
First capture	100	83	1.20
All captures	161	113	1.42*
Seine			
First capture	127	49	2.59*
All captures	152	58	2.62*
Combined			
First capture	227	132	1.72*
All captures	313	171	1.83*

salt marsh. The climate is subtropical with temperatures falling below freezing on fewer than 20 d during the winter. Tidal creeks within the salt marsh study area are subject to 2 m daily tidal fluctuations. A more detailed description of Kiawah Island is given in Gibbons and Harrison (1981).

Techniques

A variety of collecting techniques were used including dipnetting, hand capture, seining, trammel nets, and trawling. The vast majority of specimens were collected with trammel nets and seines. A total of 414 individuals were captured 588 times. Individuals were marked for future recognition, sexed, measured and released at the point of capture. Estimates of sex ratios for other populations were obtained from the literature. Ratios were tested for significant departure from 1:1 using a Chi-square test corrected for continuity at an alpha level of 0.05 (Zar 1984).

Table 4. Sex ratios of diamondback terrapins in various aquatic habitats of Kiawah Island, South Carolina. Ratios designated with an asterisk differ from 1:1 at $P \leq 0.05$.

Habitat	First capture			All captures		
	Sex			Sex		
	M	F	Ratio	M	F	Ratio
Kiawah River	11	10	1.10	13	12	1.08
Terrapin Creek	54	39	1.38	119	73	1.63*
Fiddler Creek	122	68	1.79*	159	86	1.85*
Oyster Creek	7	3	2.33	7	4	1.75

Table 5. Sex ratios of diamondback terrapins as reported in selected references. Seasonal variation in sex ratios is reported when available. Male to female ratios designated with an asterisk differ significantly from 1:1 at $P \leq 0.05$.

Reference	Locality	Males	Females	M:F ratio	Comments
This study	South Carolina	265	149	1.78*	—
Cagle (1952)	Louisiana	57	13	4.38*	—
Seigel (1984)	Florida	5	42	0.12*	Banana River, Feb-Nov
		9	90	0.10*	Indian River, Feb-Nov
		4	22	0.18*	Indian River, Mar-Apr
		251	336	0.75*	1975
Hurd et al. (1979)	Delaware	176	144	1.22	1976
		195	86	2.27*	Overall ratio
Bishop (1983)	South Carolina	22	43	0.51*	1979
		132	40	3.30*	1980
		41	3	13.67*	1981
		50	2	25.00*	Hatchling sex ratio under artificial conditions at $27 \pm 2^\circ\text{C}$
Hildebrand (1929)	Captivity	239	1058	0.23*	Hatchling sex ratio under artificial conditions
Hildebrand (1932)	Captivity	209	1233	0.17*	Hatchling sex ratio under artificial conditions
Hildebrand and Hatsel (1926)	Captivity	15	85	0.18*	Hatchling sex ratio under artificial conditions

Results

A total of 265 males and 149 females were collected a total of 382 and 206 times, respectively. Each male was recaptured a mean of 0.44 times and each female a mean of 0.38 times. The proportion of recaptures did not differ significantly between the sexes (Contingency table analysis, $\chi^2 = 0.57$; $P > 0.10$). The proportions of first captures and of total captures are both significantly biased toward males ($P < 0.05$). Sex ratios were male biased in all years for which relatively large samples were available, some significantly so (Table 1). Monthly variation in sex ratio was generally male biased (Table 2). Sex ratios were also male biased for both major collecting techniques (Table 3). Seining produced estimates of male bias approximately two times greater than data for trammel nets. Sex ratios derived from the combined data were intermediate but still significantly male biased. All major habitats within the salt marsh exhibited a male-biased sex ratio (Table 4). Estimates of sex ratios for other populations range from strongly female biased to strongly male biased (Table 5).

Discussion

Sampling bias

The importance of sampling bias must be considered in any study of sex ratios (Gibbons 1970). The perception of population sex ratio can vary as a function of collecting technique, microhabitat sampled, differences in the

behavior of the sexes, determination of the age or size at maturity, or a combination of these factors.

It is easy to imagine how a certain collecting technique could be biased toward a given sex. For example, in species such as *Malaclemys* that exhibit dramatic sexual size dimorphism, use of traps or nets with a mesh size small enough to let the smaller males escape would result in a female biased estimate. This was not the case in our study since mesh size was considerably smaller than the size at which males reach sexual maturity.

The sexes may also segregate into slightly different microhabitats at certain times of the year. This may explain the heavily female-biased samples reported for *Malaclemys* populations in Florida (Table 5). Seigel (1984) set trammel nets adjacent to the only known nesting site in his study area (Seigel 1980a). The disproportionate number of female captures appears to have been the result of this sampling bias. Furthermore, the small numbers of males reported by Seigel may not reflect their actual abundance. Large aggregations of terrapins were occasionally seen in his study area, but not captured (Seigel 1980b).

Differences in the behavior of the sexes can also affect the perception of sex ratio. This is particularly important if the behaviors affect the probability of capture. For example, concentrating collecting efforts during the nesting season can result in female-biased samples of most species of turtles (Gibbons 1990). Conversely, the greater capture of males in some seasons is probably a reflection of increased mating activity by this sex (Morreale et al. 1984, Parker 1984).

Another problem that can lead to biased estimates of

sex ratios is the improper determination of sexual maturity in one or both sexes (Gibbons 1970). In *Malaclemys*, females mature later and at a larger body size than males. Assignment of maturity in females at body sizes smaller than that at which maturity actually occurs would lead to increasing female bias in the calculated sex ratio, due to the inclusion of immature females in the sample. We avoided this problem by determining the lower limit of sexual maturity in females with X-ray photography (Gibbons and Greene 1979).

Explanations such as these may be responsible for many of the female-biased sex ratios reported in Table 5. Furthermore, these problems serve to underscore the importance of conducting thorough sampling in any assessment of sex ratios.

Results for our study area show that sex ratios vary from year to year and as a function of sampling technique. In spite of this variance, samples are still male biased. In addition, overall recapture probabilities are the same for both sexes. The probability of capturing a male was greater overall than for females due to their numerical advantage. However, individual males and females were equally likely to be recaptured. Based on these results, we reject the hypothesis that male-biased sex ratios in *Malaclemys* on Kiawah Island are due to sampling bias.

Skewed primary sex ratios

In many species of reptiles, particularly turtles, sex is determined by incubation temperature (Bull and Vogt 1979, Bull 1980, Morreale et al. 1982, Vogt and Bull 1982a, 1984). These studies revealed that the eggs of many species of turtles develop as males at low incubation temperatures and females at high ones. Although pivotal temperatures vary, they are generally within the range of 26°–29°C. It is important to note that not all species of turtles are known to exhibit environmental sex determination (ESD). At least two species have heteromorphic sex chromosomes interpreted as an XX/XY sex determining system (Sites et al. 1979, Carr and Bickham 1981). In addition, some species not known to possess heteromorphic sex chromosomes do not exhibit sex ratio variation in response to different incubation temperatures (Vogt and Bull 1982b, Bull et al. 1985, Georges 1988). Other species apparently show an interaction between temperature and genetic sex determination (Merchant-Larios et al. 1989, Servan et al. 1989).

The question of sex determination has not been adequately addressed in *Malaclemys terrapin*. Sachsse (1984) reported that a group of eggs incubated at 27 ± 2°C resulted in a hatching success rate of 50% with a sex ratio of 52 males and 2 females. These results suggest that *Malaclemys* may have the same pattern of sex determination reported for many other species of turtles: larger numbers of males are produced at relatively

low incubation temperatures. Alternatively, it is also possible that differential mortality of males and females occurred during embryonic development as a result of incubation temperature. This phenomenon was reported by Burger and Zappalorti (1988) for pine snakes (*Pituophis melanoleucus*). They found that male:female sex ratios of live hatchlings varied from 0.11 at 21°C to 1.40 at 32°C under controlled conditions; however, the sex ratio of live and stillborn embryos combined was not significantly different from unity. In contrast, Vogt and Bull (1982a) concluded from laboratory studies of 14 genera of turtles that survival of embryos to hatching was sufficiently high to reject the hypothesis of differential embryonic mortality as a result of incubation temperature. It is difficult to interpret Sachsse's (1984) results for *Malaclemys* as proof for ESD since he did not report the sex ratio of embryos that may have died during incubation. It is also possible that unhatched eggs resulted from infertility instead of mortality. Hatching success is only 69% in *Malaclemys* nests under field conditions (Burger 1976). However, her data should be viewed with caution since she periodically uncovered nests to determine time of hatching (Burger 1977).

It is tempting to speculate that ESD would result in biased adult turtle sex ratios in nature. Vogt and Bull (1984) observed that under natural conditions nest sex ratios of two species of the turtle genus *Graptemys* tended to be all-male or all-female with an overall excess of females. Nests with males were associated with heavy vegetation and cool temperatures and nests with females were located in open areas exposed to the sun. Sex ratios varied between nesting beaches in response to the differences in the availability of these two categories of nest sites. Since all-female nests hatched in less time than all-male nests, sex ratios of emerging hatchlings were strongly female biased early in the season and strongly male biased later in the season. Subsequent to this study, Vogt (1980) reported a female-biased adult sex ratio for his population. The female-biased adult sex ratios may have been due to sampling bias since he trapped mainly near areas where females were likely to nest.

Nest site selection in *Malaclemys* was described in detail by Burger and Montevicchi (1975). When compared to randomly selected sites in their study area, actual nest sites were located in stable, high dune areas with low vegetative cover (less than 20%) more often than expected. Seigel (1980a) reported that *Malaclemys* in Florida nested on elevated dike roads. These observations on nest site selection agree with ours in that *Malaclemys* nests on Kiawah Island have only been observed on small sandy islands and beaches in the marsh with low vegetative cover, exposed to considerable insolation. If *Malaclemys* follows the normal pattern of ESD as suggested by Sachsse (1984), then the relatively open areas selected for nest sites might be expected to produce a female bias as shown by Vogt and

Bull (1984) for *Graptemys*. This is clearly not the case with our data, but such an explanation cannot be entirely ruled out for the female-biased ratios reported by Seigel (1984) (Table 5). The highly female-biased sex ratios reported in Table 5 by Hildebrand are undoubtedly due to the artificial conditions under which eggs were incubated.

We suggest that in animals such as turtles, that mature late in life and have a relatively long lifespan (Gibbons 1987), variation in nest site selection and environmental temperatures during a female's reproductive life will tend to balance out any differences in year-to-year hatchling sex ratios. Evidence in support of this hypothesis was provided by Zweifel (1989) for the painted turtle *Chrysemys picta*. He reported that the sex ratio (based on the number of offspring surviving until development of secondary sexual characters) of broods of a single female turtle varied from all males to all females during a five year period. However, the total summed to unity. Mrosovsky et al. (1984a) found that sex ratios of hatchling loggerhead turtles (*Caretta caretta*) in South Carolina and Georgia varied from no females in nests laid at the beginning of the nesting season in late May, to 80% females from nests laid in early July, to 10% females from nests laid in early August. Despite such dramatic differences in sex ratios within a season, the overall sex ratio was near 1:1 when data were combined with nesting frequency data over six years. Similar results were reported by Mrosovsky et al. (1984b) for two other species of sea turtles. It is doubtful that females can predict and compensate for environmental variance within a season since sex is determined several weeks after oviposition (Yntema 1979, Bull and Vogt 1981). Based on this body of evidence, we tentatively reject the hypothesis that the male-biased sex ratio in Kiawah *Malaclemys* is due to skewed primary sex ratios.

Differential mortality

Differential mortality of the sexes has often been invoked as a cause for biased sex ratios (see review in Howe 1977, Ehrlich et al. 1984, Hurly 1987, Burger and Zappalorti 1988, Elmquist et al. 1988). Evidence for biased adult turtle sex ratios due to differential mortality was reported by Gibbons (1990). He observed a predominance of female *Trachemys scripta* on a barrier island near Kiawah (Gibbons et al. 1979). The relative scarcity of males may have been a consequence of alligator (*Alligator mississippiensis*) predation. Male *Trachemys* are significantly smaller than females (Gibbons and Lovich 1990) and are presumably more susceptible to large predatory alligators in the relatively vegetation-free habitat. High female specific predation has been reported for nesting turtles (Shealy 1976, Seigel 1980c), but these authors did not comment on its possible effect on the population sex ratio.

Predation rates on nesting female *Malaclemys* can be very high. Seigel (1980c) reported that at least 10% of the females in his study site were killed in one year by predators. Interestingly, he reported heavily female-biased sex ratios (Table 5) in spite of such a high incidence of female specific mortality. We have occasionally observed the remains of female *Malaclemys* killed (presumably during nesting) on Kiawah Island. However, at this time we have insufficient evidence to conclude that females are preyed upon as heavily as suggested by Seigel (1980c).

The frequency of predator-related injuries has been used by others to estimate predator intensity (Rand 1954, Schoener 1979, Schoener and Schoener 1980). However, caution is advised in interpretation since injuries may be indicative of predator inefficiency, not intensity (Schoener 1979). A variety of mortality factors can be envisioned for *Malaclemys*, especially juveniles. However, the behavior of juvenile *Malaclemys* is presumably the same in both sexes. Because of this, rates of mortality should be similar for males and females until attainment of maturity. In our marked population of *Malaclemys* 17 females (12%) were missing one or more feet, probably as a result of predator encounters with terrestrial mammals (alligators are not found in the study area). Twenty males (8%) exhibited similar injuries. The proportion of injured individuals did not differ significantly between the sexes (Contingency table analysis; $\chi^2 = 1.35$; $P > 0.10$). Based on these results we reject the hypothesis that male-biased sex ratios in *Malaclemys* on Kiawah Island are due to differential mortality.

It is important to note that *Malaclemys* (particularly females) were heavily exploited as a gourmet food item around the turn of this century (Coker 1920). This is no longer the case at our study site and thus is an unlikely explanation for the male-biased sex ratio observed.

Differential immigration and emigration

Male turtles of many species are known to travel greater distances and move more often between populations than females (Morreale et al. 1984, Parker 1984, Gibbons 1986, Dodd et al. 1988, Ingold and Patterson 1988, Lovich 1990). These differences in activity are thought to be representative of differential reproductive strategies between the sexes. The following predictions are associated with this hypothesis (Morreale et al. 1984): 1) males become active early to increase their chances of mating with the earliest active female (see Wiklund and Fagerström 1977), 2) males move to increase their opportunities for multiple matings, and 3) during the nesting season mate searching activity by males will be reduced whereas female movements will increase as they seek nest sites. Because of this difference in the movement patterns of males and females, sex ratios may fluctuate over time in some populations. It is

important to note that departures from unity in local populations may be balanced by immigration and emigration to and from other populations.

Very little is known of movement patterns in *Malaclemys*. Hurd et al. (1979) found little evidence of immigration and emigration in the *Malaclemys* population they studied in Delaware. Our results for Kiawah were similar in that the vast majority of specimens exhibited high year-to-year site fidelity. Individual males and females were often recaptured within several meters of the original point of capture in as many as three successive years, including periods before and after tropical storms and hurricanes. Major displacements of 100–200 m were seen in only two males and four females. Based on these results, we reject the hypothesis that male-biased sex ratios are due to differential patterns of immigration and emigration between the sexes.

Differential maturity

According to Gibbons (1990), the single most important influence on the sex ratio of some turtle populations is the differential rate of maturity of the sexes that is characteristic of some species. Males of the turtle *Trachemys scripta* mature several years earlier than females in the same population (Cagle 1944, 1948, 1950, Gibbons and Lovich 1990, Gibbons et al. 1981). Gibbons (1990) demonstrated that if no other factors are involved that result either in differential mortality rates of the sexes or in differential ratios at hatching, *Trachemys* populations experiencing juvenile recruitment will have more adult males than females. Conversely, Lovich et al. (1990) observed that in the wood turtle (*Clemmys insculpta*), a species in which females mature earlier and at a smaller size than males, females outnumber males in populations for which large sample sizes are available. Thus, it appears that the sex that matures earlier will predominate numerically.

Juvenile male and female *Malaclemys* apparently grow at the same rate for the first three years (Coker 1920, Seigel 1984). Males mature at about 90 mm before the end of their third year (Cagle 1952, Seigel 1984) at which time their rate of growth slows considerably (Coker 1920, Hildebrand 1929, Cagle 1952, Seigel 1984). At the size at which males reach maturity, females are only one half their adult size (Coker 1920). Female growth continues at the juvenile rate until they mature after the sixth year at between 160–176 mm (Cagle 1952). Some females may mature in their fourth year (Hildebrand 1932) at body sizes as small as 132 mm (Montevecchi and Burger 1975, Seigel 1984). The smallest male in our population that exhibited well defined secondary sexual characters was 91 mm and three years old. The smallest female known to be gravid via X-ray photography was 138 mm and seven years old. Part of the variance in size and age of maturity among populations of this wide ranging species may be due to ge-

ographic variation in growth rate among the races for which data have been reported (Seigel 1984). In spite of this variation, male *Malaclemys* mature earlier than females in the same population.

We propose that the male-biased sex ratio in our population of *Malaclemys* is a result of differential maturity of the sexes. Other factors may modify the resultant sex ratio somewhat, but their influence appears to be minimal.

Conclusion

Biased sex ratios can result from several factors including biased sampling, skewed primary sex ratios, differential mortality, differential immigration and emigration, and differential age at maturity. We used the "strong inference" procedure of Platt (1964) (see also Cousens 1985) to formulate our conclusions. Each explanation was tested as an alternative hypothesis to determine its utility. Only differential age at maturity provides a satisfactory explanation for the strongly male-biased adult sex ratio exhibited by our study population of *Malaclemys terrapin*. The potential importance of the other factors is not diminished by this finding. However, their individual effects are apparently insufficient to explain the extent of bias observed.

Our findings suggest that adult sex ratio variation in animals with sexual differences in the timing of maturity, can be explained with a simple model. We propose that the sex that matures earlier will predominate numerically. A major assumption of this model is that the other potential factors have a minimal interactive effect on the resultant sex ratio and that the population experiences regular recruitment of juveniles.

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