

*Structure,
Demography, and
Interaction among
Populations*

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Sex Ratios and Their Significance among Turtle Populations

Abstract

Sex ratios of adults in natural populations of turtles have been reported to vary both within and among species. Long-term studies with the slider turtle (*Trachemys scripta*) indicate that sampling biases can result from a variety of causes, including season of capture, determination of maturity, and trapping method. Four demographic factors influence actual sex ratios within a population: (1) sex ratios of hatchlings, (2) differential mortality of the sexes, (3) differential emigration and immigration rates of the sexes, and (4) differences in age at maturity of the sexes. The last reason is considered to be the primary cause of biased adult sex ratios within many populations of turtles, although future studies should investigate the other possibilities.

Introduction

The sex ratio of a population is an important demographic measurement because of the potential influence that the relative proportion of the sexes can have on certain aspects of population dynamics (e.g., time spent searching for receptive mates, intrasexual competition, and annual egg productivity of a population). Both even and unbalanced secondary sex ratios have been reported for natural populations of turtles (Bury, 1979). Unbalanced sex ratios may occur naturally in some populations (Moll and Legler, 1971; Bury, 1979), but biased sampling has been suggested as being responsible for at least some of the reports of unbalanced sex ratios in the turtle literature (Ream and Ream, 1966; Gibbons, 1970c). The reports of skewed sex ratios among hatchling turtles in a variety of species following incubation at different temperatures (e.g., Picau, 1974; Bull and Vogt, 1979; Bull, 1980; Morreale et al., 1982; Vogt and Bull, 1984) also give a potential explanation for varied adult sex ratios in natural populations. The purpose of this chapter is to discuss the

Table 14.1. Comparison of sex ratios (male:female) of freshwater turtles captured at Ellenton Bay using two different collecting techniques

Species	Baited aquatic traps				Terrestrial drift fence			
	Males	Females	Sex ratio	X ²	Males	Females	Sex ratio	X ²
Slider turtle (<i>Trachemys scripta</i>)	556	282	1.97	**	592	556	1.06	NS
	314	153	2.05	**	296	206	1.44	**
Eastern mud turtle (<i>Kinosternon subrubrum</i>)	289	158	1.83	**	1,067	1,631	0.65	**
	138	70	1.97	**	298	271	1.10	NS
Chicken turtle (<i>Deirochelys reticularia</i>)	230	54	4.26	**	396	333	1.19	**
	110	25	4.40	**	128	67	1.91	**
Florida cooter (<i>Pseudemys floridana</i>)	39	15	2.60	**	115	104	1.11	NS
	10	3	3.33	NS	27	14	1.93	NS
Stinkpot (<i>Sternotherus odoratus</i>)	202	168	1.20	NS	106	156	0.68	**
	46	36	1.28	NS	24	24	1.00	NS
Snapping turtle (<i>Chelydra serpentina</i>)	68	40	1.70	**	30	45	0.67	NS
	16	6	2.67	NS	9	5	1.80	NS

Note: Only adult individuals are included. The top number for a species indicates all captures and recaptures from 1967 through 1987. The lower number is based on each individual as a single capture. Chi-square (X²) tests corrected for continuity were used to compare the preceding sex ratio (observed) for each technique in each row with a 1:1 sex ratio (expected). Abbreviation: NS, $p \geq .05$.

** $p < .01$.

various causes of the observed sex ratios of adult turtles in natural populations and to determine the evolutionary significance of equal or unequal numbers of the sexes. I base interpretations of sex ratio estimates (and they must categorically be understood to be only estimates, unless every individual is accounted for) on examples from the literature and from field studies of the slider turtle (*Trachemys scripta*) and other freshwater species on the Savannah River Plant (SRP) in South Carolina.

Defining Sex Ratios

Although a sex ratio simply represents the relative proportion of males to females, a consideration in the discussion of sex ratios is the proper quantification of how a population is classified demographically in terms of various functional categories. For example, defining the sex ratio in a sample of newborn turtles whose sexes have been identified is straightforward, because all individuals are members of the same cohort. However, with species that show dramatic sexual size dimorphism, such as slider turtles, the sexes reach maturity at widely differing ages, so that some cohort comparisons will include immature females and mature males. Although the proportion of all mature and immature turtles of both sexes in a population can provide information on other demographic features, the functional sex ratio is based only on individuals that have reached maturity. Therefore, it is necessary to know the size and age at maturity of individuals within a particular population if functional adult sex ratios are to be established.

Factors Influencing Perceived and Actual Sex Ratios in Turtle Populations

The sex ratio perceived by an investigator is influenced by biases that result from sampling or interpretation as well as by the actual sex ratio resulting from changes that occur as a consequence of normal population processes. The potential effect of either of these processes and the interaction between them must be considered in any examination of adult sex ratios in natural populations.

SAMPLING BIASES AFFECTING PERCEIVED SEX RATIOS

The influence of sampling bias should be a primary consideration for any investigator in the determination of sex ratios in natural populations of turtles or most other animals. Different impressions of what the sex ratio is in a population can result from collecting technique, differences in behavior of the sexes, determination of age or size at maturity, or a combination of these factors. Several examples can emphasize this point. In thorough sampling efforts of populations of slider turtles on the SRP, the proportional number of captured adult males and adult females varied seasonally, annually, and as a result of collecting technique (Tables 14.1 and 14.2).

The methods by which turtles are collected can also severely influence the size classes or sexes that are captured. This is intuitive for many species of turtles (e.g., some *Graptemys*) in which the males are appreciably smaller than the females. Therefore, if an investigator uses traps with a mesh large enough for smaller turtles to es-

Table 14.2. Variability in perceived sex ratios (male:female) in South Carolina populations of *Trachemys scripta* resulting from sampling bias as a function of season and year

Year	Winter (Dec.-Feb.)				Spring (Mar.-May)				Summer (June-Aug.)				Fall (Sept.-Nov.)				Total year			
	M	F	Ratio	X ²	M	F	Ratio	X ²	M	F	Ratio	X ²	M	F	Ratio	X ²	M	F	Ratio	X ²
Ellenton Bay																				
1967									50	18	2.78	**	59	21	2.81	**	100	35	2.86	**
1968					42	32	1.31	NS	21	4	5.25	**					70	37	1.89	**
1969																	12	3	4.00	*
1970																	17	6	2.83	*
1975					55	74	0.74	NS	29	26	1.12	NS					77	88	0.88	NS
1976					15	27	0.56	NS	32	16	2.00	*	31	21	1.48	NS	71	54	1.31	NS
1977					19	14	1.36	NS	30	16	1.88	NS	12	6	2.00	NS	60	30	2.00	**
1978	7	10	0.70	NS	94	54	1.74	**	34	34	1.00	NS	15	10	1.50	NS	118	85	1.39	*
1979					21	7	3.00	*	10	4	2.50	NS	14	3	4.67	*	41	19	2.16	**
1980					47	37	1.27	NS	20	23	0.87	NS	10	6	1.67	NS	62	50	1.24	NS
1981					129	96	1.34	*	64	26	2.46	**					185	120	1.54	**
1982	16	11	1.45	NS	16	11	1.45	NS	10	8	1.25	NS								
1986					17	18	0.94	NS	11	23	0.48	NS					27	36	0.75	NS
All years	54	37	1.46	NS	393	270	1.46	**	273	160	1.71	**	147	67	2.19	**	511	294	1.74	**
Par Pond																				
1968					5	8	0.63	NS					12	5	2.40	NS	20	14	1.43	NS
1969																	5	3	1.67	NS
1970																	7	4	1.75	NS
1975									10	9	1.11	NS					12	9	1.33	NS
1976					6	14	0.43	NS	57	20	2.85	**	39	7	5.57	**	92	33	2.79	**
1977	40	2	20.00	**	48	28	1.71	*	40	24	1.67	NS					126	53	2.38	**
1978					11	7	1.57	NS					9	1	9.00	*	27	7	3.86	**
1979					10	8	1.25	NS	1	3	0.33	NS					19	14	1.36	NS
1980																				
1981									4	1	4.00	NS	15	6	2.50	NS	164	63	2.60	**
1982	69	17	4.06	**	89	41	2.17	**	31	11	2.82	**					59	25	2.36	**
1983					25	15	1.67	NS	27	17	1.59	NS					28	20	1.40	NS
1984													6	5	1.20	NS	7	16	0.44	NS
1985													18	5	3.60	*	23	11	2.09	NS
1986																				
All years	143	27	5.30	**	200	139	1.44	**	201	106	1.90	**	121	54	2.24	**	526	256	2.05	**
Lost Lake System																				
1967													37	32	1.16	NS	37	34	1.09	NS
1968	15	12	1.25	NS	17	16	1.06	NS	6	11	0.55	NS					34	31	1.10	NS
1969	5	7	0.71	NS					1	12	0.08	**					12	19	0.63	NS
1970									3	8	0.38	NS					3	8	0.38	NS
1975																				
1976													9	5	1.80	NS	10	8	1.25	NS
1977									14	13	1.08	NS					14	16	0.88	NS
1978																				
1979													22	1	22.00	**	22	5	4.40	**
1980					50	37	1.35	NS	30	27	1.11	NS	47	19	2.47	**	114	69	1.65	**
1981	24	10	2.40	*	44	24	1.83	*									67	34	1.97	**
1982					10	5	2.00	NS					110	24	4.58	**	119	29	4.10	**
1983	68	13	5.23	**	141	45	3.13	**	29	22	1.32	NS	15	7	2.14	NS	235	84	2.80	**
1984					40	15	2.67	**	27	13	2.08	*					67	33	2.03	**
1985					7	8	0.88	NS	59	34	1.74	*	41	18	2.28	**	101	55	1.84	**
1986					24	7	3.43	**					60	16	3.75	**	89	31	2.87	**
All years	112	49	2.29	**	301	147	2.05	**	164	158	1.04	NS	315	121	2.60	**	556	290	1.92	**
Risher Pond																				
1968									16	23	0.70	NS					16	23	0.70	NS
1969									3	9	0.33	NS	9	8	1.13	NS	12	15	0.80	NS
1970					18	24	0.75	NS	12	9	1.33	NS					21	30	0.70	NS
1975																				
1976													10	17	0.59	NS	11	17	0.65	NS
1977					10	10	1.00	NS									10	10	1.00	NS
1978					9	11	0.82	NS					10	10	1.00	NS	12	14	0.86	NS
1979													5	7	0.71	NS	6	7	0.86	NS
1980													11	11	1.00	NS	11	11	1.00	NS
1981													7	7	1.00	NS	9	11	0.82	NS
1982									11	7	1.57	NS					11	7	1.57	NS
1983					4	6	0.67	NS									4	6	0.67	NS
1984					8	10	0.80	NS	7	12	0.58	NS					17	16	1.06	NS
All years					38	45	0.84	NS	43	43	1.00	NS	28	31	0.90	NS	59	54	1.09	NS

Note: Samples are based on original captures of adult individuals in a particular season or year (winter samples include December of the preceding year) when 10 or more adult individuals were captured. Chi-square (X²) tests corrected for continuity were used to compare the sex ratio (observed) within each season and year with a 1:1 sex ratio (expected). Abbreviation: NS, $p \geq .05$.

* $p < .05$.

** $p < .01$.

cape, an obvious bias will occur. The converse, using a trap entrance too small for large females, could result in the differential capture of smaller individuals. However, some collecting techniques have a more subtle bias and require quantitative documentation of differential captures (e.g., see Ream and Ream, 1966).

A technique-by-technique evaluation of differential capture of adult turtles would offer little guidance other than that some collecting techniques can have a dramatic or minor effect on the proportional capture of either sex. This evaluation can best be made by the investigator in the context of the particular study species and collecting situation. A comparison of sex ratios of the turtle species captured at Ellenton Bay by baited aquatic traps and terrestrial drift fences is instructive (Table 14.1). The results demonstrate that even a long-term sampling effort can be strongly biased with regard to the probability of capture of an individual on the basis of its sex and could greatly influence the perceived sex ratio in some instances. For example, the numbers for individuals of Eastern mud turtles (*Kinosternon subrubrum*) captured in aquatic traps give the impression that the sex ratio is significantly unbalanced toward males, whereas the numbers captured terrestrially suggest that the sex ratio is not significantly different from 1:1. An earlier study that considered all adults captured by any means in the Ellenton Bay population revealed a significant, male-biased sex ratio (1.34, 268 males:200 females; Gibbons, 1983a), as does the total of all captures through 1987 (1.31, 405 males:308 females; this study).

The propensity of adult females to travel terrestrially during nesting results in a higher proportion of females in the samples collected with drift fences. In contrast, male *K. subrubrum* apparently are more likely to enter aquatic traps, perhaps because of a greater tendency to wander in search of females, and they therefore have a greater opportunity to encounter a trap. The result is that aquatic trapping apparently underestimates females, whereas with terrestrial trapping the opposite is true, so that the actual adult sex ratio lies somewhere in between. The sex ratio of aquatically trapped individuals of *T. scripta* is 2.05, and that of terrestrially captured individuals is 1.44 (Table 14.1), whereas the ratio based on all slider turtles at Ellenton Bay is intermediate at 1.74 (Table 14.3). This same phenomenon—aquatic traps' being more selective for males and terrestrial traps' being biased toward females—appears to be true for each of the six species at Ellenton Bay (Table 14.1). Comparisons with other types of aquatic traps or with other means of capturing turtles would also undoubtedly reveal a sex ratio bias and should be considered in establishing the perceived sex ratios.

The seasonal behavioral differences between the sexes can also have a direct effect on sex ratio perception (Table 14.2) and can interact differentially with collecting method. For example, more females of most species are cap-

Table 14.3. Influence of perceived size of each sex at maturity on adult sex ratio (male:female) in two South Carolina populations of *Trachemys scripta*

Females	Males					
	80	90	100	110	120	130
Ellenton Bay						
140	1.47	1.46	1.38	1.24	0.99	0.72
150	1.62	1.61	1.53	1.37	1.09	0.79
160	1.85	1.83	<u>1.74</u>	1.56	1.24	0.90
170	2.23	2.21	2.10	1.88	1.50	1.09
180	3.25	3.22	3.06	2.74	2.19	1.58
190	5.27	5.22	4.96	4.45	3.54	2.56
200	9.87	9.78	9.29	8.33	6.64	4.80
Par Pond						
160	1.59	1.59	1.57	1.54	1.45	1.31
170	1.66	1.66	1.64	1.61	1.51	1.37
180	1.76	1.76	1.74	1.71	1.60	1.45
190	1.91	1.91	1.88	1.85	1.74	1.57
200	2.09	2.08	<u>2.05</u>	2.02	1.89	1.71
210	2.41	2.40	2.37	2.33	2.19	1.98
220	2.70	2.69	2.66	2.61	2.45	2.22

Note: Column and row headings indicate plastron length in mm. Numbers in table indicate sex ratios based on numbers of turtles of each sex captured in each population at the indicated size categories. The actual sex ratio of each population based on known sizes at maturity of each sex is underlined. The mean size at maturity for males in both populations is 100 mm. Females in Ellenton Bay mature at about 160 mm; those at Par Pond mature at 200 mm. Sample sizes at the sizes at maturity: Ellenton Bay, 511 males, 294 females; Par Pond, 526 males, 256 females.

tured on land during late spring and early summer than in other seasons because of nesting activities. The greater capture of males in some seasons (e.g., *T. scripta* during the fall at most sites, Table 14.2) is presumably a reflection of the reported greater mating activity of males (Morreale et al., 1984; Parker, 1984; Gibbons, 1986).

Aside from the identifiable effects of collecting method and season, numerous less obvious factors presumably operate independently and interactively to result in the sex ratio perceived by the investigator. The annual variability in the sex ratio determined for four SRP populations of slider turtles (Table 14.2) demonstrates that even large sample sizes can result in dramatically different estimates of adult sex ratios in a turtle population during different years. For example, during the seven years at Ellenton Bay in which the number of adults captured was greater than 100, the sex ratio was highly significant ($p < .01$) in favor of males in three years, significant ($p < .05$) in one year, and not statistically significantly different from 1:1 in three years. Clearly, a single year's estimate should be considered circumspectly. This should not be taken as a discouragement to those of us interested in the demography of turtle populations but is intended as a word of caution in the interpretation of data.

DETERMINATION OF MATURITY OF INDIVIDUALS

Aside from the biases in sex ratio estimates resulting from sampling techniques and probabilities, an error can be

made because of the improper determination of maturity in one or both sexes. This type of mistake has been inherent in many population studies with turtles (Gibbons, 1970c) and other animals, resulting in inaccurate adult sex ratio estimates. Estimates of size and age at maturity have been made for the populations at Ellenton Bay and Par Pond (Gibbons et al., 1981), so the potential impact of errors on the accurate determination of the mean size and age at maturity can be observed for SRP slider turtles (Table 14.3). Thus, if the Ellenton Bay size at maturity for females were used with the Par Pond sample, the adult sex ratio would be calculated as 1.57 rather than 2.05. Conversely, the Ellenton Bay sex ratio, using the Par Pond size of maturity for females, would be 9.29 rather than 1.74.

The problem of differential growth rates and subsequent differences in ages or sizes at maturity among different populations of the same species within a region (Gibbons et al., 1981) confounds designation of size at sexual maturity. Studies must be tempered with the knowledge that misjudgment of size at maturity, and of its inter-population variability, can be a major influence on the determination of sex ratio estimates.

BIOLOGICAL FACTORS AFFECTING ACTUAL SEX RATIOS

Wilson (1975) cites three factors as normally determining the functional sex ratio in a population of animals, and they are applicable to turtles: (1) the sex ratio of hatchlings, (2) the differential mortality of the sexes, and (3) the difference in ages at maturity of the sexes. A fourth factor that could potentially affect the sex ratio is differential emigration or immigration of the sexes in the study population. Each of these can be considered on the basis of what is known about turtle populations and in terms of how sex ratios are likely to be influenced.

HATCHLING SEX RATIOS. Pieau (1974) first suggested that the sex of some turtles may be influenced by the temperature at which the eggs are incubated. A plethora of publications (Bull and Vogt, 1979; Morreale et al., 1982; Vogt and Bull, 1982; and many others) has demonstrated that many species of freshwater, terrestrial, and marine turtles lay eggs that develop as females at high incubation temperatures and as males at low ones. The reported pivotal temperatures vary but are generally within the range of 26°–29° C. The determination of sex has been based categorically on histological or gross examination of the reproductive organs in the hatchlings. To my knowledge, no one has conducted a controlled experiment to document that the juveniles actually develop into adults in the ratios predicted from the incubation temperatures. That is, I am not aware of any experiment in which eggs incubated at different temperatures were apportioned into two sets: (1) those dissected to determine sex ratios by histological dissection of hatchlings, and (2)

those hatched and raised to maturity, or at least to a point at which maturity is obvious in males, in order to determine if the sex ratio is consistent with what would be expected. This is a definitive experiment that deserves investigation. The use of laparoscopy would even permit such a study to be conducted on the same individuals that were sexed as hatchlings.

In species in which the primary sex ratio is a consequence of nest incubation temperatures, more of one sex could enter a population and ultimately affect the sex ratio of adults. This has not yet been conclusively documented to be a factor in determining the functional sex ratio of any natural population of turtles. However, Vogt (1980a) discovered unusually high proportions of females in *Graptemys ouachitensis* in Wisconsin. Although a sampling bias may have existed from his trapping heavily in the areas where females were likely to nest (Vogt, 1980a), he also attributed the sex ratio imbalance to the fact that females in his study area nest on open river beaches, which would result in higher temperatures and thus the production of mostly females (Vogt and Bull, 1984; Vogt, pers. com.). Limpus et al. (1983) reported a situation for loggerhead sea turtles (*Caretta caretta*) nesting on the Great Barrier Reef in which human interference of nesting beaches may have reduced the proportion of beach that normally produced females, thus potentially altering the hatchling sex ratio. The potential certainly exists, and other investigators should consider hatchling sex ratios as a possible influence on adult sex ratios.

DIFFERENTIAL MORTALITY OF THE SEXES. Once hatchlings enter a turtle population, any factor that results in differential survivorship of the sexes can affect the functional sex ratio. I see no reason to expect that juvenile turtles should show differential mortality on the basis of sex. Until the advent of maturity, when secondary sex characteristics and behavioral differences appear, natural selection would presumably operate equally on both sexes. However, at this time, no unequivocal evidence has been presented in the literature to demonstrate that one sex of juvenile turtles has a probability of mortality that is higher than, lower than, or equal to the other's.

Differential mortality of the sexes as adults, or in sexually size-dimorphic species in which one sex may be an adult while the other is a juvenile, may be an important factor. However, documentation of the actual or potential effects of differential mortality on sex ratio, and whether the patterns are consistent or vary interpopulationally, has not been reported for any species of turtle. Hurly (1987) reported a male-biased adult sex ratio in a red squirrel (*Tamiasciurus hudsonicus*) population in Ontario, Canada, and stated that it was the first example of differential mortality of the sexes in the species.

Numerous reports have been made of females that died during nesting excursions as a consequence of terrestrial

Table 14.4. Adult sex ratios (male:female) and the effect of maturation rate on sex ratio in South Carolina populations of *Trachemys scripta*

Location	All adults				All above 100 mm		
	Males	Females	Ratio	X ²	Females	Ratio	X ²
Pond B	185	78	2.37	**	131	1.41	**
Capers Island	14	45	0.31	**	45	0.31	**
Kiawah Island	19	17	1.12	NS	19	1.00	NS
Ellenton Bay	511	294	1.74	**	505	1.01	NS
Par Pond	526	256	2.05	**	406	1.30	**
Risher Pond	59	54	1.09	NS	77	0.77	NS
McElmurray's Pond	280	123	2.28	**	155	1.81	**
Cecil's Pond	82	33	2.48	**	47	1.74	**
Lost Lake System	556	290	1.92	**	380	1.46	**

Note: Turtles were captured from 1967 to 1986. Adults include all individuals above the mean size of maturity: males ≥ 100 mm plastron length, females ≥ 160 mm, for all populations except Par Pond (females ≥ 200 mm) and Capers Island and Kiawah Island (minimum sizes at maturity not determined). Because of the long-term study of some populations, some ratios include (1) individuals captured as many as 19 years apart from each other and (2) individuals that were immature at first capture but reached maturity during the study. A chi-square (X²) test corrected for continuity was used to determine level of significance. Abbreviation: NS, $p \geq .05$.

** $p < .01$.

predators (e.g., Shealy, 1976; Seigel, 1980b; Congdon, pers. com.), a differential mortality phenomenon that would result in shifts in the adult sex ratio. Differential mortality is presumably responsible for the sex ratio of the slider turtle population on Capers Island, South Carolina (Table 14.4), where the predominance of females is believed to be a consequence of heavy predation by alligators (Gibbons et al., 1979). Of the adults, smaller males are presumably more susceptible to large alligators in the relatively vegetation-free habitat and have been disproportionately eliminated from the population. This population had no juvenile recruitment from 1978 to 1986, and only large individuals of either sex remain.

Other examples of how differential size or behavior (e.g., overland mating quests by males) could result in one sex's being more vulnerable at certain times or in certain habitats can be envisioned. At this point, however, we need documentation of how differential mortality of the sexes affects sex ratios and whether the phenomenon is characteristic for the species or only peculiar to particular situations.

DIFFERENTIAL EMIGRATION AND IMMIGRATION OF THE SEXES. Male turtles of some species are more likely to travel greater distances and more often between populations than are female turtles (Gibbons, 1986; also see Chapter 16). Because of this difference in overland movement of the sexes, local populations of some freshwater turtles may be dynamic in the proportion of the sexes. The influence of emigration and immigration should affect only local populations, with a presumed balance being achieved over time among the local populations within a region. Thus, whereas populations in a region may differ in sex ratios at one season or during one year, the ratios

may be counterbalanced at other times because of emigration and immigration. This could explain much of the seasonal and annual variation observed in the four populations of *T. scripta* in South Carolina (Table 14.2). Investigators should be aware that the habitat they define as being occupied by a population may be interactive with noncontiguous habitats, so sampling errors result over short periods or during certain seasons or even different years. Thus, the actual sex ratio in a local population at a given time may not be representative of the functional sex ratio with regard to potential genetic exchange. This is a problem in many demographic studies in which the boundaries of the population cannot be precisely defined.

INFLUENCE OF MATURATION RATE. The single most important influence on actual sex ratios that has been documented in some turtle populations is the differential rate of maturity of the sexes that is characteristic of some species. Male slider turtles generally mature several years earlier than females (see Chapter 9.). Therefore, if no other factors are involved that result either in differential ratios at hatching or in differential mortality rates of the sexes, slider turtle populations experiencing juvenile recruitment will have more adult males than adult females (Table 14.4). The importance of this fact can be seen by comparing the sex ratios based only on mature females with the sex ratios that also include immature females above the male size at maturity, so that cohorts are compared (Table 14.4). The sex ratio more closely approaches 1.0 for some South Carolina populations by including these immature females. However, the resultant ratio is still significantly different from 1:1 in most cases, suggesting that other factors besides maturation rate may be involved in determining sex ratios in these populations.

Variation in Adult Sex Ratios among Sliders and Other Turtles

The discovery of consistent variation in a biological trait can give insight into its dynamics and the mechanisms that influence it. However, no strong geographical trend in sex ratio bias is evident in the few species of turtles, including slider turtles, for which several estimates are available (Table 14.5). Sufficient population records exist for too few turtle species to justify a categorical statement of whether sex ratios vary in any consistent pattern. One might speculate that if any trend were to be revealed, it would be that there are more males in cooler climates because of temperature-dependent sex determination, although local habitat variation or nest site selection could have an influence on natural nests that would override climatic trends (Morreale et al., 1982; Vogt and Bull, 1984). Also, one might conclude that if one sex had a fitness advantage over the other, natural selection at the histological level would operate to equalize the sex ratios.

Based on the estimates for slider turtles (*Trachemys scripta*), stinkpots (*Sternotherus odoratus*), eastern mud turtles (*Kinosternon subrubrum*), and chicken turtles (*Deirochelys reticularia*) in South Carolina (Table 14.5), sex ratio variability among populations within a region can be as great as that among regions. In fact, the variation within South Carolina populations of these species encompasses the range of ratios observed for them in most other regions. This suggests that geographical trends may be difficult to document if they are subtle and occur in species with high variability among regional populations. Before further speculation is made on this issue, thorough sampling must be done to determine the range of variability among regional populations as well as among different geographic regions.

The presentation of sex ratios in Table 14.5 does not reveal any clear phylogenetic trend at the family level. In fact, most species for which several samples are available vary from male-biased to female-biased sex ratios. However, many of the sex ratios given, including some of those from South Carolina, are based on small samples and on samples that are biased because of time and method of collections. Thus, adequate comparisons are difficult to make. At this time, I do not consider that any categorical statement can be made regarding any expectation that sex ratios are a trait tied to phylogenetic relationship per se. Differential sizes of the sexes at maturity are the only mechanism that can be considered a species trait that clearly affects adult sex ratios directly in some species of turtles, although differential mortality, emigration and immigration, or sexes at birth may influence the outcome in local populations.

Some of the ratios in Table 14.5 are aberrant from those expected mathematically, based on the sizes at which maturity is reached by the sexes. Using *T. scripta* as an exam-

ple, natural populations would be expected to have a significantly higher proportion of adult males, unless one or more of the other three factors are involved in altering the numbers of the sexes. In the 17 samples of *T. scripta*, 9 have more males than females ($p < .01$), 6 have sex ratios not significantly different from 1:1, and the remaining 2 have more females ($p < .01$). Of the South Carolina populations, the higher numbers of adult females are possibly explained by differential mortality of the sexes (Capers Island) and inadequate sampling (Kiawah Island). No apparent explanation can be given for the similar numbers of each sex at Risher Pond. The sample of Cahn (1937) was too small to make a valid assessment, but the large samples of Cagle (1942, 1950) and D. Moll (pers. com.) cannot be challenged in this way, suggesting either that an undetected sampling bias was involved or, perhaps more likely, that a true female-biased sex ratio occurred for some reason in these populations. Likewise, no obvious explanation is available for the higher female abundance reported by Webb (1961). The sample of Viosca (1933) was obviously a biased one, being composed of purchased animals from various populations, and should not be considered in an assessment of sex ratios for the species.

So when the 3 questionable *T. scripta* samples are eliminated (Kiawah Island; Cahn, 1937; Viosca, 1933), 9 have significantly more males, 2 have significantly more females, and 3 are not significantly different from 1:1. Therefore, 9 of 14 of the samples result in adult sex ratios that would be expected based on the differential sizes at which maturity is attained, and even they vary appreciably in the degree of the proportion of males. The variability that is apparent in the seemingly straightforward measure of sex ratios of a relatively well-studied species, whether as a result of sampling biases or natural occurrences, indicates that the interpretation of the causes of adult sex ratio in turtle populations is not a simple process and involves a complex of considerations.

Model for Natural or Sexual Selection of Sex Ratios

Data from several thoroughly assessed populations of *T. scripta* from South Carolina indicate that sex ratios in this species are weighted heavily toward males, although exceptions do exist (Capers Island). This is in contrast to the tendency for biased sex ratios of most animal species to be a consequence of greater female numbers, because of higher mortality of males (Trivers, 1972). The primary explanation for the high proportion of males observed in the South Carolina populations of slider turtles (Table 14.4) is differential maturation rates of the sexes. Male *T. scripta* reach maturity as a function of their body size after approximately 2 to 5 years of age, depending upon juvenile growth rates (Gibbons et al., 1981). Thus, fast-growing males from Par Pond reach maturity at a plastron

Table 14.5. Adult sex ratios of turtle species from published studies of natural populations

Taxon	Location	Males	Females	Sex ratio	X ²	Reference
Chelidae						
<i>Phrynops dahlí</i>	Colombia	13	19	0.68	NS	20
<i>Platemys platycephala</i>	South America	28	50	0.56	*	78
Cheloniidae						
<i>Chelonia mydas</i>	Aldabra	83	54	1.54	*	33
	Miskito Cay	132	337	0.39	**	14
	Indian Ocean	112	178	0.63	**	29
	Oman	128	114	1.12	NS	69
	Mexico	144	862	0.17	**	19
	Nicaragua	68	99	0.69	*	56
<i>Lepidochelys olivacea</i>	India	15	39	0.38	**	68
Chelydridae						
<i>Chelydra serpentina</i>	South Dakota	37	291	0.13	**	26
	SRP, S.C.	55	21	2.62	**	83
	Michigan	74	77	0.96	NS	6
		87	79	1.10	NS	76
	Quebec	27	28	0.96	NS	16
	Tennessee	14	8	1.75	NS	44
<i>Macrolemys temminckii</i>	Louisiana	25	33	0.76	NS	31
Emydidae						
<i>Batagur baska</i>	Malaysia	83	64	1.30	NS	54
<i>Chinemys reevesii</i>	Asia	119	110	1.08	NS	70
<i>Chrysemys picta</i>	Illinois	14	14	1.00	NS	10
		28	39	0.72	NS	4
		17	14	1.21	NS	10
		39	3	13.00	**	10
		55	45	1.22	**	39
	Louisiana, Arkansas	21	37	0.57	*	39
	Michigan	51	51	1.00	NS	10
		265	215	1.23	NS	24
		849	481	1.77	**	83
		875	325	2.69	**	76
		242	184	1.32	**	15
	New Mexico	55	54	1.02	NS	38
	New York	42	29	1.45	NS	43
		62	28	2.21	*	5
	Ontario	129	179	0.72	**	75
	Pennsylvania	374	375	1.00	NS	32
	Saskatchewan	64	61	1.05	NS	63
	Wisconsin	32	28	1.14	NS	38
		32	23	1.39	NS	39
		270	209	1.29	NS	21
	Tennessee	17	19	0.89	NS	39
<i>Clemmys guttata</i>	Indiana	17	15	1.13	NS	37
	Pennsylvania	61	79	0.77	NS	45
	Ohio	21	42	0.50	*	79
<i>C. insculpta</i>	Michigan	86	105	0.82	NS	50
	New Jersey	311	464	0.67	**	50
<i>C. marmorata</i>	California	246	210	1.17	NS	36
<i>C. mühlenbergii</i>	United States	22	29	0.76	NS	11
		82	75	1.09	NS	80
<i>Deirochelys reticularia</i>	Ellenton Bay, S.C.	265	95	2.79	**	83
	Lost Lake, S.C.	19	17	1.12	NS	85
	Risher Pond, S.C.	22	11	2.00	NS	83
<i>Emydoidea blandingii</i>	Massachusetts	41	33	1.24	NS	49
	Michigan	49	173	0.28	**	76
		14	55	0.25	**	28
<i>Graptemys barbouri</i>	Florida	180	131	1.37	**	41
<i>G. geographica</i>	Quebec	132	79	1.67	*	53
	Wisconsin	45	15	3.00	**	55
<i>G. nigrinoda</i>	Alabama	39	10	3.90	**	57
<i>G. ouachitensis</i>	Louisiana	48	85	0.56	*	71
	Wisconsin	68	265	0.26	**	55
<i>G. pseudogeographica</i>	Upper Missouri River	36	36	1.00	NS	25
	Wisconsin	68	109	0.62	**	55
<i>G. pulchra</i>	Southeastern United States	49	53	0.92	NS	81
<i>Malaclemys terrapin</i>	Kiawah Island, S.C.	138	84	1.64	**	83
<i>Mauremys caspica caspica</i>	Europe	56	44	1.27	NS	52
<i>M. c. rivulata</i>	Europe	30	21	1.43	NS	52
<i>M. leprosa</i>	Europe, Africa	44	38	1.16	NS	52
<i>Pseudemys concinna</i>	Florida	66	57	1.16	NS	30
<i>P. floridana</i>	Ellenton Bay, S.C.	59	45	1.31	NS	83
<i>Rhinoclemmys diademata</i>	Venezuela	11	30	0.37	**	67

Table 14.5 -- Continued

Taxon	Location	Males	Females	Sex ratio	X ²	Reference	
<i>Terrapene carolina</i>	Indiana	15	24	0.63	NS	37	
	Maryland	107	122	0.88	NS	9	
	Missouri	384	314	1.22	NS	42	
<i>T. coahuila</i>	Mexico	70	94	0.74	NS	40	
<i>Trachemys scripta</i>	Louisiana	123	102	1.21	NS	2	
	South Carolina	(See Table 14.4)					
	Mississippi	115	77	1.49	**	66	
	Illinois	403	441	0.91	NS	8	
		396	576	0.69	**	4	
		5	9	0.56	NS	3	
	Oklahoma	46	13	3.54	**	18	
	Panama	137	71	1.93	**	35	
	Belize	152	188	0.81	NS	82	
	Kinosternidae						
<i>Kinosternon flavescens</i>	Oklahoma	23	20	1.15	NS	22	
	Oliver National Wildlife Refuge, Okla.	64	88	0.73	NS	27	
<i>K. f. arizonense</i>	Donita's Pond, Okla.	20	13	1.54	NS	27	
	Arizona	7	22	0.32	**	64	
<i>K. f. flavescens</i>	Arizona, Mexico	8	15	0.53	NS	51	
	Nebraska	18	18	1.00	NS	64	
	United States, Mexico	311	263	1.18	*	64	
		158	137	1.15	NS	51	
<i>K. f. spooneri</i>	Illinois, Iowa, Missouri	60	58	1.03	NS	64	
<i>K. integrum</i>	Mexico	28	33	0.85	NS	13	
<i>K. sonoriense</i>	Tule Stream, Ariz.	99	90	1.10	NS	46	
<i>K. subrubrum</i>	Oklahoma	21	20	1.05	NS	22	
	Cowan Creek, Okla.	47	71	0.66	*	27	
	Tishomingo, Okla.	16	24	0.67	NS	27	
	Lake Texoma, Okla.	16	28	0.57	NS	27	
	Berry's Pond, Okla.	23	35	0.66	NS	27	
	Ellenton Bay, S.C.	268	200	1.34	**	62	
	SRP, S.C.	82	81	1.01	NS	62	
	Ellenton Bay, S.C.	405	308	1.31	**	83	
	Risher Pond, S.C.	27	40	0.68	NS	83	
	Rainbow Bay, S.C.	79	76	1.04	NS	83	
	<i>Sternotherus carinatus</i>	Oklahoma	22	36	0.61	NS	27
			17	15	1.13	NS	22
		Alabama	224	92	2.43	**	77
		United States	310	341	0.91	NS	47
		United States	80	97	0.82	NS	17
		43	46	0.93	NS	17	
		40	42	0.95	NS	17	
		29	36	0.81	NS	17	
		65	83	0.78	NS	17	
		51	35	1.46	NS	17	
	Jacob, Ill.	33	16	2.06	*	4	
	Elkville, Ill.	18	57	0.32	**	4	
	Oklahoma	18	18	1.00	NS	22	
	Michigan	118	115	1.03	NS	27	
	Whitmore Lake, Mich.	36	32	1.13	NS	83	
	Indiana	77	178	0.43	**	1	
	Indiana	11	19	0.58	NS	37	
	Ellenton Bay, S.C.	94	80	1.18	NS	83	
	Lost Lake, S.C.	37	29	1.28	NS	83	
	Risher Pond, S.C.	27	25	1.08	NS	83	
	Par Pond, S.C.	44	17	2.59	**	83	
	Steel Creek, S.C.	32	28	1.14	NS	83	
Pelomedusidae							
<i>Podocnemis vogli</i>	Venezuela	27	61	0.44	**	67	
Testudinidae							
<i>Chersina angulata</i>	South Africa	109	76	1.43	*	65	
	Aldabra	30	31	0.97	NS	34	
<i>Geochelone gigantea</i>	Anse Mais, Aldabra	51	94	0.54	**	23	
	Takamaka, Aldabra	80	73	1.10	NS	23	
	Turkey, Greece	48	23	2.09	*	58	
<i>Testudo graeca</i>	France	166	168	0.99	NS	72	
<i>T. hermanni</i>	Greece	121	114	1.06	NS	73	
<i>Xerobates agassizii</i>	Mexico	69	57	1.21	NS	59	
	Utah	65	50	1.30	NS	7	
<i>X. berlandieri</i>	Hargill, Tex.	31	8	3.88	**	60	
	Yurria Ranch, Tex.	36	32	1.13	NS	60	

Table 14.5 -- Continued next page

Table 14.5 -- Continued

Taxon	Location	Males	Females	Sex ratio	X ²	Reference
	Loma Tio Alejos, Tex.	75	36	2.08	**	61
	Laguna Atascosa, Tex.	67	39	1.72	**	74
Trionychidae						
<i>Trionyx muticus</i>	Kansas	1,148	168	6.83	**	48
<i>T. spiniferus</i>	Minnesota	73	98	0.74	NS	12
	Illinois	24	17	1.41	NS	4

Note: Sex ratios are based on best estimates from tables, figures, text, or personal communication with the author. Abbreviation: NS, $p \geq .05$.

References: 1, Risley, 1933; 2, Viosca, 1933; 3, Cahn, 1937; 4, Cagle, 1942; 5, Rancy and Lachner, 1942; 6, Lagler and Applegate, 1943; 7, Woodbury and Hardy, 1948; 8, Cagle, 1950; 9, Stickel, 1950; 10, Cagle, 1954; 11, Barton and Price, 1955; 12, Breckenridge, 1955; 13, Mosimann, 1956; 14, Carr and Giovannoli, 1957; 15, Sexton, 1959b; 16, Mosimann and Bider, 1960; 17, Tinkle, 1961; 18, Webb, 1961; 19, Caldwell, 1962a; 20, Medem, 1966; 21, Ream and Ream, 1966; 22, Mahmoud, 1967; 23, Gaymer, 1968; 24, Gibbons, 1968b; 25, Timken, 1968; 26, Hammer, 1969; 27, Mahmoud, 1969; 28, Gibbons, 1970c; 29, Hirth and Carr, 1970; 30, Jackson, 1970; 31, Dobie, 1971; 32, Ernst, 1971c; 33, Frazier, 1971; 34, Grubb, 1971; 35, Moll and Legler, 1971; 36, Bury, 1972; 37, Minton, 1972; 38, Christiansen and Moll, 1973; 39, Moll, 1973; 40, Brown, 1974; 41, Sanderson, 1974; 42, Schwartz and Schwartz, 1974; 43, Bayless, 1975; 44, Froese and Burghardt, 1975; 45, Ernst, 1976; 46, Hulise, 1976; 47, Iverson, 1977a; 48, Plummer, 1977; 49, Graham and Doyle, 1979; 50, Harding and Bloomer, 1979; 51, Iverson, 1979c; 52, Busack and Ernst, 1980; 53, Gordon and MacCulloch, 1980; 54, Moll, 1980; 55, Vogt, 1980a; 56, Mortimer, 1981; 57, Lahanas, 1982; 58, Lambert, 1982; 59, Osorio and Bury, 1982; 60, Rose and Judd, 1982; 61, Auffenberg and Weaver, 1969, in Rose and Judd, 1982; 62, Gibbons, 1983a; 63, MacCulloch and Secoy, 1983a; 64, Berry and Berry, 1984; 65, Branch, 1984; 66, Parker, 1984; 67, Fritchard and Trebbau, 1984; 68, Sitas et al., 1980, in Fritchard and Trebbau, 1984; 69, Ross, 1984; 70, Lovich et al., 1985; 71, Shively and Jackson, 1985; 72, Stubbs and Swingland, 1985; 73, Stubbs et al., 1985; 74, Bury and Smith, 1986; 75, Balcombe and Licht, 1987; 76, Congdon, pers. com.; 77, K. Dodd, pers. com.; 78, Ernst and Lovich, pers. com.; 79, Lovich, pers. com.; 80, Lovich and Ernst, pers. com.; 81, Lovich and McCoy, pers. com.; 82, D. Moll, pers. com.; 83, this study.

* $p < .05$.

** $p < .01$.

length of about 100 mm, similar to males from Ellenton Bay, which grow more slowly. Females in these two populations reach maturity at approximate ages of 6 to 8 years, not as a function of size. Thus, Par Pond females are greater than 200 mm in length at maturity, and those at Ellenton Bay are usually at least 160 mm. Consequently, a portion of the males of the population will have matured at least one to two years and as many as five to six years before females in the same cohorts. Therefore, the adult sex ratio is strongly influenced by the differential maturation rates of the sexes.

The impact of biased hatchling sex ratios, extreme differential mortality, or differential emigration and immigration of the sexes is more difficult to assess and has not been documented for the SRP populations at this time. Males commonly mature one to several years before females in many turtle species; hence, a higher frequency of males would be expected unless other factors override the effect. The hatchling sex ratio should not be expected to be 1:1 in any particular year, or even over long-term intervals, in *T. scripta* or other species of turtles with temperature-dependent sex determination. However, establishing the influence of hatchling sex ratios will be difficult in natural populations and is yet to be documented.

Survivorship curves of adult male and female *T. scripta* have not been shown to differ appreciably on the SRP (see Chapter 15); therefore, differential mortality patterns do not satisfactorily explain the observed sex ratio im-

balance. In fact, the numbers of males and females in age classes above that at which males reach maturity in the large Ellenton Bay population are effectively equal (Table 14.4), suggesting that mortality of the sexes within each cohort is similar in this population, with an assumption of 1:1 hatchling sex ratios. Differential survivorship of adults of both sexes is almost certain to occur in populations of many species simply because of differences in behavior patterns. Predator selection of adult females during nesting has been documented (e.g., Seigel, 1980b). Predation on males because they are smaller has been inferred in the Capers Island population of *T. scripta*. Because of the variability and unpredictability of environments, no universal rule would seem to apply as to which sex might be favored. Differential mortality of the sexes would be a population-specific phenomenon. This could be an explanation for why not all of the South Carolina populations had a 1:1 sex ratio after adjustment for the differing ages at maturity (Table 14.4), although the available data do not support or refute this contention.

Finally, the effects of differential emigration and immigration on sex ratio must be considered, although data available at this time shed only a dim light on the subject. Adult male turtles have a propensity for moving more often and for longer distances than females (Morreale et al., 1984; Parker, 1984; Gibbons, 1986; also see Chapter 16), resulting in females that are relatively sedentary within a habitat and males that have a high rate of ex-

change among areas. This can confound sex ratio estimates, depending on when and for how long sampling was done. For example, long-term sampling efforts in a single, localized area could result in a higher proportion of males in the overall region being sampled because of the higher turnover of males as they moved among habitats. Short-term sampling efforts would be biased by whether more males had departed the study area than had arrived at the particular time of the census.

The variation in estimated sex ratios for *T. scripta* during different seasons and years at Ellenton Bay is partially a function of this phenomenon (Table 14.2), because of the movement of individuals between Ellenton Bay and surrounding aquatic habitats suitable for slider turtles. A final bias that should also be considered is that resulting from the size of the study area. Clearly, the effects of emigration and immigration are reduced as more and more populated areas are encompassed in the sampling program.

Imbalanced sex ratios favoring males should be expected in adults of *T. scripta* or other species in which males mature first. Furthermore, an expected ratio can be predicted based on mean ages at maturity. Aside from the obvious possibilities of sampling biases, an alteration in this ratio would be a consequence of biased hatchling sex ratios, differential mortality, or emigration and immigration. None of the biological variables discussed, except differential sizes of the sexes at maturity, would appear to be a species trait, because all can vary as a function of conditions specific to each particular population.

Future Studies with Sex Ratios

Sex ratios in a population will continue to be an important demographic parameter to determine. Because of numerous sampling biases that can influence the investigator's perception of the sex ratio, it is essential that actual sex ratios in turtle populations be established with as much certainty as possible through thorough sampling programs. The casual reporting of sex ratios based on small, seasonal, or otherwise potentially biased samples will not further our understanding of the significance of sex ratios in turtle populations.

Because the observed sex ratio at any time is dependent on only four factors (sex ratios of hatchlings that ultimately make up the adult population, differential mortality rates of the sexes, differential emigration and immigration rates of adults of both sexes, and differential ages of maturity of the sexes), certain predictions can be made about what should be expected within a population. In sexually size-dimorphic species, the sex ratio will normally be imbalanced in the direction of a higher proportion of the earlier-maturing sex. This is based on the premise that in sexually size-dimorphic species, the smaller sex will mature at a significantly younger age than

the larger. For example, male-biased sex ratios should be particularly apparent in genera such as *Graptemys* and *Trionyx*, in which females attain dramatically larger sizes than males. When this is not the case, the first suspicion should be directed toward sampling bias, although natural factors may ultimately be determined as the cause. In turtle populations of species in which males and females are approximately the same size, the sex ratio will not be imbalanced by the maturity factor.

Actual sex ratios would differ from the condition expected from maturation rates as a result of aberrant hatchling sex ratios or because of sex-specific rates of mortality or emigration and immigration. Observation of a sex ratio that differs from that predicted for a population on the basis of maturation rates should first entail an examination of mortality rates of the two sexes and a search for evidence that they are indeed different. It is unlikely that any difference would be observed in the juvenile stages of the two sexes, because male and female turtles are presumably similar ecologically and physiologically until maturity is reached. Therefore, evidence of differential mortality of the adults should be sought. If the population interacts with others in the region, consideration should be given to whether the sexes vary in their emigration or immigration rates.

If equal mortality rates between adults of the two sexes are demonstrated in a population in which the sex ratio is different from that predicted from the maturation rates, and if emigration and immigration effects are ruled out, then differential mortality of juveniles or an unequal sex ratio among hatchlings is the only possible explanation. All of these considerations must be tempered with an awareness of how sampling methods influence the numbers of each sex captured and whether an investigator can distinguish between actual ratios and perceived ones that are strongly biased.

My prediction is that no documentation is forthcoming that reveals a significant difference in mortality between the two sexes during the juvenile stage. The shift in adult sex ratio because of a difference in sex ratio of the hatchlings from previous years could be a possible explanation in some situations (e.g., Vogt and Bull, 1984; Congdon, pers. com.) and should be looked for in natural populations. It is conceivable, for example, that unusually cool temperatures during the first part of the summer in successive years could result in an excess of male turtles in the populations of a region and could be ultimately reflected in the adult sex ratio in populations in that region. Unusually warm summers could, of course, result in an excess of females. Should this explanation seem like the appropriate one to use because of the observation of an aberrant sex ratio, a test would be to examine more than one population in the same region. If climatic temperatures are responsible, other regional populations having similar nest characteristics with regard to shading, hydric

conditions, soil type, and so forth should also show the same phenomenon.

My recommendation to investigators determining sex ratios in natural populations is to consider every possible bias in the estimate of the actual, functional, adult sex ratio before the ratios are reported in the literature as meaningful. The reporting of sex ratios that are based on small samples or that have a high possibility of having been influenced by various sampling biases should be avoided. Such information is counterinstructive to anyone attempting to attribute significance in some synthetic or conceptual manner to sex ratios in natural populations. A special caution is urged in regard to determinations of age and size at maturity of individuals of each sex in particular populations. An error in establishing maturation times can strongly influence perceived sex ratios. A careful examination of age structure and age-specific ratios should be a primary target in turtle population studies where sex ratio is an element of interest.

The sex ratio has been demonstrated to be a species attribute of turtles only with respect to the influence of differential maturation rates. That is, in species in which males ordinarily mature earlier than females, a male-biased sex ratio should be expected and could be considered a characteristic of the species. The other potential demographic influences have not been documented to follow characteristic trends in any species of turtle to date. However, such trends may indeed exist and should be sought.

In a consideration of the application of evolutionary concepts to turtle sex ratios, a theory that emerges as a

paradox in the slider turtle, as well as other species in which males mature at significantly younger ages than females, is the one first proposed by Fisher (1930) that the female should produce more of the sex that is the least costly and in shortest supply. Because the sex of a turtle egg of many species is apparently not determined until after egg laying, natural selection cannot operate on this trait unless female turtles select nest sites on the basis of anticipated sex-determining temperatures and with a proper assessment of which sex would be more successful in the population. Convincing evidence that such behavior and insight occurs in female turtles has not been demonstrated.

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