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Chelonian Conservation and Biology, 1996, 2(1):114–117
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Possible Demographic and Ecologic Consequences of Sex Ratio Manipulation in Turtles

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In a recent article Vogt (1994) advocated the use of environmental sex determination (ESD) as a conservation tool to assist in the recovery of imperiled turtle populations. His suggestion is predicated on the assumption that female turtles are more important than males since one male can inseminate many females (polygyny). With this foundation he suggested that captive breeding programs for rare and declining turtles should begin producing and releasing hatchlings at a ratio of 6–20 females for every male. Vogt's proposal was questioned by Mrosovsky and Godfrey (1995) as a "superficially attractive scheme [that] is reminiscent of headstarting," another dubious conservation tool (Frazer, 1992). In this essay I continue the cautious approach suggested by Mrosovsky and Godfrey and elaborate some of the potential demographic and ecologic consequences of manipulating sex ratios in turtle populations.

Sex Ratio Variation in Turtles. — An examination of the influence of sex ratio manipulation on turtles requires an understanding of natural sex ratio variation. Adult sex ratios in turtle populations can vary according to four underlying factors, assuming that sampling bias is not a concern (Gibbons, 1990; Lovich and Gibbons, 1990).

1. The sexes can experience differential mortality, a likely possibility in most highly aquatic species in which females are the only sex to leave the relative safety of the aquatic environment to lay eggs.

2. The sexes may exhibit differential immigration or emigration (Parker, 1984; Gibbons et al., 1990; Lovich, 1990a). Males of many species of turtles are known to move more frequently and for greater distances than females and this can produce episodic or lasting differences in sex ratios among various assemblages of turtles, especially in patchy environments (Parker, 1990).

3. Many turtles exhibit ESD, with the sex of hatchlings determined by the temperature at which eggs are incubated (Ewert and Nelson, 1991; Janzen and Paukstis, 1991a, 1991b). Although ESD can cause considerable variation in the primary sex ratio within cohorts among years, some long-term studies have demonstrated that sex ratios tend toward unity over many years (Zweifel, 1989; references in Lovich and Gibbons, 1990; Mrosovsky, 1994).

4. Bimaturism, or differences in the timing of attainment of maturity between the sexes, has been shown to influence adult sex ratios in several turtle species, including *Malaclemys terrapin* (Lovich and Gibbons, 1990), *Trachemys scripta* (Gibbons, 1990), and *Clemmys insculpta* (Lovich et al., 1990). Simply stated, the sex that matures earlier is expected to predominate numerically, assuming that other factors do not exert an overwhelming influence (Lovich and Gibbons, 1990).

Recent research (Lovich and Gibbons, in prep.) has demonstrated a relationship between sexual size dimorphism and adult sex ratios in turtles due to the correlation of both to bimaturism and the coupling of sex determining pattern to sexual size dimorphism (Ewert and Nelson, 1991). The significance of this finding is the suggestion that biased adult sex ratios are to be expected in some turtle species and that the direction and magnitude of bias is predictable: under natural conditions, adult sex ratios will tend to be male-biased in species in which females are larger than males, and female-biased when males are larger than females.

The assumption that adult sex ratios are naturally biased in some turtle species, as has been shown in numerous detailed long-term studies, has profound implications for any program that would attempt to manipulate the sex ratio to produce an excess of females (Morreale et al., 1982). A major concern would be the impact of such a program on the reproductive ecology of a species, specifically as it relates to the effects of multiple paternity, sperm competition, fertility, and intra- and inter-sexual competition on population persistence.

Multiple Paternity and Sperm Competition. — It is now well established that several turtle species exhibit multiple paternity (Harry and Briscoe, 1988; Kaufmann, 1992; Galbraith et al., 1993). Coupled with the sperm storage

ability possessed by many turtles (Gist and Jones, 1989), multiple paternity and sperm competition must be considered as significant adaptations in their reproductive strategy. In reality, the importance of these traits has been largely ignored in turtles (Galbraith et al., 1993).

Several adaptive explanations for sperm storage and multiple paternity have been proposed for turtles and are reviewed by Galbraith (1993). One of the most obvious explanations is the possibility that sperm storage is an adaptive feature of the reproductive strategy of long-lived organisms in which females may not have contact with males in some years. Combined with the possibility that frequent copulations might increase offspring viability in some reptiles as a possible result of sperm competition (Madsen et al., 1992), it is logical to assume that these traits would be strongly selected for in turtles.

Multiple paternity and sperm competition are only effective when the number of reproductive males is sufficient to facilitate multiple inseminations. Recent work by Sugg and Chesser (1994) demonstrated the importance of breeding structure on gene diversity in natural and captive populations. They showed unequivocally that multiple paternity increases the effective population size above that expected from polygyny or monogamy. Significantly, as the number of males actually mating decreases, the impact of multiple paternity also decreases.

Sperm competition, an extension of male-male conflict within the female reproductive tract, can lead to the production of offspring with greater fitness, assuming that enough males are available to assure multiple inseminations of females. However, most discussions of sperm competition have ignored the possibility of competition among various haploid genotypes of sperm within the ejaculate of a single male. Haig and Bergstrom (1995) suggested that rivalry within ejaculates limits cooperation among members of an ejaculate when they compete with sperm from rival males. Further, a gene that gains an advantage in competition within an ejaculate (called a segregation distorter) can increase in frequency even when it is associated with significant costs to organismal fitness. If the segregation distorter impairs the competitiveness of ejaculates in which it occurs, then the relative advantage of the distorter is reduced when females mate with multiple males.

The preceding discussion suggests that multiple paternity and sperm competition may be very important in the persistence of populations and cautions against manipulating the sex ratio of turtle populations to produce an excess of females.

Fertility. — Chan (1991), cited in Mrosovsky and Godfrey (1995), suggested that the poor hatch rates (30% infertility according to Mrosovsky, 1994) of leatherback sea turtles (*Dermochelys coriacea*) in Malaysia may be attributed to insufficient numbers of males to fertilize clutches. Observations by Wood and Wood (1980) on captive green sea turtles (*Chelonia mydas*) showed that the percentage of nesting females was directly correlated with the observed duration of mating. They suggested that the duration of observed mating is a partial function of the number of males that copulate with a female. Males of this species are known to engage in multiple copulations (Booth and Peters, 1972). Thus, even the act of nesting can be related to the relative abundance and behavior of male turtles.

Intra- and Inter-Sexual Competition. — Sexual selection operates to enhance features or behaviors that increase access of one sex to the other (usually of males to females). Sexual selection can result in intra-sexual competition for mates, usually in the form of male-male combat, or inter-sexual choice, usually in the form of female choice of a mate (Trivers, 1972). Abundant evidence is available to suggest the existence of both forms of sexual selection in turtles, as discussed below.

Combat among males during the breeding season has been documented for many turtles, particularly in terrestrial species and those in which males are larger than females (Berry and Shine, 1980; Gibbons and Lovich, 1990; Kaufmann, 1992; Ernst et al., 1994). Kaufmann (1992) found that fighting occurs among male wood turtles (*Clemmys insculpta*), resulting in a linear dominance hierarchy that determines access to breeding females. In this species adult sex ratios tend to be female-biased under natural conditions (Lovich et al., 1990). As such, these and other species in which males are larger than females may not be adversely affected by an additional sex ratio bias toward females, but the exact consequences of sex ratio manipulation remain unknown.

Female choice of males, through discriminatory mating, has also been demonstrated in turtles. Booth and Peters (1972) showed that female green sea turtles (*Chelonia mydas*) were capable of avoiding copulation with a variety of behavioral patterns including biting, avoidance, and refusal. The authors concluded that the female is completely in control of whether mating occurs or not. This behavior was confirmed by Crowell Comuzzie and Owens (1990) who suggested that females signal reproductive receptivity to males but also exercise mate selectivity by avoiding mounting. Lovich et al. (1990) observed that female slider turtles (*Trachemys s. scripta*) assume an active role in courtship including the use of proceptive behaviors that actively solicit male attention and may communicate receptivity.

Both forms of sexual selection require a sufficient pool of the competitive sex for intra-sex combat or choice by the discriminating sex. If sex ratios are manipulated to produce an excess of females then adaptations driven by sexual selection may be altered. The yellow-bellied slider turtle *Trachemys s. scripta* is a good example of a taxon in which adult males naturally outnumber adult females in well-studied populations (Gibbons, 1990) and numerous males compete for the attention of a female during the mating season (Cagle, 1950). Given the active role females play in courtship behavior, one must question the result of shifting or inverting the sex ratio toward an excess of females. Would an adequate number of males be available for sexual selection to operate effectively? Although the question may seem

academic, the implications are potentially profound when considering the fate of declining populations of rare turtles. For example, fewer than 30 *Pseudemydura umbrina* remain in the wild, and captive breeding is a major part of their recovery program (Kuchling et al., 1992).

Ecologic Consequences. — Sex ratio manipulation can have possible ecologic consequences as well. Resource partitioning between the sexes can result from natural selection due to differential interactions of each sex with its environment (Shine, 1989; Lovich, 1990b). Several ecological mechanisms have been incorporated into models that could account for resource partitioning, especially as it relates to the evolution of sexual size dimorphism (SSD) (Slatkin, 1984). The first is the dimorphic niche model. If there are intrinsic differences between males and females because of their different energetic needs to ensure successful reproduction or because of different social roles, then there will be different optimal morphologies for each. In the second model, bimodal niche selection, each sex has the same needs and is ecologically similar, but there are two optima toward which either sex could evolve (Schoener, 1969, 1977). The third model, and perhaps most frequently invoked ecological cause of SSD, is competitive displacement, a process similar to ecological character displacement as described by Brown and Wilson (1956) and Dunham et al. (1979). In this model the resources used by a given sex are determined to some extent by a particular trait. For example, individuals that are larger or have a larger feeding apparatus may be able to consume larger food items than smaller counterparts. It is often assumed that differences in the distribution of such a trait lessens competition between the sexes for the limiting resource (Selander, 1966; Schoener, 1966; Earhart and Johnson, 1970; Feduccia and Slaughter, 1974; Fitch, 1981).

Few studies have examined the role of inter-sexual resource partitioning in turtles. Tucker et al. (1995) noted significant dietary partitioning between the sexes of diamondback terrapins (*Malaclemys terrapin*) with females eating larger prey and a wider diversity of prey than males. Sloan et al. (1996) found differences in diet between male and female alligator snapping turtles (*Macroclemys temminckii*). Differences in prey size and distribution may lead to habitat partitioning between the sexes.

Given that the population of *M. terrapin* studied by Tucker et al. (1995) has a strongly male-biased adult sex ratio (Lovich and Gibbons, 1990) one must question the impact of artificially manipulating the sex ratio to produce an excess of females. Would the excess females upset the balance of resource partitioning by eating too much of the prey base on which the population subsists? Would resource partitioning itself break down? These are theoretical questions, perhaps, but questions that need to be considered before manipulating the sex ratio of turtle populations. In actuality, the "experiment" to test this hypothesis is already being "conducted" since terrapin populations are experiencing extremely high male mortality in crab traps (Bishop, 1983; W. Roosenburg, *pers. comm.*).

Summary

Vogt (1994) performed a valuable service to the chelonian conservation community by initiating a dialogue on the merits of using sex ratio manipulation as a conservation tool. In the spirit of continuing that dialogue I maintain that there is insufficient information at this time to evaluate fully the potential impact of sex ratio manipulation on turtle population persistence and that the information available argues against manipulation. Furthermore, Vogt's suggestion to produce predominantly female turtles would only exacerbate problems caused by predicted global warming which has the potential to eliminate the production of male offspring in some turtle species (Janzen, 1994).

The pitfalls of sex ratio manipulation in turtle populations were first highlighted by Morreale et al. (1982) who warned that artificial incubation projects for green sea turtles (*Chelonia mydas*) were releasing all male, all female, or even intersex hatchlings. They recommended against the use of artificial incubation in an effort to maintain natural sex ratios. Later, Frazer (1992) eloquently articulated the fallacy of headstarting as another conservation technique that emphasizes treating symptoms instead of causes. Too many conservationists had defined the disappearance of turtles only numerically in terms of there not being enough turtles. The "halfway technology" solution, as discussed by Frazer (1992), was simply to produce more turtles without focusing attention on causes for their disappearance. This theme was amplified by Meffe (1992) who noted the propensity of humans to embrace technology in the search for solutions to ecological problems, again focusing on symptoms and not causes.

The idea of using sex ratio manipulation to "jump-start" declining turtle populations has all the allure of technology noted by Meffe combined with the short-sightedness of the halfway approach noted by Frazer. Now the problem appears to be not just having too few turtles, but not having enough female turtles. In a world that is increasingly hostile to turtles of both sexes, I see little hope for this approach until we face the real problems of over-exploitation, pollution, habitat destruction, and rampant human population growth (Meffe et al., 1993).

Acknowledgments. — Earlier versions of this manuscript benefited from comments offered by Roland de Gouvenain, Whit Gibbons, Fred Janzen, Gary Meffe, Peter Pritchard, and Anders Rhodin. Manuscript preparation was aided by contract number DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory.

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Received: 12 November 1995. *Accepted*: 31 December 1995.