Sex Ratios of Sea Turtles

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ABSTRACT Estimates of sex ratios of hatchling sea turtles range from approximately 50% female (Chelonia mydas and Dermochelys coriacea in Suriname) to approximately 90% female (Caretta caretta in Florida). Seasonal sex production profiles (SSPPs) show how similar overall sex ratios can be achieved in dissimilar ways. Possible explanations of the data include sampling error, constraints on evolutionary adjustment of pivots or behavior to local thermal conditions, and violations of assumptions required by classical Fisherian theory.

WHY STUDY NATURAL SEX RATIOS
Having the direction of sexual differentiation determined by the environment (ESD) requires explanation at two levels: that of proximate mechanism and that of adaptive value. For temperature determination of phenotypic sex (TSD) there are several plausible candidates: temperature dependent synthesis or activity of enzymes (Standora and Spotila, '85; Desvages and Pieau, '92), heat shock proteins (Harry et al., '90), and temperature sensitive gene expression (Deeming and Ferguson, '89). It is not too difficult to imagine mechanisms. However, it is harder to think up convincing specific proposals for the adaptive value of TSD in reptiles.

When I started working on TSD, it seemed to me that speculations on its adaptive value would be better founded if one knew what the animals themselves were doing with this system. If natural sex ratios were 1:1 near the time when parental investment ends in species whose male and female offspring are equally costly, then one might take that as a confirmation of Fisher's ('30) theory and not search so hard for special functional significance. TSD might just be an alternative to the more familiar XY-XX or ZZ-ZW chromosomal mechanism of going about the matter of balancing sex ratios. But if ratios were highly skewed, that might foster different speculations.

A second reason for wanting to learn about sex ratios in nature is the need for some yardstick against which to assess conservation measures. If global warming strikes, it might become necessary to manipulate reptile eggs to avoid producing all of one sex. But what proportions should one aim for? Also, there are a number of current conservation practices that involve thermal changes, such as transplanting eggs (Mrosovsky and Yntema, '80). Knowledge of natural sex ratios would help in estimating the risks of such interventions. And if eggs are harvested for conservation through utilization—for instance, for reptile ranches—then one needs to arrange the take in a way that does not detrimentally affect sex ratios. The same applies to the selection of eggs for protection. In Malaysia, the 30% infertility of eggs of leatherback turtles (Dermochelys coriacea) has been attributed to lack of males in the population. This insufficiency has in turn been attributed to having in the past protected eggs mostly from the warmer, female producing months of the season (Chan, '91). Thus there are applied as well as theoretical reasons for wanting to know what animals themselves are doing with TSD in the wild.

SAMPLING PROBLEMS
It sounds like such a simple question, but discovering natural sex ratios is beset with empirical and interpretational traps. It is not just that one needs to sample in a thermally typical year; one also needs to know that egg laying occurred at a time of year typical for the species. This latter point is neglected in most studies. In addition, one must sample fairly in space and in time. It is also necessary to know what are the limits of the breeding population, whether the habitat is natural, and whether the population is in equilibrium. For these reasons tabulating sex ratios from different studies without reference to the sampling problems is questionable. Such meta-analyses that try to extract consensus from a number of inadequate studies are to be viewed with suspicion. The sampling problems, as they apply...
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POSSIBLE EXPLANATIONS OF SEX RATIOS

Classic sex ratio theory

When one sees how relatively even sex ratios can be achieved in different regions by various combinations of nesting seasons, pivotal levels, and thermal conditions, it might be natural to take that as evidence of the power of Fisherian principles. That fairly balanced ratios can occur in a variety of ways in these reptiles could be taken as a better way of validating classic sex ratio theory than finding even sex ratios in mammals and birds. In those cases it can always be argued that results are the inevitable outcome of sex chromosome mechanics (but see Wilson, '75).

Sampling error reconsidered

The data from Florida loggerheads put an abrupt halt to such speculations. Although the Florida data represent only one out of the four SSPPs in Figure 1, they are the hardest to dismiss as sampling error. They are based on 3 years sampling for sex and supported by 5 years of temperature monitoring (Fig. 2). The Suriname SSPPs and beach temperature recordings are for one season, and the study in GA and SC was not designed for producing sex ratio estimates and had its share of sampling imperfections. Some additional points support the belief that loggerheads in the USA are producing highly skewed sex ratios. First, about 90% of the loggerhead nesting along the southeast coast takes place in Florida (Murphy and Hopkins, '84). Even if the more northern nests were producing entirely males, there would still be a massive female bias (Mrosovsky and Provancha, '89). Second, 68% of juvenile loggerheads caught off Florida in 1984-1986 were female (Wibbels et al., '91). These juveniles would have passed through their thermosensitive period (during incubation of the egg) a number of years before the Mrosovsky and Provancha study, 1986-1991. Assuming that chances of male or female turtles being caught are similar when they are immature, the USA was producing many more female than male loggerheads in years before our sampling in Florida.

Why might loggerheads be producing highly skewed ratios and leatherbacks and green turtles more balanced ratios? Perhaps this diversity stems from an unlucky choice of an atypical year for the work in Suriname. I view this possibility as sufficiently plausible to make it important to continue work there or in other tropical areas. On the other hand, when pivotal and beach tempera-
Figure 1.
turtles are also considered (Fig. 2), there is a certain consistency to the data. The pivotal level is the temperature giving 50% of each sex when eggs are incubated at constant temperatures (Mrosovsky and Pieau, '91). In Florida, beach temperatures are well above the pivotal for most of the season. On this basis one would expect some males to be produced at the beginning of the season and few or none after that—just what was found by direct sampling for sex ratio. In Suriname, more even sex ratios would be expected because during the months when nesting is frequent, sand temperatures are sometimes below and sometimes above pivotal. For hawksbill turtles in Antigua, heavy female biases would not be expected because mean temperatures appear to be mainly below pivotal. However, it would not be safe to infer that there must necessarily be a marked male bias there, though this is a possibility. Metabolic warming toward the end of the thermosensitive period or brief excursions above pivotal level might be enough to produce a number of females (Bull, '85). The top of the egg mass is subject to greater thermal variation than the 30 and 60 cm depths measured in this study (Mrosovsky et al., '92).

The variety of relationships between pivotal and beach temperatures (Fig. 2) suggests that diversity of sex ratios in different populations should be expected. Of course, the pivotal levels obtained might also be subject to sampling error. These are no more than estimates of population pivotals, based on incubation of a few clutches in constant laboratory conditions. There is evidence that pivotals vary between clutches (Bull et al., '83; Mrosovsky, '88). However, at least for the loggerheads in Florida, it seems unlikely that the population pivotal temperature was much underestimated; otherwise, males should have been found in more of the large number of clutches from which samples were collected in the field (Mrosovsky and Provancha, '92). Thus there is sufficient internal consistency between data on pivotal levels, beach temperatures, and the actual samples for sex ratio to make it worth at least pondering explanations other than sampling error for the diversity of sex ratios in these studies.

**Fig. 1. Seasonal sex production profiles (SSPPs).** The graphs give estimates for month or half-month periods (laying dates on x axis) of the number of each sex produced at hatching, expressed as a percentage of the total number of hatchlings produced in the season. Similar areas covered by male and female SSPPs imply an even overall sex ratio (values given numerically as % female). Data on sex ratios for green and leatherback turtles come from a single year; data on relative nesting frequency at different times of the season are means of 11 years. The data, methods of sampling, and n values are given in Schulz ('75) and in Mrosovsky et al. ('84b). For leatherbacks, 7.4% of the sample of gonads showed little sign of differentiation at hatching ("indeterminate" category in Mrosovsky et al., '84b) and have been counted as males on basis of lack of germinal epithelium (Dutton et al., '85). For the green turtles, 1.1% were intersexes and have been included with the males. SSPP estimates for loggerhead turtles in GA and SC come from nesting distribution data for 6 years; the sex ratio data come from unsystematic sampling over 3 years for other purposes; some of the nests sampled had been reburied (Mrosovsky et al., '84a). Data for Florida loggerheads (Mrosovsky and Provancha, '92) are means of SSPPs calculated separately for each of 3 years; it has been assumed that the few loggerheads nesting in the first half of May produced all males and the few after the middle of August all females. For all populations, data were available for the main nesting seasons (i.e., estimates would not be greatly altered by a few uncounted turtles laying outside the study periods or by lack of sampling for sex ratio at the ends of the season). In addition, not shown in this figure, there are estimates ranging from approximately 50–75% female for some other populations of sea turtles. Some of these do not present information on nesting frequency (Rimblot-Baly et al., '87; Maxwell et al., '88), and some are based on extrapolations from data from limited parts of the season, or depend on assumptions about pivotal levels and incubation duration-temperature relationships (Standora and Spotila, '85; Spotila et al., '87; see also Benabib, '84, and comments in Mrosovsky and Provancha, '89, '92).

**No special function: Conservatism in pivotals and behavior**

Perhaps there is no particular adaptive value to TSD (Bull, '80; Mrosovsky, '80). It might simply be a device that works adequately as a way of producing some of each sex. In slowly maturing species, like sea turtles, imbalances in hatching sex ratio in thermally atypical years will be smoothed out by recruits to the breeding population coming from a number of different years. Moreover, if genetic sex determines the direction of sexual differentiation of eggs incubated close to the pivotal (Zaborski et al., '88) (see also Figs. 3, 4), then production of almost all females in a hot year will sow the seed of a corrective masculinisation in later years. Many of the females produced in the hot year will be genetically males (ZZ in most turtle species). When they mate with males (ZZ or ZW), the genetic makeup of their offspring will predispose the embryos to develop into males in years when temperatures are closer to pivotal level.

If there is no particular special value in TSD as a way of producing some of each sex, then the
Fig. 2. Relationship of pivotal temperatures (horizontal lines) to sand temperatures over the main nesting season for different sea turtle populations. To enhance comparability, all temperatures are for 60 cm; at this depth variations due to measures being taken at different times of day are minimized. This figure is designed to show, in terms of general trends, how the average sex ratio of hatchlings would be expected to vary over the season and between different beaches. The two

variety of relationships between pivotal and beach temperatures might result from pivotal being a conservative characteristic in turtles. Perhaps consequent biases in sex ratio cannot always be adequately compensated for by changes in behavior because of constraints on when and where nesting is possible. There might be little variation in behavior for natural selection to work on. Bull et al. (88) found that individual female leopard geckoes, Eublepharis macularius, did not consistently choose warm or cool sites for nesting, but these authors rightly cautioned against extrapolating from laboratory studies to field conditions. Stoneburner and Richardson (81) reported that loggerhead turtles crawled up the beach until the temperature rose abruptly by approximately 2.0°C. The temperatures measured were those of the surface. As soon as the turtle is a certain distance past the wet tide-washed area, surface temperature would tend to rise. It remains to be demonstrated that particular temperatures at nest depth are chosen and whether there are individual differences in such a choice. Individual leatherback turtles do not consistently travel particular distances up the beach from the water mark (Eckert, '87). Individual green turtles do not consistently choose one zone (such as near the treeline or near the water) of the beach for nesting (Bjorndal and Bolten, '92). Possibly natural selection might be able to exert pressure on how early or late in the year sea turtles begin their nesting (Mrosovsky and Provancha, '92). Extensive studies on variability of nesting behavior and its thermal consequences are needed.

Turning to pivotal temperatures, it is notable that those available for sea turtles are clustered close to 29°C (Table 1). The fractions of a degree

points above the month labels are temperature means for half-month bins and are for typical nesting sites. Of course, sex ratios of particular clutches will have different ratios because of variation in ambient temperature and in pivots. For green and leatherback turtles, mean of "sand" and "border" areas is shown (Mrosovsky et al., '84b); the solid line (L) represents pivotal level for leatherbacks from Rimblot-Baly et al. ('87), the dashed line (G) pivotal for green turtles from Mrosovsky et al. ('84b). For loggerhead turtles, data collected over 5 years are shown for "mid-beach sites (Mrosovsky and Provancha, '92). Data for hawksbills are for 2 years for "shaded" sites. Loggerheads and hawksbills do not typically nest as deep as 60 cm, but values for 30 cm were usually within approximately 0.5°C of the 60 cm values (Mrosovsky and Provancha, '92; Mrosovsky et al., '92). Generally similar data on 60 cm depth temperatures in French Guiana are in Rimblot-Baly et al. ('87).
in Table 1 should not be taken too seriously in comparing studies using different conditions and ways of measuring temperature. For instance, the greater temperature variation in some studies (e.g., Limpus et al., '85) might have resulted in more females being produced. For freshwater turtles, Bull ('85) has shown that even when mean temperature is the same, increased variation around this mean increases the number of females; the effect may arise because more developmental time occurs when thermal excursions are above rather than below the mean, and therefore there is more development at female producing temperatures, even though the mean temperature may be at pivotal (Pieau, '82). We are at the limits of affordable current technology for specifying pivots. Inevitably there is some thermal variation within incubators, and it is not feasible to record the temperature of each egg. But the results are sufficient to show that pivots do not vary greatly among sea turtles.

Fig. 3. Diagram of transitional range of temperature (TRT) and pivotal temperatures (vertical dashed lines) for a turtle species with ZZ males and ZW females. P1, P2, and P3 represent the pivots that might be expected from WW, ZW, and ZZ samples; 1m shows the limit below which 100% of the embryos are masculinized, 1f the limit above which 100% of the embryos are feminized (from Mrosovsky and Pieau, '91).

If a particular sex ratio were an evolutionarily stable strategy (ESS), then one would expect pivotal and beach temperatures to be related in a way that would produce similar sex ratios for populations of turtles nesting in thermally different places or times (cf. Blackmore and Charnov, '89). It was partly to look for such adaptive relationships that the study of hawksbill turtles, *Eretmochelys imbricata*, was undertaken. Hawksbills commonly nest high on the beach in the shade, and it had been thought that they might have a low pivotal temperature. This proved not to be the case, even though beach temperatures were lower than those of other populations shown in Figure 2. In studies in which pivotal levels from different parts of the range of a reptilian species have been compared, little difference has been found (review in Mrosovsky, '88; Ewert and Nelson, '91; but see Ewert et al., this issue, for some new data).

The closest indication of some modification in the pivotal temperature in sea turtles is perhaps the somewhat higher value for leatherbacks (29.5°C) in the Guianas compared with that of green turtles (28.8°C) nesting on the same beach. Since relatively more leatherbacks nest when it has begun to warm up after the rainy season, their higher pivotal makes their overall sex ratio more similar to that of green turtles than it would have been if both species had the same pivotal. However, although an estimate of green turtle pivotal for Suriname was obtained, unfortunately data delimiting the full transitional range of temperature were lacking. Sex ratios are not dependent just on pivotal, but on the shape of curve within the range of where temperature exerts effects on sex (transitional range of temperature = TRT, Fig. 3) and on how rapidly the curves approach the 100% female and 100% male asymptotes at either end of this range. The effects of a lower pivotal in greens might be counteracted by slowness to asymptote to 0% female at the lower end of the
TRT. Therefore, further study of this case is needed.

**Condition-dependent factors**

Trivers and Willard ('73) realized that selective pressures to produce more of one sex might arise if the environment affected the fitness of males and females differentially. The environment they had in mind was the nutritional condition of the mother of an ungulate. If the mother was well nourished, her offspring would be large. This might benefit a male more because by fighting off other males he would be able to mate with more females. If the mother was in poor condition, capable only of producing a small, weak calf, then it might be better to allocate her resources to a female which might produce at least some offspring, while a weak male might be excluded from breeding altogether. The critical points are that maternal condition predicts the condition and later reproductive success of the offspring and that maternal condition has differential effects on male and female fitness (Fig. 5).

This argument has been extended by Charnov and Bull ('77) to explain environmental effects occurring after the mother is out of the picture. Provided that the environment affects male and female fitness differentially, then selective pressures arise for control of sex ratio. By implication, and stated explicitly later, ESD may be favoured "because it enables the embryo to control its sex in response to the environment" (Bull, '81). Trivers and Willard ('73) also envisaged that the control of sex ratio was postponed until after the combination of XX and XY chromosomes at conception. This type of condition-dependent selective pressure may therefore be called Triversian for short, to contrast it to the more familiar Fisherian frequency-dependent selective pressures (frequency of the two sexes in the population).

Could such Triversian selection apply to TSD in turtles? It is not necessary that temperature itself directly influence survival of male and female embryos differently, so long as incubation temperature is correlated with different fitness for males and females later on. Conceivably, incubation temperature correlates with subsequent growth which in turn correlates with adult size and fitness (Ferguson and Joanen, '82; Deeming and Ferguson, '89). It should be noted that if such types of differential growth are important, they would provide plausible explanations not only of TSD, but also of skewed sex ratios (should those be substantiated). This is because with a situation such as that diagrammed in Figure 5, the average fitness of one of the sexes is higher than the average fitness of the other sex. Since both sexes contribute equally to the next generation, for the average fitness to differ between the sexes there must be different numbers of the two sexes. The sex with the lower average fitness (i.e., the sex that is produced in the poorer condition) must...
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**TABLE 1. Pivotal temperatures of sea turtles**

<table>
<thead>
<tr>
<th>Species (country)</th>
<th>Pivotal (°C)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leatherback</td>
<td>29.5</td>
<td>Rimblo-Baly et al. ('87)</td>
</tr>
<tr>
<td>Green</td>
<td>28.8</td>
<td>Mrosovsky et al. ('84b)</td>
</tr>
<tr>
<td>Green</td>
<td>28.0–30.3²</td>
<td>Standora and Spotila ('85)</td>
</tr>
<tr>
<td>Hawksbill</td>
<td></td>
<td>Mrosovsky et al. ('92)</td>
</tr>
<tr>
<td>Antigua</td>
<td>29.2</td>
<td>McCoy et al. ('83)</td>
</tr>
<tr>
<td>Olive ridley</td>
<td>approximately 30³</td>
<td>Yntema and Mrosovsky ('82)</td>
</tr>
<tr>
<td>Loggerhead</td>
<td>approximately 30⁴</td>
<td>Mrosovsky ('88)</td>
</tr>
<tr>
<td>USA</td>
<td>29.0³</td>
<td>Limpus et al. ('85)</td>
</tr>
<tr>
<td>Australia</td>
<td>28.6</td>
<td>Maxwell ('87)</td>
</tr>
<tr>
<td>S. Africa</td>
<td>29.7⁵</td>
<td></td>
</tr>
</tbody>
</table>

¹Methods of measuring temperature, constancy of incubators, moisture, and number of temperatures tested (i.e., resolution) varied between studies.
²Estimated from field studies.
³Sexing by gross morphology, not validated against histology (for comments see Whitmore et al., '85).
⁴The earlier estimate of a 30°C pivotal for USA loggerheads has been revised down to 29°C, partly because of better resolution in temperature and partly because of introducing a 0.5°C correction factor to reflect the finding that the eggs in a moist substrate tend to be cooler than the incubator.
⁵This is higher than the 27.0–29.3°C estimated from field studies for this population (Maxwell et al., '88).

be more abundant (Frank and Swingland, '88). Nevertheless, the existence of extreme sex ratio biases would remain a problem because condition-dependent selection does not operate in isolation from frequency-dependent selection (Fig. 5). The more extreme the skew, the stronger will be the counteracting Fisherian pressures, and therefore, it has been argued, large imbalances would be unlikely to be stable (Bull and Charnov, '88).

However, there is another factor that should affect sex ratios: the abundance of various kinds of conditions (environments/patches). If environments in which one sex is fitter are more common, then there will be a tendency for sex ratios to be skewed in that direction. If the environment in which one sex is fitter is not only very common, but also is one in which fitness for both sexes is very low, then large biases could develop and be stable. Most of the offspring from the poor environments might never reproduce, and those that were able to might owe this to being the fitter sex in that environment. Quantitative treatment is provided by Bull ('81). Therefore, it is possible in theory that combinations of Triversian pressures and patch frequency could result in highly skewed sex ratios being stable.

The problem with this conjecture is that when one moves from the armchair to the field, these factors are not obvious. Powerful condition-dependent factors for turtles remain to be demonstrated. For slowly maturing species it is hard to see how

![Fig. 5. Diagram showing gender-different changes in fitness (solid lines) as the condition of the offspring changes (after Bull, '81). For reptiles, incubation temperature or some correlate might be the relevant condition, but how temperature has such gender-specific effects is not understood. When the fitness of one sex exceeds that of the other, the allocation of resources for reproduction should switch between these sexes (a). For reptiles, the switch point should approximate the pivotal temperature. Density-dependent Fisherian factors still operate; therefore, the switch point should shift to b if males become abundant, because the fitness of males will be lowered (dashed line). The shapes of the fitness functions influence the extent of such shifts. For example, if the fitness of males increases steeply at low temperatures, surplus males in the population should not shift the switch point as much as if the fitness of males increases gradually.](image-url)
temperature during a short period in the middle of incubation would correlate with some factor that years later made one sex fitter than another, especially considering the variety of patterns in different reptiles relating sex ratio to temperature (Ewert and Nelson, '91). In sexually dimorphic species, being large presumably benefits one sex more. However, the correlation between the presence of TSD and sexual dimorphism in reptiles is not compelling; and whether high temperatures produce males or females does not seem to be linked to which sex is the larger as an adult (Janzen and Paukstis, '91b; see also Ewert et al., this issue). Even within crocodilians, data are not consistent on what kind of start in life is associated with different incubation temperatures. In Crocodylus johnstoni, warm temperature incubation results in hatchlings that are lighter but have more yolk (Whitehead et al., '90), whereas in Alligator mississippiensis, lighter hatchlings come from intermediate temperatures (Joanen et al., '87).

**Other Fisherian assumptions not met**

Absence of differential condition-dependent effects on fitness of the sexes is just one of a number of assumptions underlying Fisherian theory (Bull and Charnov, '88). For instance, if siblings influence each other’s fitness either by competing for mates or by helping each other, then the Fisherian assumption of random mating is not met. Within a season green sea turtles have high nest-site fidelity for a particular stretch of beach (e.g., Bosc and Le Gall, '86). If females also return to the stretch of their natal beach where they hatched, there would be opportunities for interactions between siblings (Mrosovsky, '80). However, without more information, speculations about non-random mating are tenuous.

Again one needs to distinguish between explanations of TSD and of skewed sex ratio. Sex ratio skews on account of non-random mating can occur in animals whose sex is determined by sex chromosomes (e.g., competition for resources between sedentary females is associated with male biased sex ratios in prosimians) (Clark, '78).

**Disequilibrium states**

One major reason for being open-minded about explanations of sex ratio data is that usually we do not know whether the populations studied are in an equilibrium state. If a population is severely depleted, then patches that produce the fittest turtles may not be fully occupied, and there will be opportunities for turtles that would otherwise be relegated to poorer patches to move into the better ones. When the population is abundant, then good patches will be fully occupied, and other turtles will have to adopt the best of a bad situation tactic (BBS) (see Gross, '84). When population levels fall, tendencies to occupy the better patches will be able to express themselves in more individuals. If the species had a TSD mechanism, perhaps to accommodate some condition-dependent factor, then its sex ratio could become skewed in the disequilibrium state, even if the Triversian factors were not very powerful in themselves.

In a world so much altered by people, there is a real possibility that populations under study are not in equilibrium. Harvesting, alteration of the relative frequency of different patch types, and the beginning of global warming—near to pivotal levels even a fraction of a degree C could alter sex ratios—are potential causes of disequilibrium. All this makes it extremely hard to bring data on sex ratios to bear on sex ratio theory. When a skewed ratio is found, is that a temporary departure from a Fisherian situation or a manifestation of an ESS under some other set of circumstances?

**EVALUATION AND SUMMARY**

The main conclusion is that we are far from firm conclusions in this field, or should one say bog. Figure 6 diagrams relationships between different categories of uncertainty. A few general points may nevertheless be in order.

This paper has focussed on possible explanations for the data on sex ratios rather than on explanations for the existence of TSD, although the two are interrelated (for speculations on the adaptive value of TSD see Bull, '80, '81; Mrosovsky, '80; Deeming and Ferguson, '89; Ewert and Nelson, '91; Janzen and Paukstis, '91a,b; Korpelainen, '90). The phylogenetic inertia explanation for the existence of TSD seems less attractive now that it is known that different species within a family can exhibit either TSD or GSD (Ewert and Nelson, '91a; Janzen and Paukstis, '91a).

On the other hand, the sex ratios resulting from TSD do appear to be subject to constraints. In sea turtles, the combination of relatively similar pivotal values, nest site, and nest season fixity seem to dictate overall sex ratios in a given year and the way the overall values are achieved, the SSPPs. Doubtless imaginative scenarios could be devised for why in midseason loggerheads should produce females, and greens males, but I view these more as consequences rather than reasons for TSD. One might think
that TSD would liberate species to perform all sorts of clever manoeuvres with their sex ratios. Instead it seems to have subjugated them to the vagaries of the weather, with the greenhouse effect ominously on the horizon.

Suppose that long enough sampling periods (decades) were used to average out these thermal vagaries. If skewed equilibrium sex ratios were found, then they might encourage explanations of TSD in terms of condition-dependent effects on male and female fitness, or non-random structure of mating groups, or some other violations of the assumptions of Fisherian theory. If skews were extreme, then for whatever reason those skews might be desirable, or even if skews were only temporary responses to transient conditions rather than being ESSs, it would suggest an additional function of TSD: to provide a mechanism for producing extreme skews. Korpelainen ('90) concluded that “adaptive sex ratio variation is considerably easier for organisms with ESD, and this feature is the ultimate cause for the evolution and maintenance of ESD.” Mrosovsky ('80) suggested that TSD “would allow turtles greater scope in varying sex ratio than if they were constrained by a heteromorphic chromosome system.” Why turtles might need such scope remains a mystery.

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