TEMPERATURE AND THE LIFE-HISTORY STRATEGIES OF SEA TURTLES

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Abstract—1. Sea turtles have a high fecundity, high mortality, great longevity life history strategy.
2. With the exception of the leatherback, turtle distribution is constrained by the 20 C surface isotherm.
3. All sea turtles exhibit temperature-dependent sex determination (TSD) with pivotal temperatures close to 29 C.
4. It is suggested that hatchling sex ratio will vary chaotically because of TSD.
5. Because of TSD and natal homing, sea turtles are likely to be adversely affected by global warming.
6. TSD and global warming have implications for conservation/management of sea turtles. © 1998 Elsevier Science Ltd. All rights reserved

Key Word Index: Sea turtles; temperature; temperature-dependent sex determination; chaos; global warming

INTRODUCTION

There are seven living species of sea turtles (Table 1) drawn from two families that are only distantly related; a diphyletic origin for extant sea turtles cannot be ruled out (Bowen *et al.*, 1993). Detailed scientific study has largely been limited to green, loggerhead and leatherback turtles; amongst the other species hawksbills and Kemp's ridleys are rather better known than either olive ridleys or flatbacks. All sea turtle species are endangered, so the type and number of investigations that can be carried out upon them is limited ethically and by statute. Observational or experimental replication is commonly compromised. Particularly invasive physiological or biochemical studies are rare, so turtle researchers often turn to common freshwater/brackish water forms (e.g. *Trachemys scripta, Chrysemys picta, Malaclemys terrapin, Chelydra serpentina*) as useful models, and extrapolate to marine species. Because of these constraints, generalizations about sea turtle biology need to be viewed with some reservation.

The basic sea turtle life history strategy is, however, similar in all species (Fig. 1; see Miller, 1997 for review). Female turtles mate in near-shore waters, probably storing sperm for several weeks after a single mating. They lay eggs in nests dug on tropical, subtropical or warm-temperate beaches. Parental care beyond the energetic contribution to each egg is limited to choice of nesting site and stereotyped burial and smoothing of the nest area.

Egg number per clutch is very high by reptilian standards (roughly 50–200 eggs, depending on species, subpopulation and individual; IUCN, 1982) and females of most species appear to lay several clutches per nesting season (<6–7 in green turtles) at intervals of 9–30 days, but usually do not breed every year. Eggs, much larger as well as more numerous than most freshwater species, incubate for about 2 months. They hatch at any time of the day or night, but usually emerge from the nest at night, the hatchling turtles crawling down the beach and swimming rapidly and continuously ("swimming frenzy") out to sea. Much of their subsequent life is still enigmatic, though Atlantic loggerhead turtles spend several years (perhaps as many as 10–12) drifting with oceanic currents (Caldwell, 1968; Carr and Meylan, 1980; Stoneburner *et al.*, 1982; see also Musick and Limpus, 1997 for review) before recruiting to the subadult/adult coastal populations. It is usually assumed that the other species behave in similar fashion, though there are indications that the flatback, *Natator depressa*, may not have a pelagic phase. Sea turtles show considerable species-specific diversity of feeding habit (IUCN, 1982). Growth is slow and sexual maturity is attained after many years in cheloniid sea turtles (roughly 6–10 in hawksbills and ridleys, 15–20 in loggerheads, 20–50 in green turtles), though there is some evidence that leatherbacks may grow to maturity much more quickly, reaching their far greater adult body size in as little as 13–14 yr (Zug and Parham, in sub-

Table 1. Classification of living sea turtles. Following
Bowen *et al.* (1993) and Pritchard (1997)

Family Dermochelyidae
    Genus   *Dermochelys*
                Dermochelys coriacea
                (Leatherback turtle)
Family Cheloniidae
  Tribe Chelonini
    Genus   *Chelonia*
                Chelonia mydas
                (Green turtle)
  Tribe Carettini
    Genus   *Caretta*
                Caretta caretta (Loggerhead turtle)
    Genus   *Eretmochelys*
                Eretmochelys imbricata (Hawksbill
                turtle)
    Genus   *Lepidochelys*
                Lepidochelys olivacea (Olive ridley
                turtle)
                Lepidochelys kempii (Kemp's ridley
                turtle)
    Genus   *Natator*
                Natator depressus (Flatback turtle)

mission). At maturity turtles are believed to return
to their natal beaches to breed. Adult turtles breed
for several decades; green turtles at least attaining a
century or more. In consequence, a female may lay

Fig. 1. Diagram of generalized sea turtle life history.

several thousands of eggs in her lifetime. Mortality
is known to be very high during the early stages of
the life history; large numbers of eggs and hatchl-
ings appear to be needed to saturate the appetites
of guilds of terrestrial and aquatic predators. Once
adult, predatory pressures (in the absence of man)
are low. All stages of the life history are profoundly
affected by temperature.

TEMPERATURE, DISTRIBUTION AND MIGRATION

When at sea, cheloniid distribution appears to be
constrained approximately by the 20°C surface iso-
therm. For green, hawksbill, flatback and olive rid-
ley populations, distribution is essentially tropical
and subtropical, while for the Kemp's ridley and
(especially) the loggerhead, animals spend much
time in warm temperate waters, showing tempera-
ture-linked migrations between high latitude fora-
ging grounds and lower latitude overwinterings
areas. Thus, loggerheads that spend the summer in
the coastal waters of New York State migrate south
to Florida in the autumn.

Leatherbacks have a quite different distribution.
While they breed in the tropics, they forage widely
in cool seas during the late summer and autumn,
often penetrating the arctic circle. They have been
recorded off Japan, Newfoundland, Iceland and
western Norway and are regular visitors to waters
around the UK (e.g. Nishimura, 1964; Bleakney,
1965). Leatherbacks are the most widely-distributed
of living reptiles; in the southern hemisphere they
have been reported from Chile, Peru and the waters
around New Zealand. Water temperatures associ-
ated with their high latitude feeding migrations are
in the range 5–15°C. S. A. Eckert (unpublished
data) has recently used satellite tracking to demon-
strate within-year round trip migrations of
11,000 km between the Caribbean and central north
Atlantic. It is also known that leatherbacks are
deep divers, regularly reaching 500 m, and some-
times exceeding 1200 m (Eckert *et al.*, 1984, 1986);
such dives briefly take them into water at (5°C
where they seek out gelatinous prey (Davenport,
1988; Davenport and Balazs, 1991).

Leatherbacks are endotherms, maintaining a core
body temperature of around 25°C by a variety of
anatomical/physiological adaptations (Mrosovsky
and Pritchard, 1971; Frair *et al.*, 1972; Greer *et al.*,
1973; Davenport *et al.*, 1990). These include posses-
sion of a thick layer of subcutaneous blubber, coun-
tercurrent heat exchangers in the flippers, different
compositions of peripheral and central lipids and
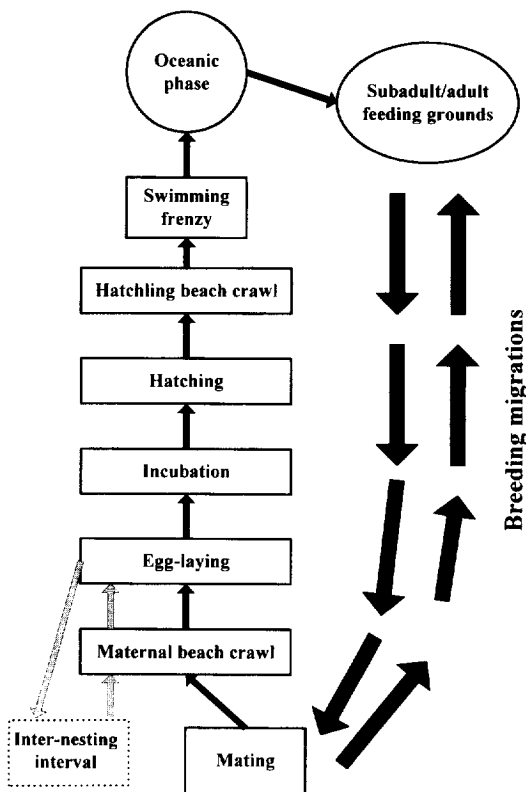an unusual oesophageal arrangement that allows

gelatinous food to be warmed before reaching the core (Davenport, in press).

TEMPERATURE AND MORTALITY

Low or high temperatures are a significant source of mortality in several turtle species. In the north Atlantic specimens of juvenile turtles (particularly loggerheads, but occasionally green turtles or Kemp's ridleys) are often found dead or dying in coastal waters because of "cold-stunning" (Schwartz, 1978; Morreale *et al.*, 1992; Meylan and Sadove, 1986). This phenomenon appears to stem from adverse weather conditions taking young turtles out of the oceanic gyres that normally keep them in warm surface waters. In the UK and western Europe prolonged strong southwesterlies are associated with subsequent loggerhead stranding episodes, as in 1990 when small loggerheads were reported from shores around the Irish Sea. Once in cooler waters, young turtles face a spiral of detrimental consequences. At around 20°C they will cease to feed (Birse and Davenport, 1987) and at 15°C locomotory integration becomes degraded (Davenport *et al.*, 1997). Finally, at sustained temperatures much below 10°C, coma will be followed by death.

Adult turtles feeding in enclosed, shallow waters close to the limits of geographical distribution are also vulnerable to cold-stunning during spells of cold weather (Witherington and Ehrhart, 1989). In these circumstances animals often survive; Witherington and Ehrhart reported mortality levels of only 8.1–11.5% during single cold snap episodes. However, in such long-lived animals the cumulative life-time risk can be high at the margins of their distributional range.

Nesting and emergence of hatchlings from the nest normally take place during the night or at dusk/dawn, when environmental temperatures are usually below 30°C even in the tropics. Terrestrial locomotion is inefficient and stereotyped (Davenport, 1987); in consequence both nesting females and newly-emerged hatchlings can sometimes become trapped by beach flotsam, whether natural or artificial. Once immobilized and exposed to the full force of the sun they are likely to die of combined hyperthermia and desiccation (e.g. Bustard, 1972).

HIBERNATION

Felger *et al.* (1976) were the first to report hibernation in sea turtles; they recorded winter dormancy in a population of green turtles living in shallow water. Later Carr *et al.* (1980) found a rather more interesting situation—loggerheads apparently hibernating, buried in the walls of submarine canyons. This suggests that loggerheads can survive without breathing for periods of weeks or more, but so far this phenomenon has not been investigated further.

TEMPERATURE AND INTERNESTING INTERVAL

Within single nesting seasons, females of all species usually nest several times. The internesting interval is shortest in the leatherback (9–10 days) and longest in the two ridleys (17–20 < 28–30 days). Interestingly, Sato *et al.* (unpublished data) have recently found that loggerheads exhibit much longer internesting intervals in Japanese waters during years when seawater temperatures are low, than in warm years. No data are yet available to determine whether this results in overall fecundity per nesting season being lower.

TEMPERATURE AND INCUBATION DURATION

As with other reptilian eggs, incubation is affected by temperature in two ways. Firstly, successful incubation is only possible within certain thermal limits. Secondly, eggs incubate faster at higher temperatures. Bustard (1972), for example, reported that green turtle eggs from Queensland would only develop successfully at constant temperatures between 25–27°C at the lower thermal limit and 35–37°C at the upper limit; incubation times ranged from 6–13 weeks depending upon environmental temperatures. It should be remembered that these are constant temperatures; the short-term survival range will undoubtedly be rather wider (see Miller, 1997 for review). Nest temperatures are variable not only on a single beach within a season and at different levels on the shore, but also vary with depth within a single nest (deeper eggs are incubated at rather lower, more stable temperatures). It is presently impossible to give "typical" nest temperatures with any confidence, beyond noting that the mean temperatures are usually between 25°C and 30°C. The influence of short periods of extreme temperature is unclear; Miller points out that the last third of incubation is particularly temperature-sensitive; eggs rarely hatch if exposed to temperatures below 23°C or above 33°C.

TEMPERATURE-DEPENDENT SEX DETERMINATION

All sea turtles, like most other chelonians, show temperature-dependent sex determination (TSD) of

their offspring's gender. They do not have morphologically identifiable sex chromosomes, although there is some inconclusive evidence (for green and Kemp's ridley turtles) for underlying weak genotypic sex determination (GSD), masked and overriden by TSD except near the pivotal temperature (Wellins, 1987; Demas *et al.*, 1990; Girondot *et al.*, 1994). Weak GSD overriden by TSD has been more firmly established in freshwater turtles (*Emys orbicularis*; Zaborski *et al.*, 1988; Girondot *et al.*, 1994). The temperature of incubation during the middle third of embryonic development determines the sex of the hatchling, with high temperatures yielding females, low temperatures yielding males (Fig. 2). This thermosensitive period coincides with the period when histological differentiation of the gonads is detectable (Pieau and Dorizzini, 1981). Sex determination is all-or-nothing; intersex hatchlings are rare. Pivotal temperatures (the temperature which yields a 1:1 sex ratio in eggs reared at constant temperature) have been determined for most sea turtle species (Table 2), but Mrosovsky and Pieau (1991) point out that these are often based on extremely small samples (such as a single clutch). Under fluctuating thermal conditions, it appears to be the proportion of time that the pivotal temperature is exceeded that determines sex. The transitional range of temperatures (TRT: constant temperatures of incubation at which both male and female hatchlings are produced) is narrow for all
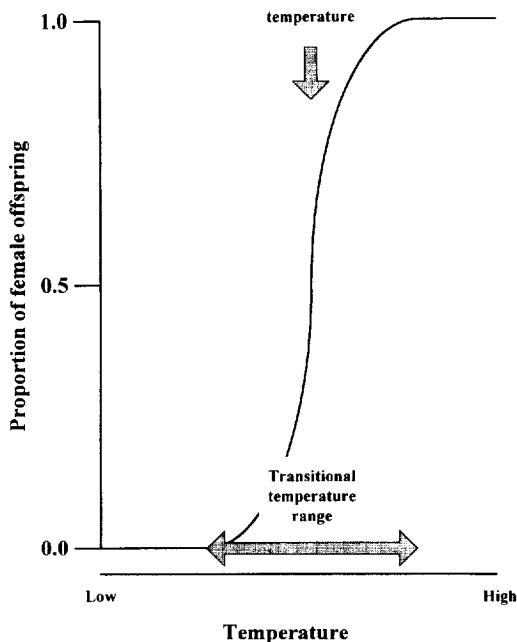
Table 2. Pivotal temperatures of sea turtle species

Species	Pivotal temperature (°C)	Source
Chelonia mydas	28.26	Ackerman (1997)
Caretta caretta	28.74	Ackerman (1997)
Lepidochelys olivacea	29.13	Ackerman (1997)
Eretmochelys imbricata	29.20	Mrosovsky *et al.* (1992)
Dermochelys coriacea	29.50	Mrosovsky (1994)

species (see Ackerman, 1997). For example, for the loggerhead Maxwell *et al.* (1988) showed that the difference in mean temperature during the critical period between wholly male and wholly female clutches was only 1.1 °C. It needs to be emphasised that, since most clutches are not reared in the TRT, the majority of nests yield hatchlings that are mostly (if not all) one sex. It has been suggested that single-sex clutches are of adaptive value, since they will minimize the risk of in-breeding associated with sibling mating. However, this seems to be a negligible risk for such long-lived animals which are unlikely to return simultaneously to the natal beaches.

A striking feature of the pivotal temperatures shown in Table 2 is their similarity; despite the separation of species for many millions of years, all have pivotal temperatures clustering closely around 29 °C. The author believes that this similarity reflects the great similarity of nest environment amongst sea turtles; all dig nests about 0.5 m deep that substantially dampen temperature fluctuations by comparison with air temperatures (Turnage, 1939). Presumably, over long periods, selection operates to determine pivotal temperature (thus compensating for long-term climatic changes), so the similarity of nesting environment would force a convergence of pivotal temperature.

The biochemical mechanisms that underly TSD have been extensively studied in turtles (see Crews *et al.*, 1994; Crews, 1996 for review), though most data have been collected from common emydid turtles (e.g. *Trachemys scripta*) rather than sea turtles. Figure 3 shows a simplified summary of the process. Sex is determined by an appropriate steroid hormonal cascade (as in animals exhibiting GSD), but the nature of the cascade is determined by temperature, presumably activating genes encoding for steroidogenic enzymes (e.g. reductases and aromatases) and steroid hormone receptors. Interestingly, production of either female offspring, or male offspring is an active process—in contrast to the "female default" situation in mammals.

Fig. 2. Diagram of temperature-dependent sex-determination in sea turtles (after Mrosovsky and Pieau, 1991).

Masculinizing
temperatures (low)

Feminizing
temperatures (high)

Testosterone

Reductase   *Aromatase*

Dihydrotestosterone   **Estradiol**

male-producing hormone
cascade

female-producing hormone
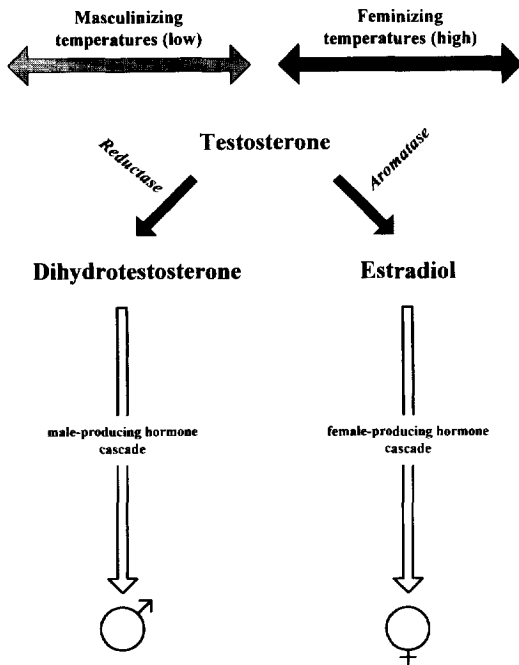cascade

♂   ♀

Fig. 3. Simplified biochemistry of temperature-dependent sex-determination in sea turtles (after Crews *et al.*, 1994).

In the real world, environmental temperatures vary diurnally and seasonally, clutches are laid at different times in a breeding season at different places on the shore where nest temperatures and clutch sex ratios differ (Spotila *et al.*, 1987; Maxwell *et al.*, 1988), while eggs are packed tightly into a nest, so metabolic heating can perhaps become a significant factor towards the end of the thermosensitive period (but see Maxwell *et al.*, 1988). Unsurprisingly, seasonal and interannual changes in sex ratios have been reported (e.g. Mrosovsky *et al.*, 1984; Maxwell *et al.*, 1988; Horikoshi, 1992), with cool periods yield males and vice versa. Bull and Charnov (1988) demonstrated that TSD can produce sex ratios that differ from the 1:1 ratio predicted from GSD (Fisher, 1930), and that such skewed ratios might be adaptive (though they were not specifically considering sea turtles). For about 70 yr there has been a general understanding that "in populations of turtles, females usually outnumber males" (Yntema, 1976), though many of the field or laboratory studies performed are open to criticism. Sex ratios of adult sea turtles are difficult to assess, though some studies have failed to show significant deviations from a 1:1 ratio (e.g. Limpus *et al.*, 1985). Wibbels *et al.* (1991) reported that an apparently random sample of immature, oceanic stage loggerheads off Florida had a sex ratio of 2:1 (females:males). Two questions can therefore be

posed for sea turtles: (1) are sex ratios skewed if averaged over several seasons/years? (2) if a skew exists, can an adaptive function for it be suggested? However, before attempting to answer these questions, two important caveats have to be entered. First, since it seems very likely that the freshwater ancestors of sea turtles exhibited TSD, sea turtles may simply be committed to a reproductive strategy that is of no particular advantage to them (Bull, 1980; Mrosovsky, 1980). Secondly, most workers have assumed that turtle populations are in equilibrium (a prerequisite for the 1:1 Fisherian ratio), though Mrosovsky (1994) points out that Man's influences may have resulted in disequilibrium. Aside from this possibility, there are good fundamental reasons for thinking that that sea turtle sex ratios may *never* be in equilibrium. Temperature of egg incubation is, *a priori*, affected by at least four factors: (1) weather/climate during the nesting season, (2) tidal height (perhaps influencing characteristics of the female beach crawl), (3) vegetational cover at the top of the beach (controlling shading of nests), (4) turtle nesting behaviour. It is well known that weather/climate and tidal cycles are inherently chaotic (e.g. Lorenz, 1963), i.e. they feature elements of both predictable pattern and unpredictable randomness over a wide range of time scales (days to millenia). The quantity of vegetational cover on a given beach is also likely to be controlled by weather (stripped by hurricanes, consolidated by periods of more stable conditions), and hence be chaotic in turn. It is not yet known whether female turtles can exert control over incubation temperature, perhaps by choosing warmer or cooler nesting sites, but given a chaotic thermal future it is difficult to envisage the advantage gained by such choice, particularly in species that do not mature for decades, and in which inter-generational mating must be common. Equally, if we accept that incubation temperature varies in chaotic fashion, then a search for an average sex ratio will be quite futile, since sex ratio will also vary chaotically and *never* be in equilibrium. We should *expect* hatchling sex ratio to vary between years (already known), decades (suspected) and centuries/millenia (beyond our patience!). The paper of Janzen (1994) on painted turtles (*Chrysemys picta*) is of relevance here; predicted sex ratios (derived from ambient temperature levels) for the period 1942–1993 ranged from 0% females to 100% female, with an unbiased mean of 52% female, but a chaotic variation about the mean was obvious (and made discernment of any overall trend impossible).

For most sea turtle species the question of long-term sex ratio average could not be answered con-

clusively anyway; there are inherent ethical, legal or logistical problems in sampling adult populations, while the methodology for reliably sexing hatchlings or juveniles without sacrifice has not been available for long enough (e.g. Mrosovsky, 1994).

Assigning causes or adaptive values to a systematically skewed sex ratio (if real) is not easy either. Individual green turtles have been shown to grow at extremely variable growth rates (Bjorndal and Bolten, 1988), though specific growth rates for an individual appear to be temporally stable (Davenport and Scott, 1993a,b). A potential source of variation in fitness between the sexes [which would permit an adult sex ratio different from 1:1 (Bull and Charnov, 1988)] would be a sexual dimorphism of growth rate, but Bolten et al. (1992) found no evidence to support such a dimorphism. Equally, there appears to be no reliable evidence of sexual dimorphism of mature size in any sea turtle, not least because males are much rarely measured than females. Janzen (1995) has recently conducted trials that revealed interesting differences in performance (swimming speed, tendency to run from predators) of hatchling snapping turtles *Chelydra serpentina*) between hatchlings derived from different thermal incubation regimes. Such indications of difference in "fitness" have not so far been sought in sea turtles.

The author of the present review adds the following propositions to the debate on (possibly) female-biased sex ratios:

- Male hatchlings take longer to produce (because their incubation temperature is lower). They are therefore exposed to the risk of attack by terrestrial predators or saprophytic fungi for a significantly longer period than faster-developing female embryos. Even though parental investment in "male" or "female" eggs might be equal, and survival be unaffected by incubation duration *per se*, this would automatically favour a skewed sex ratio in favour of females.

- Cold years cause lengthened internesting intervals, at least in loggerheads (Sato et al., unpublished data). If this means that seasonal fecundity is also reduced, then cold years will not only yield males rather than females, but the absolute numbers of hatchlings will be reduced. Conversely, warmer, more "female" years will be associated with higher total numbers of hatchlings.

TEMPERATURE AND EMERGENCE OF HATCHLINGS

Turtle hatchlings almost invariably emerge from the nest at night, though they hatch at any time. Hendrickson (1958) and Bustard (1967) showed that newly-hatched green turtles start to dig upwards through the sand as soon as they hatch, but on reaching sand of 30 C they become torpid and cease digging until the temperature falls below 30 C again. This causes those turtles that hatch during the day to wait until the cool of night before emerging. Bustard (1967) demonstrated that the response was a little more complicated than a simple reaction to temperature; hatchlings in the nest show a phenomenon known as "social facilitation" – waves of activity or inactivity pass though the hatchling community. So, when the topmost hatchlings become torpid in a nest, this inactivity spreads to hatchlings a little lower in the nest, even though they are somewhat cooler. The net result is that hatchlings emerge at night *en masse*, rather than in small numbers. This probably helps to reduce predation.

TURTLES AND ANTHROPOGENIC GLOBAL WARMING

Most environmental scientists accept that significant global warming will occur over the next century or more because of anthropogenic emissions of greenhouse gases. There is, however, no consensus about the likely degree of such warming (0.6–8.0 C have been suggested; see Janzen (1994) for review), though it would appear that effects will be greatest at middle latitudes. Sea turtles would be predicted to be uniquely sensitive to unusually rapid global warming (Mrosovsky et al., 1984; Davenport, 1989) because of three features of their life history: slow growth to sexual maturity, TSD and natal beach homing. Global warming, perhaps already taking place, will have significant effects on climate during a small number of turtle generations, too quickly for adaptive response by turtle populations. Because of TSD, increases in mean nest temperatures of no more than a few tenths of a degree Centigrade would be likely to bias reproduction in favour of production of females. Mrosovsky and Provancha (1989) reported that >93% of hatchlings produced on beaches in Florida in recent years have been female, compared with 56% in an earlier study in Georgia and South Carolina (Mrosovsky et al., 1984), perhaps indicating the early stages of this phenomenon (though see the discussion of TSD and chaotic hatchling sex ratios above). This is particularly important since over 90% of the logger-

head breeding in the western hemisphere takes place on Floridan beaches.

Chan (1991) reported a sequence of events for leatherback turtles at the Terengganu rookery in Malaysia that gives a hint of the long-term consequences of female-biased clutches (Mrosovsky, 1994). For decades, virtually all eggs at Terengganu were taken by egg collectors, except for small numbers that were reared in protected nests. These protected nests were mostly set up in the warmer months when female offspring would be produced. The adult female leatherbacks now lay eggs that are 30% infertile—perhaps indicating an insufficiency of males.

Production of increasingly female clutches would be less serious for turtles if they could readily switch nesting to cooler beaches. Homing of females to the same beach for repeated nesting within and between years has long been documented (e.g. Carr, 1967), but natal homing (i.e. nesting of females on the beaches that they themselves hatched on) has largely been assumed, but not proven. However, conclusive evidence for such homing has now been found directly for Kemp's ridleys (Shaver, 1996) and indirectly for loggerheads (Schroth et al., 1996; see also Lohmann et al., 1997 for review). The paper of Schroth et al. (1996) is especially significant. Based on measurements of genetic diversity of nuclear and mitochondrial DNA they established the following features of populations of loggerhead turtles in the eastern Mediterranean:

- Colonies of turtles separated by only tens of km are genetically distinct.
- Limited gene flow between turtle colonies is male-mediated; female natal homing is precise. Male-mediated gene flow is too low to prevent genetic substructuring.
- There are two haplotypes of loggerheads present in the eastern Mediterranean. Identical with loggerhead haplotypes found in the Atlantic, their presence indicates that demographic isolation maintained by natal homing during the postglacial period over which loggerheads could have entered the Mediterranean (this corresponds to a period of ca 10^4 yr, equivalent to ca 500 turtle generations).

From these data it would seem unlikely that turtles can respond to rapid global warming by shifting to different breeding beaches. However, this conclusion needs to be qualified. Nesting beaches in the microtidal Mediterranean are probably physically more stable structures over time than the beaches of oceanic islands or exposed oceanic coasts (e.g. Hughes, 1974). Strong philopatry ("place

sense"; Carr, 1975) is likely to be of advantage in stable but diverse habitats, but not in unstable habitats characterized by great variations in juvenile survival rate. Tellingly, the oceanic leatherback turtle, that nests mainly upon exposed beaches, appears to be less faithful to nesting sites than other sea turtles (Pritchard, 1973; Eckert et al., 1989).

Alternative hypotheses, that turtles may respond to climate change by changing their pattern of nesting within seasons (nesting in cooler periods of the breeding season would yield more males), or may select inherently cooler nest sites are presently unsupported by direct evidence. Some freshwater turtles (e.g. Graptemys sp.) occur over a range of latitudes, yet do not differ in pivotal temperature, so are implicitly capable of such behaviour at the population level. On the other hand, Janzen (1994) reported that the behaviour of a single population of the painted turtle Chrysemys picta is stereotyped, with no change in season of breeding or type of nest site selected.

Sea turtle species are of great antiquity so have clearly coped with climate change in the past—why should they not do so in the near future? First, there are far fewer turtles today than before humans had effects upon them. Over-exploitation and habitat loss, particularly during the past 300 yr, have substantially reduced populations. Second, past climate changes appear to have been relatively gradual. Turtle nesting beaches are ephemeral over geological time scales, and the survival of turtle species must always have relied on animals failing in nest site fidelity. Such failures are not uncommon (see Eckert et al., 1989 for review), but are unlikely to be frequent enough in the cooler direction, to be significant over as little as a century. Rapid temperature rises and depleted populations are likely to interact to overwhelm the species' resilience.

Global temperature rise is also likely to have indirect effects on sea turtles. It seems probable that climate change will be associated with increased storminess, and possibly alterations in oceanic current patterns. It is already known that there can be relationships between turtle breeding patterns and weather—Limpus and Nicholls (1988) demonstrated a link between fluctuations in green turtle breeding and fluctuations in the Southern Oscillation (a weather pattern of temperature, rainfall and atmospheric pressure linked to El Niño). Alterations in current patterns could have dramatic effects on sea turtles, since they rely so much on currents for migration and dispersal.

J. Davenport

TEMPERATURE AND THE CONSERVATION OF SEA TURTLES

Mrosovsky (1982) long ago raised problems of temperature and management of depleted sea turtle populations. From the 1960s onwards, three management practices have been common; removal of eggs ("transplantation") to areas protected against predation, rescue of "doomed" nests (i.e. nests dug below the high tide level), and "headstarting" (artificial incubation and subsequent rearing of hatchlings to a size at which mortality due to predation would be less likely). Often, eggs have been incubated in styrofoam boxes, usually indoors and at lower temperatures than in natural nests (Morreale et al., 1982; Mrosovsky, 1982; Dutton et al., 1985), thus yielding male-biased sex ratios. In other cases, transplantation of eggs has been carried out only during part of the nesting season and yielded female-biased clutches (Mrosovsky, 1994). Even though natural optimum sex ratios are unknown (and probably unknowable), it would obviously be desirable for conservation programmes to deliver a mixture of sexes. A sensible precautionary principle would be to aim for a 1:1 sex ratio.

Mrosovsky et al. (1995) recently described another interaction of temperature and turtle breeding that has implications for conservation. In Florida they found that beach temperatures at the depth of loggerhead nests were depressed by 1–2°C by the shading effects of condominiums. It was suggested that the effects would be minimal in the height of the summer, but would favour production of male hatchlings in the earlier, cooler, parts of the nesting season. Presumably, similar considerations would apply to any other nesting beaches subject to adjoining ribbon building development.

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