Thermal Biology of Sea Turtles[1]

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SYNOPSIS. Sea turtles are not confined to the tropics but may experience and tolerate widely different temperatures. This paper discusses the role of temperature in determining sexual differentiation of the embryos, incubation duration, emergence from the nest, activity, growth, survival, hibernation, internesting interval and distribution of sea turtles. Methods of measuring temperatures of adult turtles are considered in detail. Particular attention is devoted to the question of sex ratio and whether temperature determination of sexual differentiation has adaptive value.

INTRODUCTION

Sea turtles are commonly thought of as tropical animals. This view requires modification (Bleakney, 1965). Loggerhead turtles (*Caretta caretta*) have a sub-tropical nesting range. Green turtles (*Chelonia mydas*) and loggerheads hibernate in cool water. Leatherbacks (*Dermochelys coriacea*) swim far into the northern and southern hemispheres and New England waters have recently been proposed as "critical habitat" for the Atlantic ridley (*Lepidochelys kempi*) and other species (Lazell, 1980). Marine turtles are not confined to the tropics but can experience and survive widely different temperatures. Study of their thermal characteristics is therefore likely to provide insight into their life cycles. Even in the tropics smaller temperature changes have important effects on the reproductive biology and behavior of turtles.

Temperature is known to influence sex ratio, incubation duration, emergence from the nest, activity, growth, survival, hibernation, internesting interval and distribution. These topics will be discussed below. Of course temperature is not the only factor of importance in these facets of the life cycle. However, striking effects are already apparent from the relatively few existing studies.

INCUBATION DURATION

When turtle eggs are kept at constant temperature, incubation duration is longer at cooler temperatures; over the range of 26–32°C, a 1°C change decrease adds about 5 days to incubation (see Mrosovsky and Yntema, 1980, for a review). In natural conditions, it has been estimated that a 1°C decrease adds about 8.5 days. In the latter study the temperature of the eggs was only inferred from readings in adjacent soil taken twice daily. Metabolic warming of the eggs compared to a control site near the eggs, but not too near to be warmed by them, has been well documented (Carr and Hirth, 1961; Bustard, 1972; Raj, 1976; Kraemer, 1979), but factors affecting the amount of warming have not been looked at systematically.

Incubation of chelonian eggs has been thoroughly reviewed by Ewert (1979); he suggests that risk of flooding may be one evolutionary pressure for the relatively short incubation durations in sea turtles. In general, there is nothing remarkable about the effects of temperature on incubation duration of sea turtle eggs. More extensive data would be useful, however, because then duration could be used as an index of temperature prevailing in the egg mass. This could be a valuable tool in working on the effects of temperature on sex ratio.

SEX RATIO

Following demonstrations with freshwater turtles that the temperature of the
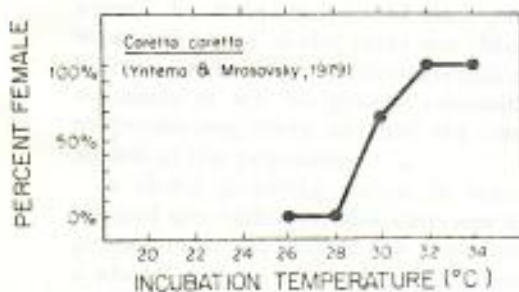
FIG. 1. Sex ratio as a function of incubation temperature in loggerhead turtles (data from Yntema and Mrosovsky, 1979).

eggs during incubation has dramatic effects on the sex ratio (Pieau, 1972; Yntema, 1976), it has been shown that sea turtles (*Caretta caretta*) are affected in similar ways (Fig. 1; Yntema and Mrosovsky, 1979). At higher temperatures there are more females. Pivotal temperatures were defined as those over which the sex ratio changed greatly.' At these temperatures the ratio is highly sensitive to temperature with even 1°C making a considerable difference. Categorization of sex is made from microscopic differences in the gonads of the hatchlings (Yntema and Mrosovsky, 1980). Two pieces of evidence suggest that sex at hatching reflects sex later on. First, at the Cayman Turtle Farm, sex ratios were highly skewed in different directions in different batches even several years after hatching (Owens and Hendrickson, 1978). Second, sex in freshwater turtles *Emys orbicularis*, kept up to 59 mo was the same as that of animals from the same clutch studied at hatching (Pieau, 1976). The matter needs more extensive study, but at present there is nothing to indicate that sex in turtles changes later in ontogeny (see also Bull and Vogt, 1979). Several species including three sea turtle species (Bickham, 1979) have been shown to lack distinguishable sex chromosomes. Of course differences might still be revealed by other methods, but given the lack of marked dimorphism in the chromosomes and the effects with temperature, it is reasonable to suppose that sex is environmentally rather than genetically determined (see also Mittwoch, 1975)

This phenomenon raises many questions:

1) Are temperatures giving a 1:1 ratio the same for populations of turtles nesting at different latitudes? Presumably not, because turtles nesting on cooler beaches would have different demographic profiles, but perhaps there is some inflexibility in the pivotal temperatures. This could act as a limiting factor in the selection of nesting beaches.

2) Could there be any within season change in temperatures giving a 1:1 ratio or are more male turtles produced at the cooler ends of the nesting season, *e.g.*, with loggerheads in South Africa or the U.S.A. (Hughes and Brent, 1972; Kraemer, 1979)? Or do pivotal temperatures span a broad enough range to give both sexes throughout the season?

3) Is the sex ratio really 1:1 in nature? Given exploitation of turtles by man and the greater vulnerability of females at nesting, it may be impossible to discover what is the sex ratio of undisturbed populations. At least there is now a method of determining the ratio at hatching.

4) Does the behaviour of the nesting female have a major effect? When do turtles select nest sites beneath vegetation, and how much does this influence temperature of the eggs beneath? Judging by the near doubling of incubation duration in windy shady places (Bustard, 1972), nest site selection should make a considerable difference to sex ratio (see Mrosovsky and Yntema, 1980, for a quantitative treatment).

5) Does the physiology of the female influence sex ratio? Is clutch mass or size, for instance, a significant factor? Incubation plus emergence times of large clutches are slightly shorter than those of small clutches in hawksbill turtles, *Eretmochelys imbricata* (Garnett, 1978).

6) Will cooler eggs at the edge of the clutch (Bustard, 1972) tend to produce more males? Do predators such as crabs take eggs preferentially from the edge of clutches?

7) Might temperature at incubation contribute to the wide and unpredictable fluctuations in numbers of turtles nesting on a given beach from year to year, with

warm spells augmenting the numbers of females arriving many years later?

Many of these questions can be tackled individually. Some with implications for conservation procedures have already been considered elsewhere (Mrosovsky and Yntema, 1980). But it would be more satisfactory to have some guidance from an overall understanding of the adaptive value of having sex ratio dependent on temperature. Postponing sexual differentiation to a time when there might be advantages in being either male or female is one possible reason for environmental determination of sex (Charnov and Bull, 1977) but this is not obviously pertinent to turtles because determination of sex is only postponed until incubation. Rather than search for other possible adaptive advantages of environmental determination of sex, it may be wise first to question the assumption that turtles are perfectly adapted. There may be constraints, limits in genetic variance, that are barriers to evolving other systems (see Lewontin, 1979). Temperature determination of sex, even if it leaves much to meteorological caprice, might work adequately but not have any special advantages. It is plausible that this is really the correct answer to the question of adaptive advantage of environmental determination of sex in turtles.

There are, however, two points that raise cautions about accepting this view unreservedly at present. First, it has been claimed that there is at least one species of turtle, *Trionyx spiniferus*, whose sexual differentiation is not temperature dependent (Bull and Vogt, 1979). Second, there is more to it than most turtle species simply being encumbered with this way of determining sex because they have been unable to evolve anything better. If that were the case, surely the importance of temperature could at least have been limited, but turtles are not merely dependent on temperature, they are so highly dependent that a change of as little as 2°C can make a huge difference in sex ratio. There may indeed not be much value in speculating about some overall adaptive value of having sex determined by temperature, but given that turtles use this method there may well be sur-

vival value in the quantitative aspects of the system. Perhaps physiological constraints are primary here. For instance, if female and male producing temperatures were not sharply divided, intersexes might result too frequently. A system with such a characteristic might nevertheless be put to other uses.

One possible value in having a sharp division between male and female producing temperatures could be that it provides an opportunity to vary sex ratios, either by spatial or temporal selection of nest sites for instance. Evolutionary theory tells us that in populations as a whole the primary sex ratio should be equal, assuming that parental investments in producing a male and female are equal (Fisher, 1930; Williams, 1979). This assumption holds in turtles since sex is not even determined at the time the female turtle leaves the eggs.

In certain circumstances, however, skewing of sex ratio by an individual may be advantageous. In particular, if there is a wide variance in the reproductive success of the male (such as occurs when a dominant male establishes a harem and excludes other males from breeding), then a sex ratio in favour of males might be advantageous if environmental conditions were benign. If there was a good chance of producing a strong healthy male offspring that was successful in competition for females, many genes might be passed on to future generations. But if the mother was raising young in marginal conditions, it might be better to produce more females. Probably at least some of these might bear young, while a weak male might not have the chance of mating at all (Trivers and Willard, 1973). An assumption in this view is that the condition of the young at the time of parental investment ends will be carried over to their condition when they are mature. With sea turtles, because maturation is estimated at more than 30 years (Balazs, 1979; Limpus, 1979), this becomes a problem, though not one that cannot be surmounted with a little imagination.

Skewing of sex ratio might conceivably also be advantageous to an individual if the sex ratio in the population became imbal-

anced. An individual could then produce more offspring of the rarer sex (Maynard Smith, 1978). With environmental determination of sex no genetic committment to producing more of that sex need be added to the population.

A third possible value in having a skewed sex ratio—in this case one that is permanently skewed in the population as a whole—relates to predator satiation. Female turtles on shore move slowly and are easily attacked. Even before the coming of man, turtles on land were probably taken by other predators such as large carnivores. Jaguars still kill sea turtles (Schulz, 1975). Sharks lying just offshore also attack turtles. If predator satiation by producing many eggs and hatchlings is important in the life strategy of turtles, then it would be advantageous to have more females in the population. The problem is to see how this could be achieved without resorting to group selection. Mortality after parental investment has ended should not act as a pressure skewing sex ratios. However, an individual might increase her chance of contributing toward the next generation by producing more females if those females helped each other. This is not inconceivable given current suggestions of predator satiation and nest site fidelity. Two daughters returning to the same beach, perhaps the very same stretch of that beach, might well have more than twice the chance of getting some of their offspring past the predators than a single turtle has. It would be interesting to have more information on the genetic similarity of turtles nesting on a given stretch of beach.

This last suggestion is a version of a more general argument that kin structure of a population may alter inclusive fitness benefits in producing a particular sex if kin alter each other's environment. Another instance of this general argument is the suggestion that competition for local resources by sedentary related female prosimians skews the ratio in favor of males (Clark, 1978). In the latter mammalian case, the sex ratio does not depart very greatly from unity. It may be that having sex determined by temperature would al-

low turtles greater scope in varying sex ratio than if they were constrained by a heteromorphic chromosome system for determining sex. Pronounced skewing of the sex ratio might then occur as a response in any or several of the situations described above.

These speculations are tenuous. It is hoped that nevertheless they will provide a useful starting point in considerations of the functional aspects of temperature determination of sex in turtles, and attract attention to two questions: Why is the system so very sensitive to temperature and what are sex ratios in natural populations?

NOCTURNAL EMERGENCE OF HATCHLINGS

Hatchling turtles usually emerge at night. Hendrickson (1958) suggested that heat inhibited activity during the daytime. This suggestion has been tested by measuring activity of hatchling green turtles in Surinam: At high temperatures they were less active and these high temperatures corresponded fairly well with temperatures commonly prevailing at the sand surface during the day (Mrosovsky, 1968). It was proposed that above a critical level of about 28.5°C activity was suppressed and the hatchlings held in their nests till the cool of night. However, it has been correctly pointed out that in Surinam soon after dawn the sand surface is often below 28.5°C (Mrosovsky, 1968; Schulz, 1975). The possibility was raised that hatchlings have a negative thermotaxis. This would inhibit emergence in the early morning because the sand surface warms quickly. However, it is also conceivable that a simple temperature inhibition of activity could still account for the fewness of early morning emergences. Because of the lag in temperature changes below the surface, the coolest temperatures at 30 cm depth occur during daylight hours (Mrosovsky, 1968). These cool temperatures could permit activity which would be shut off as the turtles worked their way towards the warmer surface. On any given night only turtles fairly near the surface already would experience cool enough temperatures to emerge and they would be likely to emerge fairly soon after sundown. If not near the surface

their activity might be inhibited till the next day when they could make some upwards progress before encountering the warm surface of the daylight hours.

Inhibition of activity by high temperatures is easily demonstrated (Mrosovsky and Shettleworth, 1968). However more thought is needed on how it should best be measured and how it relates to nocturnal emergence. It is also quite possible that other factors influence emergence, or that once started, the juvenile frenzy overrides thermal inhibition. There are, however, reasons for thinking that temperature rather than the other obvious candidate, light (which might penetrate the upper layers of sand: Schulz, 1975) is in some way important in controlling nocturnal emergence. If light was used for this purpose, turtles would have to have a negative reaction towards it. But it is known that hatchlings have a strong positive reaction towards light and that this is the basis of their sea-finding behaviour (Mrosovsky and Shettleworth, 1968). Occasional emergences during rainy days (Carr, 1967) is the price paid for a system that guides the animals to the water so effectively.

TEMPERATURES OF ADULT TURTLES

Marine turtles are much easier to study on land so it is not surprising that temperature data are much more extensive for this phase of their life cycle. Virtually nothing is known about their thermal biology at sea. However, inferences can be made from the existing data provided consideration is given to the different ways that have been used to measure temperature. In this paper whenever new data are presented, the methods have been essentially the same as those used previously (Mrosovsky and Pritchard, 1971) unless otherwise specified.

Cloacal temperature

This is relatively easy to take, but the depth of immersion of the probe is an important variable. For instance, in green turtles the median of the differences between readings from a probe inserted 6 cm into the body cavity through the plastral scutes and readings in the same individual
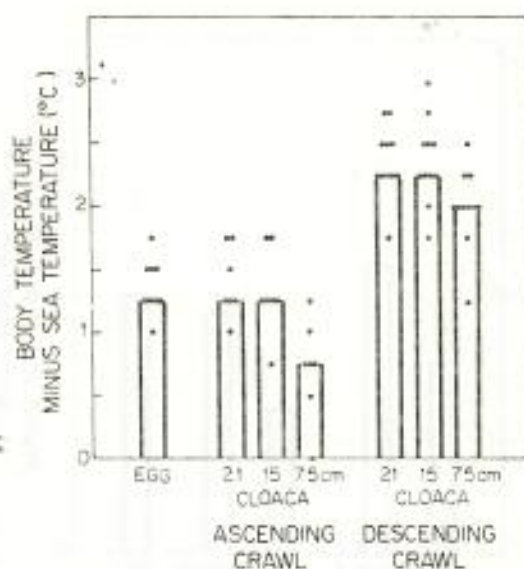

FIG. 2. Relationship between sea and body temperature measured in different ways and at different stages during the nesting of loggerhead turtles. Data were collected at Jupiter Island, Florida, 28–31 May 1974. Histograms show medians. Cloacal temperatures were taken for each animal at each of the three different depths shown. Eight of the 11 individuals studied in the descending crawl previously contributed data to the histogram for egg temperatures. Nine of the 11 animals studied post-laying were crawling back toward the sea, 2 had carried out extensive covering of the eggs and were probably just about to descend. Ascending crawls include false crawls.

from a probe immersed 6 cm into the cloaca was 1.1°C for ascending turtles, n = 4, and .75°C for turtles that had just covered their eggs, n = 5 (Mrosovsky and Pritchard, 1971). Clearly, a probe immersed only 6 cm in the cloaca does not record core temperature. The same is true for loggerhead turtles (Figs. 2, 3); however, provided the probe is inserted 15 cm, pushing it in further does not give higher values. Presumably the reading at 15 cm reflects deep body temperature, though not necessarily that of the muscles. With nesting leatherback turtles Sapsford and Hughes (1978) state that after 16 ± 6 cm immersion temperature does not increase further. However, other data suggest that it may be necessary to insert the probe about 24 cm, perhaps a little more to measure core temperature at nesting (Table 1;
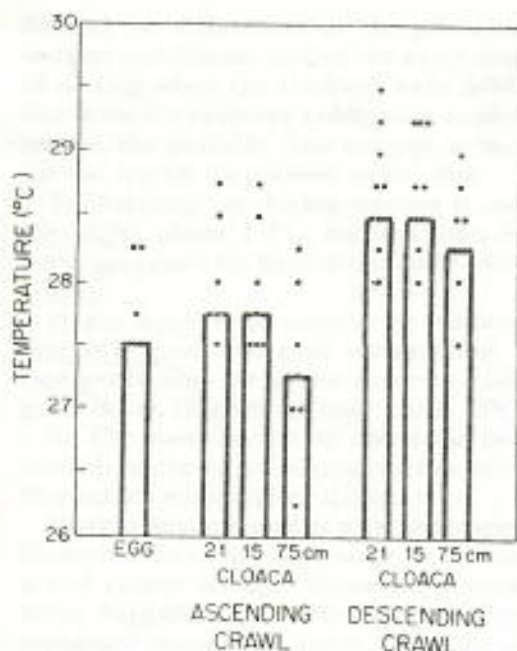
FIG. 3. Temperatures of loggerhead turtles measured in different ways and at different stages of nesting. Histograms show medians, dots data for individuals. Data were collected at Jupiter Island, Florida, 28–31 May 1974. For further details see Figure 2.

TABLE 1. *Temperature (°C) of leatherback turtles measured within 5 min of emerging from the sea to nest in Mexico, November 1978.*

Animal # Beach	C 01157 Tierra Colorada*	C 01162 Petatillo
Sea	28.25	26.25
Cloacal, 7.5 cm	29.0	28.5
Cloacal, 15 cm	29.75	29.25
Cloacal, 21 cm	30.0	29.5
Cloacal, 24 cm	30.0	29.75
Max. cloacal − sea	1.75	3.5

* Median egg temperature at Tierra Colorada was 31.1 (30.5–33.5 range, n = 10) and excess of egg temperature over sea temperature was 2.75°C (range 2.2–5.1).

For a <u>male</u> leatherback in cool water, a cloacal reading at 20 cm gave a value 5.75°C less than core temperature (Frair *et al.*, 1972).

Egg temperature

Taking egg temperature as a way of assessing body temperature has practical advantages. It is unnecessary to disturb the turtles so that the work can be combined with other studies. It is particularly useful for leatherbacks which are troublesome to restrain or turn for other temperature measurements. The ease of taking egg temperatures makes this a convenient method of comparative work on different turtle populations.

Fortunately egg temperatures provide a relatively good, though not perfect, reflection of body temperature. In studies in the Guianas (Mrosovsky and Pritchard, 1971) deep body temperatures were taken in the

same individuals in some other way after the animals had finished covering over the nest chamber but before concealment activities had begun, that is fairly soon after the readings from the eggs had been made. For leatherbacks the median difference between body and egg temperatures was only .1°C (range 0–.5°C, n = 4). For green turtles the median difference was .5°C (range .25–.75°C, n = 3), again in favour of the body temperature. This tendency for the body to be slightly warmer than the egg might be due to heat production during covering the eggs, or to the eggs cooling down during their passage through the cloaca. In all measures of egg temperature reported here or previously, the first few eggs have always been avoided in case they had spent extra time in the peripheral and cooler parts of the cloaca. However, there are no obvious indications that eggs from the earlier part of a clutch are cooler. In one green turtle laying 104 eggs at Pulau Selingaan, Sabah, the temperature of the first egg and every tenth egg thereafter was recorded: all eggs were 30.0°C, except for the 21st, 81st, 91st and 101st which were 29.75°C (sea = 28.5°, air = 26.0°C).

Thus egg temperature is a convenient, fairly accurate way of taking body temperature. However, it must be noted that the reliability checks mentioned above only concern temperature at, or very near to, the time of laying. We can now turn to

considering whether egg temperature is or is not a good index of the body temperature of the turtle at other times.

Do turtles warm up during nesting?

This is a useful question not only because the answer helps define their thermal characteristics but also because it would tell us if temperatures taken on land can be used to estimate how warm turtles are when in the water.

Brattstrom and Collins (1972) believed that metabolic activity resulting from nesting raised temperatures of green turtles on Heron Island, Australia, by a median of 2.0°C (range 1.7–2.6°C, n = 4). They inferred this from cloacal temperatures at 7.5 cm depth (Brattstrom, personal communication) taken "just before and just after egg laying and nest construction" in the same individuals. However, they did not consider the possibility that a mass of warm eggs passing through the cloaca might warm it up. This could be especially important with the relatively peripheral cloacal sites they used; these would be cooler than the eggs. Another factor to be considered is that the wet cloaca might cool off when the animal comes ashore.

Although Brattstrom and Collins' data can be interpreted in terms of redistribution of heat within the animal, they may nevertheless be right. Metabolic heat production may warm up nesting turtles, but studies using deep body temperature are necessary to prove this. Existing data on core temperatures taken at various stages of the nesting sequence do not agree on this point. Hirth (1962) did not find any difference between the cloacal (13 cm) temperature of green turtles in Costa Rica before and after laying. These turtles had been out of the water 3–20 min or 1–2 hr when their temperatures were taken. In both groups the median value was 30.0°C (n = 7 per group, sea at 28 ± .5°C). Mrosovsky and Pritchard's (1971) data on green turtles in the Guianas agree with this. Core temperatures of turtles crawling up the beach, before starting any digging (median 29.6°C, n = 4) were close to those of turtles after covering the egg chamber
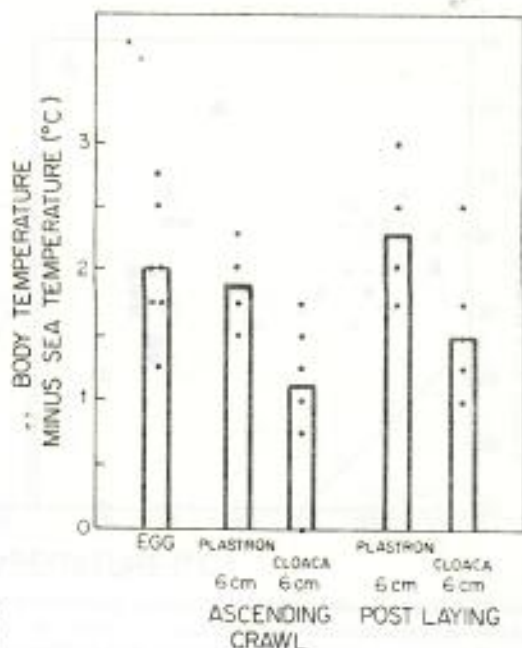

FIG. 4. Relationship of sea to body temperature measured in different ways and at different stages of nesting of green turtles in the Guianas. Histograms show medians, dots data for individuals. The same animals contribute to different histograms in some cases (data from Mrosovsky and Pritchard, 1971).

(median 30.0°C, n = 5). See also Fig. 4 for temperatures expressed relative to that of the sea, where the latter is available.

However, in another study, on loggerhead turtles, evidence of warming up during nesting was obtained (Figs. 2, 3). Since most of the animals in the post-laying sample had been turned for measurements on their way back to the sea, after they had finished the nesting itself, and since the egg temperatures were not much different from those on the ascending crawl, the greatest heat production probably occurs in the period immediately after the laying of the eggs. This is consistent with recent data on green turtles: the 20 cm cloacal temperature just as the turtles began their descending crawl was 1.5°C (median, n = 5) above egg temperatures of the same animals (Spotila et al., 1979; Spotila, personal communication). Differences in these various studies ma

depend on differences in the prevailing weather conditions, and on the exact stage of nesting when the readings were made. But to meet a reviewer's obligation to summarise, the available data suggest, at least for the species mentioned so far, that:

1) Warming up during nesting is usually slight, about 1.0°C, but less than the 2.0°C proposed by Brattstrom and Collins (1972).

2) For loggerhead turtles egg temperature is a good index of temperature at emergence and for green turtles a fairly good index (higher by only about .5°C).

3) The contribution of metabolic heat towards warming of nesting turtles probably occurs mainly after laying.

More systematic studies with better specification of weather and stage of nesting are of course needed. However, it sometimes happens that an unplanned, even unwanted occurrence turns out to be almost as instructive. The following anecdote provides strong reasons for thinking that metabolic heat production is capable of raising a turtle's temperature markedly when it is nesting. A leatherback turtle (C 01138) at Tierra Colorada, Mexico, started to dig an egg chamber but, perhaps because it was disturbed, began to return to the sea. Egg poachers intervened as it reached the surf and managed to stop it, whereupon it started to dig another chamber which promptly filled up with water. Biologists, giving up hope of a successful nesting, disturbed the animal further by tagging and measuring it. The poachers remained dissatisfied and encouraged the turtle to move back up the beach where it dug its third egg chamber and laid. The eggs were 33.5°C, the highest egg temperature ever recorded for a sea turtle, and 5.0°C warmer than the sea.

Having discussed some of the methodological problems and important variables, we can now try to tackle some more interesting questions about the thermal biology of adult turtles.

Are leatherbacks warm-blooded?

Given the frequent appearance of leatherbacks in northern waters (Nishimura 1967, Brongersma 1972) it would be instruct-

tive to know if they have any special thermal properties. If indeed they can maintain temperatures well in excess of ambient, then it becomes less plausible to argue that these northern occurrences are composed of aberrant animals.

Egg temperatures of leatherbacks in the Guianas are about 1°C higher than those of other sea turtles using the same beach (Mrosovsky and Pritchard, 1971). On the basis of the correspondence between egg temperatures and body temperatures of green turtles emerging from the sea, this finding had been taken as signifying that leatherbacks were warmer in the water also. It was then calculated, making assumptions about k values in Newton's Law of cooling, that a five-fold increase in heat production above the level in tropical waters would enable leatherbacks to be at 25.75°C in 12°C water (Mrosovsky and Pritchard, 1971). However, the anecdote recited above calls this line of reasoning into question. Perhaps higher egg temperatures of leatherbacks are due to greater retention by this species of heat generated during nesting. Since cooling constants in Newton's law of cooling are less for air than water, a leatherback being warm on land is less impressive than one being warm in the sea. More specifically, heat production on land would have to be raised four-fold to maintain the same excess temperature above the ambient when the turtle was in the water, because cooling rates in water are probably at least four times greater (Weathers and White, 1971). A further five-fold increase, making a total twenty-fold increase, would then be needed to maintain 25.75°C in 12°C water. Although the total heat production needed in cool water would be the same whether leatherbacks in the tropics are warmer when they emerge or only warm up during nesting, in the second case a twenty-fold increase in heat production over that at nesting would be required. This seems unlikely because Prange (1976) has found that oxygen consumption at maximum swimming speed in immature (735 g) green turtles is only 3–4 times greater than resting levels. Thus, if the egg temperatures of leatherbacks are relatively high

Key:
- · GUIANAS ⎤
- ▲ MALAYSIA ⎬ EGG TEMPERATURES
- ✗ MEXICO ⎦
- ⊛ " , ASCENDING CRAWL
- ⊙ TONGALAND, NESTING OR LAYING
- ⊕ " , ASCENDING CRAWL
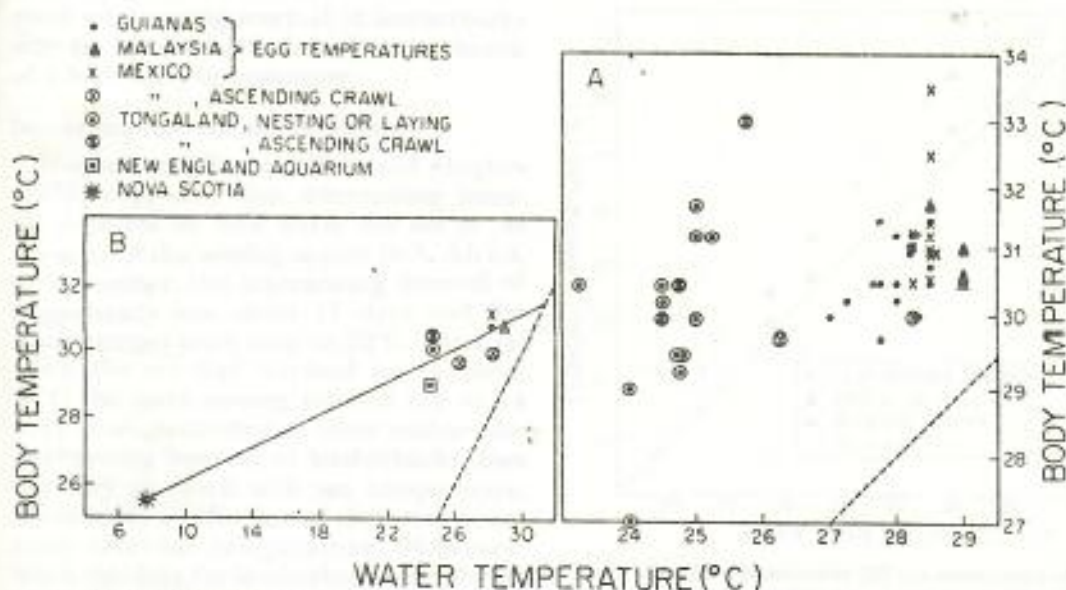- ▣ NEW ENGLAND AQUARIUM
- ✳ NOVA SCOTIA

FIG. 5. Relationship of body to water temperature of leatherback turtles. Dotted lines show equal body and water temperatures. A, data on individual nesting turtles. B, median of egg or cloacal temperatures for various locations as a function of median water temperatures, together with data from individuals emerging to nest and from individuals captured in northern waters. Sources of data: Guianas, Mrosovsky and Pritchard (1971); Malaysia, collected at Trengganu, 7–10 July 1975; Mexico egg temperatures, collected at Tierra Colorada, 22–26 November 1978; Mexico ascending crawl, see Table 1; Tongaland, Sapsford and Hughes (1978); New England Aquarium, 281 kg female found entangled in lobster trap 28 July 1972, near Rockland, Maine, moved to aquarium in Boston 31 July, blood samples and 6 cm intraplastron temperature taken 2 August, turtle generally quiet and inactive, died 7 August; Nova Scotia, intraplastron temperature (Frair et al., 1972).

because they have warmed up during nesting, it makes it less probable than previously supposed that they could maintain high temperatures in cold water.

Temperatures of leatherbacks directly after leaving the sea could help clarify the issue. These are not easy to obtain, but on a few occasions the necessary combination of circumstances were present (Table 1; Fig. 5). Unfortunately, the data are equivocal. While one animal at Tierra Colorada was a little cooler than other leatherbacks on the same beach at the time these were laying their eggs, another animal, at another beach, that at Petatillo, was 3.5°C warmer than the water, suggesting that sizeable excess temperatures can exist in leatherbacks. But the beach at Petatillo slopes very gently so that the temperatures in the shallows may not reflect the temperatures further out at sea as well as they do in the Guianas (M&P 1971) and no data on egg temper-

atures are available for this beach. In Tongaland Sapsford and Hughes (1978) measured the cloacal temperature, 32 cm, of a leatherback that had just emerged; it was 5.5°C warmer than the sea (Fig. 5). It would not be surprising if heat production on land contributes somewhat towards the high egg temperatures of leatherbacks but that they are also relatively warm on emerging from the sea.

A different approach to discovering if leatherbacks are warm-blooded is to study them when they are in cool northern waters, rather than extrapolating from their temperatures in the tropics, but this is just as difficult because they are not common enough to be found easily at sea. Very limited data from animals brought into aquaria suggest that leatherbacks can be as much as 18°C above an ambient of 7.5°C (Frair et al., 1972; Fig. 5) but do not tell us how long such differences could be maintained.
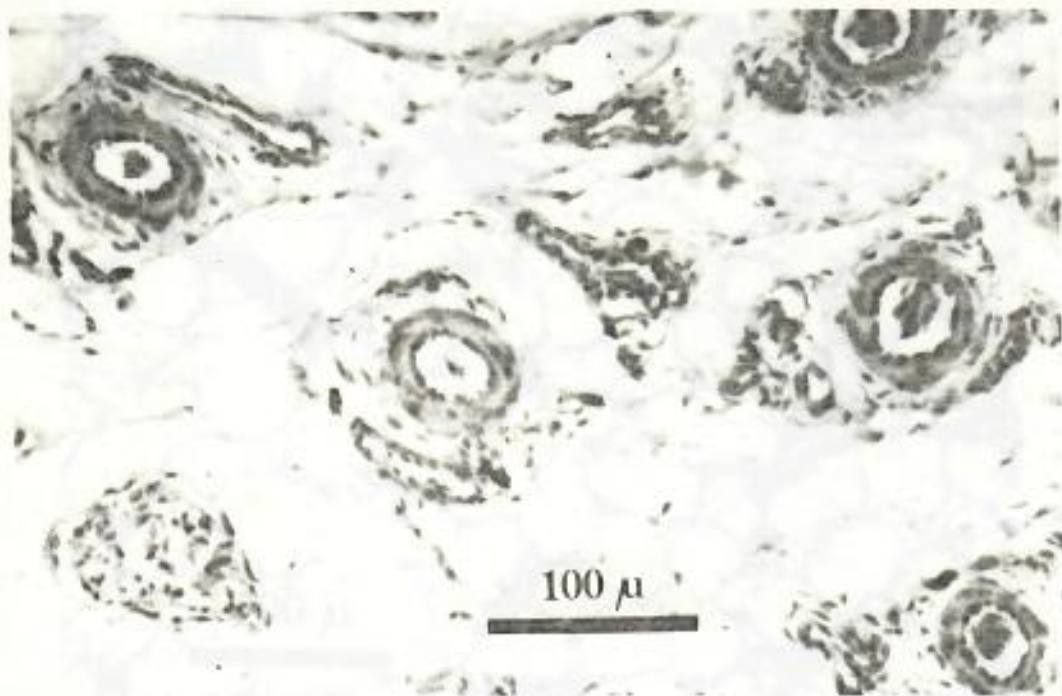
FIG. 6.   Counter-current heat exchanger from front flipper of a hatchling leatherback; H & E, 10 μm.

Maintenance of excess temperatures in cool water is consistent with various anatomical features possessed by leatherbacks: a counter-current heat exchanger system in the flippers (Greer *et al.*, 1973; see also Fig. 6), the thick oily layer around the body and a large size. The latter is probably a major factor because of the influence of size on cooling rates. Temperatures of a small immature leatherback in the Miami Seaquarium (see Foster and Chapman, 1975; Witham, 1977, for housing conditions) gave no special indication of thermal prowess when compared with turtles of other species weighing about the same (Fig. 7). Hatchling leatherbacks in 27.0°C water are barely warmer, 0.1°C, than ambient and no different from hatchlings of other species (Mrosovsky and Pritchard, 1971).

It would be interesting to know how much leatherbacks can increase their metabolic rate and whether they possess any mechanisms equivalent to non-shivering thermogenesis. The green fat of leather-

backs (Fig. 8) and of various species of freshwater turtles has been examined histologically in collaboration with U. Rowlatt and A. English. Sometimes green fat has a multilocular appearance reminiscent of brown fat (Rowlatt *et al.*, 1971) but there are differences such as the concentration of the pigment in special cells. In freshwater turtles, *Pseudemys scripta elegans*, no evidence was found that green fat was warmer than other tissues during cooling (Mrosovsky and Lang, unpublished). But these experiments were not extensive and it remains possible that some special heat generating tissue might have evolved in the leatherback, a species that already has the necessary size and insulation to retain that heat. This would not preclude other functions for green fat. The colour of this tissue is not always a green-grey but sometimes quite a bright yellow. Perhaps these variations underlie the unexplained colour differences in turtle urine noted by Bjorndal (1979).

Finally again in a speculative tone, the

short internesting interval of leatherbacks may be seen as an index of maintenance of a high body temperature.

Internesting interval and temperature

Hughes and Brent (1972) and Hughes (1973) suggested that internesting interval depends on how warm the sea is. At the start of the nesting season in S. Africa, in November, the internesting interval of loggerheads was about 17 days and the water temperature near to 22°C. Later on when the sea had warmed up to about 26°C the inter-nesting interval fell to 14 days or so. According to these authors the internesting interval of leatherbacks does not vary so much with sea temperature, presumably a reflection of their more constant internal temperature. However, when the data for leatherbacks are plotted out, in the slopes of the lines with respect to temperature are quite similar to those for their loggerhead sample, but the actual internesting intervals for leatherbacks are shorter (Fig. 9).

Independently I have been interested in the short internesting interval of leatherbacks in the Guianas compared to that of the other species there, and the inverse relationship between internesting interval and temperature for these species (Fig. 10). Of course these may be species characteristics rather than depending directly on temperature differences. Perhaps the long incubation period (64–65 days) of leatherback eggs compared to that for green (54–58 days) and olive ridley turtles (53 days) in Surinam (see Schulz, 1975) might reflect compensation for eggs not being so far developed when laid. However, apart from the within-species temperature correlations for loggerheads cited above, it is relevant that when green turtles were taken from the Guianas to an artificial breeding pool at Mariculture Ltd., Grand Cayman Island, their modal internesting interval was only 10 days (Ulrich and Owens, 1974; Simon et al., 1975). It seems very likely that a shallow pool (3.1 m deep) would become quite warm despite the 18 changes of water per day.
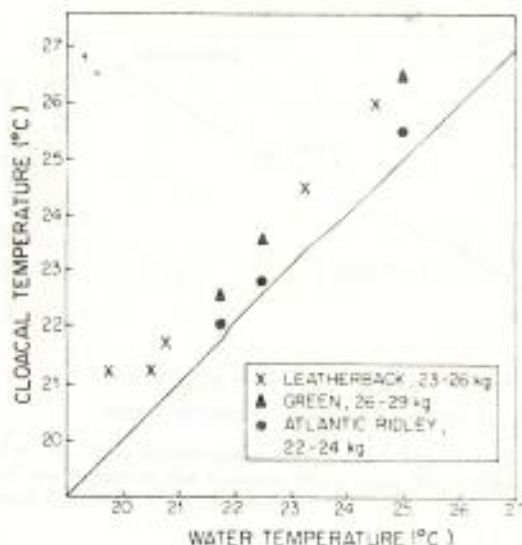

FIG. 7. Cloacal temperatures (20 cm immersion) of an immature leatherback and two other sea turtles of similar weight. Data collected by P. Foster and the author at the Miami Seaquarium, 21 November 1974–4 March 1975.

The idea that temperature is an important factor in determining internesting intervals has testable implications. For instance at Mon Repos, Queensland, Australia, flatback turtles nest every 14–15 days while the internesting interval of loggerheads there is about 2 days shorter (Limpus, 1971). The flatbacks should have lower body temperatures. The short internesting intervals of leatherback turtles is certainly consistent with the view that they are warmer than other species when in the water.

Thermal characteristics of loggerhead turtles

Loggerheads nest in sub-tropical rather than tropical regions. For instance, there are important rookeries on Masirah Island, Oman (Ross, 1978), >20°N, and in the southern U.S.A.; loggerheads can even nest in New Jersey, about 39°N (Lazell, 1976). Differences between body temperatures at nesting and water temperatures do seem to increase if the turtles come from colder water, but the effects are not very striking (Fig. 11). In contrast, Saps-
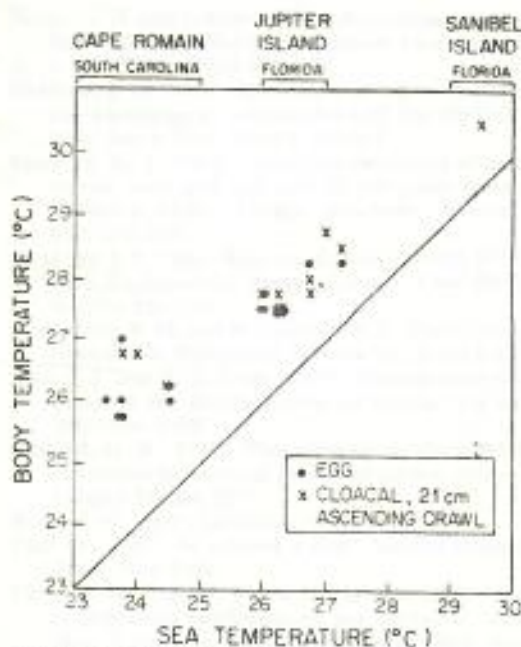
FIG. 11. Relationship of sea and body temperatures of loggerhead turtles nesting at three different locations in the U.S.A. Data were collected 26 May–5 June 1974. Cloacal and egg temperatures are from independent samples.

temperatures is unknown (see Hainsworth and Wolf, 1978, for a review of temperature preferences).

In another study on the effect of temperature on growth, Hughes (1974) found that 1-mo-old loggerheads from S. Africa kept for 2 wk at 14 and 15°C lost weight, and ate little. Those at 17 and 18°C gained weight, but slowly in comparison to other animals at 24°C. Three out of 5 of the animals at 14°C died within 3 days of being returned to 24°C water at the end of the 2-wk experimental period. It was suggested that tolerance to 14°C might enable hatchlings to survive localized upwellings of water that can be as low as 14°C. Numbing by prolonged cold might account for hatchlings being washed ashore at Cape Agulhas.

LETHAL TEMPERATURES

Data on this matter are not extensive. Presumably the temperatures survived depend on how long the turtles are exposed to them. It appears that hatchlings are better able to tolerate cold temperatures than

adults. The main information comes from Schwartz's (1978) observations on turtles kept in outdoor pools in N. Carolina during natural temperature variations. He reported that hatchling loggerheads survived up to 12 hr at 4.0°C, the adults less than 24 hr at 5.0°C. Green turtles died at 5.0–6.5°C, the animals with larger carapace lengths (56 cm) dying at the upper end of this range. Atlantic ridleys at 30 cm or more carapace length died within 24 hr at 6.5°C; the smaller ones tolerated 5.0 for a while before dying.

At temperatures above those at which the animals died, they took up an unusual floating posture, with the posterior part of the carapace above the water, the head pointing down and the front flipper often extended outwards. Floating occurred in ridleys at 10.0–13.5°C and in green and loggerhead turtles at 9.0–9.9°C but young loggerheads did not float till 5.0–9.0°C and the hatchlings only 3.5–4.5°C. All these values refer to water temperatures, not body temperatures, though probably they were fairly close.

Cold stunning of turtles occurs naturally during particularly severe winters. In 1977, in Mosquito Lagoon, Florida, green and loggerhead turtles began to float at the surface at water temperatures of 7.3–10.0°C. When temperature fell to 4.0°C large numbers of turtles were found, nearly all immature; undoubtedly many would have died if not rescued (Ehrhart, 1977).

Dying through overheating appears to be a danger turtles face when they have difficulty returning to the sea or reaching it for the first time as hatchlings, but upper lethal temperatures are not known. Data from basking turtles and from adult turtles nesting by day, such as Atlantic ridleys or the Cousin Island population of hawksbills (Diamond, 1976), could provide information about tolerance of high temperatures without having to kill animals. Crossing a 100 m or so stretch of beach in the day would not necessarily be a problem for hatchlings provided they started off cool, because they travel rapidly, about 1 m/15 sec for green turtles (Mrosovsky et al., 1979) Hatchlings of this species can survive rectal temperatures of 36–40°C for

more than 15 min (Bustard, 1970). However, if hatchlings starting out across the sand were already warm, from lying near the surface before emerging for instance, overheating could be a real danger, especially since this itself would further slow down the turtles (see p. 532 above).

HIBERNATION

Torpid easily handled green turtles have been found in the muddy edges of under-sea troughs and other specific sites among boulders in the Gulf of California (Felger et al., 1976). Because this torpor occurs during the cooler parts of the year (water below about 15°C), it can be called hibernation.

Other species of sea turtle have also been found hibernating. Large numbers of loggerheads, mostly immature, and a few Atlantic ridleys have been caught by trawling in a channel near Cape Canaveral (Carr et al., 1980). Water temperature was about 11°C. This is not incompatible with the temperatures for survival and floating (<10°C) reported by Schwartz (1978) for young loggerheads. Moreover, body temperatures were 13–15°C, maybe more, the "deep cloacal" temperatures reported being an imprecise measure. Apparently the turtles burrowed their way into mud at the sides of the channel which was warmer than the water itself. Indeed, it was suggested that the turtles select this place because the mud is softer than the hard clay rich surface outside the channel.

These findings raise many interesting physiological and demographic questions. Sea turtles do not have cloacal bursae (Smith and James, 1958) so that a search for some other aquatic respiratory structure might be worthwhile. It would also be interesting to know whether hibernation is a crisis response occurring in particularly cold winters, or a regular part of the life cycle of certain populations, and how it relates to migration.

DIRECTIONS FOR THE FUTURE

It has been said that "more had been learned by tagging turtles than in any oth-er way" (Carr et al 1978). It would be foolish to dispute this claim if only because

tagging has been more widely used than other methods. But there is a danger that tagging, enumeration of nesting intervals, seasonal returns, carapace lengths, pioneered by Archie Carr and so instructive in his hands, will, precisely on that account, become something of a ritual, the sea turtle researcher's paradigm. Take internesting interval for example. The literature is full of data on this subject but it becomes a dead end if not related to something else. Temperature is one way of doing this, but this in turn must be related to something else, how deep the animal is swimming perhaps, or its size, etc. With so many people studying turtles now, there is room for greater diversity of methods and problems. More extensive work on some of the subjects sketchily covered in this paper would surely help clarify the life strategies of the sea turtles. A particularly interesting topic, now that hatchlings can be sexed, is the sex ratio, with all its demographic and evolutionary ramifications. And if a thermal tag could be developed . . . surely not prohibitively difficult if initially only maximum and minimum temperatures encountered were recorded . . . tagging itself could be given a new lease of life!

REFERENCES

Balazs, G. H. 1979. Growth, food sources and mi-

temperatures of *Dermochelys coriacea* and other sea turtles. Copeia 1971:624–631.

Mrosovsky, N. and S. J. Shettleworth. 1968. Wavelength preferences and brightness cues in the water finding behaviour of sea turtles. Behaviour 32:211–257.

Mrosovsky, N. and C. L. Yntema. 1980. Temperature dependence of sexual differentiation in sea turtles: Implications for conservation practices. Biol. Conserv. (In press)

Nishimura, S. 1964. Considerations on the migration of the leatherback turtle, *Dermochelys coriacea* (L.), in the Japanese and adjacent waters. Publ. Seto Mar. Biol. Lab. 12:177–189.

Owens, D. W. and J. R. Hendrickson. 1978. Endocrine studies and sex ratios of the green sea turtle, *Chelonia mydas*. Florida Marine Research Publications (Florida Department of National Resources) 33:12–14.

Owens, D. W. and C. L. Ralph. 1978. The pineal-paraphyseal complex of sea turtles 1. Light microscopic description. J. Morphol. 158:169–179.

Pieau, C. 1972. Effets de la température sur le développement des glandes génitales chez les embryons de deux Cheloniens, *Emys orbicularis* L. et *Testudo graeca* L. C. R. Acad. Sci. Paris 274:719–722.

Pieau, C. 1976. Donnees recentes sur la differenciation sexuelle en fonction de la température chez les embryons d'*Emys orbicularis* L. (Chelonien). Bull. Soc. Zool. France 101 suppl. 4:46–53.

Prange, H. D. 1976. Energetics of swimming of a sea turtle. J. Exp. Biol. 64:1–12.

Raj, U. 1976. Incubation and hatching success in artificially incubated eggs of the hawksbill turtle, *Eretmochelys imbricata* (L.). J. Exp. Mar. Biol. Ecol. 22:91–99.

Ross, P. 1978. Marine turtle survey, 1977, Sultanate of Oman. Marine Turtle Newsletter. No. 7:4–5.

Rowlatt, U., N. Mrosovsky, and A. English. 1971. A comparative survey of brown fat in the neck and axilla of mammals at birth. Biol. Neonate 17:53–83.

Sapsford, C. W. and G. R. Hughes. 1978. Body temperature of the loggerhead sea turtle *Caretta caretta* and the leatherback sea turtle *Dermochelys coriacea* during nesting. Zool. Africana 13:63–69.

Sapsford, C. W. and M. van der Riet. 1979. Uptake of solar radiation by the sea turtle, *Caretta caretta*, during voluntary surface basking. Comp. Biochem. Physiol. 63A:471–474.

Schulz, J. P. 1975. Sea turtles nesting in Surinam. Zool. Verhand. No. 143:1–143.

Schwartz, F. J. 1978. Behavioral and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina. Florida Mar. Res. Publ. No. 33, Florida Dept. Natural Resources, 16–18.

Simon, M. H., G. F. Ulrich, and A. S. Parkes. 1975. The green sea turtle (*Chelonia mydas*): Mating, nesting and hatching on a farm. J. Zool. Lond. 177:411–423.

Smith, H. M. and L. F. James. 1958. The taxonomic significance of cloacal bursae in turtles. Trans. Kansas Acad. Sci. 61:86–96.

Spotila, J. R., E. A. Standora and R. E. Foley. 1979. Body temperatures of green turtles: Free swimming and active on land at Tortuguero Costa Rica. Amer. Zool. 19:982. (Abstr.)

Standora, E. A., J. R. Spotila, and R. E. Foley. 1979. Telemetry of movement and body temperature data from green turtles, *Chelonia mydas*, at Tortuguero, Costa Rica. Amer. Zool. 19:981. (Abstr.)

Threlfall, W. 1978. First record of the Atlantic leatherback turtle (*Dermochelys coriacea*) from Labrador. Can. Field. Nat. 92:287.

Trivers, R. L. and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Ulrich, G. F. and D. W. Owens. 1974. Preliminary observations on the reproduction of *Chelonia mydas* under farm conditions. Proc. World Mariculture Soc. 5:205–214.

Weathers, W. W. and F. N. White. 1971. Physiological thermoregulation in turtles. Am. J. Physiol. 221:704–710.

Whittow, G. C. and G. H. Balazs. 1979. The thermal biology of Hawaiian basking green turtles (*Chelonia mydas*). Amer. Zool. 19:981. (Abstr.)

Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. Proc. Roy. Soc. Ser. B 205:567–580.

Witham, R. 1977. *Dermochelys coriacea* in captivity. Marine Turtle Newsletter No. 3:6.

Yntema, C. L. 1976. Effects of incubation temperatures on sexual differentiation in the turtle, *Chelydra serpentina*. J. Morphol. 150:453–462.

Yntema, C. L. and N. Mrosovsky. 1979. Incubation temperature and sex ratio in hatchling loggerhead turtles: A preliminary report. Marine Turtle Newsletter No. 11:9–10.

Yntema, C. L. and N. Mrosovsky. 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. Herpetologica 36:33–36.

NOTE ADDED IN PROOF

D. C. Jackson and H. D. Prange (1979, Ventilation and gas exchange during rest and exercise in adult green sea turtles, J. Comp. Physiol., 134:315–319) have found oxygen consumption of exercising adult green turtles to be almost 10 times the standard resting value. This makes it more plausible that leatherback turtles would be able to increase their metabolism enough to maintain relatively warm body temperatures in cool waters.

Balazs, G. H. and E. Ross. 1974. Observations on the basking habit in the captive juvenile Pacific green turtle. Copeia 1974:542–544.

Bickham, J. W. 1979. Karyotypes of sea turtles and the karyological relationships of the cheloniidae. Amer. Zool. 19:983. (Abstr.)

Bjorndal, K. A. 1979. Urine concentrations of ammonia, urea and uric acid in the green turtle, *Chelonia mydas*. Comp. Biochem. Physiol. 63A:509–510.

Bleakney, J. S. 1965. Reports of marine turtles from New England and eastern Canada. Can. Field Nat. 79:120–128.

Brattstrom, B. H. and R. Collins. 1972. Thermoregulation. Int. Turtle and Tortoise Soc. J. 6:15–19.

Bull, J. J. and R. C. Vogt. 1979. Temperature-dependent sex determination in turtles. Science 206:1186–1188.

Bustard, H. R. 1970. The adaptive significance of coloration in hatching green sea turtles. Herpetologica 26:224–227.

Bustard, R. 1972. *Sea turtles*. Collins, London.

Carr, A. 1967. *So excellent a fishe*. Natural History Press, New York.

Carr, A., M. H. Carr, and A. B. Meylan. 1978. The ecology and migrations of sea turtles, 7. The West Caribbean green turtle colony. Bull. Am. Mus. Nat. Hist. 162:1–46.

Carr, A. and H. Hirth. 1961. Social facilitation in green turtle siblings. Anim. Behav. 9:68–70.

Carr, A., L. Ogren, and C. McVea. 1980. Apparent hibernation by the Atlantic loggerhead turtle off Cape Canaveral, Florida. Biol. Conserv. (In press)

Charnov, E. L. and J. Bull. 1977. When is sex environmentally determined? Nature 266:828–830.

Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. Science 201:163–165.

Diamond, A. W. 1976. Breeding biology and conservation of hawksbill turtles, *Eretmochelys imbricata* L., on Cousin Island, Seychelles. Biol. Conserv. 9:199–215.

Ehrhart, L. M. 1977. Cold water stunning of marine turtles in Florida east coast lagoons: Rescue measures, population characteristics and evidence of winter dormancy. Am. Soc. Icthyol. Herpetol. Abstracts of meetings in Gainesville, Fla.

Ewert, M. A. 1979. The embryo and its egg: Development and natural history. *In* M. Harless and H. Morlock (eds.), *Turtles, perspectives and research*, pp. 333–413. Wiley, New York.

Felger, R. S., K. Clifton, and P. J. Regal. 1976. Winter dormancy in sea turtles: Independent discovery and exploitation in the Gulf of California by two local cultures. Science. 191:283–285.

Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford.

Foster, P. and C. Chapman. 1975. The care and maintenance of young leatherback turtles, *Dermochelys coriacea*, at the Miami Seaquarium. Int. Zoo. Yearbook 15:170–171.

Frair, W., R. G. Ackman, and N. Mrosovsky. 1972. Body temperature of *Dermochelys coriacea*: Warm turtle from cold water. Science 177:791–793.

Garnett, M. C. 1978. The breeding biology of hawksbill turtles (*Eretmochelys imbricata*) on Cousin Island, Seychelles. Research Report, Int. Council for Bird Preservation (British Section).

Greer, A. E., J. D. Lazell, and R. M. Wright. 1973. Anatomical evidence for a countercurrent heat exchanger in the leatherback turtle (*Dermochelys coriacea*). Nature 244:181.

Hainsworth, F. R. and L. L. Wolf. 1978. The economics of temperature regulation and torpor in nonmammalian organisms. *In* L. C. H. Wang and J. W. Hudson (eds.), *Strategies in cold: Natural Torpidity and thermogenesis*, pp. 147–184. Academic Press, New York.

Hendrickson, J. R. 1958. The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak. Proc. Zool. Soc. Lond. 130:455–535.

Hirth, H. F. 1962. Cloacal temperatures of the green and hawksbill sea turtles. Copeia 1962:647–648.

Hughes, G. R. 1973. The sea turtles of south east Africa. Ph.D. Diss. University of Natal.

Hughes, G. R. 1974. The sea turtles of south-east Africa II. The biology of the Tongaland loggerhead turtle *Caretta caretta* L. with comments on the leatherback turtle *Dermochelys coriacea* L. and the green turtle *Chelonia mydas* L. in the study region. Oceanographic Res. Inst. Investigational Report No. 36, Durban, S. Africa.

Hughes, G. R. and B. Brent. 1972. The marine turtles of Tongaland. 7. The Lammergeyer 17:40–62.

Kraemer, J. E. 1979. Variation in incubation length of loggerhead sea turtle, *Caretta caretta*, clutches on the Georgia coast. Master's Thesis, University of Georgia.

Lazell, J. D. 1976. *This broken archipelago*. Quadrangle, The New York Times Book Co.

Lazell, J. D. 1980. New England waters: Critical habitat for marine turtles. Copeia. (In press)

Lewontin, R. C. 1979. Sociobiology as an adaptationist program. Behav. Sci. 24:5–14.

Limpus, C. L. 1971. The flatback turtle, *Chelonia depressa*, Garman in southeast Queensland, Australia. Herpetologica 27:431–446.

Limpus, C. L. 1979. Notes on growth rates of wild turtles. Marine Turtle Newsletter No. 10:3–5.

Maynard Smith, J. 1978. *The evolution of sex*. Cambridge University Press, U.K.

Mittwoch, U. 1975. Chromosomes and sex differentiation. *In* R. Reinboth (ed.), *Intersexuality in the animal kingdom*, pp. 439–446. Springer-Verlag, Heidelberg.

Mrosovsky, N. 1968. Nocturnal emergence of hatchling sea turtles: Control by thermal inhibition of activity. Nature 220:1338–1339.

Mrosovsky, N., A. M. Granda, and T. Hay. 1979. Seaward orientation of hatchling turtles: Turning systems in the optic tectum. Brain, Behav. Evol. 16:203–221.

Mrosovsky, N. and P. C. H. Pritchard. 1971. Body