

The Ecological Strategies of Sea Turtles¹

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SYNOPSIS. By employing concepts such as "option" and "strategy" from game theory, this study derives an ecologically-oriented dendrogram of the probable evolutionary history and the present relationships of sea turtles. An "armored tank" strategy is seen as differentiating the first ancestral testudines from the stem reptiles and providing enduring advantages while simultaneously imposing basic restrictions on all later forms. A "flipper" strategy is postulated as basic to development of the sea turtle line, again imposing limitations while conferring selective advantage. Modern sea turtle species are grouped into three lineages representing strategies of habitat-type resource partitioning (a split-habitat, migratory pattern, a neritic residence pattern, and a pelagic residence pattern). Within the split-habitat, migratory group, further resource-partitioning by food-type separates the herbivorous *Chelonia mydas* populations from omnivorous *Eretmochelys imbricata* and the (apparently) carnivorous *Chelonia depressa*. Herbivory is seen as integral to the split-habitat, migratory strategy and *C. mydas* is considered the most "traditional" species, with the migratory habit secondarily lost in the other two. At the same time, the enhanced philopatry selected for by the migration strategy is viewed as responsible for the fact that *C. mydas* seems to have the most active race-formation of the three species. Further habitat-type partitioning in the neritic group, together with food-type partitioning, separates *Caretta caretta* from the two *Lepidochelys* species. *L. kempi* is represented as a consequence of Panamanian separation from *L. olivacea* following the last establishment of the isthmus as a land barrier. The third, pelagic residence, strategy is represented by *Dermochelys coriacea*, with little further differentiation of the line. The paper attempts to show that the evolution of sea turtles has been ecologically logical, that most conceivable niches for marine turtles are presently filled successfully, and that some predictions may be made with regard to gaps in our existing information.

INTRODUCTION

Although I suspect that few biologists will be in much doubt about the subject of this discussion, the title itself is troublesome because of the use of the word "strategies." The word stems from the Greek *stratos* (army, host) and *agein* (to lead); its English meaning is either strictly military or a transferred meaning from this, and it is misused here. It implies rational choice, and an example of correct usage is a comment on the conduct of medical research attributed by Bates (1951) to Alan Gregg of Rockefeller Foundation: "Strategy is the art of deciding when and on what one will engage his strength, and tactics is the skill, economy, promptitude and grace with which one utilizes his strength to attain the ends chosen by strategy." Yet the word has

gained currency in discussion of ecological and evolutionary phenomena; recent publications (Waddington, 1957, is the earliest reference I happen to know about) speak of reproductive strategies, foraging strategies, sex ratio and gene strategies, *r* and *K* strategies, ecological and evolutionary strategies, even community and ecosystem strategies . . . all with reference to entities and processes which we agree cannot make rational choices. Louw (1979) correctly points out that these usages of the word "strategy" are semantically wrong and philosophically misleading—besides, I strongly suspect that most of the users mean "stratagem" (synonym: trick for achieving a goal) rather than "strategy" (art of deciding, etc.). What we are really talking about in most cases are complexes of adaptive evolutionary changes, each of which has relative positive and negative values in any one ecological circumstance. These adaptive complexes (phenotypes) are moves in an "existential game" (Slobodkin and Rapoport, 1974), the rules of

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which are the principles of natural selection and probability, and the object of which is to "turn resources into babies" (Colinvaux, 1973) so that recruitment rate at least equals death rate; past moves, possibly under different ecological circumstances, place varying limitations on present options; there are clearly defined losers, and the winner's reward is the opportunity to keep on playing. There is no cognition, no rational choice, no prediction—chance and necessity are all-controlling.

Smith (1979) coins the term "phenotype set" which I would have preferred to "strategy," but then goes on to give this useful phrase a distinct hierarchical context and to speak of the possible behavioral strategies within the phenotype set. Mitchell and Williams (1979) note the difference between the dictionary definition and the biological usage of the word "strategy," but then go on to consolidate the usage. I reluctantly agree with Murtagh (1979) that it is a necessary evil for lack of a simpler way to label evolutionary designs in context with present-day thought on the subject. It has become jargon, and, while I lament the birth of this bastard in our family of words, I have little choice but to acknowledge its existence as a counterpart of the *nomina conservanda* of systematics. "When I use a word," Humpty Dumpty said, in rather a scornful tone, "it means just what I choose it to mean—neither more nor less" (Carroll, 1935).

In the discussion which follows, I attempt an heuristic approach to the evolutionary history of sea turtles, speaking as of a complex game played with nature over the past 200 million years. I try to show how, given various mixes of opportunities and limitations implicit in each "move" of the game, and given the strategies "chosen" by the ancestral sea turtle line, a logical outcome seems to be the present mix of species and their various niche spaces. Limited knowledge and limited space permit no more than an account which hits only the high spots of the game and is simplistic in many respects—I consider only a few major aspects of body form and attendant function in the ances-

tral lines, and include speculation in the form of "best guesses" when describing the ecological niches of extant species. The point is to present, not documented fact, but a way of thinking about sea turtles which is consistent with present evolutionary and ecological theory and which squares in a logical way with sea turtle biology as we presently understand it. If the main framework is correct, it should accept embellishment in detail without damage, and it may in itself predict the content of various information gaps which now exist. It is conceivable that a haemoglobin chemist or an endocrinologist might weave the same fabric from different lines of evidence.

THE GENERAL CHELONIAN "STRATEGY"

Obviously, the extant species of sea turtles did not have unlimited possibilities for developing the phenotypes (ecological patterns and attendant morphologies) which they show today; earlier "options" selected during their evolutionary history conferred certain genetic parameters within which the present species had to develop. Whether of positive, negative, or neutral value in any one life circumstance, these parameters from the past are basic to what we can detect today.

The prime "option" selected by the sprawl-legged ancestral chelonian line more than 200 million years ago was the "armored tank" mode of body form—the drastic modification of the entire anatomy to provide for encasement in a rigid box of defensive armor, presumably for defense against large, toothed predators. Pritchard (1979) gives a succinct account of early chelonian evolution and mentions a number of important references. I cherish Romer's (1945) statement that: "The chelonians are the most bizarre, and yet in many respects the most conservative, of reptilian groups. Because they are still living, turtles are commonplace objects to us; were they entirely extinct, their shells—the most remarkable defensive armor ever assumed by a tetrapod—would be a cause for wonder. From the Triassic the turtles have come down to present times practically unchanged; they have survived all the vicis-

situdes which have swamped most of the reptilian groups and are in as flourishing a condition today as at any time in the past." (In 1945, and with his long view of paleontological history, Romer can hardly be faulted for not recognizing the disastrous effects of man on these otherwise-flourishing species.)

The highly successful "armored tank" defense mode adopted by the ancestral chelonians involved a number of drastic anatomical modifications which committed the line irrevocably to several important limitations on their evolutionary future (see Zangerl, 1969). About a dozen vertebrae were eliminated from the trunk region; the ribs were freed from the sternum and spread laterally, and the limb girdles were drastically modified to lie partly inside the rib elements. In the process of fusing the axial skeleton to the bony shell box, practically all the dorsal trunk musculature was lost and the remnants of the ventral trunk musculature were modified for respiratory action to make up for the loss of the expansible thoracic cage. The tail was drastically shortened to permit retraction into the bony box. With these changes, all possibilities for resuming undulatory swimming motion were lost. Expansion room in the cloacal area was severely limited by the bony box and the necessary conditions for giving birth to large, living young (as in the ichthyosaurs and most sea snakes) could not be met in the chelonian line, so they remained tied to the land for deposition of cleidoic eggs.

It is interesting (albeit somewhat mysterious to me) that, as in the evolution of birds, when the anterior appendages became sufficiently modified for other purposes to no longer serve efficiently for grasping and anchoring prey, while at the same time there was broad amplification of keratin formation by the epidermis, cornified beak structures appeared and teeth disappeared—presumably forever.

THE MARINE COMMITMENT

While the move into the marine world by the ancestors of marine turtles undoubtedly exploited an important, favorable opportunity for the general chelonian

mode to occupy new niche-space, it did produce a new set of life challenges which—under natural selection—had to be accommodated by further phenotypic "strategy." The fossil record appears to give evidence of a number of separate attempts by chelonian lines to invade the sea; I believe that a single group was ultimately successful to the extent of having representatives living today.²

Compared with the swamp, river, and land habitats in which the chelonian "armored tank" strategy proved so successful, the vast extent of the ocean environment and its relative monotony (lack of local spatial heterogeneity) must have presented a major new challenge; mobility must have become a prime factor for selection. Given the irrevocable loss of trunk musculature, etc. mentioned above, the best adaptation (phenotypic "strategy") to provide the requisite swimming speed and efficiency seems to be the limb modifications we see in all living sea turtles (see Zangerl and Sloan, 1960). The stiffened, elongate foreflippers which enable the animals to "fly" through the water with forward propulsion from both up and down strokes, with the rudder and elevator action provided by the modified hindflippers, meet the need in a rather elegant way. Given the anatomical circumstances imposed by the chelonian mode, I can think of no superior adaptation for covering large distances. A number of other morphological and physiological modifications (*e.g.*, the curious, cornified papillae lining the esophagus, etc.) also come to mind in association with the commitment to marine life, but these appear to be subordinate to the major change in flipper form and function.

And the penalties of success? With the full development of the swimming flippers as a strategy for life in the spacious sea, all possibility of any reasonably efficient mo-

² I disagree with Pritchard's (1979) phylogenetic diagram showing separation between dermochelyid and cheloniid lines in the Jurassic. I follow Ernst and Barbour (1972) in believing that the ancestors of *Dermochelys* evolved much later from the cheloniid line, probably in Eocene times (see also Zangerl and Turnbull, 1955; Romer, 1956; Gaffney, 1975).

bility on land had to be sacrificed. Not only was flight from land predators made ridiculously inefficient, but the necessary hypertrophy of the pectoral muscles for powering the foreflippers interfered with complete retraction of the head, partially invalidating the original "armored tank" advantage. Maternal care of a nest (as in crocodylians) became virtually impossible, yet the animals remained tied to terrestrial egg deposition.

There must have been strong selection at this time for the development of behavior patterns leading to choices of isolated beaches for nesting, where there were minimal risks of predation by land animals on the vulnerable adults and the unprotected nests. It is interesting to note that the Zangerl and Sloan (1960) account of the primitive cheloniid *Desmatochelys lowi* Williston from the Cretaceous not only analyzes its primitive "flying" flipper developed from the ancestral chelonian type, but also describes the fossil site as probably an island in the Benton Sea which then covered the South Dakota region where the fossil was found.

Unprotected nests mean precocial young which must meet, unassisted, the challenges of the environment. For baby sea turtles leaving the nest and crawling to the sea, this implies the devastating early mortality rates so characteristic of marine species. A strongly concave survivorship curve, with high mortality during the early life stages, was presumably inescapable under such circumstances (see Pearl, 1929; Krebs, 1972).

I believe it was here in the evolutionary history of sea turtles, coincident with the "flipper commitment," that the reproductive strategy common to all living sea turtles developed. All our living species produce large numbers of eggs which are deposited, one oviducal load following another, in a sequential series of subterranean nests dug by the female under conditions of peril and then left without further attention. I believe there was no alternative but to resort to this "numbers game" so different from that shown by almost all other reptiles, and to develop the (sometimes complex) behavioral patterns

of nesting beach selection with which we are familiar.

The required production of large numbers of eggs, combined with the necessity for long distance travel to reach nesting beaches offering the requisite isolation, poses a general problem in energetics. It seems that all sea turtles must have a relatively large body mass to solve the imposed problem of energy allocation for reproduction—apparently, there can be no small-sized marine turtles as we know them.

The foregoing describes what I believe Smith (1979) would call the "phenotype set" of the living sea turtles—the complex of morphological and behavioral characters common to all seven species. They are all large animals with elongate, "flying" front flippers and "rudder" hind flippers for efficient, sustained, long-distance travel in the sea; all have unusually high fecundity by reptilian standards, with precocial young suffering high initial mortality, etc. From this point onward, the story is of radiation within the major set and the formation of minor, species-level phenotype sets or strategies fitted to different ecological niches. There is no reason to doubt that this process, which I view as essentially one of resource partitioning in the broad sense, has gone on continually since the time true sea turtles first appeared. In terms of the "game" paradigm employed here, this amounts to the constant testing of the opponent (the changing environment) through secular time by deployment of new minor variants of the sea turtle mode, with continual extinctions of some phenotypes and establishment of others, but with some group of sets always surviving to continue the testing. The forms living today are the temporary membership of this changing series.

THE MODERN SPECIES OF SEA TURTLES

The seven presently recognized species of sea turtles are placed in five genera, representing two families. It is useful to visualize a branching evolutionary tree which extends into the present time-slice at seven points and has n twigs terminating in times past. The names we apply are only labels

hung on various lower branches and twig-ends, placed to indicate meaningful relationships, but nevertheless arbitrary. I have no argument with the common, modern placement of family labels (see Footnote 2, preceding); I am reasonably content with the four generic labels on the cheloniid branchlets and the single label on the dermochelyid branchlet, but I belong to a sizable company of students who have strong doubts that all the extant twig-ends are suitably hung with species labels. Present studies in my laboratory (Hendrickson, 1980) on the chemical composition of the shell keratins from different populations indicate that *Chelonia mydas carrinegra* Caldwell, for instance, should be reinstated and elevated to full species status (a fitting action for the present symposium honoring Archie Carr!). In the present paper, however, I shall confine my remarks to the seven "official" species listed in most current works, merging *carrinegra* with the rest of species *mydas* in the genus *Chelonia*.

The seven species have a great deal in common, as described above, but they also show considerable differences in their realized ecological niches along with related, minor differences in morphology. I find it useful to view these differences as the consequence of a partitioning of the spectrum of resources available to the sea turtle phenotype set in past and present times, and will attempt description of each species in this context.

Schoener (1974) concluded that niche segregation by resource partitioning according to habitat-type dimensions is in general more important than partitioning by food-type dimensions, which is in turn more important than partitioning by temporal dimensions. This seems to apply to the ecological evolution of sea turtles, and to have an attractive correspondence with Zangerl's (1958) and Zangerl and Turnbull's (1955) arrangement of the cheloniid sea turtles according to paleontological evidence.

A basic division of the habitat resources in the world ocean may be made between the neritic waters of continental shelves and oceanic islands on the one hand and the vast spaces of open, deep sea on the

other. Biological energy fluxes and associated possibilities for food resources are highest in the continental shelf habitat-type with its input of nutrients from the adjacent continental land masses, lower in the coastal waters of oceanic islands, and lowest of all in the open ocean pelagic waters. At the same time, the general sea turtle phenotype set places high value on isolated beaches for nesting because of the requirement for reduced terrestrial predation pressure. One strategy for coping advantageously with this situation, particularly for herbivores whose richest pasturage (sea grasses) is usually in shallow areas of coastal deposition where isolated island beaches with few predators are scarce, is development of structural, physiological and behavioral adaptations to permit migration between feeding and remote nesting areas across the intervening expanses of open water. A good example is the *Chelonia mydas* (L.) population which feeds on the Brazilian coast and nests on Ascension Island (see Carr, 1975). This appears to be the strategy adopted by the group of species which Zangerl (1958) places in his Tribus Chelonini on the basis of what he interprets as "pelagic" modifications. The remainder of the cheloniids are placed by Zangerl (1958) in his Tribus Carettini, which he considers to be less modified for open ocean travel. To me this latter group represents the alternative option available to carnivores unrestricted by distribution of pasturage plants; they can maintain residence in continental neritic waters and trade off the advantages of remote nesting for the metabolic savings implicit in not making extensive migrations.

Zangerl's (1958) separation of cheloniids into tribes, based largely on paleontological evidence, is acceptable to me as a broad separation of niche space. He places it in Oligocene/Miocene times, although other workers might place it earlier (see Ernst and Barbour, 1972).

In Zangerl's (1958) Tribus Chelonini belong *Chelonia mydas* (Linnaeus), *C. depressa* Garman, and *Eretmochelys imbricata* (Linnaeus). In his Tribus Carettini belong *Caretta caretta* (Linnaeus), *Lepidochelys olivacea* (Eschscholtz) and *L. kempi* (Garman). He does not consider *Dermochelys coriacea* (Lin-

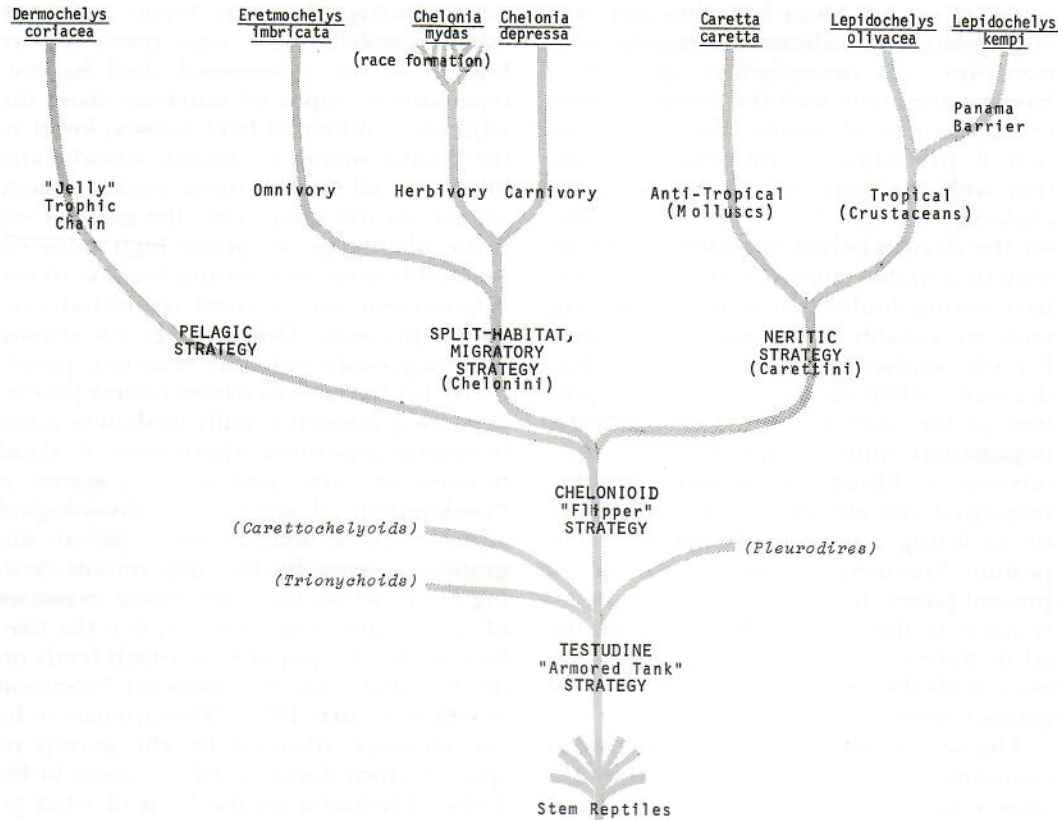


FIG. 1. Ecological strategies in sea turtle evolution.

naeus); I conceive of this species as an aberrant, highly specialized offshoot from the chelonioid stem which adopted a third option with regard to habitat partitioning among sea turtles, possibly in Eocene times (Romer, 1956; Ernst and Barbour, 1972; Gaffney, 1975). The strategy for *Dermochelys* consists of forsaking benthic feeding grounds entirely and specializing in adaptations for planktonic feeding and permanent residence in the open ocean waters (except for the obligate terrestrial nesting common to all testudines); this is discussed further in the species account for *Dermochelys*. Figure 1 illustrates my concept of the evolution of ecological strategies in sea turtles preceding and following this major three-part division.

Further habitat specializations presumably occurred subsequent to the above-described strategic "choices" made by the ancestors of modern sea turtles, often coincident with food-type resource parti-

tioning and sometimes significantly altering the original niche-space. Such later change seems to have been particularly common in the chelonins (Tribus Chelonini), presumably because the development of highly directed, philopatric migration behavior enhanced the genetic isolation of populations and provided greater opportunity for fixation of new strategic "moves" at the population level. It is difficult to explain in any other way the chelonin group tendency toward race-formation and speciation in a connected world ocean. Such radiation, originally contributed-to by the migrational habit, apparently included in a number of instances a reversal of the base trait and adoption of non-migratory habits where shifts in diet permitted survival without the energy-expensive migrations (see below).

In the species accounts which follow, I shall treat the taxa and lesser population units from the above point of view, delin-

eating their individual ecological niches (strategies) as I see these on the basis of available information on sea turtle natural history.

Dermochelys coriacea (Linnaeus),
the leathery turtle

This is a true pelagic animal, highly adapted for life in the open ocean. Among the more obvious morphological adaptations of *Dermochelys coriacea* for pelagic life are its powerfully developed swimming flippers (differently proportioned and differently structured from those of other sea turtles), its sculptured carapace ridges (which I take to be adaptations for handling problems of laminar flow associated with sustained swimming at speed), and its large size with consequent low surface-to-mass ratio permitting maintenance of adequate core body temperatures in cool waters (Frair *et al.*, 1972). All these features support a wide-ranging life on the high seas, where accessible food items of suitable size are sparsely distributed or patchy. I view this line as an early branch off the chelonin stem which found a food niche in the open ocean and rapidly evolved for sustained residence there.

Dermochelys coriacea has become so specialized that it is more strictly limited to its open sea habitat and specialized diet than the other living sea turtles are tied to their particular niches. It is apparently an obligate jelly-feeder (medusae and other gelatinous plankton); little other food has been found in stomachs, and captive young animals do poorly on other diets. It is interesting to note that this specialized diet, on first consideration seeming so unlikely a source of adequate sustenance for such a giant, probably places the leathery turtle at the top of a distinctive marine food chain based upon nannoplankton responsible for more than half of the total primary production of pelagic waters, which chain is largely independent of the more commonly recognized trophic systems supporting whales, tunas, etc. (Greve and Parsons, 1977).

Behaviorally, leathery turtles demonstrate the extent of their adaptation to a three-dimensional, liquid world by an ap-

parent incompetence for dealing with solid obstacles; captive juveniles which I reared for up to 18 mo seemed to have no "reverse gear," reacting to contact with the solid walls of their tanks by swimming harder and battering themselves unceasingly against the obstacle. Limited success in captive maintenance was possible only by building an inner wall of flexible, polyethylene film in a circular tank and creating a strong rotary flow in the water mass.

The behavioral adaptations for pelagic life make the general testudine group constraint of terrestrial nesting even more of a challenge for this species than for the others. Leathery turtles nest, for the most part, on mainland beaches with deep water approaches where strong, on-shore currents produce steep-fronted beach profiles; such circumstances permit access to nesting elevations above high tide levels by comparatively short crawls. The extreme difficulty which this incomparable swimmer experiences during land locomotion accounts, I suggest, for the fact that *Dermochelys* shows the most extreme stereotypy of all sea turtles during its period of emergence from the sea for nesting.

Chelonia mydas (Linnaeus),
the green sea turtle

As noted above, although the *C. mydas* migrating between Brazilian feeding grounds and Ascension Island nesting beaches are considered here to typify the "chelonin option" of long distance travel between separated habitats, there are numerous variations on this pattern. The Costa Rican/Nicaraguan population so thoroughly studied by Archie Carr (see Carr *et al.*, 1978 and earlier papers cited there) shows well-defined migration, but remains coastally oriented and does not cross open ocean waters to reach its nesting ground on the (relatively isolated) mainland bar beach at Tortuguero. The Hawaiian and Galapagos populations appear to be permanent residents of these oceanic island groups, feeding mainly on algae instead of sea grasses. A number of other variations on the presumed standard pattern have been described, but these examples serve to illustrate the point. This

species appears to be more clearly divided into distinct, variant populations than are other sea turtles.

Broadly speaking, it is possible to characterize the species *mydas* as one distinctive by its herbivory. All populations, regardless of their variation from the migratory pattern postulated for the original chelonin strategy, appear to show strong philopatric behavior and remarkable site-fixity in nesting. Another behavioral feature which seems to distinguish green sea turtles from the other sea turtles is the digging of a distinct "body pit" as deep as or deeper than the carapace, in which the female rests in an approximately horizontal position before beginning the excavation of the discrete cavity in which the eggs are deposited. The end result seems to be the positioning of the egg mass at a relatively lower level in the beach sand than in other species, sizes of the ovipositing females being approximately equal.

All green sea turtle hatchlings are distinctively countershaded black above and clear white below—a feature in which they differ from other cheloniid hatchlings and which Bustard (1970) interprets as adaptive for juvenile life on the open ocean.

There is still much uncertainty about nesting cycles of sea turtles (see Hughes, 1980) but I expect that, when more facts are available, it will be found that *C. mydas* tends to lay more eggs per season, with longer periods between nestings, than do other sea turtle species. (Hirth, 1971, arrives at a trial calculation of 17% of body weight for the eggs a female *C. mydas* deposits during one nesting season.) Such a trend toward "big-bang" reproduction would be consistent with the heavy energy investment implicit in the chelonin migratory pattern which I consider to be best represented among extant species by the green sea turtle.

Chelonia depressa Garman,
the flatback turtle

This distinctive, large-headed Australian species with a depressed and reflexed carapace is presumed here to represent a fairly recent offshoot from the *C. mydas* line (see Fig. 1). Most of what little is

known about it is contained in reports by Bustard and Limpus (1969), Limpus (1971), and Bustard (1973, 1979). I believe it is a population which evolved to species status on the northern coasts of Australia and has since spread southward along both eastern and western coasts to occur sympatrically with *C. mydas* in some areas. The main elements of *C. depressa*'s ecological strategy appear to be related to non-migratory habitation of an especially isolated region of shallow coastal waters where the nesting beaches were free of large, terrestrial carnivores. There is no firm information on diet, but some aborigines believe the flatback feeds largely on sea cucumbers (Cogger and Lindner, 1969, cited in Bustard, 1973), and several reports indicate that the flesh is unpleasant by comparison with green turtle flesh—an observation commonly made when green turtle diets tend toward carnivory. One also recalls the relatively large head of *C. depressa* and the tendency toward large-headedness in the carnivorous caretins (see below).

Evolving in the absence of placental carnivores (before the advent of the dingo with aboriginal man), the principal vertebrate predators on flatback nesting beaches were presumably birds, important threats only to hatchlings. The flatback has apparently lost most of its heavy, keratinous armor, to the point where fairly light scratches will draw blood. Bustard (1973, 1979) indicates that it is frequently a day-nester, influenced more by tides than by ambient light. It lays a smaller clutch of larger-sized eggs than other *Chelonia*, and these hatch into significantly larger hatchlings, too large for the available bird predators to swallow comfortably (Bustard, 1973). The hatchlings differ markedly from *C. mydas* hatchlings in coloration as well as in morphology, being gray dorsally rather than black. Bustard (1970) interprets this to mean that young flatbacks do not go to open, pelagic waters for juvenile residence—a feature which would accord with a non-migratory strategy. I expect that, when data from tagging programs on the flatback become available, the species will be found to show a high frequency of annual nesters.

Eretmochelys imbricata (Linnaeus),
the hawksbill turtle

The hawksbill is represented here as another specialized offshoot from the *Chelonia* line, probably separated from the main stem for a longer period than *C. depressa*, but still having a strong genetic similarity to *C. mydas*. Intergeneric mating can produce viable offspring. Earlier this year, I had the opportunity to examine a group of about 18 animals on the Cayman Turtle Farm which were clearly the results of a hybrid cross between *Chelonia mydas* and *Eretmochelys imbricata*. The turtles (something over 2 yr old when I saw them) had hatched from a batch of wild-laid eggs imported from Surinam in a routine shipment for farm stock during the period before the farm stopped all recruitment from the wild. The 5–8 kg individuals showed wide gradations and mixes of characters between *C. mydas* and *E. imbricata* (one wonders if they will be fertile when mature?!).

The hawksbill's strategy for survival seems to be that of a coral-reef-scrounging-omnivore tied closely to coral reef habitats which supply both feeding and nesting requirements within a small spatial range. Most of the adequately documented reports of human poisoning after consumption of sea turtle flesh relate back to this species, no doubt in correlation with its omnivorous food habits. Although there is a regrettable lack of quantitative information on hawksbills from tagging programs, there is general agreement that it is basically a solitary nester which does not engage in distant migration. Bustard (1979) reports hawksbill populations in the Torres Straits which nest on coral cays only a few miles apart, yet are "readily distinguishable on carapace morphology, coloration, and shell thickness." The strategy tying the species strongly to coral reef areas is adequate to explain why hawksbills are found nesting mainly, but not only, on islands. The general pattern of living where the reefs are would provide less consistent isolation from land predators than is common for the other species; this, in turn, conforms with the observations

that hawksbills are largely solitary nesters which show exceptional alertness and freedom from stereotypy during the nesting process (Carr *et al.*, 1960).

Caretta caretta (Linnaeus),
the loggerhead turtle

This species and the two species of *Lepidochelys* belong in Zangerl's (1958) Tribus Caretini and represent what I consider to be the third major strategic choice made by ancient sea turtles—neritic residence with adoption (continuation?) of carnivory (Fig. 1). Between the genera *Caretta* and *Lepidochelys* there seems to have been a two-fold partitioning of resources, dividing both habitat regions and principal food items. Both genera show less evidence of race-formation than do the chelonin genera.

The ecological strategy of the loggerhead appears to be one of antitropical distribution and mollusc-feeding. Although loggerheads range widely and appear to tolerate low temperatures better than any other species except the leathery turtle, their main concentrations are over productive sea bottoms on the eastern sides of continental masses where the general water movement is from the tropics toward cooler regions (exception: the Mediterranean populations). Loggerheads characteristically nest on mainland beaches (exception: the Japanese populations). While there do seem to be migrational movements in this species, they appear to be more a seasonal drift-and-return process than directed movement between distinctly different habitats as in the chelonin mode. The heavy head and jaw structure of the loggerhead are presumably direct adaptations to their molluscan diet, although there are numerous reports of *Caretta* feeding on other prey, including jellies at the sea surface and mangrove leaves in the shallows.

Lepidochelys olivacea (Eschscholtz),
the olive ridley turtle

So little is known of the non-nesting life of the olive ridley that any attempt to describe its full ecological niche, or strategy, must necessarily resort to educated guess-

work with regard to some important details. The species shows an interesting complementary distribution and diet to its fellow caretin, the loggerhead, in that *L. olivacea* is strongly tropical in distribution (at least for nesting) and seems to feed mainly on decapod crustaceans (Fig. 1). Like *Caretta*, both species of *Lepidochelys* are, for the most part, mainland nesters. The olive ridley apparently resides farther offshore than the loggerhead during the non-breeding portion of its life; many reports of "green turtles" far out at sea in the Eastern Pacific are, I believe, based on sightings of olive ridleys. Apparently, this animal dives deeply to feed on benthic crustaceans in neritic waters, but I suspect that it also may spend long periods floating on favorable currents over deep abyssal waters, feeding on crustaceans such as the red lobsterette (*Pleuroncodes*) which come to the surface at night, as well as on larger plankton it may contact during the day. If this be true, the species is tending to move out of the initial caretin neritic habitat and into the pelagic world of *Dermochelys*, but only in a strictly tropical zone.

One of the more remarkable features of both *L. olivacea* and its sibling species *L. kempfi* is the reproductive strategy of predator-swamping by aggregating in large groups offshore and, upon suitable stimulus provided by wind or stormy weather, coming ashore *en masse* to nest in a saturation maneuver on one section of beach. Anyone who has endured the conditions on an exposed beach during a high wind is probably willing to believe that most of the large land carnivores would shun the beach at such times, and can testify to the rapidity with which the turtle tracks (and, presumably, odors) are obliterated in the wind-swept sands. The turtles are quite capable of nesting individually or in small groups, but these massive *arribadas* (arrivals) seem to be typical whenever there are large numbers of individuals in the nesting population. Richard and Hughes (1972) suggest that the sites chosen for *arribadas* may be more a matter of focus by current patterns than philopatry or site fixity on the part of the turtles. Tagging returns indicate a fairly high frequency of

annual nestings, conforming with the caretin mode of less energy expenditure for major migrations leaving more energy available for reproductive effort.

Lepidochelys kempfi (Garman),
the Kemp ridley turtle

I view this species as a special, recent offshoot of the *L. olivacea* line following final emergence of the Panamanian land barrier and isolation from the major East Pacific populations of *L. olivacea*. The Kemp ridley is confined to the Gulf of Mexico as a reproducing entity, and the entire breeding population nests on a limited section of coastline in the state of Tamaulipas, Mexico. Scattered reports of stomach contents from Kemp ridleys indicate a diet consisting mainly of portunid swimming crabs. Like the olive ridley, the Kemp ridley is prone to formation of massive nesting *arribadas*, but these characteristically take place during the day for *L. kempfi* instead of at night, as in *L. olivacea*.

One interesting feature of the ecological niche of *L. kempfi* involves the question of whether the Panamanian isolation which presumably triggered its evolution as a distinct species carried with it a major negative effect. While the Atlantic and Pacific ocean systems were connected across what is now the Panamanian Isthmus, the westward flow of the Atlantic North Equatorial Current presumably "spilled" into the Pacific system. With the emergence of the isthmus barrier in early-to-middle Pliocene (about 3.5 to 4 million years ago), the energy generated by deflection from this barrier must have made the Florida Current and Gulf Stream more powerful flows, moving water out of the Gulf of Mexico habitat of *L. kempfi* and into the north Atlantic circulation (Berggren and Hollister, 1974). At the present time, there are abundant records of *L. kempfi* on the eastern U.S. seaboard and even in western Europe. One must ask whether these individuals, carried outside their critical habitat into what must be highly disadvantageous environments, are ever able to make their way back to the Gulf of Mexico to join in the reproductive effort of the species. Or is this a gigantic "leak" in the system, con-

tinually extracting an important fraction of the population and making such waifs, reproductively speaking, "dead" to the species? The majority of the animals recorded are well beyond the small juvenile stages and, therefore, past the early period of high mortality; they are valuable individuals in terms of potential recruitment to the breeding population.

SUMMARY

In an attempt to understand the complexities of sea turtle evolution and interpret the histories and relationships of the extant seven species of sea turtles, it is useful to employ a technique of game theory, treating the various conceivable evolutionary possibilities as options and the selected adaptations of populations and species as strategies. Following this approach, it is possible to identify a basic "testudine option," or strategy, which had great survival value but also imposed certain permanent limitations on descendants of the line (*e.g.*, possibilities for undulatory swimming were forfeited, cleidoic eggs became mandatory, etc.). When the successful descendants of the testudine line invaded the major oceanic habitat, the successful strategy also carried distinctive limitations (required high fecundity with precocial young and massive early mortality). Further development of the line in a changing environment produced three major strategy classes by a process of resource partitioning. The first group, identifiable from fossil evidence, developed adaptations for herbivory in mainland shallow waters combined with energy-expensive migrations to remote islands for nesting. From this group, by further ecological strategies, or adaptations, have come *Chelonia mydas*—a relatively "orthodox" descendant, *Eretmochelys imbricata*—a variant which has given up migration and turned to omnivory as a member of the coral reef community, and *Chelonia depressa*—a local form adapted to a life without strong pressure from land carnivores and apparently itself turned carnivorous. The second group, also identifiable from fossil evidence, adapted to a carnivorous life on the continental shelves, without travel to distant

nesting beaches. From this line, by resource partitioning of habitat space and diet came *Caretta caretta* and the two *Lepidochelys* species. With the rise of the Panamanian barrier, *Lepidochelys kempi* differentiated in the Gulf of Mexico, leaving the remaining world population as *L. olivacea*. The third group, represented by the pelagic *Dermochelys coriacea*, has undergone no further speciation by our existing standards.

I conclude that, not only does the evolutionary history of sea turtles make good ecological sense, but that the group meets the logical expectation of successfully filling all the major niche space available to sea turtles at present.

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