

COMMENTARIES AND REVIEWS

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Are Leatherbacks Really Threatened With Extinction?

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The paper by Spotila et al. (1996) in this issue is extremely valuable. It brings together data from a wide variety of recent sources to give a global picture of leatherback turtle (*Dermochelys coriacea*) nesting distribution and numbers. It also puts leatherback population dynamics, and their responses to various anthropogenic stresses, on a theoretical basis for the first time. It is difficult to create good population models and easy to critique them, and the courage of those who offer such theoretical constructs to the public for open criticism is to be applauded. It is in the spirit of attempting to provide some fragmentary “course correction” in our collective, erratic, but (we hope) ultimately asymptotic approach to the truth that I offer the comments below.

Spotila et al. and I have taken the same raw material — global information on leatherback numbers and trends — and come up with different conclusions. My belief is that we do not yet have the necessary data on which to base a theoretical construct that has predictive value, and therefore we should look at those populations for which adequate population trend data exist, and look for common threads or stresses in those cases for which serious population decline has occurred.

Doing this, my conclusion is that the leatherback is a vigorous and dynamic species, more flexible than cheloniid turtles in many ways (for example, in rapid maturation and in the ability to make substantial intra-seasonal shifts in nest sites), and able to show quite rapid response to protection. The well-documented examples of serious decline in nesting populations, such as at Terengganu (Malaysia) and Playa Grande (Costa Rica), are cases where almost all of the eggs laid by the entire nesting colony had been harvested for many years. There is no turtle — indeed, no organism — that can tolerate such interception of its reproductive effort.

Specific points where I question the assumptions and methodologies of Spotila et al. are as follows:

1) The assumption that the leatherback, like *Emydoidea* and *Chelydra*, is long-lived is, in fact, undemonstrated. Evidence suggests the opposite — that the species matures very rapidly (Rhodin, 1985; Zug and Parham, 1996), and that most females tagged while nesting are encountered on not more than two or three nesting seasons, with the record documented post-maturation survival only on the order of about two decades. An individual I tagged in French Guiana in 1970 was found freshly dead 19 years later in New Jersey. Hughes (1996) records a female returning to nest in Tongaland over a period of 18 years. In the context of either turtles specifically, or larger marine organisms in general, these figures do not indicate an unusually long-lived animal. And of course, average longevity for the species is very short, probably measurable in weeks rather than years, in that it has to include all the hatchlings that are consumed as they disperse.

2) The Crouse et al. (1987) life tables for the loggerhead incorporate real-world numerical data for the various intermediate life-stages, based upon the extensive availability of incidentally captured specimens in these size ranges. Such are not available for the leatherback, a species for which the intermediate life stages remain essentially unknown.

3) The term “extinction” is a very absolute one. It should not be used casually. The extirpation of leatherbacks throughout extensive parts of their global range does not constitute “extinction.” Projections of any global species to extinction, based upon a few years of trend data, need to take into account the concept of the “demostat,” an idea discussed extensively by Hardin (1993). This concept refers to the tendency of animal populations to expand until they reach an asymptotic level, to which they will tend to return after reduction following stress or temporary increase. Without a demostat, virtually all animal populations would either rise to infinity or drop to zero.

In reality, most populations of most species most of the time will oscillate around a modal value, with deviation from this value ultimately corrected as limiting factors come into play. When entirely new conditions permanently change the rules of the game, the demostat

will be re-set in a new position — perhaps a much lower one, if new sources of mortality are introduced. But it will not normally hit zero, except when reproduction has, for some reason, been totally thwarted, or in the case of species whose habitats have been destroyed, or oceanic island species whose demographics are so sensitive and absolute population levels so low as to tolerate no disturbance at all.

Many of the leatherback populations that have declined sharply are now protected. In the well-documented cases, such as Playa Grande and Terengganu, nesting populations declined because people took almost all of the eggs. So today, these populations include rather few nesters but, with current protection of the eggs, recruitment should potentially be quite good. Man has had no known influence upon any of the juvenile and subadult stages of the leatherback, and thus the survival of hatchlings as they pass through these stages, lacking data to the contrary, may be assumed to be essentially unchanged from pre-human conditions. So the hatchlings of today may generate demographically acceptable numbers of adults after they have had time to mature. True, these adults of the future may then face many dangers at the hand of man, and the maturation time remains debatable, but the overall concept is not compatible with species-wide “imminent” extinction.

4) Care must be taken when extrapolating population trends from nesting data taken over two, or just a few, seasons, for two reasons. One is that all marine turtle species except the ridleys have a variable remigration interval that is almost always longer than one year, and that may be three, four, or five years. Even in a stable nesting population there will be “good” and “bad” nesting years, and the difference between these extremes may be considerable, so multi-year averages will be necessary to detect real trends. Moreover, extrapolation of the trend into the future should not just be a linear extrapolation of the past, but will need to take into account what is happening to the population today, in terms of egg, subadult, and adult survival, with events on the nesting beach itself probably more important than any other single factor.

Spotila et al. recognize these considerations, but they fall short of applying them. Thus, many of the trends they identify conclude with data for 1994, which by all accounts was indeed an extremely poor nesting year at least throughout the eastern Pacific. Yet 1995 was better than 1994, and it would have been very helpful to have included 1995 data, if only to show that the 1995 values extrapolated from previous linear trends would have been considerably lower than they in fact were. And, conversely, future population trends extrapolated linearly from the 1994–95 data alone would have been encouraging indeed!

5) There may well be long-term natural cycles of considerable amplitude in leatherback populations. It is easy to conceive of natural factors that could serve to

reduce the recruitment success of very large or dense nesting populations; these factors include destruction of eggs by other females nesting on the same spot, buildup of resident hatchling predator concentrations on both beaches and nearshore habitats, food competition, and so on. The apparent worldwide rarity of nesting leatherbacks only a few decades ago (Deraniyagala, 1939; Carr, 1952) may in part reflect simply that most colonies remained undiscovered, but it may in part reflect reality. There may have been fewer leatherbacks then. The oldest residents at one of the most important nesting beaches today (i.e., Playa Grande, Costa Rica) report that this beach used to be a ridley arribada beach until the ridleys were displaced by the insurgent leatherback colony.

6) It is not realistic to “fill in the gaps” in leatherback demographics and population models by inserting data or concepts from such distantly related forms as *Emydoidea* or *Chelydra*. Beyond the fact that these are also reptiles with carapaces, leatherbacks have nothing in common, in terms of ecology, demography, or reproductive strategy, with these taxa. There is a point in the accumulation of information on a species where one may make an attempt at a first population model, but in my opinion, for the leatherback that point has not yet been reached. One simply has to make too many wild guesses about the basic parameters of leatherback biology for the results to be credible.

7) Currently, I perceive no evidence of overall decline in the leatherbacks of the Atlantic, and on many nesting grounds (e.g., Trinidad, Guyana, Surinam, St. Croix) there has been significant increase in recent decades. In the Indian Ocean, Hughes (1996) has documented steady increases of nesting animals in Tongaland for several decades. Moreover, these animals represent only a component of a population whose nesting extends well into Mozambique, but about which we lack recent information. Elsewhere in the Indian Ocean, leatherback colonies are few and small, but there is no evidence of really large colonies even in the past, and I believe the primary limiting factor for leatherback nesting in the tropical and subtropical Indian Ocean is the ubiquity of coral reefs along both mainland and insular shores.

The problem is in the Pacific. Here the nesting decline, especially in the eastern Pacific, is real, even though I probably chanced to hit an unusually good nesting year during my 1980 flight along the Mexican Pacific coast, the population estimates derived from which (Pritchard, 1982) have possibly been used as baseline data for subsequent estimates to a greater degree than the quality of the data would justify. Nevertheless, this same flight indicated that adults were being killed on many of the beaches, and subsequent ground-truthing indicated that egg collection was also rampant. These two factors alone would have decimated the population, and the numerous at-sea factors documented by Spotila

et al. only served to make the situation worse, and the decline steeper.

8) Spotila et al. assume that the risk of predation upon a given life stage is proportionately greater when the duration of that life stage is longer. Furthermore, the population models presented assume that there is a fixed percentage loss of subadult leatherbacks per year, and that this will progressively decimate subadult populations whether they take 5 or 15 years to mature. In reality, the key point is that it is probable that the relatively brief time during which a hatchling progresses into the standing juvenile and subadult population (i.e., the first few months of life), and the time immediately after it leaves this population (i.e., the first breeding season), are times of probable very high mortality. On the other hand, the mortality of the established juvenile and subadult animals themselves may be so low as to be insignificant compared to these assuredly high front-end and back-end mortalities. The young leatherback needs to pass through these stages rapidly because only when it is large can it function physiologically in the very cold waters where feeding is often best. There is no evidence that these stages are intrinsically dangerous.

Nevertheless, the concept that a population that can mature in five years is more vulnerable than one that matures in fifteen years needs some discussion. It may be true that, if leatherbacks mature very rapidly (e.g., in five years), they are subject to the higher mortality to which adults are exposed sooner, but an immature animal is demographically useless until it matures. The key parameters will be a) average duration of the productive adult years (i.e., mean number of nesting seasons), and b) the percentage of individuals that survive to reach maturity. Duration of adult survival, time to first maturity, and the odds against a neonate surviving to maturity may have a fairly complex relationship. Spending too much time as a hatchling or post-hatchling is probably very dangerous, but many vertebrate species that grow slowly and reach maturity only after many years (elephants, humans, whales) have at least potentially great adult longevity, and many solve the problem of high juvenile mortality by having few but large young. Furthermore, long maturation, even with some finite level of annual attrition, may present an advantage in certain situations, for example in the case of a nesting colony of a sea turtle species that is exposed to a catastrophic or saturation level of beach exploitation (nesting females plus eggs) for a finite period, followed by abrupt cessation of exploitation. If the juveniles in the "pipeline" had a long enough maturation time, they might stay at sea throughout this period, and the population might recover. But if all the surviving juveniles matured and returned to their natal beach for a rendezvous with doom within the period of intensive slaughter, the population would clearly be extirpated. Real world examples of this pattern include several cases where green turtle soup canneries have operated intensively but for finite periods on or near nesting beaches. The turtle populations were not extirpated,

presumably because green turtles take several decades to mature, and by the time the later-maturing individuals returned to nest, the cannery was closed.

9) Spotila et al. make the assumption that leatherbacks "need" to lay many eggs because of their intrinsically high mortality during the first year of life. This assumption may not be correct. Certainly, the high egg productivity of sea turtles makes their demographic responses potentially very different from those of *Emydoidea* or *Chelydra*. The high percentage mortality experienced in places where hatchlings are abundant may not be identical to the situation in places where nests are occasional and hatchlings so few that resident predators are unlikely to expect them nor count on them to provide their daily sustenance. There are a number of chelonian species, including *Heosemys spinosa*, *Chersina angulata*, *Malacochersus tornieri*, and *Rhinoclemmys punctularia*, that live in environments that offer many predators, but that often lay only a single egg. Perhaps sea turtles lay numerous eggs simply out of intraspecific competition — after all, Darwinian competition works on individuals, not populations, and the object of the exercise for the individual turtle is to have maximal genetic representation in the next generation, not to feel responsible for the future of the species, or the population, as a whole.

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