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MODULATED REPRODUCTIVE PERIODICITY IN *CHELONIA*[1]

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Abstract. After 15 yr tagging at the nesting ground of *Chelonia mydas* at Tortuguero, Costa Rica, 447 remigration returns have been recorded. These confirm previous indications that some Tortuguero females return to nest every 2 yr and some every 3 yr, with the latter being the more frequent cycle. Returns after absences of 4 yr are so frequent that it seems probable that a regular cycle of this magnitude also exists. Longer absences recorded (up to 9 yr) probably can be attributed to missed encounters or to weak site tenacity by the returning turtles. A growing list of two-time and three-time returns shows that although an individual usually maintains a constant cycle, modulation of this may occur, and that the change may be either from 3 to 2 yr, or vice versa. It is suggested that the modulation reflects ecological conditions on the feeding ground. A sudden extensive shift to a 2-yr cycle, by turtles that had been nesting on a 3-yr cycle, probably contributed to the heavy nesting that occurred in 1969, after several previous weak seasons.

After each season at the Tortuguero breeding ground of the green turtle, *Chelonia mydas*, some females return to nest two years later and some come back after a three-year absence. The three-year cycle is the more frequent (Table 1). No return after a single year has ever been recorded at Tortuguero (Carr and Ogren 1960)—or, apparently, at any other nesting ground of *Chelonia* anywhere in the world. Neither the departure from the annual breeding regimen nor the dichotomy in the existing periodicity is understood. Nonannual or irregular rhythms occur in the breeding cycles of some birds. Sooty terns breed at Ascension Island every 9.7 months (Chapin and Wing 1959); and according to Robert McFarlane (personal communication) the same species returns to nest at Wake Island at intervals of from 6 to 12 months. Condors and some of the albatrosses may breed every other year (Thomson 1964, p. 107) and the King Penguin breeds twice every 3 yr (Thomson 1964, p. 107).

In *Chelonia* the length of the internigration period may be related to both feeding ecology on the residence ground and the pattern of ocean currents in the travel area, and changes in its length might be determined by variations in these. The physiological problems of migratory reproduction would seem fundamentally the same in the green turtle and in migratory birds. There are differences in the breeding ecology of the two, however, and it may be in these that an explanation of both the longer reproductive cycle of *Chelonia* and the duality in its cycle-period should be looked for. One difference is the multiple-renesting characteristic of sea turtles, which may involve five or more emergences at intervals of from 12 to 14 days. Another is that much of the cyclical reproductive venture, which may require up to 4,000 km of round-trip travel, the laying of some 500 eggs or more—representing at least one fifth of the body weight—and a stay of several weeks at the nesting locality, is apparently passed without access to a source of food. It has seemed likely, therefore, that the breeding cycle is modulated in accordance with conditions on the feeding range, that physiological preparation for the migration can never be completed in 1 yr, and that even slight ecologic changes may shift the preparation period from 2 to 3 yr, or vice versa.

TABLE 1. Interval-frequency in 447 remigration returns of *Chelonia* to Tortuguero, Costa Rica, 1958–1969

Intervals (yrs)	Number	Percent
1	0	0
2	117	26.1
3	196	43.8
4	79	17.6
5	22	4.9
6	23	5.1
7	8	1.7
8	1	0.2
9	1	0.2

From the beginning of our migration research with *Chelonia* it has thus seemed of fundamental interest to learn whether an individual female adheres to a fixed schedule of breeding migrations, or may change from one cycle to the other—that is, might nest one time after a 2-yr interval and the next time wait 3 yr, or vice versa. It was clear that to elucidate this point, records of consecutive post-tagging returns by individual females would be required; and that if the cycle-shifts should prove to be rare, it might be necessary to

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await the accumulation of a large number of two-time returns before a shift was recorded. The first of these was seen at Tortuguero in 1965, when a female green turtle changed from a 2-yr to a 3-yr cycle (Carr 1967). The records that have accumulated since then include 42 two-time returns and three returns of three times each (Table 2). Among these there were 11 shifts from the 3-yr period to that of 2 yr, while the above-mentioned case noted in 1965 remains the only one in which the shorter period was followed by the longer. However, much of the preponderance of the 3–2 shift was contributed by eight cases that occurred in 1969, a year in which the total number of turtles returning after a two-year absence was the largest for any year since 1958, and more than twice the overall average for the 12 yr of the study. There seems to be no doubt that this fluctuation in periodicity was at least partly responsible for the relatively heavy nesting that occurred on Tortuguero Beach in 1969.

Except for the attrition that should logically reduce the number of 3-yr cycles somewhat—simply because a female is more likely to be lost to the population in a 3-yr period than in one of 2 yr—it might seem that the ratio between breeding-cycle frequencies could be determined by simply tagging a large number of turtles in one season and then comparing the number of those that returned two years and three years later. During later years of the study, however, longer remigration intervals have appeared (see Table 1). At first it appeared probable that these were merely multiples of the 2-yr and 3-yr cycles, in which intervening arrivals had been missed during an entire season by the beach patrols. It now seems that this may have been an oversimplification.

For example, an unexpectedly large number of 4-yr intervals has been recorded (Table 1). These could be simply 2–2 cycles with an intermediate contact having been missed. Although site-fixity is strong in Tortuguero green turtles, and although each female nests, on the average, between four and five times during her season at the breeding ground; and although tag crews patrol nightly throughout the season on the same 6.4 km (4 miles) of the nesting beach, it would nevertheless be possible for a turtle to escape attention for an entire season. However, the number of 4-yr remigration intervals that now have been recorded appears too high to be attributed to missed contacts, and the dichotomy in breeding periodicity would seem likewise to be evidence that trichotomy may also occur. The interchangeability of the 2-yr and 3-yr cycles in a given female suggests that the dichotomy is ecologically regulated. If it is true that 3yr is simply the usual time needed for a turtle to ready herself for the physiological feat of reproductive migration, and if it is true also that exceptionally favorable conditions may simply shorten the period to 2 yr, might not unfavorable conditions lengthen it to 4? Although, there is at present no way to prove that the 4-yr reproductive cycle really exists, both logic and the negative evidence available suggest that it does, and that even more protracted postponement of reproductive migration may be indicated by the intervals of 5 yr and more shown in Table 1.

TABLE 2. Interval-frequency in two-time and three-time returns of nesting green turtles, Tortuguero, Costa Rica, 1958–1969

No. of years returning	Intervals (yrs)	Frequency observed
Two-time returns	3–3	11
	2–2	10
	3–2	10
	4–2	4
	3–4	2
	3–6	2
	2–3	1
	4–3	1
	2–5	1
Three-time returns	4–2–2	1
	2–2–2	1
	3–3–2	1

Attrition was mentioned as a factor bound to change the relative frequency of 3-yr and 2-yr cycles, in favor of the latter. The same factor would be even more effective in reducing the number of 4-yr intervals recorded, and this effect would increase as the intervals grew to 5 and more years. Except for this effect of attrition, the recorded totals of 2- and 3-yr intervals are a reliable sample, because neither is a multiple of any shorter interval, and so cannot be based on a missed encounter. All the longer intervals, however, could represent cryptic multiple remigrations, and this effect would offset, in some degree, the decrease due to attrition. The figures in Table 1 should be looked at with this in mind.

As long-distance tag recoveries accumulate, it may become possible to associate certain individuals or sections of the Tortuguero nesting colony with particular residence ranges, and so to correlate frequencies of, and shifts in cycle interval with the geographic derivation and travel routes of the migrants involved. When this is possible we will be closer to an understanding of the ecologic factors responsible for both the dichotomy of the cycle and the modulation it undergoes.

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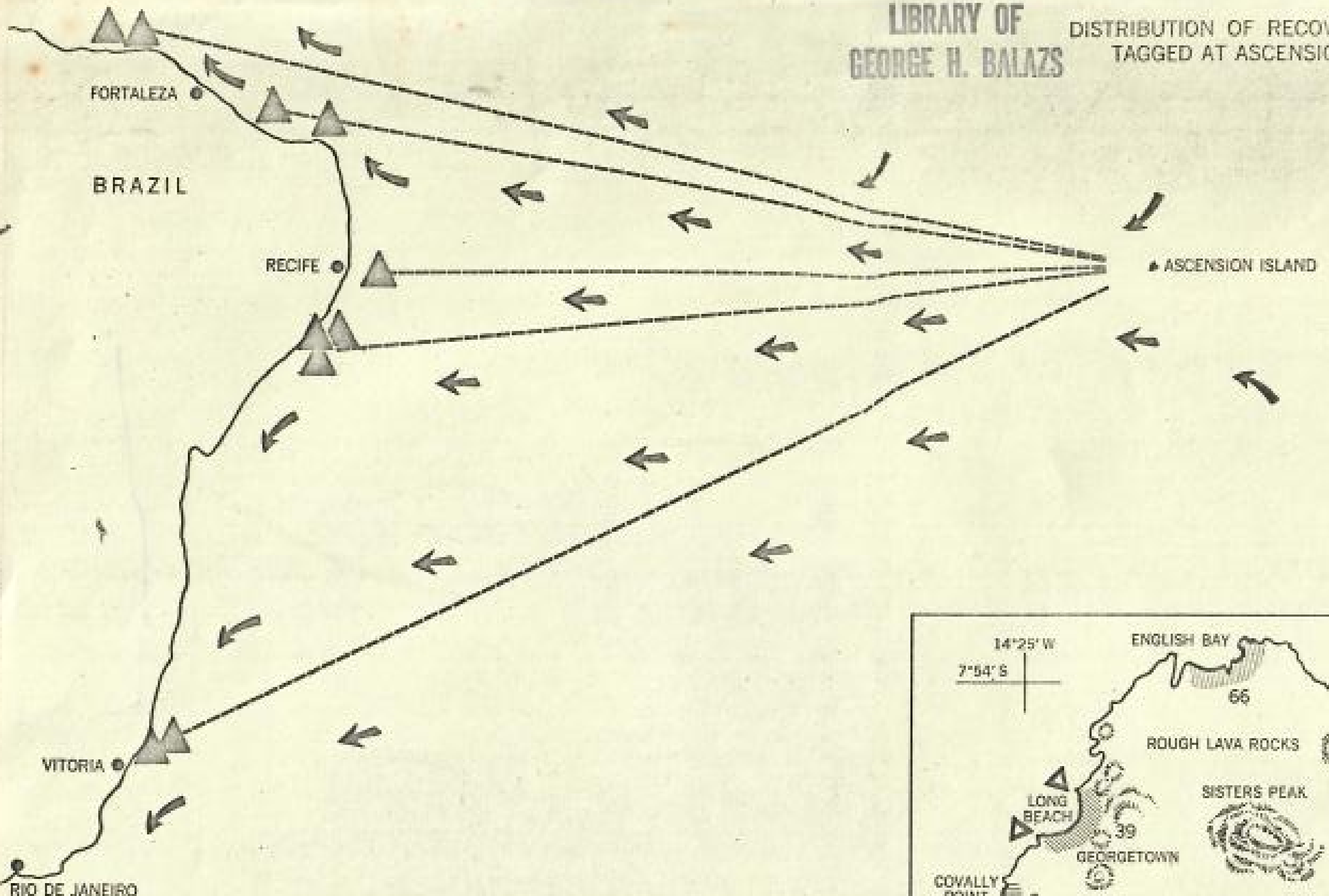

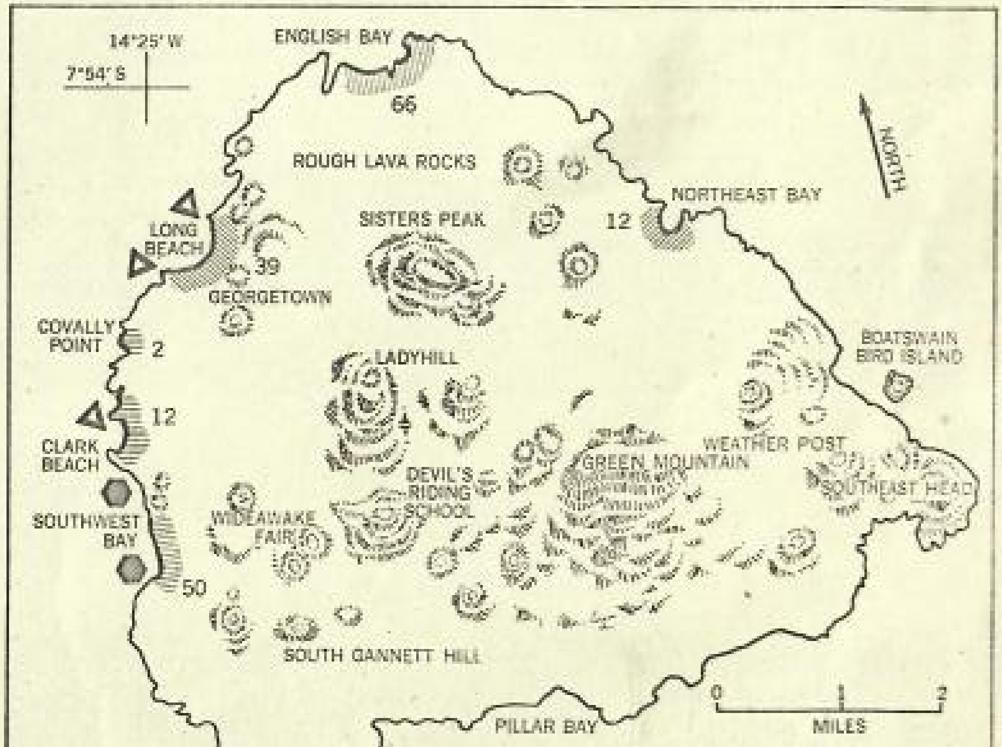

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