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Nesting Activity of the Loggerhead Turtle (*Caretta caretta*) in South Carolina I: A Rookery in Transition

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Surveys of nesting activity of *Caretta caretta* were performed during nesting seasons from 1972 to 1976 on Kiawah Island, SC. A hatchery, operating from 1973–1976, reduced the effect of raccoon predation on nests and usually yielded a high percentage of hatchlings. Nightly beach patrols from 1973–1976 helped reduce raccoon predation among nests left on the beach; egg poaching ceased during the study period. Nesting females were tagged from 1973–1976 to obtain information on the size of the annual nesting population, in-season renesting, and internesting wanderings. A decline in nesting activity from 1973–1976 could not be correlated with any specific human activity, and appears to have reversed itself since 1976. An average of 34.0 ± 3.7 adult and adolescent loggerhead carcasses washed ashore each year. Occurrence of dead turtles was closely related to intensive commercial shrimping activity in nearshore waters. Kiawah Island is undergoing development as a resort, but the builders have followed many of the management recommendations established relative to *Caretta*. This could explain the stabilization of nesting activity since 1976, and indicates that prudent beach development need not inhibit reproduction by *Caretta*.

As with other genera of marine turtles, data on the Atlantic loggerhead, *Caretta caretta* (Linne) have been collected largely through a variety of mark-recapture studies and beach surveys at identified nesting areas. Population data have been obtained from long-term tagging programs (LeBuff and Beatty, 1971; Hughes, 1974 a, b; Richardson et al., 1978) modelled on the study of *Chelonia mydas* at Tortugero, Costa Rica (Carr and Giovannoli, 1957). Short-term studies have generated valuable data on annual nesting activity (Caldwell et al., 1959; Carr and Ogren, 1959; Kaufmann, 1975), habitat perturbations (Caldwell, 1962; Worth and Smith, 1976) and predation (Ehrhart, 1976; Davis and Whiting, 1977). Although there is a significant population of loggerhead turtles in South Carolina (Caldwell, 1959), there has been no previous sustained quantitative study of a specific nesting beach. We have conducted five years of nesting and predation surveys on Kiawah Island, South Carolina, and four years of tagging and hatching operations. This paper reports results of that work.

Kiawah Island lies 9 km southwest of Charleston, South Carolina, with a nearly east-west orientation (Fig. 1). Kiawah is a beach ridge barrier island which has prograded along two-thirds of its 16 km length since 1939 (Hayes, 1975), and provides nests with relative safety from erosion. Archaeological evidence suggests that *Caretta* has utilized the Kiawah beach since at least 2,000 BC (J. D. Combes, pers. comm.).

C. caretta has been declared an internationally endangered species (IUCN 1970) and holds "threatened" status under both the Federal Endangered Species Act and the South Carolina Non-game and Endangered Species Program. In 1972, daily beach patrols revealed that the Kiawah loggerhead population faced three major pressures that could endanger its survival: egg predation by raccoons, nearshore drowning of adults and adolescent turtles in shrimp trawler nets, and frequent human disturbance on the nesting beach. These results provided the basis for a tagging and hatchery program on Kiawah which was carried out from 1973 to 1976. Our objectives were to identify nesting habitat, to enumerate nesting females and to determine and enhance hatchling production. During this time, the ownership of the island was transferred and resort development begun, which provided an opportunity to observe the effects of development on *Caretta* activity.

Methods and Materials

Beach patrols.—In 1972 daytime patrols recorded nesting and non-nesting emergences, nest

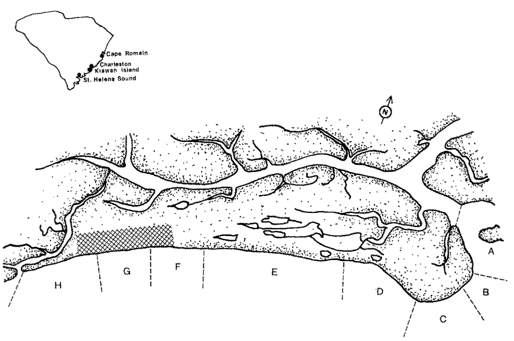

Fig. 1. Kiawah Island, South Carolina. Total length of the island is 16 km. Letters designate beach sectors (see text). Hatching indicates site of present resort development. Inset shows location of Kiawah Island relative to important features in South Carolina.

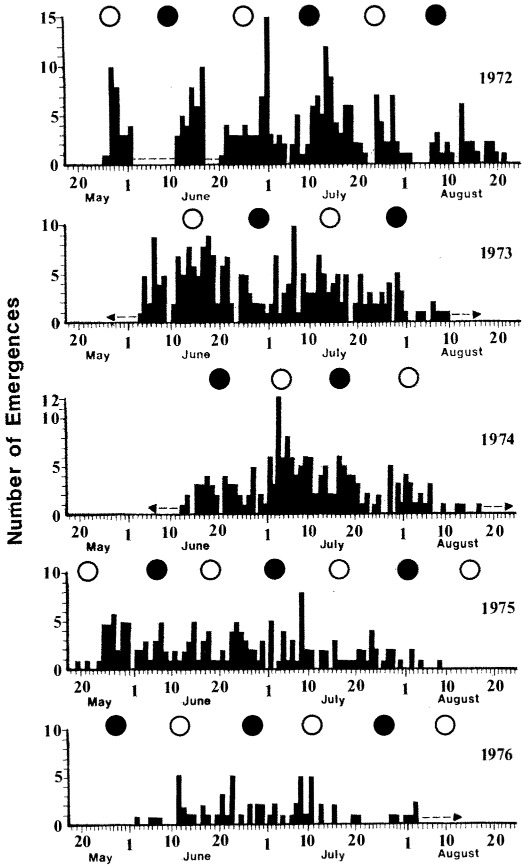

Fig. 2. Annual nesting activity on Kiawah Island, S.C., 1972–1976. Open circles indicate times of full moon, closed circles represent new moon. Dotted lines and arrows show times when nesting could have occurred, but was not monitored.

predation and carcass washups. From 1973 to 1976, dusk-to-dawn nightly patrols with all-terrain vehicles enabled us to tag nesting females, secure nests for protection and observe nesting behavior. Patrols generally began in late May or early June and continued until nesting was completed during the second or third week of August (Fig. 2). All known emergences were mapped, and a sample of wild nests was staked and followed through incubation to hatching.

Tagging.—Female loggerheads were tagged during oviposition whenever possible, but some individuals had to be turned over, either after nesting or on the return crawl of a non-nesting emergence. Archie Carr supplied #49 Monel cattle-ear tags (1973–1976) and H. O. Hillestad supplied Henley Jumbo Rototags (1974–1976), which were applied according to the techniques of Carr and Caldwell (1956) and Bass et al. (1965), respectively. Prior to tagging, the tag site was perforated with a standard leather punch to permit inspection of the locking mechanism during and after application. Measurements of curved carapace length and width, straight-line skull length and width, clutch size, nest cavity and track dimensions were recorded whenever conditions permitted. Morphological abnormalities and distinctive carapace epifauna were noted.

Hatchery.—The 1973–1974 hatcheries consisted of wire pens in the dune field where whole fresh clutches of eggs were transplanted into holes dug by hand to match the original nest cavities. Extensive embryonic mortality in 1974, caused by heavy rainfall, prompted a change in the 1975 and 1976 hatchery procedures. Eggs were packed in styrofoam coolers, stored in a shelter, and periodically moistened according to the techniques of Mariculture Ltd. (G. Ulrich, pers. comm.). All eggs were moved to the hatchery within 8 hours of oviposition. Hatchlings were released above the high water mark at various locations on the beach in the evening, within 24 hours of emergence from the sand. Each clutch was inventoried after hatching activity ceased.

RESULTS

Nesting activity.—Nesting began in mid-May each year, reached a peak between 25 June and 9 July, and ended by 22 August (Fig. 2). Pro-

TABLE 1. NESTING ACTIVITY OF LOGGERHEAD TURTLES AT KIAWAH ISLAND, S.C., 1972–1976.

	1972	1973	1974	1975	1976	Total
Emergences	275	310	379	258	68	1,290
Body pits	205	215	230	154	44	848
Nests (%)	196 (71.3)	194 (62.6)	204 (53.8)	135 (52.3)	38 (55.9)	767 (59.5)
Dry runs (%)	79 (28.7)	116 (37.4)	175 (46.2)	123 (47.7)	30 (44.1)	523 (40.5)
% Body pits that contain nests	95.61	90.23	88.70	88.76	86.36	90.44

nounced peaks in nesting activity occurred at 10–14 day intervals in 1972 and seemed to follow the semi-lunar tide cycle, but no such peaks or correlation existed in subsequent years. An emergence or crawl refers to a turtle's departure from the surf and subsequent activity on the beach whether or not eggs are deposited. A dry run or false crawl is any emergence which does not result in a nest. Between 1972 and 1976, there were 1290 emergences, of which 767 (59.5%) were nests; the other 532 (40.5%) were dry runs (Table 1). The proportion of dry runs was substantially lower in 1972 (28.7%) than in the other four years, in part because 1973–1976 night patrols recorded fresh dry runs that occurred entirely below mean high water. Such tracts were usually erased by the tide prior to the daytime beach visits in 1972. Only 81 (15.5%) of the 523 dry runs featured a body pit, the shallow ovoid depression excavated by a turtle prior to oviposition. From 1972–1976, 90.4% of all emergences with body pits actually contained nests.

A chi-square test was applied to nesting data to determine whether nests were uniformly distributed among beach sectors (Table 2). Distribution in 1972 and 1976 was essentially uniform, although Sector A had concentrations slightly in excess of expected values both years. Sector G had moderately light nesting during 1972, then exceeded expected concentrations in 1976, despite accelerated resort construction and increased human activity immediately landward of the dunes.

Nest distribution was significantly non-uniform ($P = 0.025$–0.050) in 1973, 1974 and 1975 (Table 2). In 1973, nest concentration in Sector C was much greater, and that in Sector F was much less than expected. In both 1974 and 1975, nesting was heavier than expected in Sectors A and E, and lighter than expected in Sector H.

Tagging.—Turtles were intercepted on an average of 60.4 ± 11.7% (mean ± SE; Range: 45.6% (1976) to 78.6% (1975)) of all emergences from 1973–1976. Sectors A, B, and C were patrolled less frequently in all years, which resulted in lower interception rates in those areas ($\bar{x}$ = 18.4 ± 9.9%). All individuals ob-

TABLE 2. CHI-SQUARE TABLE SHOWING SPATIAL NEST DISTRIBUTION ON KIAWAH ISLAND, S.C., 1972–1976. Chi-square values at the bottom of the table indicate wheher sectors were significantly different (*). Values with superscripts indicate sectors which had higher (+) or lower (−) nesting activity than expected.

Sector	1972	1973	1974	1975	1976
A	1.34+	0.08	3.66++	3.00+	1.78+
B	0.26	3.22−−	0.40	0.01	0.50
C	0.16	6.05++	1.25	0.77	0.04
D	0.35	0.20	1.33	0.94	0.04
E	0.06	0.06	4.08++	4.07++	0.57
F	0.68	5.96−−	0.32	0.11	1.88−
G	3.50−−	0.80	1.80	0.86	4.00++
H	0.16	0.99	4.39−−	5.19−−	0.78
Chi-square value	$6.52^{n.s.}$	17.34*	17.23*	14.95*	$9.59^{n.s.}$
Level of significance	$P = 0.10$	$P = 0.025$	$P = 0.025$	$P = 0.050$	$P = 0.10$

TABLE 3. CUMULATIVE TAGGING DATA FROM KIAWAH ISLAND, S.C., 1973–1976. Values in parentheses are the number of dry runs (non-nesting emergences) and nests, respectively.

	1972	1973	1974	1975	1976	Total
Total # tagged females	—	61	68	59	23	211
Single interceptions (dry runs, nests)	—	37 (8, 29)	54 (6, 48)	37 (17, 20)	18 (4, 14)	146 (31, 115)
Two-time interceptions	—	10 (6, 14)	5 (1, 9)	11 (5, 17)	4 (2, 6)	26 (12, 40)
Three-time interceptions	—	7 (6, 15)	7 (5, 16)	2 (1, 5)	0	16 (12, 36)
Four-time interceptions	—	4 (4, 12)	1 (1, 3)	2 (2, 6)	1 (0, 4)	7 (7, 21)
Five-time interceptions	—	0	1 (1, 4)	1 (1, 14)	0	2 (7, 21)
Six-time interceptions	—	1 (2, 4)	0	3 (4, 14)	0	4 (6, 18)
In-season renesters (%)	—	22 (36%)	14 (20%)	19 (32%)	5 (22%)	60 (28%)
Out-of-season remigrants (%)	—	0	0	1 + 11* (20.3%)	2 + 7* (39.1%)	21 (10.2%)
Nests/female** ($\bar{x}$ = 2.54 ± 0.58)	—	3.21	3.01	2.29	1.65	—
Dead turtles (washups)	29	47	24	35	35	170

* Eleven (1975) and seven (1976) females were observed with scarring at the tag site but no tag. All other remigrants bore tags.
** Calculated by dividing nests/yr (Table 1) by tagged females/yr.

served after 12 July of each year had been tagged previously that season.

Two hundred eleven females were tagged in the four years ($\bar{x}$ = 51 ± 12.2 yr^{-1}, Table 3). Sixty individuals (28.4%) were intercepted two to six times in a single season. Emergence data for 22 of these multiple-return females (1973–1975) indicate an average distance between successive emergences of 3.2 ± 1.8 km. Another 151 individuals (71.6%) were observed only once in a given season at Kiawah. Although 50 animals that were overturned to be tagged before nesting were not seen again, another 48 individuals so treated returned to nest within 1–12 ($\bar{x}$ = 2.4 ± 0.8) days. This lot includes one female that nested six times in 1975, one that nested five times in 1974, and four that nested four times in 1973 and 1975.

Only three females nested in more than one of the four years. Turtle C2478 was observed nesting once in 1973 (118 eggs), and once in 1975 (132 eggs). Turtle D2705 nested twice in 1974 (108 eggs each time) and returned in 1975 to nest at least once (121 eggs). Turtle D2699 nested once in 1974 (127 eggs), and once in 1976 (139 eggs), the night after she made a dry run. Eighteen females showed signs of tag loss or tissue necrosis in the tagging region in 1975 or 1976; no such abnormalities were noted on turtles during the previous two years.

The ratios of annual number of nests to tagged females ranged from 3.21 nests/female in 1972 to 1.64 nests/female in 1976 ($\bar{x}$ = 2.54 ± 0.58; Table 3). There was a steady decline in this ratio during the study period.

Predation.—Although the ghost crab, *Ocypode quadrata,* was locally abundant, destruction of turtle eggs by this species was limited to scavenging. Likewise, the robust feral hog population on Kiawah was not a significant agent of nest predation. Egg poaching by humans occurred once and was thwarted once in 1973, and did not occur again. Nest predation was thus primarily effected by the raccoon, *Procyon lotor marina,* and ranged from 10 to 97% (Fig. 3). In 1975, there was an 85% winter die-off of the Kiawah raccoon population (M. Pelton, pers. comm.). Except for that year, the decrease in wild nest predation from 1972–1976 closely paralleled the declining number of nests left on the beach as a greater proportion of nests was moved to the hatchery. Beach surveys in May indicated that there was a 2–3.5-week lag between the onset of turtle nesting (8–15 May) and the occurrence of destruction by raccoons. Predation estimates among the first 45 nests in 1973–1975 ranged from 15.6% to 26.7% ($\bar{x}$ = 21.5%).

Predation rates in Sectors A, B and C, which were lightly patrolled due to inaccessibility on high tides, were compared with those in Sectors D–H, which were patrolled more regularly, with a Mann-Whitney U Test (Table 4). In 1972, all sectors were patrolled equally by day, and no significant difference in predation levels

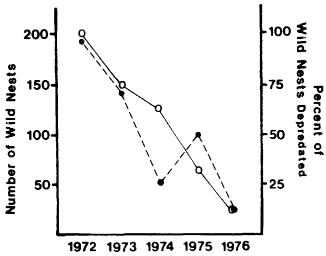

Fig. 3. Frequency (closed circles) and percent predation (open circles) of wild nests on Kiawah Island, S.C., 1972–1976.

in the two areas existed ($P = 0.5$). In each of the other four years, however, predation on wild nests was markedly higher in Sectors A–C.

Hatchery.—Between 1973 and 1976, 197 nests were placed in hatcheries on Kiawah Island (Table 5). The mean clutch size declined significantly ($P = 0.05$; Kruskal-Wallis Test) from 1973 and again from 1974 to 1975 and 1976. Hatch rates in 1973 (80.61%) were higher than for wild nests ($P = 0.10$). In 1974, 93% of the entire egg production on Kiawah was lost. All 90 nests in the hatchery, as well as 36 wild nests, were inundated by a torrential August rainfall which flooded the entire island for more than 3 weeks and drowned the developing embryos. Of the nine wild nests that hatched in 1974, seven were at elevated sites (dune tops). They had normal hatch rates between 66–97% ($\bar{x} = 81.2 \pm 4.1$). During the four years the hatchery operated, 9,682 hatchlings (73% of all eggs handled, except in 1974) were released.

Offshore mortality.—From 1972–1976, an average of 34.0 ± 3.7 (total = 170) dead turtles washed ashore on the 16 km study beach each year (Table 3). In 1972, six of the 31 carcasses had gunshot or bludgeon wounds, but only two carcasses were so marked between 1973–1976. Overall, 134 (78.8%) carcasses had carapace lengths between 45 and 82 cm, indicating that they were juveniles or sub-adults (Carr and Goodman, 1970; Hillestad et al., 1977). The area off the Kiawah Beach is a highly productive shrimp fishery; shrimp trawlers congregate there and encounter loggerheads in the shallow nearshore habitat during the shrimping season. The relationship between intensive trawling activity at Kiawah and subsequent carcass washups is strong, but difficult to quantify except by isolated examples. In 1974, 13 turtles washed ashore between 2 May and an unscheduled mid-June closing of the inshore shrimping season. During the 3-week closure no strandings occurred, but three days after the season reopened in July, 11 carcasses washed ashore. In 1976, no dead turtles were observed prior to the opening of the inshore season on 15 May, but six dead turtles washed up May 18. On 10 June 1976, 31 trawlers were working off Kiawah and two days later 13 carcasses washed ashore. No dead turtles washed ashore more than two days before or five days after the opening and closing dates of the inshore shrimping season in any year during the study.

TABLE 4. PERCENT OF UNMANIPULATED (WILD) NESTS DEPREDATED, KIAWAH ISLAND, S.C., 1972–1976. Mann-Whitney U-statistic compares predation on rarely patrolled (light) sectors (A–C; see Fig. 1) versus commonly patrolled (heavy) sectors (D–H). Sectors were not patrolled at night in 1972.

Sector	Patrol intensity	1972	1973	1974	1975	1976
A	Light	95.8	85.0	71.0	75.0	75.0
B	Light	93.5	90.0	52.5	50.0	66.7
C	Light	95.0	81.3	90.0	92.0	50.0
D	Heavy	98.0	68.2	78.2	75.0	33.3
E	Heavy	100.0	80.0	36.5	25.5	25.0
F	Heavy	94.5	56.5	22.1	33.3	20.0
G	Heavy	91.0	50.0	30.0	66.7	12.5
H	Heavy	80.0	75.0	38.0	30.0	16.6
Mann-Whitney U-statistic		7.0	0.0	2.0	2.5	0.0
Level of significance @		0.50 (n.s.)	0.018	0.071	0.098	0.018

Table 5. Results of Hatchery Effort on Kiawah Island, S.C., 1973–1976.

	1973		1974		1975		1976	
	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild
No. of nests recovered	55	189	90	114	35	100	17	21
Total no. of eggs year^{-1}	7,297	—	11,192	—	4,027	—	1,979	—
Mean no. of eggs nest^{-1} ± SE	133.2 ± 2.3		124 ± 2.1		115 ± 4.7		116 ± 5.5	
No. of hatchlings released	5,880	—	0	—	2,789	—	1,013	—
Mean hatch rates ± SE	80.6 ± 1.8	67.2 ± 2.8*	0	84.2 ± 4.1*	70.6 ± 3.6	69.3 ± 3.5*	51.2 ± 2.9	

* Wild nest hatch rates based on N = 5 (1973), 9 (1974), 38 (1975) nests.

Discussion

Nesting activity.—The duration and seasonality of nesting activity on Kiawah agrees with descriptions from Cape Romain, South Carolina (Caldwell, 1959) and Cape Sable, Florida (Davis and Whiting, 1977). The regular frequency ($\bar{x}$ = 12 ± 1.8 days) of activity peaks in 1972 could have been due to factors within the Kiawah population (i.e., group nesting), rather than to any broad-scale environmental effect, but verification of this without extensive tagging data is impossible. Nesting at South Island, South Carolina, 80 km north of Kiawah indicates a similar periodicity in 1972 (P. Wilkinson, pers. comm.), but the dates of peak activity on the two beaches do not coincide. Group nesting resembling that noted by Caldwell et al. (1959) and Caldwell (1962) was observed among several females each year from 1973–1975, but was not extensive in any season.

The mean internesting interval for 44 turtles on Kiawah from 1973–1976 was 13.0 ± 0.7 days, which is similar to the results Caldwell et al. (1959), and Gallagher et al. (1972) have reported from other southeastern U.S. beaches. On Kiawah, three females each nested three times in 1974, all on 14-day intervals (but different dates), and all within 0.65 ± 0.29 km of their previous nest. By August 3, two of these females had four nests incubating along a 0.1 km stretch of beach, but such site fidelity was the exception rather than the rule for Kiawah loggerheads.

Nest and dry run percentages (Table 1) at Kiawah differ from those reported by Davis and Whiting (1977). Although nighttime beach activity may have prevented some turtles from nesting each year, the majority returned to nest during the same or subsequent nights (also Caldwell et al., 1959). Most turtles were handled after oviposition, and 49% of those handled prior to oviposition returned to nest in the same season. The markedly lower dry run rate in 1972 (28.7%) was due not to an absence of nighttime activity, but rather to erasure of numerous short dry run tracks by the tide prior to daytime beach patrols. Therefore, opposition to nighttime beach work simply on the basis of an apparent increase in the number of false crawls (Davis and Whiting, 1977) seems unwarranted. In the case of Kiawah, the benefits derived from tagging and rapid transport of nests to the hatchery outweighed negative effects caused by nighttime presence of investigators on the beach.

The chi-square values for nesting by sector (Table 2) show that nest distribution at Kiawah is neither consistent nor uniform from year to year. Heavier nesting concentrations at Sectors A (1974–1976) and C (1973) are difficult to explain, except that both sectors are relatively isolated from human and vehicular beach traffic. Both areas are quite unstable, however, making them poor nest sites in terms of potential loss of eggs to storm erosion. The nest concentration in Sector E (1974–1975) is more understandable, as this beach has prograded steadily since the 1920's and has an extensive dune field landward of a wide stable beach platform (Hayes, 1975). Low nest concentrations in Sector H (1974–1976) could be related to the area's instability. It is comprised of a rapidly prograding recurved spit that has formed since about 1930, with maximum susceptibility to storm destruction (Hayes, 1975).

An apparent four-year trend of low-level nesting in Sector G ended in 1976, when nests were concentrated there despite the initial resort development landward of the Sector G dunes. The developers of the island followed management recommendations for turtle nesting (Dean and Talbert, 1975), which might have helped to effect this distribution, and suggests that development of the island is not solely responsible for the nesting decline observed during the study period. Furthermore, the decline appears to have ended. Aerial track counts since 1976 indicate that nesting is now about 80–110 nests per year, which is significantly above the 1976 level.

Tagging.—The lowest rate of track interception occurred in 1976, when only 68 emergences occurred on 16 km of nesting beach in 75 days. These rates do not reflect the true proportion of the annual nesting population that was observed in any year. As with earlier studies (Ehrhart, 1976; Hughes and Brent, 1972), the lack of untagged turtles after mid-July indicated that virtually 100% of the Kiawah nesters each season were intercepted at least once.

Tag loss affected the results of the Kiawah study, as it has numerous other tagging efforts (Hughes, 1976; Pritchard, 1976). The Jumbo Roto tags used in 1974 and 1975 were so abraded 2–3 weeks after application that tag numbers and return instructions were often illegible. The Monel alloy appeared to be more durable, but corrosion of the locking mechanism may have caused tag loss among the 11 tagless 1973 remigrants found in 1974. Further tag-recapture studies using marine turtles should test new types of tag materials, designs and alternate tagging sites.

Of the three tagged remigrants, one (D2705) nested in consecutive years. Although rarely noted in the literature (LeBuff, 1974), consecutive-year nesting may occur in a small proportion of many *Caretta* populations, and Dix and Richardson (1972) suggested that it could be a normal part of a population's modulated reproductive pattern. The other two Kiawah remigrants returned after a 2-year absence, but this does not provide sufficient data to determine the remigration cycles of the Kiawah population as a whole. Kaufmann (1975) hypothesized a 2-year nesting cycle among *Caretta* in Columbia based on a small number of remigrants, but we agree with Carr and Carr (1970) and Dix and Richardson (1972) that modulation of nesting cycles could be common and adaptive for turtle populations.

Population estimates based on short-term efforts and a fixed or standard number of nests per female (Worth and Smith, 1976) are subject to error, as demonstrated by Table 3. The steady decline in nests/female during this study suggests that population estimates on individual nesting beaches should be made cautiously until reliable assessments of recruitment and remigration are obtained, as Hillestad et al. (1977) have done with Georgia loggerheads.

Our results suggest that Kiawah loggerheads either nested less frequently than expected, or more likely nested at other beaches. Decline in nesting effort per female, as well as modulation of the nesting cycle, could be forms of bet-hedging (Stearns, 1976) in a population whose nesting habitat is unpredictably perturbed or variable between seasons (Mountford, 1971). Coastal barrier islands, such as those in South Carolina, have been shown to vary in degree of erosion and beach area from year to year (Stephens et al., 1976). It would be advantageous for turtles nesting on such islands to show less site fidelity than green turtles, which nest on relatively stable beaches. Two females from Kiawah were netted by trawlers at Cape Romain (75 km north) 14 days after being tagged on nests, and a third was taken in St. Helena Sound (60 km south) after a 13-day absence.

That these females were such substantial distances from Kiawah just before their predicted renesting suggests that they could nest on other beaches. In addition, turtles tagged on Fripp Island and South Island (one each) nested at Kiawah in 1973. Preliminary telemetry studies also suggest that some turtles utilize more than one nesting area in a single season (T. Murphy, pers. comm.). The mean distance between successive emergences of 22 renesters on Kiawah (3.2 ± 1.8 km) could result in turtles nesting on two or more adjacent islands during a single season. These findings support the contention that nest site fidelity in *Caretta* is considerably more flexible than in other chelonians (Carr and Carr, 1972; Worth and Smith, 1976; Carr and Stancyk, 1975).

Predation.—Egg predation by raccoons devastated the 1972 rookery, as has been reported elsewhere (Ehrhart, 1976; Hopkins et al., 1979). Predation was substantially higher than levels observed at Cape Sable, Florida (Davis and Whiting, 1977). Human habitation and production of alternative food sources such as garbage increased through the study period, as did the hatchery effort. We think these factors contributed to the steady decline in predation on wild nests (Fig. 3).

The difference between predation rates in seldom-patrolled beach sectors (A–C) and those in heavily patrolled areas (Sectors D–H) in 1973–1976 is compelling evidence that night beach patrols and relocation of nests disrupted egg predation by raccoons. Egg poaching is infrequent at Kiawah, and ceased during the study period. The contention that beach patrols can cause an increase in false crawls (Davis and Whiting, 1977) loses significance in light of the positive effect of reduced predation and poaching. In addition, we found, as did Caldwell et al. (1959) and McAllister et al. (1965), that turtles frightened off the beach before nesting generally emerged to nest later the same night or on subsequent nights.

As the human population at Kiawah increases, encounters between visitors and residents who watch turtles on the beach could result in the type of rookery abandonment alleged by Caldwell (1962) at Jekyll Island, Georgia. Continued adherence to management recommendations (Dean and Talbert, 1975) as the Kiawah resort development effort grows could minimize or preclude such a result. Indeed, Mann (1978) argues that intensive beach development does not necessarily lead to reduced nesting in Southeast Florida. The direct negative effect on nesting which might be predicted as a result of conventional resort development has not yet been observed at Kiawah.

Hatchery.—The hatchery at Kiawah gave results similar to efforts undertaken at other localities (Hillestad et al., 1977; Hughes, 1971, 1972). Although hatch rates were highest with the 1973 in-beach hatchery, incubation of turtle eggs in containers is currently favored because of the consistently high hatch rates and elimination of variables (Raj, 1976). Both methods have pitfalls. It is necessary to relocate in-beach hatchery sites yearly to escape contamination associated with decaying eggshells (Richardson, pers. comm.). This system is also susceptible to flooding by elevation of the freshwater table. Oxygen diffusion across the chelonian egg membrane cannot occur once the egg chamber has been submerged and becomes anaerobic (Ackerman, 1975). The 100% mortality in the 1974 Kiawah hatchery following heavy rains paralleled the observations of Ragotzkie (1959) at Sapelo Island, Ga. and Klukas (1967) at Cape Sable, Florida.

Although a container hatchery protects eggs from the vagaries of the physical environment, the effect of the containers on normal development is unknown. If incubating turtles obtain homing cues to their natal beach during development, a styrofoam box could prevent them from obtaining the proper information (Carr, pers. comm.). Containers also modify temperatures, and Yntema (1976) has shown that slight temperature changes can greatly affect sex ratio in freshwater turtles. Such effects might occur in sea turtles as well (Mrosovsky, 1978). Nevertheless, hatcheries are convenient means of increasing hatchling productivity. Less labor-intensive methods to reduce nest predation are discussed elsewhere (Stancyk, et al., in press).

Offshore mortality.—Sea turtle mortality caused by commercial fisheries has been identified as a major factor in the decline of nesting populations of several marine turtle species (Carr et al., 1978). The correlation between concentrations of nearshore trawlers and the subsequent beaching of turtle carcasses which we observed at Kiawah is supported by the findings of Hillestad et al. (1977) in Georgia. From 1973–1975, one turtle died off Kiawah for every two that nested on the island, and in 1976 this ratio was 1:1. The fact that a large percentage of strandings are juveniles and young adults could have a substantial negative effect on the growth rate of a population, since the individuals with the highest reproductive values in the population are being eliminated (Wilson and Bossert, 1971).

Other investigators (Ulrich, pers. comm.; Wilkinson, pers. comm.) have suggested that set-nets employed by coastal fishermen could be responsible for the massive turtle mortalities in South Carolina. This fishery is concentrated in the Santee River Delta/Winyah Bay area some 80 km north of Kiawah, and its contribution to offshore mortality there could exceed that of the shrimp fishery. In the Kiawah area, however, the majority of strandings appear to coincide with intense shrimping activity which occurs off the Kiawah beach. Strandings may also be concentrated on Kiawah due to the dominant prograding character of the beach and local offshore currents that deliver copious amounts of flotsam and jetsam to the strand line (Ulrich, pers. comm.). Statewide aerial surveys, however, show substantial concentrations of carcasses on numerous erosional beaches where fishery pressure is intense.

Conclusions.—The Kiawah nesting beach appears to be in an unstable transition period. It is the closest active nesting site to Charleston Harbor, South Carolina, and could support nesting as long as conservation efforts and adherence to management recommendations are maintained. As Kiawah's resort development advances eastward toward more heavily-nested beach sectors (A–E; Fig. 1), the extent of its impact on loggerheads could become more evident.

In addition to the loss of nesting habitat, the loggerhead population off Kiawah suffers destruction of nests by raccoons, and of subadults and adults by drowning in fishing nets. Predation varies over time and is often exacerbated by human activities. Methods that control predation, secure nesting habitat or increase offspring production are available, but require monitoring and maintenance effort to prevent interference with normal development. Resuscitation methods and new excluder trawls may help to reduce the impact of fishing mortality. The effect of these conservation efforts cannot be accurately assessed, however, until further tagging studies reveal more about the age structure, sex ratio and size of loggerhead turtle populations in South Carolina.

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The Consequences of Within-year Timing of Breeding in *Ambystoma maculatum*

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Embryonic and adult mortality, as a function of within-year timing of breeding, was studied in the spotted salamander, *Ambystoma maculatum*. Separate groups of salamanders bred at three different times in 1978 between 26 January and 28 March. Embryonic survival associated with the earliest breeding salamanders (wave 1) was very low (23%) compared to the later two waves (93% and 98%). The number of eggs per egg mass was greater in wave 1 egg masses than in wave 2 or 3 egg masses. Adult mortality caused by a pond freeze occurred among the earliest breeding salamanders (wave 1). Adults killed by the freeze had significantly larger snout-vent lengths than did survivors. It was concluded that within-year variation in timing of breeding can have a major effect on reproductive success.

ALTHOUGH within-year timing of breeding was not discussed in two recent reviews of life history traits (Stearns, 1976, 1977), the importance of such timing has been recognized (Perrins, 1965; Lack, 1966; Janzen, 1967). Within-year variation in time of reproduction can play a major role in reproductive success. This report documents within-year variation in timing of breeding and the effects of unpredictable or independent environmental events on reproductive success for one species of salamander. Since optimization theory has failed to explain the observed diversity of life histories, documentation and analyses of the effects of a stochastic environment on reproductive success are necessary (Ricklefs, 1977).

The spotted salamander, *Ambystoma maculatum,* was used in this study because not all adults breed at the same time within a breeding season (Baldauf, 1952; Husting, 1965) and developmental success of egg masses is easy to monitor. Since *A. maculatum* breeds in temporary ponds (Bishop, 1941), its reproductive activities are subject to unpredictable and potentially independent environmental events (Wilbur and Collins, 1973).

MATERIALS AND METHODS

Study area.—This study was conducted at a temporary pond 3.8 km SW of Duke University's West Campus. The pond is located at Gate 9 in the Duke Forest, Durham County, NC. Gate 9 pond contained no fish species as potential predators on embryos or larvae, but did contain *A. opacum* larvae as a potential competitor.

Egg counts.—From January to May 1978, Gate 9 pond was visited three or four times per week. Following an oviposition period, egg masses arbitrarily selected for study were gathered into water filled plastic tubs, photographed with Kodak Pan-X high speed film, and returned to the pond for long term study of embryonic mortality. The developed negatives were placed under a dissecting scope with gridded oculars, and the number of eggs per egg mass was counted. Because the gelatinous sheathing of