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Temporal Distribution and Periodicity in Hawksbill Turtles (*Eretmochelys imbricata*) Nesting at Cousin Island, Republic of Seychelles, 1971–1997

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ABSTRACT. – We report on 27 years (1971–97) of data collected on nesting hawksbills (*Eretmochelys imbricata*) at Cousin Island, Seychelles, the site of what may be the most intensive long-term study of a hawksbill rookery. Nesting beach surveys indicated 75.8% of recorded emergences occurred between 24 October and 23 January, coinciding with peak annual rainfall; and > 85% occurred during daylight hours. Since 1973, 463 of 632 tagged turtles were identified during 2970 subsequent nesting emergences. The maximum recorded interval between first and last observed nestings was 17–20 years. Estimated mean clutch frequency per season was at least 3.6 (up to a possible 7 per turtle), with a mean of 15.1 days between clutches. Turtles made 1.8 recorded nesting attempts per clutch, with attempts early in the season being relatively less successful. Previously tagged remigrant females laid significantly more recorded clutches per season than untagged neophyte turtles, but the difference may not be age-related. For individual turtles identified during two to seven separate nesting seasons, we detected no change in clutch frequency over time as measured by interval lengths (i.e., remigration intervals) separating successive nesting seasons. Our data show that the predominance of relatively short two- and three-year remigration intervals was not an artifact of tag loss, although the proportion of intervals greater than seven years may be underestimated. Diurnal behavior combined with a high frequency of nesting emergences make Seychelles hawksbills particularly vulnerable to exploitation, but high clutch frequency can also enable significant increases in nesting activity at sites where turtles are protected.

KEY WORDS. – Reptilia; Testudines; Cheloniidae; *Eretmochelys imbricata*; sea turtle; nesting behavior; clutch frequency; tag loss; conservation; remigration interval; longevity; reproduction; Cousin Island; Seychelles

The hawksbill turtle (*Eretmochelys imbricata*), although circumtropical in distribution, now nests diffusely throughout most of its range having been widely exploited for its shell and to a lesser extent for its meat and eggs (Groombridge and Luxmoore, 1989). It is listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and is one of only two species of sea turtle classified as Critically Endangered on the IUCN Red List (Baillie and Groombridge, 1996; Meylan and Donnelly, 1999). The hawksbill is a long-lived species that can take up to 20–40 years to reach sexual maturity (Limpus, 1992; Crouse, 1999). Until a decade ago when intensive work began at Jumby Bay in Antigua, Campeche in Mexico, and at Milman Island in Australia, most published studies of breeding hawksbills involved relatively small data sets collected over short periods of time (Witzell, 1983). Two exceptions were the long-term studies initiated at Tortuguero, Costa Rica, in 1956 and at Cousin Island, Seychelles, in 1970. The recapture rate of tagged hawksbills on the beach at Tortuguero, however, has been low (Bjorndal et al., 1985, 1993), leaving Cousin Island as the site of the most intensive long-term study of a hawksbill rookery. Published accounts of data collected at Cousin between 1970 and 1983 have included those by Diamond (1976), Garnett and Frazier (1979), Brooke and Garnett (1983), Phillips and Wood (1983), Frazier (1984), Mortimer (1984), and Wood (1986).

Long-term studies of long-lived species provide the opportunity to examine the interaction between age and reproductive output, an issue of particular concern in an animal as endangered as the hawksbill. Sea turtles are iteroparous within a nesting season, and if they survive they may remigrate to their breeding beach during subsequent (but usually not consecutive) nesting seasons. This, along with the overall longevity of turtles (Gibbons, 1987), make them ideal subjects for such an analysis. Published accounts of long-term studies of turtles, however, have yielded conflicting conclusions about the relationship between fecundity and age. Although no correlation was found between age *per se* and clutch size among freshwater turtles (Gibbons, 1982; Gibbons et al., 1982; Congdon and van Loben Sels, 1993), older female Blanding's turtles *(Emydoidea blandingii)* (> 55 yrs old) reproduced more frequently than did younger females (minimum age < 36 yrs) (Congdon and van Loben Sels, 1993). In marine turtles, a positive correlation between age and fecundity has also been reported (Frazer, 1984; Bjorndal and Carr, 1989), based in part on studies showing a tendency for remigrants (i.e., individuals bearing tags or tag scars from a previous nesting season) to lay significantly more egg clutches per season than neophytes (i.e., individuals showing no sign of having been tagged in previous seasons) — the assumption being that, on average, neophytes are younger than remigrants (Schulz, 1975; Carr et al., 1978; Frazer, 1984; Mortimer and Carr, 1987; Tucker and Frazer, 1991).

The present study is an analysis of 27 years of data collected at Cousin Island between 1971 and 1997 that focuses on some of the temporal aspects of hawksbill nesting behavior. Our paper examines diel and seasonal activity patterns on the nesting beach, individual and age-dependent variations in clutch frequency both within and between breeding seasons, and discusses how these parameters relate to the conservation and management of hawksbill rookeries.

METHODS

Study Site. — The Republic of Seychelles in the western Indian Ocean comprises some 114 islands (Statistics Division, 1985), including 40 granitic islands in the northeastern part of the country where more than 99% of the human population resides, and where an estimated 500–800 female hawksbills nested annually in the early 1980s (Mortimer, 1984). Cousin Island (4°20'S; 55°40'E), one of the smallest of the granitic islands (28.6 ha), was acquired in 1968 by the International Council for Bird Preservation (ICBP) and managed since then as a strict nature reserve, the first of its kind in the granitic Seychelles. In 1993, ICBP became BirdLife International and transferred the island to BirdLife Seychelles in early 1998.

Data Collection. — Records of the dates and locations of hawksbill nesting emergences were kept by the resident wardens on Cousin Island beginning in 1970 (Frazier, 1984). During September through March each season, all 1570 m of nesting beach on the island were patrolled, usually several times a day during daylight hours. From 1976 onwards, the time of day of nesting emergences was recorded along with the numbers of trial nests dug and, whenever possible, an explanation for failed nesting attempts. Each nesting emergence was assigned to one of four categories of behavior: 1) "LAID" during which eggs were laid after digging one or more nests; 2) "Did Not Lay (DNL)" during which one or more nests were dug but no eggs laid; 3) "Half Moon (HM)" emergences (Carr et al., 1978) during which digging did not occur although no disturbance factors were apparent; and 4) "Emergence Stopped by Obstacle (ESBO)" during which no digging occurred because the female was discouraged by obstacles on the beach (i.e., logs, rocks, erosion platforms, etc.).

Since 1973, workers have applied a metal tag bearing a unique identification code to the trailing edge of one or both front flippers of each nesting hawksbill encountered during beach patrols, while taking care not to disturb the turtle until she completed nesting activities. For previously tagged animals, tag numbers or old tag scars were noted, and missing tags were replaced. Tagging methods changed over time, as follows: 1973 to mid-1981, single monel calf ear tags (style #49); mid-1981 to mid-1990, double monel hog ear tags (style #681); mid-1990 to mid-1996, double inconel hog ear tags (style #681); and since 1997, double titanium sea turtle tags. (Monel and inconel tags were obtained from Kentucky Band and Tag Company, USA, and titanium tags from Stockbrands Company, Australia.) Precipitation data at Cousin Island were gathered by the wardens during five seasons between 1982 and 1987.

Organization and Analysis of the Data. — The following sources were used to describe diel and seasonal distribution of nesting behavior: 1) for diel distribution, we used times of emergences recorded between 1976 and 1992; 2) to define the nesting season, we used dates of all nesting emergences recorded between 1971 and 1992; and 3) to describe the seasonal distribution of the four categories of nesting behavior (LAID, DNL, HM, and ESBO), we used nesting emergences recorded between 1976 and 1992.

Based on data collected between 1973 and 1992 we determined the number of days separating successful (LAID) emergences. Not every nesting emergence was witnessed by the taggers, so we derived estimates of the numbers of egg clutches each turtle laid per season by using only data collected during that season with the highest rate of tagging efficiency. Tagging efficiency was calculated to be the percentage of the total turtle tracks recorded during daily beach surveys for which the turtle had been identified by the taggers. The accuracy of this calculation is dependent on regular beach surveys. Three separate estimates of mean number of clutches per turtle were derived as follows: 1) by using all recorded turtle observations; 2) by excluding turtles recorded only during a single but unproductive (HM, DNL, or ESBO) emergence, on the assumption that successful nesting probably occurred at a different island; and 3) by extrapolating clutch numbers by including "missing nests" (in cases where intervals between observed nestings indicated that the taggers had probably missed a nesting emergence) and also by excluding turtles recorded only during a single unsuccessful emergence (as in method 2). In addition, we used method 3 to compare the relative number of egg clutches recorded for remigrant and neophyte turtles between 1973 and 1992.

For turtles identified during multiple nesting seasons ("MNS turtles") between 1973 and 1997, the numbers of years separating the first and last recorded nesting emergences

Table 1. Diel distribution of 3298 hawksbill nesting emergences occurring between 1976 and 1992. Means and standard deviations (SD) of the percent of annual nesting emergences that occurred at night and during two-hour intervals throughout the day are shown for 16 nesting seasons.

Emergence Time	Percent of Annual Nesting Emergences Mean	SD
Night (1800–0759 hrs)	13.8	3.4
0800–0959 hrs	12.7	3.0
1000–1159 hrs	13.5	3.3
1200–1359 hrs	15.2	4.8
1400–1559 hrs	20.1	3.3
1600–1759 hrs	24.8	3.6

of each turtle were compiled to determine the minimum periods during which individual adult female hawksbills remained reproductively active. The numbers of years separating successive nesting seasons (i.e., remigration intervals) were also compiled to determine predominant interval lengths and to discern any change in interval length as turtles aged. To detect changes in the lengths of successive remigration intervals over time we used the One Way Repeated Measure ANOVA and the Scheffe's Test (run by SAS Proc Mixed).

To test the possibility that tag loss biased the data in favor of shorter remigration intervals, intervals recorded for the following two groups of turtles were compared: 1) those that could be identified by a single tag for a period of eight or more years; and 2) all MNS turtles tagged prior to the 1990–91 season (thus also having the potential to be identified during a period of at least eight years). In a preliminary effort to quantify tag loss (which would reduce the likelihood that a turtle would be identified in a subsequent nesting season), six tagging methods that differed in terms of tag type and single- versus double-tagging were evaluated using a Fisher's Exact test adjusted for multiple testing (Westfall and Young, 1993; SAS Proc Multtest). The procedure compared what percentage of turtles tagged by each method was encountered and identified during a subsequent nesting season.

RESULTS

Diel and Seasonal Distribution of Nesting Behavior. — Table 1 shows the diel distribution of the 3298 hawksbill nesting emergences occurring between 1976 and 1992 for which time of emergence was recorded. Fig. 1 shows the relationship between seasonal patterns of precipitation during five seasons (1982–87) and nesting activity recorded at Cousin Island during 20 seasons (1971–92).

The percentage of the 3624 nesting emergences that were classified into the four categories of behavior described above are as follows: 1) LAID, 55%; 2) Did Not Lay (DNL), 26%; 3) Half Moon (HM), 16%; and 4) Emergence Stopped by Obstacle (ESBO), 3%. Thus, the average turtle made 1.8 nesting emergences for each egg clutch laid. Turtles dug significantly more nest holes during unsuccessful DNL emergences (mean = 1.72; SD = 1.16; range = 0.5–9; $n = 679$) than during successful LAID emergences (mean = 1.36; SD = 0.69; range = 1–6; $n = 1811$) (t-test; t-statistic = -7.53; $p < 0.0001$). The seasonal distributions of the four types of emergences shown in Fig. 2 were compared using a Kolmogorov-Smirnov two sample test. The distribution of successful LAID emergences differed significantly from that of both DNL (K-S D = 0.0883; $p < 0.001$; $n = 2902$) and HM (K-S D = 0.1095; $p < 0.001$; $n = 2576$) emergences. In contrast, the seasonal distributions of LAID and ESBO emergences did not differ significantly (K-S D = 0.0816; $p > 0.05$; $n = 2082$).

Nesting Periodicity Within-Season. — For turtles recorded on the beach more than once within a nesting season, Fig. 3 shows the number of days separating successful

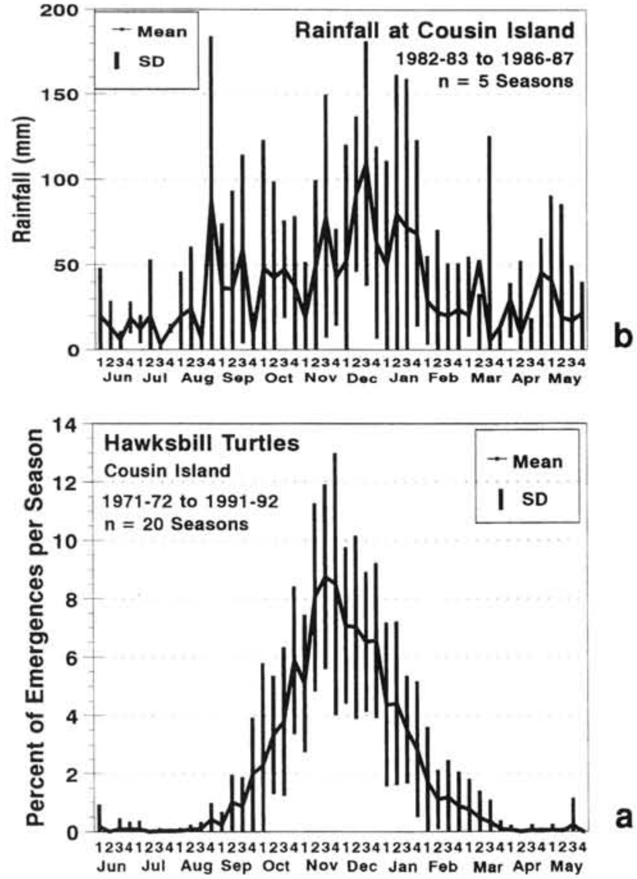


Figure 1. Relationship between the seasonal distribution of hawksbill nesting activity and precipitation at Cousin Island. Indicated are means and standard deviations (SD), on a weekly basis per month, of: a) the percentage of annual nesting emergences that occurred during 20 nesting seasons; and b) the amount of rainfall (in mm) recorded on the island during 5 seasons.

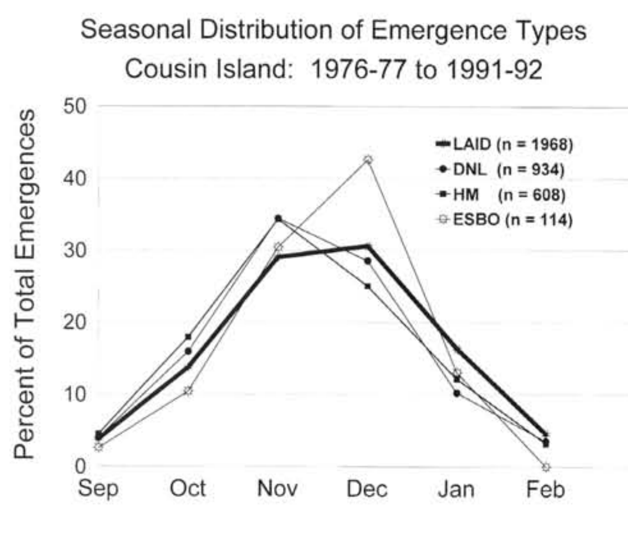


Figure 2. Seasonal distribution of four types of hawksbill nesting emergences recorded at Cousin Island during 16 nesting seasons: 1) "LAID" during which eggs were laid; 2) "Did Not Lay (DNL)" during which one or more nests were dug but no eggs were deposited; 3) "Half Moon (HM)" during which no digging occurred and no disturbance factors were apparent; and 4) "Emergence Stopped by Obstacles (ESBO)" during which no digging occurred apparently because the females were discouraged by external stimuli.

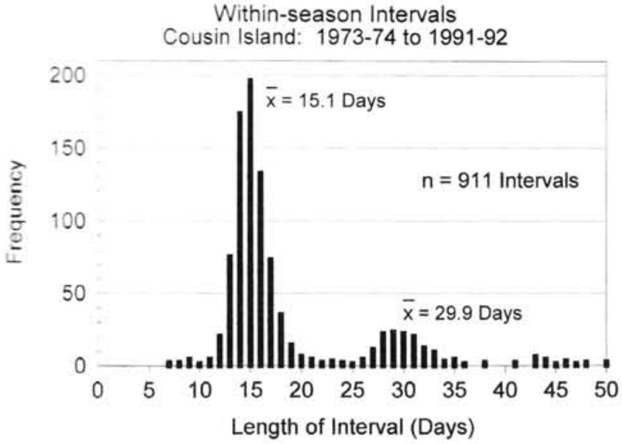


Figure 3. The number of days separating within-season nesting emergences seven or more days apart.

(LAID) emergences witnessed by the tagging team. In some cases actual oviposition was not observed. Intervals of less than 7 days are assumed to involve unsuccessful nesting attempts and are not shown while those greater than 23 days are assumed to reflect missed nestings not witnessed by the taggers. An average of 15.1 days (SD = 1.9; median = 15; mode = 15; range = 7–23) separated successful renesting emergences by individual turtles.

During the 23 seasons between 1973 and 1996, calculated tagging efficiency ranged from 20.6% to 68.0%, with a mean of 47.7% (SD = 10.8). The highest rate of tagging efficiency was recorded during the 1982–83 nesting season, when beach surveys were conducted regularly, and 68.0% of total nesting emergences and 80.4% of successful nesting emergences were witnessed by the taggers. Thus, data from the 1982–83 season were used to estimate mean numbers of egg clutches laid by turtles per season.

These estimates, as calculated by three methods (described above), were the following (see Table 2): 1) using all recorded observations (mean = 3.1; median = 3; mode = 1); 2) excluding turtles recorded only during a single but unsuccessful (no eggs laid) emergence (mean = 3.3; median = 3; mode = 4–5); and 3) extrapolating clutch numbers by including missing nests (in cases where intervals between observed nestings were multiples of 12–17 days) and also excluding turtles recorded only during a single unsuccessful emergence (as in method 2) (mean = 3.6; median = 4; mode = 5).

Average annual clutch frequencies of remigrants (mean = 3.3; $n = 230$) were significantly higher than for neophytes (mean = 2.4; $n = 419$) (Mann Whitney U Test; $z = 6.9610$; $p < 0.0001$; $n = 649$) during the period 1973–92.

During 25 seasons between 1973 and 1997, a total of 632 turtles were tagged at Cousin Island, of which 463 (73.3%) were seen during multiple nesting emergences. Overall, the numbers of recorded nestings per turtle per season ranged from 1 to 6, while the numbers of extrapolated possible nestings ranged from 1 to 7.

Inter-Seasonal Periodicity. — Of the 632 turtles tagged at Cousin Island since 1973, 203 (32.1%) were witnessed during multiple nesting seasons (MNS turtles). The numbers of years separating the first and last recorded nesting emergences of each turtle are shown in Table 3, and ranged from 1 to 17–20 years. The numbers of years separating successive witnessed nesting seasons (i.e., remigration intervals), ranged from 1 to 10 years. In total, 373 remigration intervals were recorded among the 203 MNS turtles, with two- and three-year intervals together accounting for 86% of all intervals recorded.

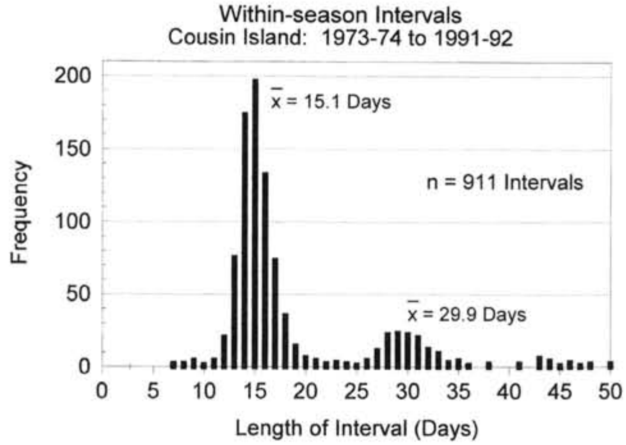
For the 46 turtles encountered during four or more separate nesting seasons, Table 4 shows the means and standard errors (SE) of the lengths of successive remigration intervals. For each subgroup of turtles the mean length of the first interval was the longest, but neither the One Way Repeated Measure ANOVA nor the

Table 2. Results of three methods used to estimate the minimum numbers of clutches laid per turtle during the 1982–83 nesting season: (1) Using all observations; (2) Excluding turtles seen only during a single, unsuccessful (no eggs laid) nesting emergence; (3) Using same turtles as method 2, but extrapolating clutch numbers to include "missing nestings" where intervals between observed nestings are multiples of 12–17 days.

	Method of Calculation					
	(1)		(2)		(3)	
	Clutches	Turtles	Clutches	Turtles	Clutches	Turtles
	1	7	1	5	1	5
	2	4	2	4	2	1
	3	4	3	4	3	5
	4	6	4	6	4	5
	5	6	5	6	5	8
	6	1	6	1	6	2
Total		28		26		26
Mean	3.1		3.3		3.6	
Median	3		3		4	
Mode	1		4.5		5	

Table 3. Intervals in years between first and final sightings of 203 individual nesting hawksbills encountered during more than one nesting season at Cousin Island during the 25-year period between 1973 and 1997. * = turtle encountered in 1976 bearing an old tag hole from a previous nesting season (probably either 1973 or 1974).

Interval Length (yrs)	Frequency No. Turtles	Percent
1	3	1.5
2	29	14.3
3	47	23.2
4	28	13.8
5	26	12.8
6	25	12.3
7	8	3.9
8	4	2.0
9	9	4.4
10	6	3.0
11	11	5.4
12	2	1.0
13	1	0.5
14	1	0.5
15	1	0.5
16	1	0.5
17 (19 or 20)*	1*	0.5



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For the 46 turtles encountered during four or more separate nesting seasons, Table 4 shows the means and standard errors (SE) of the lengths of successive remigration intervals. For each subgroup of turtles the mean length of the first interval was the longest, but neither the One Way Repeated Measure ANOVA nor the

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10	6	3.0
11	11	5.4
12	2	1.0
13	1	0.5
14	1	0.5
15	1	0.5
16	1	0.5
17 (19 or 20)*	1*	0.5

Table 4. For the 46 turtles encountered during four or more separate nesting seasons, the means and standard errors (SE) of the lengths of the 1st, 2nd, and through the *i*th recorded remigration intervals separating consecutive recorded nesting seasons are presented for four subgroups, where *i* is the minimum number of remigration intervals shared by all turtles in each subgroup. The value of *i* ranges from 3 through 6. The *p* values for the One Way Repeated Measure (ANOVA) and Scheffe's Tests ($\alpha = 0.05$) comparing the 1st through the *i*th remigration intervals within each subgroup of turtles are shown.

				Mean (SE) for each Remigration Interval					
	n	ANOVA	Scheffe's	1st	2nd	3rd	4th	5th	6th
3 or more intervals	46	0.1061	NS	2.76 (0.18)	2.39 (0.07)	2.48 (0.10)	—	—	—
4 or more intervals	24	0.3425	NS	2.63 (0.13)	2.33 (0.10)	2.54 (0.12)	2.42 (0.13)	—	—
5 or more intervals	8	0.1778	NS	3.00 (0.27)	2.38 (0.18)	2.50 (0.19)	2.50 (0.27)	2.25 (0.16)	—
6 intervals	4	0.4231	NS	3.25 (0.48)	2.50 (0.29)	2.50 (0.29)	2.50 (0.50)	2.25 (0.25)	2.25 (0.25)

Scheffe test showed any statistical difference between the lengths of the 1st, 2nd, or up to the *i*th remigration interval within each subgroup.

Bias in Recorded Remigration Intervals Caused by Tag Loss. — Fig. 4 addresses the concern that tag loss might bias the data in favor of shorter remigration intervals if tags fall off before longer intervals are recorded. It compares the frequency distributions of the remigration intervals recorded among those turtles that could be identified by a single tag throughout a period of 8 or more years (15 turtles involved in a total of 39 remigration intervals) with those of all MNS turtles tagged prior to the 1990–91 season (113 turtles involved in a total of 259 remigration intervals). The graph demonstrates little difference between the two groups of turtles in terms of intervals ranging from 1 to 7 years long. On the other hand, a higher proportion of 8 to 10 year intervals was evident among those turtles identifiable by a single tag during a period of at least 8 years.

Table 5 compares the identification rates among turtles tagged by six different tagging methods which varied by tag type and number of tags applied to each turtle. The data suggest that although inconel #681 tags may be slightly superior to both monel #49 and monel #681, the most important factor was not tag type, but whether turtles were single- or double-tagged.

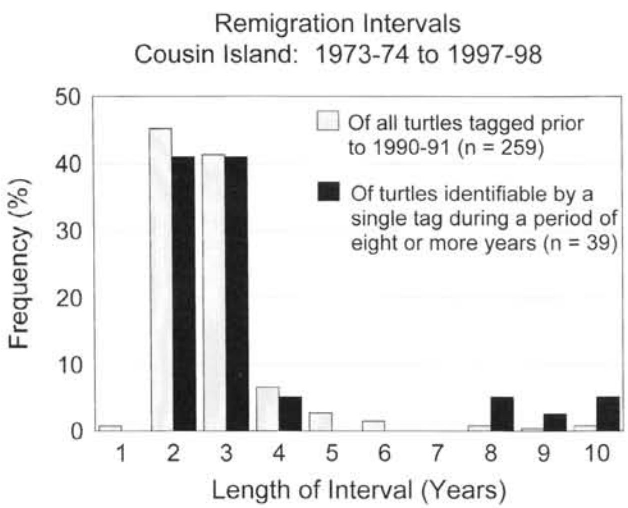

Figure 4. Frequency distributions of remigration intervals recorded for hawksbills nesting at Cousin Island between 1973 and 1998. The black bars show the distribution of the 39 intervals recorded for the 15 MNS turtles identifiable by a single tag throughout a period of eight or more years. Hatched bars show the distribution of the 259 intervals recorded for all 113 MNS turtles tagged prior to 1990.

DISCUSSION

Diel and Seasonal Distribution of Nesting Behavior. — More than 85% of hawksbill nesting emergences at Cousin Island in 1976–92 occurred during daylight hours (Table 1) with frequency increasing throughout the day and then dropping off abruptly at 1800 hrs (see also Garnett, 1978). Although on a global scale hawksbills typically nest at night (Witzell, 1983), diurnal nesting seems to be prevalent in the western Indian Ocean, being most pronounced in the Seychelles, the Chagos Archipelago (Mortimer and Day, in press), and East Africa (Frazier, 1982; Humphrey and Salm, 1996). Huang (1982) claimed that hawksbills also nest diurnally in China. Occasional daytime nesting is reported from the Red Sea (Hirth and Abdel Latif, 1980), the Solomon Islands (Vaughan, 1981), and the Torres Strait (Bustard, 1979). Mortimer and Broderick (in press) determined that nesting hawksbills in Seychelles and Chagos are both characterized by high frequency of mtDNA variant haplotypes not recorded elsewhere in the world. The gene that codes for diurnal nesting may not reside in the mitochondrial DNA, but the fact that hawksbill populations with predominantly diurnal nesting behavior constitute phylogenetic clusters in terms of mtDNA is noteworthy.

Hawksbill nesting at Cousin Island can occur in any month of the year, but during the 20 seasons between 1971 and 1992, 88.0% of nesting emergences were recorded during the four-month period between 1 October and 31 January, and 75.8% of nesting emergences occurred during the three-month period from 24 October to 23 January. The peak nesting season at Cousin Island coincides with the northwest monsoon when the heaviest and most predictable precipitation occurs (Fig. 1). This is consistent with the positive correlation between successful nest construction and rainfall which has been demonstrated for both Cousin Island hawksbills (Garnett, 1978) and Aldabran green turtles, *Chelonia mydas* (Mortimer, 1988, 1990).

Analysis of the seasonal distributions of the four types of nesting emergences (LAID, DNL, HM, and ESBO) (Fig. 2) showed that a greater proportion of unsuccessful DNL and HM emergences occurred early in the nesting season.

Table 5. Comparison of the rates of identification of turtles tagged using six different tagging methods which varied according to tag type and number of tags applied to each turtle. Identification rate was calculated to be the percentage of tagged turtles that were identified on the nesting beach during a subsequent nesting season with at least one readable tag still present. The results of Fisher two-tailed tests are presented in the table; significance is indicated by permutation adjusted p values where $\alpha = 0.05$ (in bold).

Tag Type	Monel #49	Monel #49	Monel #681	Monel #49	Monel #681	Inconel #681
Series	"G"	"A"	"M"	"A"	"M"	"QQH"
Tags per Turtle	Single	Single	Single	Double	Double	Double
Years Tagged	1973–79	1979–80; 1990	1982–90	1990	1981–90	1990–92
Turtles Tagged (n)	140	26	28	35	179	80
Identification Rate	20.7%	19.2%	14.3%	40.0%	44.1%	50.0%
Monel #49 "G" Single	—					
Monel #49 "A" Single	1.0000	—				
Monel #681 "M" Single	0.9900	1.0000	—			
Monel #49 "A" Double	0.2020	0.4920	0.2140	—		
Monel #681 "M" Double	**0.0001**	0.1550	**0.0410**	1.0000	—	
Inconel #681 "QQH" Double	**0.0001**	0.0690	**0.0160**	0.9550	0.9550	—

This presents a pattern similar to that observed in green turtles at Ascension Island (South Atlantic Ocean) where HM emergences occurred most frequently early in the nesting season (Mortimer, 1981), and suggests that endogenous factors may inhibit successful nesting early in the season. The fact that the seasonal distributions of LAID and ESBO emergences did not differ significantly is consistent with the assumption that ESBO behavior is randomly induced by external stimuli.

Nesting Periodicity Within-Season. — The data presented in Fig. 3 confirm the 15–16 day interval between within-season nesting emergences previously reported at Cousin Island by Garnett (1978). The following renesting intervals were reported for hawksbills at other sites: 14 days in 1987 and 15 days in 1988 at Jumby Bay, Antigua (Richardson et al., 1989); 15.3 at Mona Island, Puerto Rico (Olson, 1985); 16.8 days (Bjorndal et al., 1985) and 19.4 days (Carr and Stancyk, 1975) at Tortuguero, Costa Rica; 18.5 days in Nicaragua (Nietschmann, 1981); 14.7 days in the Torres Strait (Limpus et al., 1983); and 14.6 days in the Solomon Islands (McKeown, 1977).

Even our maximum estimates of the numbers of egg clutches laid per turtle during the 1982–83 nesting season, (mean = 3.6; median = 4; mode = 5) (Table 2), are probably too low for the following reasons: 1) within-season tag loss occurred; 2) any nestings occurring either prior to the first or after the last recorded emergence of a turtle would not have been counted as missed nests; 3) within-season nesting migrations do occur between islands in the granitic Seychelles (Mortimer, Bresson, and Hitchins, unpublished data) and would have resulted in unrecorded nestings; and 4) during the 1982–83 season, some Cousin Island turtles may have been slaughtered prior to laying their full complement of egg clutches. Prior to 1994, hawksbills could legally be harvested outside the nature reserves of Seychelles, and some poaching even occurred within the Cousin reserve. Thus, we conclude that the average hawksbill in the granitic Seychelles probably deposits between 4 and 5 egg clutches annually, with a potential maximum of 7 clutches laid by a very few individual turtles. Our average is higher than the 2–3 nestings reported for hawksbills at Tortuguero, Costa Rica (Bjorndal et al., 1985), and in Oman (Ross, 1981), but is consistent with the statistical means of 4.8 and 4.4 and the mode of 5 reported at Jumby Bay, Antigua (Richardson et al., 1989). It is unclear to what extent the observed variation between populations is due to inadequate sampling, mortality from human exploitation, low nest site fidelity, or true biological differences in fecundity.

Inter-Seasonal Periodicity. — Cousin Island hawksbills can remain reproductively active for at least 17 years as indicated by turtle G818 which was encountered during seven separate nesting seasons between 7 November 1976 and 23 December 1993. In fact, her nestings probably spanned at least 19 or 20 years, for when first sighted in 1976, she already had a tag scar from a previous nesting season, probably either 2 or 3 years earlier. This record of 17–20 years is the longest period of reproductive activity yet reported for any hawksbill turtle.

Fig. 4 demonstrates that the predominance of two- and three-year remigration intervals and the dearth of four- to seven-year intervals are not artifacts of tag loss. On the other hand, it also shows that tag loss may mask some remigration intervals longer than seven years. Although identification rates are improved by double-tagging (Table 5), all existing tagging methods are imperfect (Bjorndal et al., 1996).

The fact that remigrants laid more recorded clutches per season than neophytes provides inconclusive evidence that clutch frequency increases with age. Alternate explanations for the observed differences are that: 1) high tag loss may occur among so-called neophytes, and some may even shed tags without scarring (as is the case among green turtles at Tortuguero, Costa Rica, where only 37% of lost tags were detected by tag scars [Bjorndal et al., 1996]).; 2) remigrant turtles may be animals that show a particularly strong site fidelity to Cousin Island, and thus are more likely to be witnessed by the tagging team; 3) human-induced mortality may have eliminated some animals, especially those that showed less than perfect site fidelity to Cousin Island. Until the early 1990s, most turtles nesting on islands other than Cousin were likely to be killed. Because rates of tagging efficiency varied so much from season to season, we were not able to accurately quantify the number of clutches individual turtles laid in consecutive nesting seasons. More work is needed to evaluate the relationship between within-season clutch frequency and age.

On the other hand, the likelihood that a nesting turtle would be identified at least once by the taggers during any season in which she nested was probably high, given that the average turtle may lay as many as four to five clutches per season and crawl onto the beach during additional unsuccessful nesting emergences. Thus we were able to evaluate one aspect of how the reproductive frequency of individual turtles changed over time, by measuring the lengths of successive remigration intervals. The fact that our data (Table 4) could not detect a change in interval length over time suggests that this component of nesting frequency neither increased nor decreased with the age of the turtles. This is consistent with the lack of reproductive senescence observed among certain freshwater turtles (Gibbons, 1982; Gibbons et al., 1982; Congdon and van Loben Sels, 1993).

Implications for Conservation and Management. — Our findings have important implications for the conservation and management of hawksbills in Seychelles. They suggest that the average hawksbill may lay more clutches per year (4–5), make more nesting emergences prior to laying a clutch of eggs (1.8), remigrate to the nesting beach at more frequent intervals (2–3 years), and remain reproductively active for a longer period of time (up to 20 years) than many had previously suspected. It follows that a female hawksbill may have the potential to lay about 25 to 50 clutches in her lifetime, during the course of which she might make about 45 to 90 emergences onto a nesting beach. The value of such a female to the population is thus tremendous, but the frequency of her nesting emergences makes her particularly vulnerable to exploitation at sites where adequate protection is not afforded.

Because females can make so many nesting emergences within a season, an unexploited rookery may appear to host more animals than it actually does. Conversely, once effective protection is afforded to a previously exploited rookery, the increase in nesting activity can be dramatic, in that natural recruitment and remigration at last have a chance to accumulate. During more than two decades of protection, nesting activity at Cousin Island has approximately tripled (Mortimer and Bresson, 1994; Mortimer, Bresson, and Tideman, unpublished data).

Diurnal nesting by Seychelles hawksbills enhances their vulnerability to both purposeful slaughter and unintentional disturbance by humans, but does not make them immune to the negative impacts of nocturnal beach lighting (Witherington and Martin, 1996). Light pollution disorients hatchling hawksbills and might even interfere with nest site selection by daytime nesting females. Where human activity at a rookery is properly regulated, however, diurnally nesting hawksbills can provide a unique and much appreciated tourist attraction as they now do at both Cousin and Bird islands in the Seychelles (Mortimer, in press).

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