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The Green Turtle, *Chelonia mydas*, in Queensland, Australia: the Bramble Cay Rookery in the 1979–1980 Breeding Season

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Abstract. – The study summarizes the results of one season of research on *Chelonia mydas* at Bramble Cay, Australia, in 1979–80. Saturation tagging and measurements of effectively all nesting turtles (n = 687) was accomplished. A subset of turtles was selected for weighing and counting of clutches. There was a distinct summer nesting season. Nesting success improved following rain. The average nesting female had a curved carapace length of 105.9 cm, weighed 121 kg, returned to lay successive clutches after a renesting interval of 12.4 d, and laid an estimated 6.2 clutches per season. The average clutch contained 102.2 eggs and 0.04 yolkless eggs and had an incubation period of 56.6 d. Hatchling emergence success was 68.5%. The date of arrival for commencement of nesting for the season was a significant function of the number of clutches the female would lay during the season and of her size. Renesting interval was a function of when in the season a clutch was laid. Loss of some clutches occurred through beach erosion. The full season's tagging census data were examined to determine optimal times for sampling a rookery when only a portion of the nesting season may be surveyed.

Key Words. – Reptilia; Testudines; Cheloniidae; *Chelonia mydas*; sea turtle; reproduction; nesting; seasonality; census; scale counts; conservation; Queensland; Australia

Research on the Bramble Cay turtle rookery was conducted as part of a wider investigation into turtle farming in the Torres Strait. The project was started in 1969 by H.R. Bustard as head of the Applied Ecology Unit of the Australian National University. In 1973 responsibility for managing the project was transferred to Applied Ecology Pty. Ltd. (AEPL), associated with the Federal Department of Aboriginal Affairs (Carr and Main, 1973; Smart, 1973). The primary aim of the farming project was to develop a viable cottage industry involving turtles for Torres Strait Islanders living on their reserve islands. Secondary aims were to reduce the hunting pressure on wild turtles and to supplement wild populations by releasing farm-reared animals. The studies on Bramble Cay were conducted primarily to assess the environmental impact of harvesting *C. mydas* eggs for the farms from that rookery. Bramble Cay was visited for short periods by AEPL staff during the 1974–75, 1975–76 (Kowarsky, 1978) and 1976–77 breeding seasons. A research program to cover the full breeding season was designed by the company's turtle biologist, C.J. Parmenter. He led teams on the cay from early October to March in 1977–78 and 1978–79 (Parmenter, 1980a,b). One of us (DC) led the field team during the 1979–80 season which was the final year of the project. The Australian Government terminated the turtle farming and research program in 1980. AEPL itself closed in 1981 and some research data were transferred to the custody of the Australian National Parks and Wildlife Service.

Many parameters associated with census of a marine turtle nesting population and quantification of numerous reproductive parameters can only be effectively measured via study of the nesting population encompassing the many months of a breeding season. Such comprehensive studies of the breeding biology of the green turtle, *Chelonia mydas*, are rare (Hirth, 1997). Studies for entire nesting seasons at the Bramble Cay *C. mydas* rookery characterized the AEPL research program during the 1970s. Regrettably, much of the original data cannot be located and appears to have been lost. However, a substantial amount of original data collected during the 1979–80 season have been recovered, and are presented in the present study. These data provide more than just the rare opportunity to examine the reproductive biology of *C. mydas* for an entire breeding season. From an historic perspective, the data from the 1979–80 season provide a detailed description of reproduction of this relatively remote population from ca. 20 years in the past. The data also provide the first detailed description of the reproductive characteristics of the northern Great Barrier Reef genetic stock of *C. mydas*.

STUDY SITE

Bramble Cay is an uninhabited island in northeast Torres Strait (9°09'S, 142°53'E), Queensland, Australia (Fig. 1), at the northern extremity of the Great Barrier Reef and 54 km from the Papua New Guinea coast. It lies 35 km from the nearest regularly used *C. mydas* rookery of Anchor Cay in northeast Torres Strait, 88 km from the nearest large rookeries in the Murray Islands and 274 km from the very large rookery at Raine Island to the south. Bramble Cay has been described in varying detail from visits in 1924 (Jardine, 1928), 1978 (Limpus et al., 1983b) and 1987 (Walker, 1988). At the time of the 1979–80 study described here,

Figure 1. Map of Torres Strait, Queensland, Australia, showing the location of Bramble Cay relative to the major *Chelonia mydas* rookeries at Raine Island and Bountiful Island.

Bramble Cay was a low, oval-shaped, vegetated sand cay. The vegetation consisted of grasses, herbs, and creepers, and there were exposed areas of phosphatic limestone rock in the interior. There were no trees or shrubs at the time of the study. There was a stainless steel navigation tower towards the center of the island and a small fibro-cement hut on a concrete slab foundation towards the southwestern side (Fig. 2) which was the base of operations for the research team. The sand cay is situated at the western margin of the coral reef on which it lies. While most of the cay is surrounded by a coral reef flat, a small portion of the western side of the cay is exposed directly to deep, reef-front waters. The carbonate sand of the nesting beach is whitish and is derived from the surrounding coral reef, being composed primarily of fragmented skeletons of corals mixed with broken mollusc shells and foramaniferans.

METHODS

The research team was present on Bramble Cay from 9 October 1979 until 29 March 1980 (171 observation nights). The spring high tide line and the margin of the vegetation were mapped each month using a hand compass and pedometer. The entire beach was patrolled nightly at intervals of less than two hours from dusk to dawn or until the last turtle left the island. On some nights in October and March, when nesting activity was low, patrols ceased before dawn if the tide was so low as to prevent turtles accessing the beach before sunrise. Every nesting turtle that emerged from the water and entered the nesting habitat above the high tide line was recorded on almost every night. Only turtles coming ashore for nesting were captured. No turtles were captured over the surrounding coral reef. Following oviposition, or

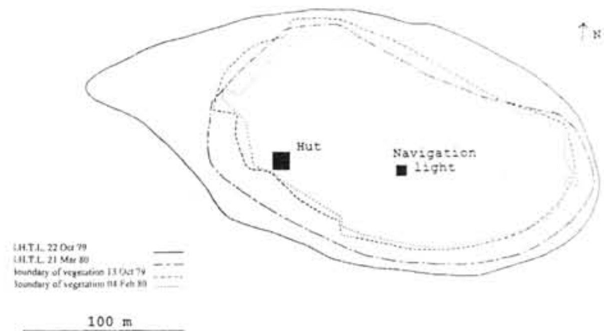

Figure 2. Map of Bramble Cay, 1979–80 turtle breeding season. S.H.T.L. denotes spring high tide level.

while returning to the water, each turtle was marked with two numbered monel tags (National Band and Tag Company [NBTC], 1005 #49; "A" prefix) applied to the trailing edge of each front flipper between digits four and five (tagging position 1, Limpus, 1992). A sub-sample of 25 green turtles (*Chelonia mydas*) (termed "priority turtles") were marked with an additional smaller monel tag (NBTC, 1005 #681; "B" prefix) on the margin of the webbing between the fourth and fifth digits of a hind flipper. These latter turtles could be quickly identified without disturbing them by approaching from behind and feeling the hind flipper. These priority turtles were selected as each laid her first clutch for the season and were intended for use in a detailed study of changing egg production and changing weight of the female through the course of a nesting season.

Each time a turtle came ashore she was tagged and/or the tag numbers were recorded along with the following information: date of capture, island sector, nesting success. Date of capture was recorded for the 24-hr period commencing at noon of each calendar day, i.e., date of capture did not change at midnight. To avoid selecting a turtle as a priority when she may have commenced nesting prior to the commencement of the study, selection of priority turtles was delayed until 21 days of tagging census had been completed and then only untagged turtles were selected as priorities.

The island was divided into eight equal-angle sectors based on true north and measured on compass bearings from the lighthouse near the center of the island. These sectors were delineated clockwise with numbered posts 1–8, with sector 1 between 270° and 315°. Nesting activity and the fate of clutches were recorded with respect to the sectors. Nesting success was scored for each nesting crawl using the following categories: successful nesting (laying a complete clutch of eggs); unsuccessful nesting (no eggs laid); partially successful nesting (the turtle was disturbed prior to completion of oviposition and the complete clutch was not laid; the disturbance was caused either naturally by other turtles or by the researchers; the recovered data does not distinguish among the various sources of disturbance); and undetermined nesting success (uncertainty as to whether or not eggs were laid).

Measurement methods used in this study followed closely the standard methods used in nesting beach studies by the Queensland Turtle Research Project, Queensland Parks and Wildlife Service and AEPL (Limpus et al., 1983a).

Measurements of turtles included: midline curved carapace length (CCL) and curved carapace width at the widest part (CCW) measured with a flexible fiberglass tape measure (± 0.5 cm); plastron length (PL) measured along the midline from anterior to posterior skin/plastron margins with a flexible fiberglass tape measure (± 0.5 cm); post-ovipositional weight (WT) of the adult turtle before she returned to the sea was measured with a spring balance (± 0.5 kg) supported from a pole and attached to the flippers of the turtle by ropes. Clutches were counted by excavating nests within six hours of oviposition and the eggs handled with the minimum of rotation and jarring to minimize movement-induced mortality of the eggs (Parmenter, 1980c). Clutch number defined the successive clutches laid by a turtle during a nesting season. Clutches laid in areas where they were at risk from erosion or inundation were moved whenever possible to a lower-risk habitat on the southwest of the island, adjacent to the vegetation (Parmenter, 1980a). Each relocated clutch was reburied in an artificial nest of approximately the same size, depth, and shape as a natural nest. While clutches were not disturbed for any purpose more than six hours after laying, most were usually moved within three hours. Yolkless eggs were not included within the clutch count. Multi-yolked eggs, including double and triple-yolked eggs, were each counted as a single egg and included in the clutch count. Each priority turtle was weighed following each oviposition and the number of eggs in the clutch counted for each successful nesting throughout the breeding season. Some additional clutches were counted from non-priority turtles. Renesting interval was calculated as the interval in days between the completion of a successful nesting and the next nesting attempt. After a preliminary examination of the 1979–80 Bramble Cay data and because *C. mydas* normally has a renesting interval of about 14 days (Hirth, 1997), renesting intervals from 19 to 35 days were presumed to include one unrecorded successful nesting (= 1 clutch) and for renesting intervals from 36 to 50 days it was presumed that two clutches were missed. Clutch numbers were calculated taking these presumptions into account. Dates were transformed for analyzes by counting the days through the breeding season, starting with 9 October as day 1. The arrival date of a female was recorded as the first date she was observed making a nesting crawl at Bramble Cay. Similarly, her departure date was taken as the last date she was recorded on a nesting crawl for the season. The scute patterns on the head and carapace of most nesting turtles were recorded following the terminology of Pritchard (1979).

Table 1. Mean monthly minimum and maximum air temperatures measured in the shade at Bramble Cay during the 1979–80 turtle nesting season.

	Air temperature (°C)	
Month and year	Monthly minimum (mean ± SE, range, *n*)	Monthly maximum (mean ± SE, range, *n*)
October 1979	25.3 ± 0.1, 24.0-26.3, 19	30.4 ± 0.2, 29.0-33.0, 19
November 1979	25.7 ± 0.1, 25.0-27.0, 24	30.7 ± 0.1, 30.0-32.5, 27
December 1979	26.3 ± 0.2, 24.0-27.5, 27	31.3 ± 0.2, 28.5-34.5, 27
January 1980	25.4 ± 0.3, 20.0-27.5, 27	30.4 ± 0.2, 28.5-33.0, 27
February 1980	24.9 ± 0.2, 22.5-27.0, 24	30.1 ± 0.2, 28.0-31.0, 24
March 1980	25.0 ± 0.2, 23.5-27.0, 24	29.6 ± 0.1, 28.0-31.0, 24

Over the first four months, 245 nests with counted clutches were marked with wooden stakes so that the nests could be located towards the end of their respective incubation periods. After 45 days, a circular wire netting fence approximately 0.6 m in diameter and 0.3 m high was placed over the nest to collect the emerging hatchlings for counting. Hatchlings were released at night within a few hours of their emergence from the nest. After hatchings had emerged from the nest, or after 65 days, the nest was opened and contents counted.

Daily minimum and maximum air temperatures were measured in the shade at Bramble Cay during the 1979–80 turtle nesting season using a max/min dry bulb thermometer. Rainfall was recorded daily. Tidal data were obtained from Queensland Transport (maritime operations) for Stephens Islet (9°30'S, 143°33'E), 55 km southwest of Bramble Cay. The closest location to Bramble Cay with long-term temperature and rainfall data was Thursday Island, 220 km to the southwest, and these data were obtained from the Australian Bureau of Meteorology.

RESULTS

Study Site

The Torres Strait regional climate, represented by the long-term weather data from Thursday Island, is summarized in Fig. 3. Torres Strait is characterized by relatively uniform maximum and minimum air temperatures throughout the year and a distinct summer wet season from Decem-

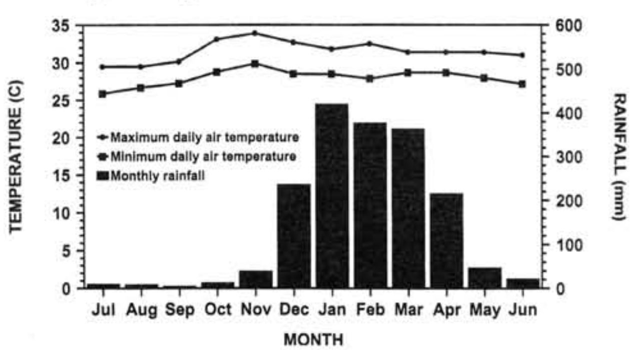

Figure 3. Monthly averages of temperature and rainfall for the 40-year period 1950–91 at Thursday Island.

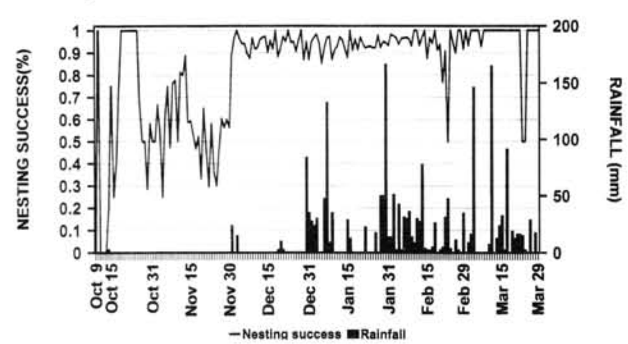

Figure 4. The impact of rainfall on nightly nesting success for green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season.

Table 2. Dimensions of Bramble Cay measured during Applied Ecology Pty. Ltd. turtle research projects at the island. Data for the 1977–78 and 1978–79 turtle nesting seasons were obtained from AEPL internal reports prepared by C.J. Parmenter.

Island parameters	Turtle nesting season 1977–78	1978–79	1979–80
Initial area	4.67 ha (6 Oct 77)	4.08 ha (15 Oct 78)	4.93 ha (22 Oct 79)
Final area	3.26 ha (26 Feb 78)	3.06 ha (29 Mar 79)	3.31 ha (21 Mar 80)
Total area loss	30.2%	25.1%	32.9%
Loss of non-vegetated beach	65.9%	66.5%	81.0%
Initial circumference	-	717 m	820 m
Final circumference	-	619 m	-

ber until April. Mean monthly minimum air temperatures were above 25°C year round, while the mean monthly maximum air temperatures did not exceed 35°C.

Monthly mean daily air temperatures at Bramble Cay during the 1979–80 turtle nesting season (Table 1) ranged approximately 5°C between minimum and maximum. These monthly mean temperatures were consistently 2–4.5°C cooler than the corresponding monthly mean values measured at Thursday Island for 40 years, 1950–91. The daily rainfall recorded at Bramble Cay during the present study (Fig. 4) was consistent with the 40-yr average rainfall data recorded at Thursday Island (Fig. 3) with a commencement of the wet season in December.

The tidal cycle for northeast Torres Strait during the study period was typical of other areas in the Great Barrier Reef. There were approximately two high tides and two low tides daily with, during the summer months, the daytime high tide being higher than the nighttime high tide. The maximum tidal range during the summer spring tides was 3.68 m and the minimum tidal range was 0.06 m during neap tides. The large tidal range that occurs in these waters results in the coral reef flat that surrounds most of the island being exposed on most low tides while 1–3 m of water cover the reef flat on high tides. Therefore most of the island was only accessible to nesting turtles during the upper half of the tidal cycle.

Northwesterly winds commenced during January, bringing rain almost every afternoon and eroding the northwestern side of Bramble Cay. The winds changed back to southeasterly in late February. The southeast winds ceased during the second week of March and, following this, the

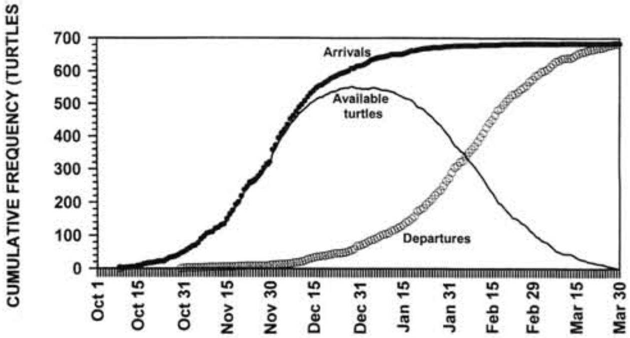

Figure 6. Cumulative arrival and departure of nesting female green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season.

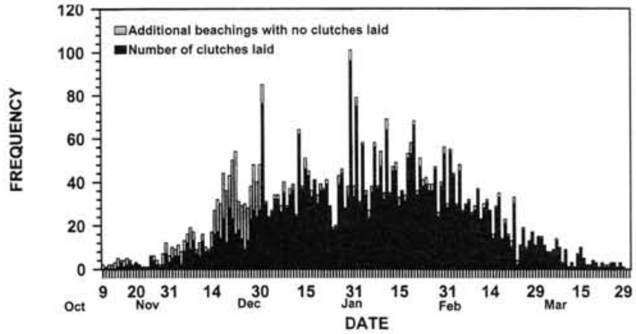

Figure 5. Nightly census of nesting green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season.

island was impacted by some violent northwesterly storms which caused massive erosion of the northern and western beaches. As recorded in the previous two turtle nesting seasons (Parmenter, 1980a), the island was dramatically reduced in size and altered in shape with this change in prevailing winds (Fig. 2, Table 2). At the commencement of the 1979–80 breeding season, Bramble Cay was considerably larger than in the 1978–79 season and slightly larger than in the 1977–78 season (island data supplied on base map by AEPL). This difference in size appears to have been mainly because of a wider beach around the southeastern quarter of the cay.

Turtle Biology

A total of 687 *C. mydas* were recorded making 4387 beachings and successfully nesting 3753 times on Bramble Cay between 9 October 1979 and 29 March 1980. No turtle was recorded attempting to come ashore for nesting during daylight hours and there was no evidence of turtles attempting to bask on the beach as occurs for *C. mydas* at other remote rookeries in the Gulf of Carpentaria (Limpus et al., 1994b) and in the Leeward Islands of Hawaii (Balazs, 1980). Although this was the fourth consecutive breeding season of intensive tagging of nesting turtles at Bramble Cay, there were no recaptures of tagged nesting turtles from the previous years of tagging nor were there recaptures from concurrent Queensland Turtle Research studies at other sites,

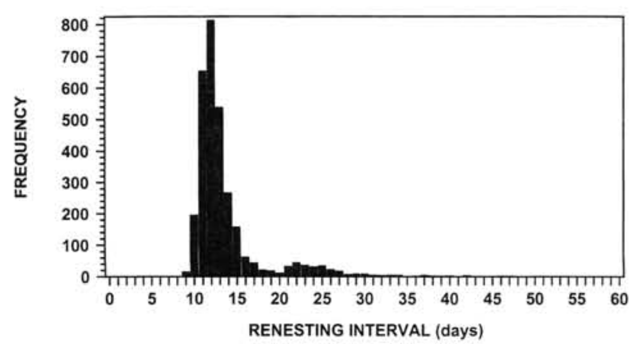

Figure 7. Frequency distribution of renesting interval for nesting female green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season ($n = 3077$). Renesting interval is measured as the interval between the date of a successful nesting and the date of the next nesting attempt.

Table 3. Summary of measurements of nesting female *Chelonia mydas* and their eggs at Bramble Cay, 1979–80 breeding season.

	Mean	S.D.	Range	*n*
Nesting females:				
Curved carapace length	105.9 cm	4.8	94.0-119.0	681
Curved carapace width	96.0 cm	4.8	79.0-112.5	681
Plastron length	83.7 cm	4.1	76.0-97.0	70
Weight (post-oviposition)	121.0 kg	16.3	85-183	375
Renesting interval	12.4 d	1.67	9-19	2781
Eggs:				
Estimated clutches per female	6.2	2.1	1-10	684
Eggs per clutch	102.2	18.4	60-182	615
Yolkless eggs per clutch	0.04	0.29	0-4	662
Incubation period	56.6 d	-	49-63	32
Hatchling emergence success	68.5%	-	0-99%	47

including Raine Island. In addition, no tagged turtles from this Bramble Cay study have been recovered nesting in a later breeding season at Bramble Cay or elsewhere.

There was strong summer nesting seasonality (Fig. 5), with the majority occurring during the wet season, December through to March (Figs. 3, 4). The breeding season had already commenced with nine *C. mydas* tracks visible from previous nights when the team arrived at the island on 9 October. However, there was only one area of recently disturbed sand indicative of a successful nesting. There was a progressive increase in nightly beachings to the peak of the nesting season in late December – early January when the mean nightly number of nesting crawls was 42.6 (SD = 16.8, range = 19–101, $n = 31$ nights commencing 16 December). Mean number of clutches laid nightly during the same period was 40.0 (SD = 16.1, range = 18–96, $n = 31$ nights). After January the nightly number of nesting crawls progressively decreased to intermittent nesting when the team departed on 30 March. The last arrival of an untagged turtle was recorded on 10 March. This changing density of nesting throughout the breeding season occurred because all turtles did not commence their nesting at the same time, there being a progressive arrival of new turtles throughout the season (Fig. 6). Approximately 90% of the nesting turtles had arrived by the end of December. As individual turtles completed laying their complement of clutches for the season, they departed at different times, as well. The first female to depart laid her last clutch at Bramble Cay on 30 October. At no time during the season were all of the females available for census as measured by the difference between the cumulative totals of arrivals and departures of the nesting females (Fig. 6). The maximum availability of nesting females (80.5%; 553 turtles), based on the daily difference in arrivals and departures, occurred during the last two weeks of December. In late March, during the last two weeks of the team's presence on the island, 27 (3.1%) of the nesting females were still nesting. This provides an indication of the maximum error in any measure that assumes that all turtles had completed their nesting season by the end of the study.

Table 4. Frequency distribution of success of nesting attempts by sector for *Chelonia mydas* nesting on Bramble Cay, 1979–80 breeding season.

Sector	Successful nesting	Unsuccessful nesting	Partially successful nesting	Undetermined nesting success	Total nesting emergences
1	1013	44	20	2	1079
2	432	18	5	1	456
3	258	4	3	0	265
4	553	22	9	3	587
5	348	26	4	0	378
6	169	5	1	2	177
7	154	12	2	0	168
8	371	17	3	0	391
no sector recorded	455	372	6	28	861
Total	3753	520	53	36	4362

For the entire season, 3753 of 4362 nesting attempts (85.5%) resulted in successful nesting, 520 (11.8%) resulted in unsuccessful nesting with no oviposition, 56 (1.3%) resulted in partially successful nesting, while for 43 nesting crawls (1.0%) the nesting success was not recorded. There were significant changes in nightly nesting success during the season (Fig. 4). Causes of failed or disturbed nesting attempts included soft dry sand that collapsed into egg chambers, buried objects precluding the digging of an egg chamber (e.g., rocks or drift wood), disturbance when turtles walked into or over each other and unintentional disturbance by researchers. An examination of nesting success data through the season showed that nesting success was low (usually < 70%) during the first 8 weeks of the census and was consistently high (usually > 90%) from early December onwards (Fig. 4). The abrupt change in nightly nesting success coincided with the onset of the wet season in early December. This suggests that the primary reason for poor nesting success in the early season at Bramble Cay was dry sand. There are benefits with respect to nesting success because this population functions with its peak nesting season coinciding with the wet season.

Following a successful nesting, turtles returned to lay the next recorded clutch at 9 to 18 days ($n = 2763$; 73.6%), at 19 to 28 days ($n = 270$; 7.1%), or at > 29 days ($n = 62$; 1.7%) (Fig. 7). The primary mean renesting interval for the return of a nesting female following a successful oviposition was 12.4 days (Table 3). Although these results are indicative of strong site fidelity to Bramble Cay, they do not preclude some of the turtles nesting on other beaches in the region. Although there was no organized search of adjacent islands

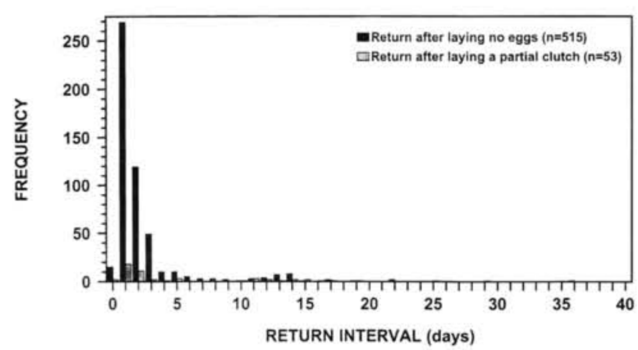

Figure 8. Frequency distribution of return interval following an unsuccessful nesting attempt in which no eggs were laid and following a disturbed nesting during which a partial clutch was laid for nesting female green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season.

Table 5. Summary of frequency distribution for scute counts of nesting adult *Chelonia mydas* at Bramble Cay 1979–80 breeding season. Post-vertebral scute count was included within the marginal count.

Scutes	Scute count	Frequency
nuchal	1	608
vertebrals	5	587
	6	15
	7	2
	8	3
costals	4/4	600
	4/5	1
	5/4	3
	5/5	3
marginals	10/12	1
	11/11	6
	11/12	4
	12/11	2
	12/12	569
	13/13	3
post-ocular	2/2	5
	3/2	1
	3/3	17
	3/4	16
	4/3	16
	4/4	449
	4/5	36
	5/4	36
	5/5	31
pre-frontal	1	5
	2	596
post-parietal	1	6
	2	508
	3	62
	4	29
inframarginals	3/4	1
	4/4	55

for tagged nesting turtles, at least one Bramble Cay female was recorded nesting at another island in this breeding season: A4864 (CCL = 100.0 cm) laid two clutches at Bramble Cay (6 December and 1 January) and was killed for food by local residents on 14 January when she came ashore to lay eggs on Darnley Island (50 km away and 13 days after laying her second recorded clutch at Bramble Cay).

For the 520 recorded unsuccessful nesting emergences during which no eggs were laid (Fig. 8), in 93.3% ($n = 486$) the respective female returned the same night or within the next few nights for another attempt to lay the same clutch of eggs (mean = 1.7 days, SD = 1.3, range = 0–9). In 5.2% ($n = 27$) the female returned to lay within a normal renesting interval (mean = 13.41 days, SD = 2.0, range = 10–19) while for 3 females (0.6%) the next recorded nesting emergence occurred after 20–90 days. Four females (0.7%) were not recorded to attempt any subsequent nestings; each of these had only arrived at the island late in the season after 1 January.

In 57 instances turtles were disturbed while laying and they returned to the sea after having laid an incomplete clutch. Of these (Fig. 8), 37 (64.9%) returned within the next few nights to complete oviposition of that clutch (mean = 1.8 days, SD = 1.3, range = 0–5), 14 (24.6%) returned within 10–19 days, 2 (3.5%) returned within 20–90 days, while 4 (7.0%) were not recorded returning for a subsequent nesting attempt.

Following an unsuccessful nesting attempt there was a high probability (93.0%) that the female would return for another nesting attempt to the same island. For those few cases (< 6%) in which females delayed their return for the length of a normal renesting interval or longer following an unsuccessful nesting attempt, there is no certainty that all eggs from those particular clutches were lost. While some turtles may have dropped the disturbed clutch at sea, others may have laid a clutch at another beach or may have retained the same clutch for an entire renesting cycle. Less than 1% of instances of unsuccessful nesting attempts could be interpreted as having resulted in an aborted nesting season in which no further clutches were laid following the disturbance. Similarly, following a disturbed nesting attempt, the majority of females (65%) could be expected to have returned to the same beach to complete the laying of the remainder of that clutch. However, as for unsuccessful

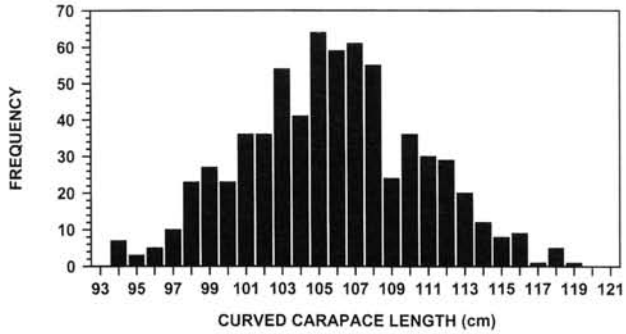

Figure 9. Frequency distribution of midline curved carapace length of nesting female *Chelonia mydas* at Bramble Cay, 1979–80 breeding season ($n = 679$).

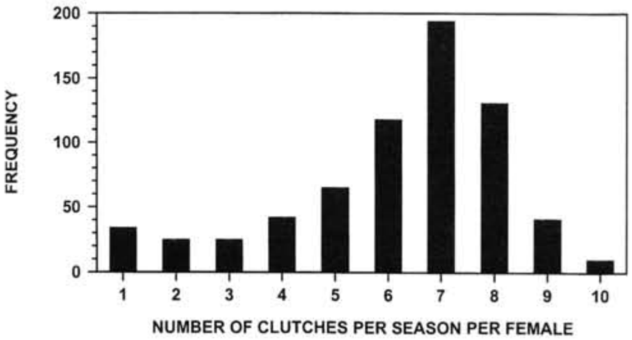

Figure 10. Frequency distribution of the number of clutches laid per female per season for green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season ($n = 684$).

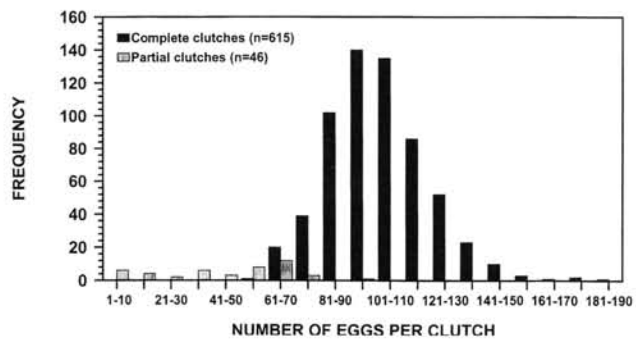

Figure 11. Frequency distribution of the number of eggs per clutch for green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season.

Table 6. Correlation analysis of morphometric data from nesting female *Chelonia mydas* at Bramble Cay, 1979–80 breeding season. The regression equation is in the form $y = ax + b$. See text for abbreviations for the measurements.

y	x	a	b	f	df	p	r^2
CCW	CCL	0.777	13.485	1055	1,676	< 0.001	0.609
PL	CCL	0.601	19.469	134	1,66	< 0.001	0.671
PL	CCW	0.661	19.998	105	1,66	< 0.001	0.614
Log(WT)	Log(CCL)	2.336	-2.650	442	1,215	< 0.001	0.673

nesting attempts, whether or not the females that failed to return dropped the remnants of the clutches at sea cannot be determined from these data. Up to 7% of the cases of disturbed nesting could have resulted in either an aborted nesting season in which no further clutches were laid following the disturbance or the females may have abandoned Bramble Cay and shifted to another beach for the remainder of the breeding season.

In summary, the present study indicates that these nesting female *C. mydas* were well able to cope with disturbance during nesting attempts while experiencing minimal loss of egg production. No analysis of the distribution of successful versus unsuccessful nesting attempts by sector has been made because the sector was not recorded for 71% of the unsuccessful nesting attempts and 12% of successful nesting attempts (Table 4).

The scute patterns of the nesting turtles are summarized in Table 5. The carapace scales were non-imbricate. Although there was some variability, the scute patterns at Bramble Cay generally reflected the typical pattern for the species globally (Hirth, 1997).

The size of the nesting females for the season is summarized in Table 3 and Fig. 9. The average nesting female had a CCL = 105.9 cm. The females were estimated to have laid an average of 6.2 clutches per season (Fig. 10). Clutch size averaged 102.2 eggs (Table 3; Fig. 11). Of 615 clutches counted, only 20 contained yolkless eggs (range 1–4, Table 3). The mean number of eggs laid during a disturbed nesting attempt was 44.0 (SD = 24.9, n = 46, range = 2–96).

There was a significant linear correlation between curved carapace length and width for the nesting females (Table 6, Fig. 12). Similarly, there was a significant linear correlation between plastron length and curved carapace length and width, respectively (Table 6). There was a significant correlation between log(CCL) of the nesting females and log(WT) following oviposition (Table 6, Fig. 13). In each of these comparisons, 30–40% of the variability was not explained by the relationship (Table 6).

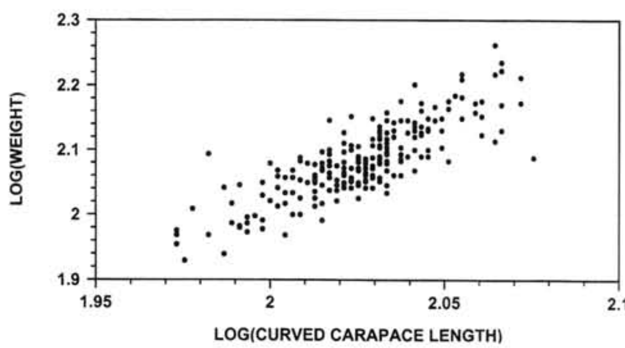

Figure 13. Scatter plot of the size with respect to log(CCL) and log(WT) for nesting female green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season (n = 217).

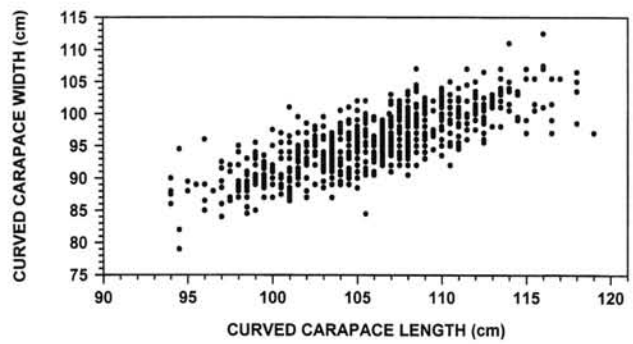

Figure 12. Scatter plot of the size with respect to carapace length and width of nesting female green turtles, *Chelonia mydas*, at Bramble Cay, 1979–80 breeding season (n = 678).

A surface response regression analysis showed that the date of arrival for a female to commence laying was a significant linear predictor of the number of clutches the female would lay for the season and a quadratic function of her size (Table 7). A quadratic function of number of clutches and an interaction term between number of clutches and female size did not improve the relationship. Bigger turtles tended to commence nesting earlier in the nesting season than smaller turtles (Fig. 14) and turtles that commenced nesting early in the breeding season tended to lay more clutches than turtles that were first recorded laying late in the season (Fig. 15). However, this relationship still left most of the variability in arrival date unexplained. There was no significant relationship between the size of nesting females and the number of clutches laid for the season (Fig. 16). There was a significant relationship between renesting interval and a quadratic function of the date of laying the clutch at the commencement of the renesting interval (Table 8). Female size, the number of clutches laid, and when in the season she arrived did not add a significant contribution to this relationship. Most of the variability in renesting interval throughout the season remained unexplained by this relationship. Renesting intervals tended to be longer at the beginning and end of the breeding season than in the middle.

Counts of eggs per clutch relative to the number of clutches laid for the season and clutch number are summarized in Table 9. The relationship between the number of

Table 7. Summary of results of hierarchical surface response regression analysis of arrival date for the female against female size (CCL, cm) and the number of clutches the female laid in the season (TCLUT) for the best fit model: cases = 678, df = 674, overall F = 54.36, p = 0.0000, r^2 = 0.1948, residual mean square = 442.2.

Predictor variables	Coefficient	S.E.	Student's t	p
constant	767.92	300.14	2.56	0.0107
TCLUT	-4.5850	3.9776E-01	-11.53	0.0000
CCL	-12.150	5.6629	-2.15	0.0323
CCL^2	5.3617E-02	2.6691E-02	2.01	0.0450

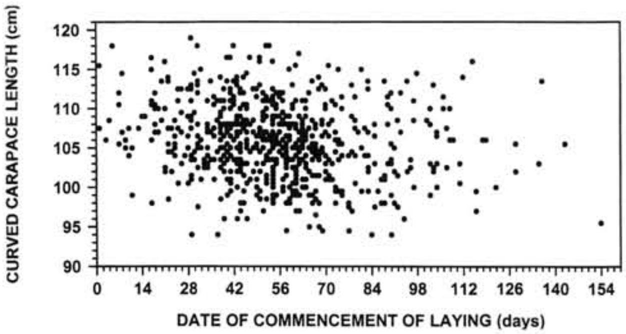

Figure 14. Scatter plot of the size of each nesting female green turtle, *Chelonia mydas,* with respect to her date of commencement of laying at Bramble Cay, 1979–80 breeding season; day 1 = 9 October 1979.

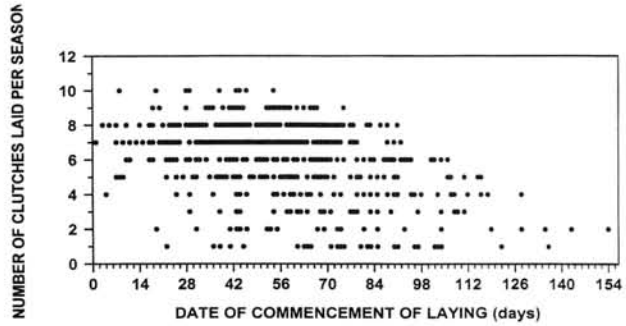

Figure 15. Scatter plot of the number of clutches laid per season by each nesting female green turtle, *Chelonia mydas,* with respect to her date of commencement of laying at Bramble Cay, 1979–80 breeding season; day 1 = 9 October 1979.

eggs in a clutch and potential predictors, such as: (1) size of the turtle, (2) number of clutches she laid for the season, (3) clutch number, (4) date of oviposition and (5) arrival date for the turtle, was reviewed using a robust regression tree model (Breiman et al., 1984). In the best fit model (with 2 terminal tree nodes) only size of the female was a significant predictor of the number of eggs in a clutch. Smaller turtles (CCL < 105 cm) laid clutches with a median count of 94 ($n = 209$) while larger turtles (CCL ≥ 105 cm) laid clutches with a median count of 106 ($n = 384$).

The changes in post-ovipositional weight of females as they laid their successive clutches through the breeding season are summarized in Table 10. There was no significant difference in the mean weight change per female per clutch laid (one way ANOVA: $F_{23,90} = 0.36$, $p > 0.25$). The mean change in ovipositional weight per clutch laid was -0.915 kg (SD = 2.70, range = -11.5 to +7.5, $n = 112$ clutches from 24 females). Because the data on weight and diameter of eggs laid by these females during this weighing experiment have been lost, the change in weight of the female relative to the weight of eggs produced could not be analyzed.

The technique of marking clutches using marker posts at the nests and recovering hatchlings by using wire mesh fences around nests when clutches were approaching hatchling emergence time had been quite successful in previous seasons, but were inadequate this season because of the high density of turtles on the beach on many nights. Nest marking posts were broken and knocked over while the wire mesh fences around full term nests were regularly flattened or torn out, especially in areas of high nesting density. Of the 245 stakes erected only 90 survived throughout incubation. Only 32 accurate incubation periods were recorded. Raw data for incubation periods and hatchling emergence success from the nests for individual clutches have been lost and only some summaries prepared by the project leader in early 1980 remain. The mean incubation period from laying to hatchling emergence was 56.6 days (Table 3); the mean emergence success of hatchlings onto the beach surface was 68.5% of the eggs laid per clutch (Table 3). The incubation sample reported above is biased for clutches laid in areas of low density nesting. While the exact location of each nest was not recorded, recording the sector and the position on the dune profile enabled an estimate of whether an incubating clutch was lost during subsequent erosion or flooding of the beach. Of the 3753 clutches recorded laid in the 1979–80 breeding season, 1259 (33.5%) clutches were estimated to have been laid in locations that would have resulted in the total loss of the eggs through erosion or flooding of the nest sites (73 of the clutches were not classified with respect to security of the nest site). The actual clutch loss for the season was less than this because 354 clutches that were laid in obviously unsafe locations were relocated immediately to safe artificial nest sites on the southwestern side of the island at the margin of the vegetation. Clutches laid in sectors 1–3 on the broad area of unvegetated sand at the western side of the island (see Fig. 2) accounted for most of the erosional loss of clutches. Egg loss from nesting turtles digging into existing clutches also occurred but was not quantified.

Two ghost crab species, *Ocypode ceratophthalmus* and *O. caudimanus*, that were common on the island, were observed to kill hatchlings on the beach at night, and crested

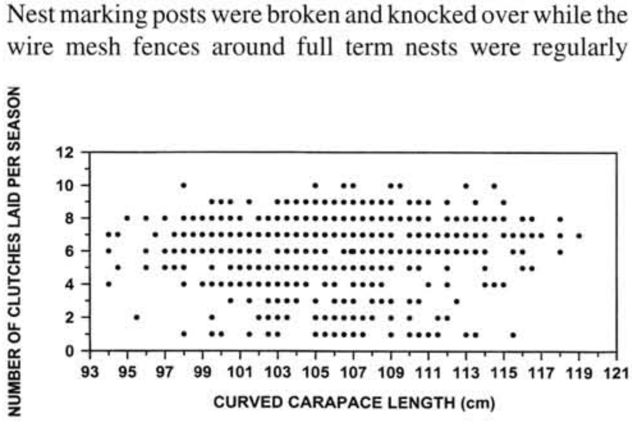

Figure 16. Scatter plot of the number of clutches laid per season with respect to size of breeding female green turtles, *Chelonia mydas,* at Bramble Cay, 1979–80 breeding season ($n = 678$).

Table 8. Summary of results of a hierarchical unweighted least squares linear regression analysis of renesting interval against date of laying the clutch at the commencement of the renesting interval (DAYS) for the best fit model: cases = 2783, df = 2780, overall F = 141.5, $p = 0.0000$, $r^2 = 0.0924$, residual mean square = 2.559.

Predictor variables	Coefficient	S.E.	Student's t	p
constant	-15.704	2.0285E-01	77.42	0.0000
DAYS	-7.4317E-02	4.9732E-03	-14.94	0.0000
$DAYS^2$	3.7605E-04	2.8962E-05	12.98	0.0000

Table 9. Mean numbers of eggs per clutch for successive clutches laid by *Chelonia mydas* nesting at Bramble Cay, 1979–80 breeding season. Data primarily from "priority" turtles.

	Clutch Number									
	1	2	3	4	5	6	7	8	9	10
Turtles laying ten clutches for the season										
Mean	96.333	97.0	101.5	-	-	113.0	-	86.0	106	81
SD	11.015	7.211	7.778			5.0		31.113		
n	3	3	2			3		2	1	1
range	85-107	89-103	96-107			108-118		64-108		
Turtles laying nine clutches for the season										
Mean	93.0	106.7	94.0	101.5	104.0	101.8	103.14	95.86	96.143	
SD	14.064	24.369	12.6	15.45	9.41	7.855	21.37	16.15	21.02	
n	11	6	6	8	4	5	7	7	7	
range	75-120	86-145	81-115	75-129	92-112	90-112	75-138	76-120	64-113	
Turtles laying eight clutches for the season										
Mean	100.95	98.81	109.43	103.0	108.92	103.17	119.11	109.0		
SD	20.86	20.88	15.52	14.61	23.55	16.17	25.41	23.37		
n	37	21	14	9	12	12	9	13		
range	61-148	62-133	85-140	84-123	81-152	77-133	96-173	75-146		
Turtles laying seven clutches for the season										
Mean	95.41	104.97	104.706	106.741	99.0	109.8	106.0			
SD	16.58	20.53	12.86	20.62	13.38	15.96	13.53			
n	51	31	17	27	23	30	19			
range	66-158	73-182	89-142	72-176	61-125	79-139	88-133			
Turtles laying six clutches for the season										
Mean	95.12	97.0	97.58	98.69	105.75	101.19				
SD	22.85	19.01	15.93	18.33	16.03	15.25				
n	25	16	12	13	16	16				
range	61-154	69-128	72-130	66-122	81-140	65-128				
Turtles laying five clutches for the season										
Mean	103.0	100.75	102.67	102.67	114.13					
SD	13.45	16.07	24.72	24.18	15.66					
n	11	8	6	6	8					
range	82-124	73-129	61-133	78-132	92-141					
Turtles laying four clutches for the season										
Mean	101.11	110.2	102.75	106.6						
SD	22.10	15.58	7.14	19.13						
n	9	10	4	5						
range	67-130	87-141	97-113	90-132						
Turtles laying three clutches for the season										
Mean	84.0	107.0	98							
SD	21.21	12.17								
n	2	3	1							
range	69-99	99-121								
Turtles laying two clutches for the season										
Mean	103.8	108.13								
SD	11.476	17.62								
n	5	8								
range	90-120	90-145								
Turtles laying one clutch for the season										
Mean	107.0									
SD	9.55									
n	8									
range	96-120									

terns (*Sterna bergii*) took hatchlings from the beach and the sea during the day. A number of black-tipped reef sharks (*Carcharhinus* sp.), a second unidentified species of small shark, and Papuan trevally (*Caranx papuensis*) were caught off the beach with stomach contents including turtle eggs which had been washed off the beach during erosion events and hatchlings eaten as they swam across the reef flat. Both types of feeding behavior were confirmed by direct observations. Although it was active throughout the turtle nesting habitat at night, the endemic rat *Melomys rubicola* (Limpus et al., 1983b) was never observed to eat turtle eggs or hatchlings. Several nesting female *C. mydas* had distinctive, fresh shark-bite wounds, some still bleeding. One untagged nesting adult and approximately six clutches of eggs were taken from Bramble Cay for food by Darnley Islanders during the season.

Four turtles tagged while nesting during the 1979–80 breeding season at Bramble Cay were subsequently reported captured and eaten by coastal peoples in feeding sites 40–476 km distant (Table 11). At the completion of the breeding season, these turtles had migrated to feeding sites in Torres Strait, southeastern Papua New Guinea, and the northern Great Barrier Reef, or were migrating to sites further away.

DISCUSSION

Recent advances in genetics research have shown that the globally dispersed species *C. mydas* comprises a series of distinct stocks that rarely interbreed (Bowen et al., 1992; Norman et al., 1994a). When genetic analysis was conducted at a series of rookeries from each of the widely separated breeding aggregations of *C. mydas* in Australia, it was demonstrated that while widely separated groups of rookeries function as independent populations, rookeries in close proximity within a cluster of breeding aggregations cannot be differentiated (Norman et al., 1994b). In particular, these studies have demonstrated that the *C. mydas* breeding aggregations at Bramble Cay, Raine Island, and No.8 Sandbank in

Table 10. Post-ovipositional weight changes with laying of successive clutches for *Chelonia mydas*, Bramble Cay 1979–80 breeding season. CCL (cm) and WT (kg) denote curved carapace length and post-ovipositional weight of the nesting female, respectively. No. Cl. = number of clutches laid during weighing period.

Date		WT (δWT since previous weighing)									Total	No.	Mean δWT/clutch
1st capt.	CCL	1	2	3	4	5	6	7	8	9	δWT	Cl.	(SD, range)
16/11/79	104.0	140.0	138.0 (-2.0)	134.5 (-3.5)	133.0 (-1.5)	135.0 (+2.0)	132.0 (-3.0)	133.0 (+1.0)	135.0 (+2.0)	131.0 (-4.0)	-9.0	8	-1.13 (2.46, -4.0 - +2.0)
22/12/79	99.5	112.0	110.5 (-1.5)	108.0 (-2.5)	106.0 (-2.0)	105.0 (-1.0)	103.0 (-2.0)	102.0 (-1.0)	103.0 (+1.0)	104.0 (+1.0)	-8.0	8	-1.00 (1.34, -2.5 - +1.0)
02/11/79	112.5	146.0	144.0 (-2.0)	144.0 (0.0)	143.0 (-1.0)	140.5 (-2.5)	141.0 (+0.5)	141.0 (0.0)	140.0 (-1.0)		-6.0	7	-0.86 (1.11, -2.5 - +0.5)
03/11/79	112.5	150.0	145.0 (-5.0)	138.0 (-7.0)	143.0 (+5.0)	141.0 (-2.0)	138.0 (-3.0)	143.0 (+5.0)	141.0 (-2.0)		-9.0	7	-1.29 (4.64, -7.0 - +5.0)
03/11/79	106.5	122.0	120.0 (-2.0)	120.0 (0.0)	118.0 (-2.0)	122.0 (+4.0)	119.0 (-3.0)				-3.0	5	-0.60 (2.79, -3.0 - +4.0)
02/11/79	107.5	121.0	119.0 (-2.0)	117.5 (-1.5)	119.0 (+1.5)	119.0 (0.0)	119.0 (0.0)	117.0 (-2.0)			-4.0	6	-0.67 (1.40, -2.0 - +1.5)
10/11/79	103.0	115.0	110.0 (-5.0)	109.5 (-0.5)	109.5 (0.0)	109.0 (-0.5)	110.0 (+1.0)	113.0 (+3.0)			-2.0	6	-0.33 (2.64, -5.0 - +3.0)
12/11/79	113.5	152.0	143.0 (-9.0)	143.0 (0.0)	141.0 (-2.0)	138.5 (-2.5)	136.0 (-2.5)	138.0 (+2.0)			-14.0	6	-2.33 (3.71, -9.0 - +2.0)
13/11/79	106.5	120.0	117.0 (-3.0)	116.5 (-0.5)	119.0 (+2.5)	115.0 (-4.0)	115.0 (0.0)				-5.0	5	-1.00 (2.30, -4.0 - 0.0)
18/11/79	104.0	114.0	112.0 (-2.0)	109.5 (-2.5)	111.0 (+1.5)	108.0 (-3.0)	111.0 (+3.0)	111.0 (0.0)			-3.0	6	-0.50 (2.20, -3.0 - +3.0)
08/12/79	100.5	114.5	114.0 (-0.5)	112.0 (-2.0)	113.0 (+1.0)	111.0 (-2.0)	109.0 (-2.0)				-5.5	5	-1.10 (1.34, -2.0 - +1.0)
26/12/79	107.5	112.5	120.0 (+7.5)	117.0 (-3.0)	114.0 (-3.0)	112.0 (-2.0)	112.0 (0.0)	111.0 (-1.0)			-1.5	6	-0.25 (3.97, -3.0 - +7.5)
08/11/79	97.5	104.0	101.0 (-3.0)	100.5 (-0.5)	102.0 (+1.5)	101.0 (-1.0)	99.0 (-2.0)				-5.0	5	-1.00 (1.52, -3.0 - +0.5)
01/11/79	104.0	-	116.0	117.0 (+1.0)							+1.0	1	+1.00 (0,+1)
25/11/79	103.0	119.5	116.0 (-3.5)	114.5 (-1.5)	103.0 (-11.5)	110.0 (+7.0)	114.0 (+4.0)				-5.5	5	-1.10 (7.60, -11.5 - +7.0)
25/12/79	98.0	95.5	96.0 (+0.5)	93.0 (-3.0)	95.0 (+2.0)						-0.5	3	-0.17 (2.57, -3.0 - +2.0)
21/12/96	106.5	112.5	112.0 (-0.5)	112.0 (0.0)	111.0 (-1.0)	111.0 (0.0)					-1.5	4	-0.38 (0.41, -1.0 - +0.5)
22/12/79	104.0	121.0	119.0 (-2.0)	118.0 (-1.0)	117.0 (-1.0)	119.0 (+2.0)	116.0 (-3.0)				-5.0	5	-1.00 (1.87, -3.0 - +2.0)
20/11/79	96.0	124.0	121.0 (-3.0)								-3.0	1	-3.00 (0,-3)
03/12/79	107.0	141.0	140.0 (-1.0)	136.0 (-4.0)	135.0 (-1.0)	135.0 (0.0)					-6.0	4	-1.50 (1.50, -4.0 - 0.0)
24/12/79	97.5	104.0	100.0 (-4.0)	101.0 (+1.0)	98.0 (-3.0)	98.0 (0.0)					-6.0	4	-1.50 (1.50, -4.0 - +3.0)
06/11/79	94.0	94.5	91.0 (-3.5)	91.0 (0.0)	93.5 (+2.5)						-1.0	3	-0.33 (3.01, -3.5 - +2.5)
26/11/79	104.0	116.0	118.0 (+2.0)	-	117.0 (-1.0)						+1.0	3	+0.33 (-)
08/11/79	102.5	120.0	118.0 (-2.0)								-2.0	1	-2.00 (0,-2)
07/01/80	107.0	110.0									-	0	

the northern Great Barrier Reef (GBR) could not be distinguished from one another using mtDNA studies. In contrast, the *C. mydas* that bred at these northern GBR rookeries were significantly different genetically from each of the breeding aggregations of the southern GBR, southern Gulf of Carpentaria, and Western Australia. The Bramble Cay *C. mydas* nesting population is therefore regarded as an outlying component of the much larger nesting population that nests at Raine Island and Moulter Cay (Limpus et al., 1993). The present study provides the first detailed report of the reproductive biology of this northern GBR *C. mydas* genetic stock.

The high density summer nesting by *C. mydas* recorded at Bramble Cay for the 1979–80 breeding season is typical of marine turtle breeding on the small coral cays of the outer northern Great Barrier Reef (Limpus et al.,1991). There has been no adequate explanation of the underlying causes of the variability in breeding distribution and seasonality of marine turtles. Many Indo-Pacific *C. mydas* rookeries are characterized by year-round nesting with a mid-year, dry season peak of nesting activity, e.g., Pangumbahun on mainland Java in Indonesia (Schulz, 1984); Sarawak Turtle Islands, small inshore continental islands, in Malaysia (Chin, 1975); and Sulu Sea Turtle Islands, small inshore islands of Sabah (Malaysia) and the Philippines (Palma, 1994). See Hirth (1997) and Miller (1989) for more extensive reviews of nesting seasonality outside of Australia. Year-round nesting with a mid-year (dry season, winter) peak of nesting activity also characterizes *C. mydas* breeding in the continental islands of the Wellesley Islands of the southern Gulf of Carpentaria at 15°S latitude (Limpus et al., 1994c, and CJL, unpubl. data).

This Gulf of Carpentaria stock is the closest independent stock to the northern GBR stock which includes the Bramble Cay Rookery. However, Bramble Cay (9°S) does not support year-round nesting but has a distinct summer (wet season) peak of nesting with little or no winter (dry season) nesting. This highly seasonal nesting occurs even though temperatures at Bramble Cay (Fig. 3) are suitable year-round for successful incubation of marine turtle eggs (Miller, 1985). The exceptionally large nesting population at Raine Island (11°S) also has a mid-summer peak of nesting but the population is so large as to have long tails to the beginning and end of the nesting season distribution resulting in sporadic nesting even in mid-year (Limpus et al., 1991). Highly seasonal summer nesting also characterizes the *C. mydas* nesting populations of the southern GBR stock

Table 11. Summary of post-nesting migration records of adult female turtles from Bramble Cay, 1979–80 breeding season; * = previously published records (Limpus et al., 1992); PNG = Papua New Guinea.

Date tagged	Nesting history	Recapture date	Locality	Distance traveled	Fate
21 Nov 79	Laid 8 clutches, last recorded 13 Feb 80	06 Mar 80*	Kimusi-w reef, Torres Strait, Australia 9°22'S, 143°03'E	92 km	Killed, eaten
17 Dec 79	Laid 7 clutches, last recorded 15 Mar 80	31 Mar 80*	Morris Island, Great Barrier Reef, Australia 13°24'S, 143°43'E	476 km	Killed, eaten?
24 Dec 79	Laid 6 clutches, last recorded 17 Feb 80	08 May 80*	Kokopi, Western Province, PNG 9°22'S, 143°13'E	75 km	Harpooned, eaten
03 Feb 80	Laid 4 clutches, last recorded 18 Mar 80	29 Nov 84	Gaba Gaba, 40 km NW of Port Moresby, PNG 9°16'S, 146°54'E	347 km	Unknown, presumed eaten

(23°S) (Bustard, 1972) and the Leeward Hawaiian Islands (24°N) (Balazs, 1980). The regional differences in nesting seasonality at these rookeries cannot be explained by latitude alone but may well be influenced by an underlying genetic factor as well as the regional climate of the nesting beaches. The environment of the nesting beach can moderate nest temperatures from that expected for the latitude. For example, white coralline sand makes for cooler nest temperatures, increased incubation periods, and increased proportion of male hatchlings as compared to beaches with darker mineral sands (Miller and Limpus, 1981; Limpus et al., 1983c; Guinea, 1994a). Rain can also cool the beach and produce similar effects, but it can also improve nesting success by providing greater adhesion of sand grains (Reed, 1980). Some nesting beaches have nest temperatures extending into the lethal range for incubating marine turtle eggs for part of the year (Guinea, 1994b). While these factors need to be considered when attempting to understand why marine turtles breed where and when they do, it must be recognized that Bramble Cay is a peripheral rookery of the much larger Raine Island – Moulter Cay nesting population. Therefore the conditions at Bramble Cay may not be the primary factors determining the seasonality of its nesting population. Attempts to explain the variability in seasonality observed among *C. mydas* rookeries globally should address the question from a stock perspective, taking into consideration the genetic relatedness of the stocks, size and distribution of the subpopulations within a stock, latitude, regional rainfall patterns, and the characteristics of the individual rookeries that influence the microclimate of the nests.

The extreme seasonality of the breeding season, the small size of the nesting beach, and the remoteness of the island from other islands made Bramble Cay an ideal site for studying the reproductive biology of *C. mydas* in fine detail. Total tagging census studies at marine turtle rookeries that include a near complete census of nesting success of each female on each nesting crawl are uncommon and this is particularly so for *C. mydas*. The results from this 1979–80 Bramble Cay study provide a rare opportunity to investigate methodologies for census and quantification of reproductive parameters at a *C. mydas* rookery. These data clearly demonstrate that there was no time when all females for that season were present at the rookery (Fig. 6). The minimum time that would have been required at the island to sight every nesting female was approximately 4.5 months, from 30 October until 10 March. Visits to the rookery for shorter periods would have sampled only a fraction of the total population, the proportion being a function of when in the season and for how long the visit occurred. Although the maximum daily availability of nesting females (cumulative arrivals minus cumulative departures) peaked at approximately 80% of the annual nesting population, not all "available" *C. mydas* visit the rookery on a single night. Rather, they visit over a two-week nesting cycle. If a two-week sampling period was used, chosen because of the difference in nightly nesting numbers that result from the tidal cycle and the approximately two-week-long internesting cycle, the optimal time to have sampled this rookery would have been in the last two weeks of December through to the first two weeks of January (Fig. 6). About 85% of the nesting population could have been sampled in either of these periods (using the difference between cumulative departures at the beginning of the sampling period and cumulative arrivals by the end of the period as a measure of the maximum availability of turtles).

These Bramble Cay data also demonstrate that several frequently measured parameters for marine turtles are a function of date during the breeding season. When a population is sampled for only part of a breeding season, the resulting values for some parameters may not be an accurate summary of the same parameters when measured for the entire season. Renesting interval tended to be longer in the early and late nesting season and shortest in the mid-season. Turtles arriving early in the season tended to be bigger (CCL) and to lay more clutches for the season than turtles arriving later in the season. In addition, there was also a tendency for larger turtles to lay larger clutches. Indeed, the total number of clutches per female per season cannot be quantified without a tagging census for an entire season. Nightly nesting success was a function of whether or not the wet season had commenced. Sampling a rookery with varying duration sampling periods at different times of the breeding season in different years will not be conducive to providing valid comparative data for the population. It would appear most reasonable to sample any given rookery at the same standard time within the breeding season in successive years. Replicate tagging census data sets for a series of entire breeding season samples are needed to test for similarity of results from a standard sampling period across the seasons and for determining the relationship between results from the sampling period and those from the entire season. Until these replicate data are available, when a census of an entire breeding season is not possible it is recommended that as long a sampling period as possible should be employed, spanning two-weekly time intervals. The number of turtles encountered will be maximized for the minimum duration census if it is conducted at the peak of the nesting season. When sampling periods and timing are not comparable, caution should be exercised when making statistical comparisons between breeding populations and seasons.

The within-season variability of parameters observed at Bramble Cay is not unique. Balazs (1980) recorded low nesting success (usually < 50%) in the early nesting season for the Hawaiian French Frigate Shoals *C. mydas* population, with increasing nesting success as the season progressed. *Caretta caretta* nesting at Mon Repos in south Queensland displays considerable within-seasonal variability in renesting interval, total clutches per female per season, eggs per clutch, and egg diameter (Limpus, 1985). It is not our intention at this time to compare results of nesting studies from the many *C. mydas* rookeries that have been studied with a diversity of sampling regimes. See Hirth (1997) and van Buskirk and Crowder (1994) for such reviews. If these reviews are examined from a stock perspective, it is apparent that there is considerable variability in many of the parameters among the stocks. These parameters are often required for population modelling exercises. In such cases, they should not be extrapolated across stock boundaries but measured within each stock.

This study has recorded the highest estimate of the number of clutches laid per female per breeding season (6.2 clutches) for wild *C. mydas* (van Buskirk and Crowder, 1994; Hirth, 1997; Miller, 1997). This value is not significantly different from the 5.9 clutches per female per breeding season recorded for captive *C. mydas* at the Cayman Turtle Farm (Wood and Wood, 1980) which was the previously highest value recorded for the species (one-way Anova: $F_{1,854} = 2.96$, $0.1 > p > 0.2$).

The failure to record any remigration recaptures of *C. mydas* during the six breeding seasons of tagging studies at Bramble Cay from 1974 through 1980 was unexpected, especially since the last three seasons were examined with total tagging census. Bustard (1974), using single tagging with the same design monel tag in the same tagging position on the front flipper, also obtained low remigration recapture rates for *C. mydas* nesting at Heron Island. He reported "only 1–2% of the green turtles from Heron Island population returned to their own island in a subsequent nesting period and mostly after a period of 4 years at sea". Studies at *C.mydas* nesting at Ascension Island, Atlantic Ocean, also reported a very low remigration recapture rate of < 2.1% of turtles tagged and high tag loss with monel tags (78% of identified remigrants in the 1977–78 season) (Mortimer and Carr, 1987). It is now possible to identify two major factors which would have contributed to these low remigration recapture rates. Monel tags (NBTC 1005 #49) have a high loss rate, especially when applied in the distal tagging position of the front flippers (Limpus, 1992; Bjorndal et al., 1996). Much higher remigration recapture rates are recorded with non-corrosible titanium tags applied to *C. mydas* at eastern Australian rookeries (Limpus et al., 1994a) and inconel tags applied at Hawaiian and Caribbean rookeries (Bjorndal et al., 1996). In addition, only a very small proportion of *C. mydas* at the eastern rookeries remigrate in less than 4 years (Limpus et al., 1991, 1994a). It is concluded that the lack of remigration records within the 6 years of AEPL tagging studies at Bramble Cay is a measure of the inappropriateness of the monel tag for long-term studies for *C. mydas* rather than a measure of a low remigration rate at that site. The low reporting rate for long-term post-nesting migration captures (Table 11) is also probably influenced by the high rate of monel tag loss within a few years of their application and does not necessarily reflect low hunting pressures on these turtles (Limpus et al., 1992).

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