MARK-RECAPTURE ESTIMATION OF THE LEATHERBACK SEA TURTLE (*Dermochelys coriacea*) NESTING POPULATION AT MATURA BEACH, TRINIDAD

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Abstract

Many researchers believe that Caribbean leatherback sea turtle (*Dermochelys coriacea*) populations are increasing. Since Trinidad currently hosts the world's third largest leatherback nesting assemblage, accurate population estimates are needed for this area. Nature Seekers, Inc., a community-based environmental management organization, has been monitoring leatherback nesting on Matura Beach since 1990 and began its tagging project in 1999. The tagging project's main goal was to determine the number of turtles nesting each year, but saturation tagging has not been possible given the resources available. However, as a season progresses, untagged turtle encounters constitute a smaller percentage of the overall leatherback encounters. The steady increase in percent of previously tagged turtles encountered during the season indicates that a significant portion of the population is being tagged and makes within season mark-recapture population estimation possible.

This project examines the rate of recapture of tagged turtles, trends in the timing of recapture events, and the requirements for mark-recapture estimates of leatherback nesting populations. The probability of encountering an individual leatherback varies based on the time of the season and the number of days since it was last encountered. To account for this variability, each season was divided into cohorts based on a nine day nesting cycle. Closed capture, time dependent population estimates were derived for each cohort using Program Capture. Data from the 2000, 2001, and 2003 nesting seasons yielded mark-recapture population estimates averaging 62 percent greater than the minimum number of turtles encountered. This is consistent with the 40 percent beach coverage estimate provided by Nature Seekers at the initiation of this analysis. The 20 to 24 day average time between encounters of individual leatherbacks also supports the theory that Nature Seekers observes slightly less than half of the nesting events on Matura Beach since leatherbacks are known to nest every nine to ten days.

Developing models to estimate sea turtle populations in situations where saturation tagging is not possible is critical for determining the status of endangered leatherback sea turtles. Future efforts should be directed toward improving nesting beach coverage, developing more accurate tagging effort indices, examination of the degree of nesting beach population closure, and the development of leatherback encounter probability models.

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I. Introduction

Many researchers believe that Caribbean leatherback sea turtle populations are increasing. Since Trinidad currently hosts the world's third largest leatherback nesting assemblage, accurate population estimates are needed for this area. Saturation tagging is not currently possible on Trinidad's nesting beaches, so the development of mark-recapture models to estimate the annual nesting population could greatly enhance our understanding of recent trends in the leatherback population.

1. Leatherback Sea Turtles

The leatherback sea turtle (*Dermochelys coriacea*) is the largest living species of sea turtle and the only surviving species of the Dermochelyidae family. Leatherbacks are essentially pelagic and range from subpolar to tropical waters. Individual leatherbacks may swim over 10,000 km per year and circumnavigate entire ocean basins (Eckert, S.A., 1998). While their pelagic range is extensive, leatherback nesting beaches are limited to the tropics. They typically nest on dynamic tropical beaches with high-energy wave action, deep sand, no fringing reef, and deep adjacent waters (Ogren, et al., 1989). A female sea turtle often returns to her natal beach to nest as a mature adult (Lohmann, et al., 1997). This natal beach homing strategy is likely responsible for the genetic distinctness of leatherback populations within ocean basins (Dutton, et al., 1999).

Leatherbacks may nest on Trinidad's beaches from late January through September, but peak nesting occurs during May and June (Fournillier and Eckert, 1999). Females lay approximately six nests per season with a nine to ten day re-nesting interval. Therefore, a female may remain near her nesting beach for as long as three months

(Chan, Eckert, Liew, and Eckert, 1990 and Eckert, 2002). The average remigration interval for nesting leatherbacks is 2.3 years (Miller, 1997).

2. Leatherback Monitoring Projects and Protection Regulations in Trinidad

The Republic of Trinidad and Tobago is an island nation off the coast of Venezuela in the Caribbean Sea. Although greens, loggerheads, hawksbills, and Kemp's ridleys all inhabit the country's waters and may nest on its beaches, leatherback sea turtles are the most abundant and have been the focus of most nesting beach protection programs. Records of Trinidad's sea turtle exploitation date back to the 1600s with capture both at sea and on nesting beaches. Due to their massive size, most intentional leatherback captures occur on land meaning that the harvest consists solely of reproductive females. However, as nesting beach protective regulations have improved, unintentional offshore captures in gillnets and trawls have gained attention. Beyond the direct capture of sea turtles, natural and human-induced habitat modifications also affect the leatherback population (Fournillier and Eckert, 1999).

A. Trinidad's Community Based Sea Turtle Management

After years of ineffective top-down sea turtle protection regulations, Trinidad's Wildlife Section first considered community-based management in 1989. The government decided in 1990 to declare Matura and Fishing Pond Beaches Prohibited Areas under the Forest Act (Chapter 66:01). Access to Prohibited Areas during the leatherback nesting season, March 1 through August 31, requires a permit issued by the Wildlife Section. Prohibited Area regulations ban fire, excessive noise, high-power lights, and vehicles from the beach as well. Camping, picnicking, and fishing are limited but not completely prohibited (Ashton and Jacobson, 1996).

As the Prohibited Area declaration was passed, community members began organizing to retain some local control of resource management. Although few people depended on the sea turtle harvest for their subsistence, leatherbacks had historically played a seasonal role in the economies of these communities (Bacon, 1973). Nature Seekers, Inc., Fishing Pond Environmental and Community Group, and the Grande Riviere Environmental Awareness Trust were three of the major groups formed during this time due to concern over the loss of income and recreational opportunities associated with the Prohibited Area designation. The Forestry Division catalyzed the founding of these organizations in an attempt to increase community conservation efforts through ecotourism ventures. High volunteerism rates and strong conservation leaders emerged from the initial community meetings (Nathai-Gyan, 1993). The community groups negotiated with the government for beach access rights. The Wildlife Section agreed to grant beach access if the community would serve to protect the turtles from poachers. Furthermore, the government significantly invested in the training of group members as eco tour guides and enhanced the capacity-building aspects of these community-based management groups (Nathai-Gyan, 1993). Nature Seekers, Inc., offered the first guided sea turtle tours at Matura Beach in 1990.

The tour guides soon realized that poaching was a serious threat to the success of turtle tourism and their new source of income. Nature Seekers began organizing a volunteer poaching patrol to assist the government guards. By 1993, these volunteers had eliminated poaching at Matura. However, as the tourism business increased in the late 1990s, poachers returned. They realized that volunteers' efforts would be focused on guiding the large number of tourists rather than preventing poaching, and four leatherbacks were slaughtered in 1996 alone (Fournillier and Eckert, 1999). Despite this small resurgence, community-based efforts seem to be the most successful method thus far in controlling turtle poaching.

Several factors could play a role in the success of this management strategy. First, it is often true that local people know who the poachers within the community are much better than government officials do. Enforcement by fellow community members can be done without the threat of severe criminal penalties. Community-based methods are also more likely to lead to a change in local attitudes and perceptions. Nature Seekers invests extensive time in education efforts at local schools. The children then return to their families and influence the beliefs of their parents. Through the efforts of Nature Seekers, eight former leatherback poachers have now become conservation minded tour guides (Sammy, 1993).

B. Nature Seekers, Incorporated's Matura Beach Tagging Project

Nature Seekers organizes teams to patrol the beach each night of the nesting season and gathers information on the basic physical characteristics of nesting females and the location and success of nesting attempts. After a two month experimental period in 1998, Nature Seekers initiated a full time tagging program in 1999 with both flipper and passive integrated transponder (PIT) tagging of nesting females. Five organizations including the High Commission of Canada, the UNDP GEF Small Grant Programme, the Forestry Division, the Institute for Marine Affairs and the Wider Caribbean Sea Turtle Conservation Network initially supported the tagging project at Matura (Sammy, 1999). The support of these organizations allowed Nature Seekers to tag and monitor turtles throughout the six month nesting season, but the large nesting population, the isolation and length of the nesting beach, erosion, tidal conditions, and the limited number of monitors prevented tagging all turtles present (Fournillier and Eckert, 1999). Earthwatch, an organization that provides financial resources and volunteers to science projects throughout the world, began sponsoring Nature Seekers' efforts in 2003. The contributions of three Earthwatch teams consisting of eight to twelve volunteers working in two week blocks during the peak of the 2003 nesting season dramatically increased beach coverage (S. Eckert, pers. comm.).

3. Nesting Beach Population Estimation

Almost all resource management decisions are based on population models (Frazier, 1989). Generating a more accurate estimate of the nesting leatherback population at Matura Beach could lead to more informed policy and management decisions. Population numbers give regulations purpose and help set goals for the future (Kerr, 1998).

A. Tagging Project Goals

The primary goal of the Matura Beach Tagging Project was to estimate the number of leatherbacks nesting at the beach each year. However, saturation tagging has not been achieved due to the large number of turtles, the length and isolation of the beach, erosion and tidal conditions, and the limited number of patrollers. Therefore, the number of turtles tagged each season represents a minimum estimate of the annual nesting population size.

B. Alternatives to Saturation Tagging

Since saturation tagging is not possible with the resources currently available, other methods must be developed for estimating leatherback population sizes.

i. Short-Term Intensive Tagging

Rhema Kerr (1998) investigated the effectiveness of short-term intensive saturation tagging in comparison to full season projects. Using hawksbill sea turtle nesting data from Jumby Bay, Antigua, she discovered that 18 day surveys produced similar population estimates and were more cost effective. This strategy, however, would not be useful on Matura Beach. With the resources currently available, saturation tagging is not possible even over short periods of time at Matura. Kerr's project at Jumby Bay involved only 21 to 38 hawksbills annually, whereas Matura Beach hosts thousands of nesting leatherbacks. Beach conditions and the great number of turtles present would prevent achieving 18 day saturation tagging without dramatic increases in the number of beach patrollers.

ii. Mark-Recapture Models for Population Estimation

Peterson first utilized the basic mark-recapture techniques in 1896 (Ogle, 1996). Under the Peterson method, each animal from a single sample is marked and returned to the population. After some time period, a second sample is taken from the population and examined for marks. Information is gained both from the recapture of marked animals and from comparisons of the percentage of marked versus unmarked animals at each sampling time (Pollock, et al., 1990). Population estimates are based on the idea that the proportion of animals in the recapture sample that have been marked is the same as the proportion of animals in the entire population who were marked. The Peterson method assumes the population is closed, all animals have the same probability of being captured, marking an animal does not affect its catchability, marks are not lost between sampling periods, and all marks are recorded at the time of resampling. Various other mark-recapture methods have been derived to adjust for open populations, multiple resampling events, and other confounding factors (Ogle, 1996).

The goal of estimating nesting populations at Matura can best be met by developing mark-recapture models for population estimation. The highest percentage of untagged turtles is expected during the beginning of each nesting season. As the season and tagging efforts progress, tagged turtles are reencountered on their return nesting events. Examining the change in percent tagged throughout the season allows for predictions of the number of nesting females present using mark-recapture models.

II. Materials and Methods

1. Data Source

Nature Seekers, Inc., supplied the National Sea Turtle Database of Trinidad and Tobago for this evaluation. This database contains information gathered from nightly nesting and tagging reports during the 1999 to 2003 seasons of the Matura Beach leatherback tagging project. Additional information was provided on sightings of Matura tagged leatherbacks observed in other locations.

2. Study Site

Matura Beach, an 8.85 km beach on the east coast, is one of Trinidad's three major leatherback nesting beaches. Historically, egg poaching and female slaughter have been problems at Matura. Around 30 percent of the turtles nesting on the beach during the 1970s were killed for meat. Nature Seekers, Inc. was established in 1990 to monitor and protect the leatherback population of Matura Beach. The beach was divided into eighteen zones for the purpose of monitoring nesting activity (Fournillier and Eckert, 1999).

Figure 1: Map of Trinidad's Leatherback Nesting Beaches (Sammy, 1999)

* Leatherback tagging occurred in the project location marked in red.
Blue dots represent other locations of leatherback sightings in Trinidad.

3. Tagging Data

My analysis focuses on data from 1999, 2000, 2001, and 2003. Full season tagging projects began at Matura in 1999. Data from the 2002 nesting season was not examined because Nature Seekers was unable to purchase tags that year. Using the National Sea Turtle Database, I extracted the number of leatherback encounters within each season and the dates and number of days between encounters of each individual turtle.

I also examined the number of leatherbacks observed at Matura and another location during a single nesting season in order to determine the degree of population closure.

4. Effort Data

In order to estimate the tagging effort during each season, I used the number of patrol days covered each year by the Nature Seekers' annual budget. For the 2003 nesting season, the patrol days contributed by Earthwatch volunteers were added to the Nature Seekers totals. During the 2001 nesting season, a substantial prize was offered to the person who tagged the most turtles, so the annual budget estimates may not adequately reflect the true effort during that season.

5. Mark-Recapture Analysis

I focused my mark-recapture analysis on single season nesting population estimates since an individual leatherback does not nest every season. Since the probability of encountering a turtle varies based on the date it last nested, I used a cohort system to ensure that each turtle had the same probability of encounter on each sampling day. Each season's data was divided into nine cohorts based on the fact that most reencounters occur nine days after the previous nesting date. Each cohort was composed of the encounters occurring on a nine day cycle as shown in table 1 with the date of the first encounter of the season being designated the first of sampling for cohort 1. One-way ANOVA's were performed to determine whether the mean number of turtles or the mean number of encounters differed among the cohorts.

Table 1: Cohort System for Maintaining Equal Reencounter Probabilities

Sunday	**Monday**	**Tuesday**	**Wednesday**	**Thursday**	**Friday**	**Saturday**
Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 5	Cohort 6	Cohort 7
Cohort 8	Cohort 9	Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 5

An encounter history file was created for each cohort within each year. This file was then used to determine a population estimate using Program Capture within Program MARK. Program Capture generates population estimates along with 95 percent confidence intervals for closed capture mark-recapture studies. I used the Darroch M_t model in which capture probabilities vary by time or trapping occasion (White, et al., 1982). A season's cohort estimates were then averaged to provide a single estimate of that season's nesting population.

III. Results

1. Leatherback Encounters and Tagging Results

A. Annual Summary Statistics

Since the beginning of the tagging project in 1999, over 1,500 leatherback encounters have occurred each season. Table 2 shows the number of turtles encountered each season and the number of reencounters of turtles seen multiple times within the season. Since the initiation of the tagging project, at least 873 turtles have been observed nesting each season with a maximum number of 2,456 turtles recorded in 2001. In 1999, 41 percent of the turtles initially tagged were reencountered later in the season. Around 20 percent of the turtles nesting in 2000 and 2001 were encountered on multiple occasions. Only 12 percent of the total number of turtles observed were encountered again within the 2003 nesting season. This table also shows the mean and median number of days between sightings of tagged turtles when false crawls are included and excluded. False crawls are events when female leatherbacks emerge from the ocean but do not successfully nest. For this analysis, an encounter was considered a false crawl if the turtle was reencountered within five or fewer days.

Table 1: Leatherback Encounter Summary Statistics for Matura Beach, Trinidad

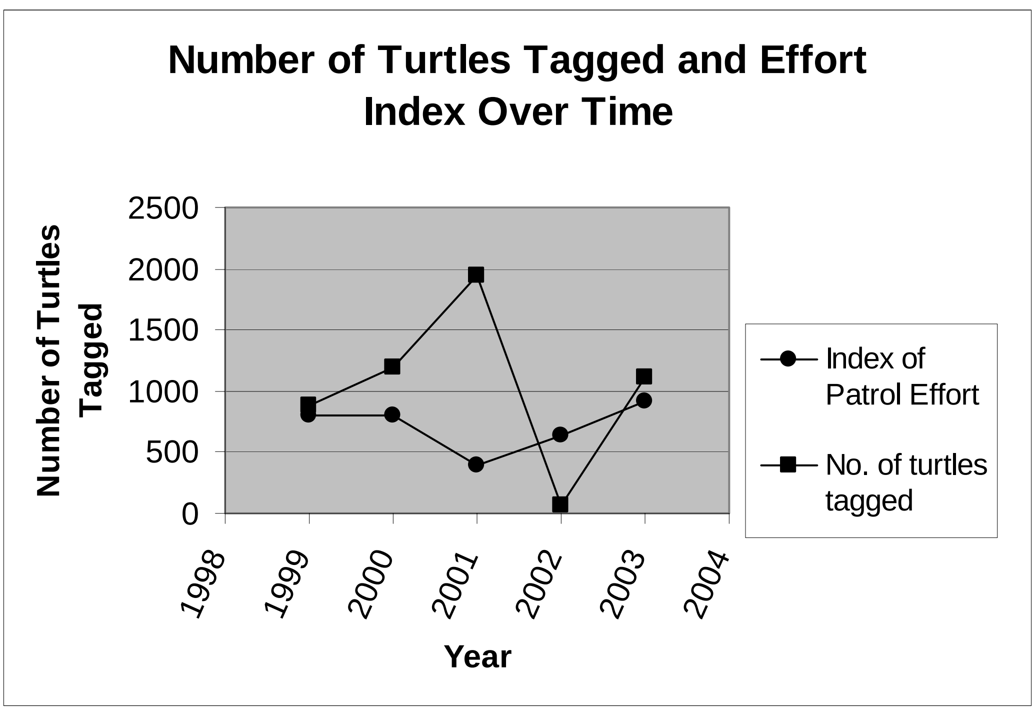
	1999	**2000**	**2001**	**2003**
Total # of Turtles Encountered	873	1271	2456	1859
Total # of Encounters	1503	1659	2951	2161
# of Turtles Reencountered	362	298	504	227
# of Reencounters	562	383	615	301
Mean # of Days between Reencounters (with false crawls)	19.48	23.30	21.98	20.79
Median # of Days between Reencounters (with false crawls)	17	20	18	16.5
Mean # of Days between Reencounters (without false crawls)	20.58	24.56	22.83	23.44
Median # of Days between Reencounters (without false crawls)	18	20	19	20

* Reencounters considered false crawls if internesting interval is less than or equal to 5 days. False crawls are events when a turtle leaves the ocean but fails to successfully lay a clutch of eggs.

B. Tagging Effort

Figure 2 demonstrates the relationship between the number of turtles tagged during a season and tagging effort. Effort estimates are based on time card data for Nature Seekers taggers. Earthwatch volunteer hours have been added to the 2003 effort calculation. Effort to tagging relationships for 2001 and 2002 seasons are known to be biased. Researchers offered a substantial prize for the person tagging the most turtles in 2001, so many more hours of tagging were conducted than are reflected by the time card effort estimates. During 2002, Nature Seekers did not have the funds to purchase tags, so patrol effort reflects beach monitoring and not tagging effort.

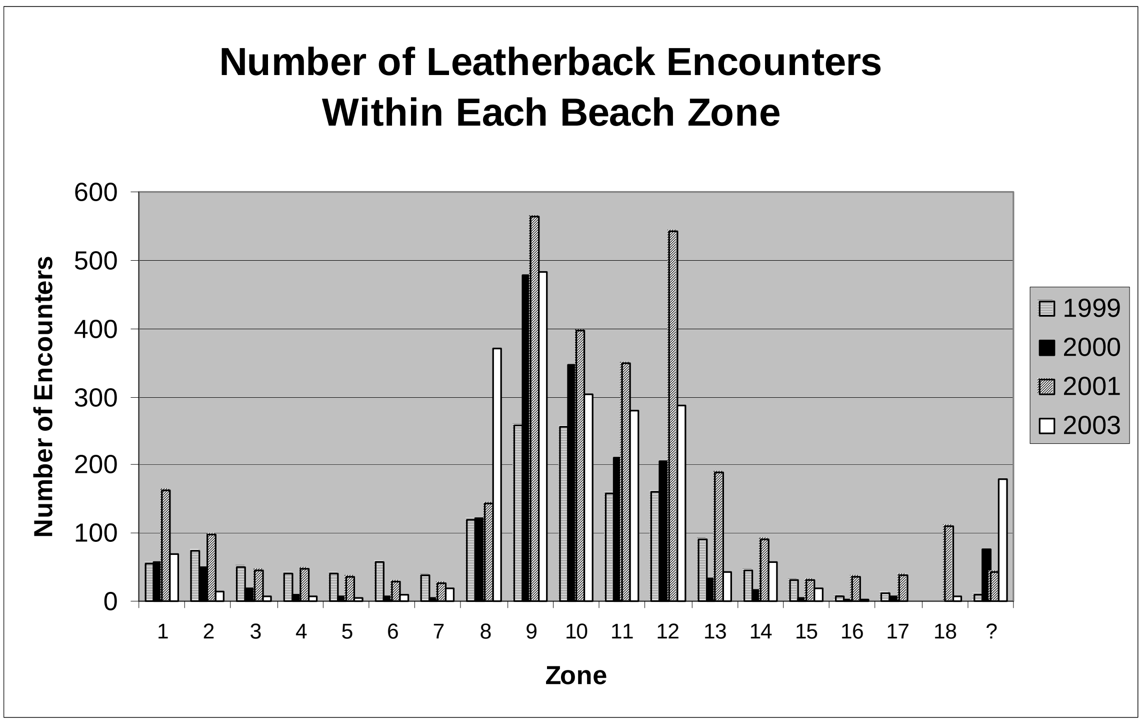
Figure 2: Number of Turtles Tagged and Index of Effort over Time



C. Location of Leatherback Encounters on Matura Beach

Nature Seekers divided Matura Beach into 18 zones in order to monitor the location of nesting activities. Figure 3 depicts the number of encounters within each zone during the four years of my analysis. Most of the encounters occurred between zones eight and thirteen. During 2003, no zone was recorded for 179 leatherback encounters.

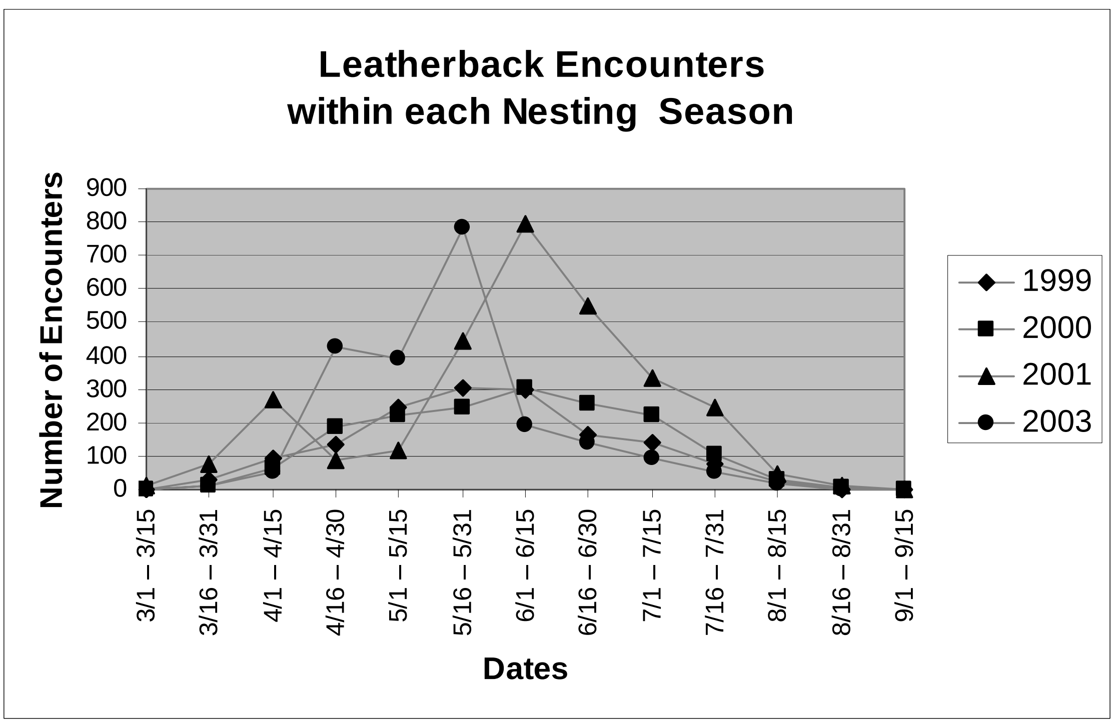
Figure 3: Leatherback Encounters within each Matura Beach Zone



D. Leatherback Encounter Trends throughout the Season

The probability of encountering an individual female leatherback varies based on the time of year and the number of days since the last encounter of that turtle. Figure 3 shows the number of leatherback encounters on Matura Beach over time. As expected the number of encounters increased during the beginning of the season, reached a peak in late May or early June, and then decreased through the end of the season. The sudden drop in the number of encounters in late April 2001 is likely the result of decreased monitoring effort. Nature Seekers recorded no paid patrols during the months of March and April 2001. The encounter rate then reached a dramatic high due to the announcement of the tagging contest and prize. The 2003 peaks coincide with the addition of Earthwatch volunteer teams to the normal Nature Seekers patrol effort.

Figure 3: Number of Leatherback Encounters over Time



As shown in figure 4, neophyte, or untagged turtle, encounters followed the same general trend seen in overall leatherback encounters. The highest encounter probabilities were found in May and June. Once again, encounter rates were low in April and May of 2001 due to low effort, and peaks were present in 2003 during the periods of Earthwatch volunteer activity.

Figure 4: First Encounters of Turtles within a Single Season

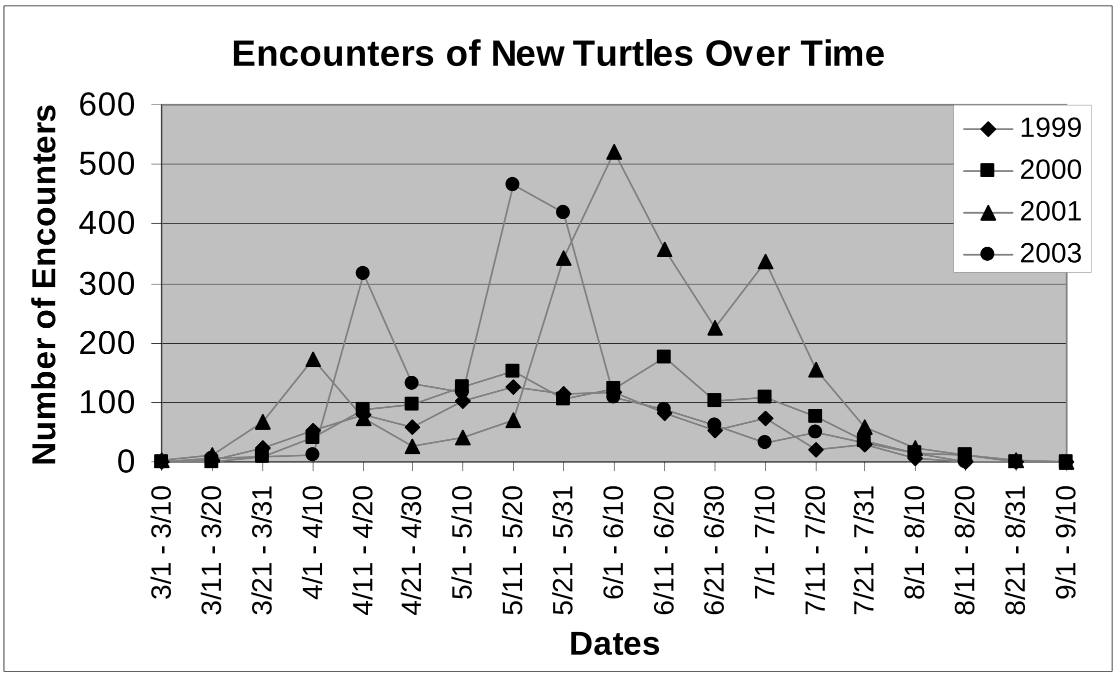
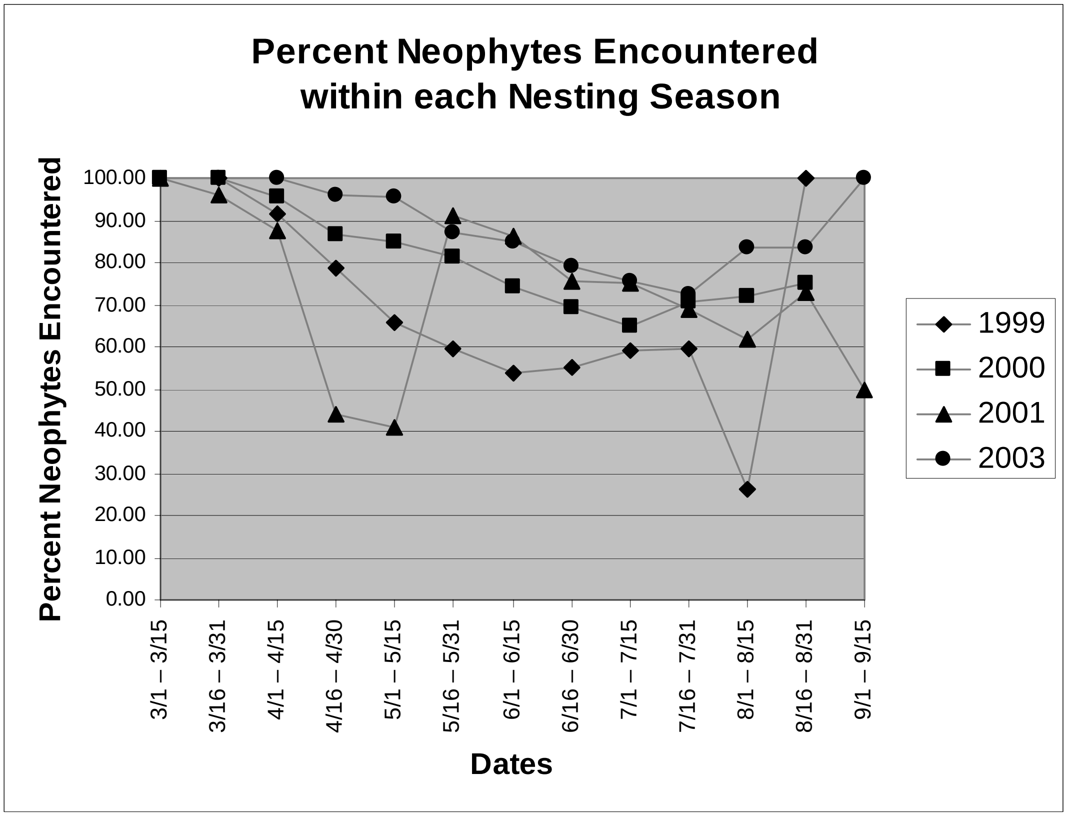


Figure 5 shows that as the season progresses, neophyte encounters constituted a smaller percentage of the overall leatherback encounters. The steady increase in percent of previously tagged turtles shown in this figure made within season mark-recapture population estimation possible.

Figure 5: Within Season Neophyte Encounter Percentages over Time



E. Renesting Intervals

The average renesting interval for leatherbacks is 9.8 days. Table 2 shows the probability of reencountering a leatherback after a specified number of days within each season. For each year, the greatest probabilities of reencountering a turtle occur nine and ten days after the initial capture. A smaller increase in reencounter probability is seen between days eighteen and twenty. This would indicate that one nesting event was missed between encounter events.

Table 3: Probability of Reencountering a Leatherback after a Specified Number of Days

# of Days *	1999	2000	2001	2003
0	**0.0106**	0.0055	0.0059	0.0091
1	**0.0158**	0.0063	0.0021	0.0070
8	**0.0232**	0.0087	0.0059	0.0075
9	**0.1077**	**0.0307**	**0.0291**	**0.0215**
10	**0.0697**	**0.0197**	**0.0317**	**0.0145**
11	**0.0243**	**0.0189**	**0.0177**	0.0070
12	**0.0106**	0.0039	0.0089	0.0027
17	**0.0180**	0.0047	0.0038	0.0022
18	**0.0275**	**0.0142**	**0.0114**	0.0032
19	**0.0222**	**0.0165**	**0.0127**	0.0032
20	**0.0232**	**0.0149**	**0.0101**	0.0059
21	**0.0190**	**0.0126**	0.0097	0.0054
27	**0.0127**	0.0079	0.0079	0.0038
28	**0.0180**	0.0071	0.0071	0.0059
29	**0.0148**	0.0063	0.0063	0.0054

*Only days with probabilities >0.01 for at least one year shown
Numbers in **bold** represent probabilities > 0.01

F. Matura Tagged Turtles Encountered Elsewhere

Between 1999 and 2003, 311 Matura tagged leatherbacks were observed on other nesting beaches. Thirteen of these turtles were seen on beaches in other countries, and 298 were spotted on other nesting beaches in Trinidad. Ninety-two percent of the observations on other beaches within Trinidad occurred on Fishing Pond Beach just south of Matura. Table 4 shows the percentage of leatherbacks observed at both Matura and another nesting beach in Trinidad within a single season.

Table 4: Population Closure within Trinidad

	Number of Turtles Nesting at Matura and Another Beach in Trinidad	Percentage of Matura Turtles Nesting at Another Beach in Trinidad
1999	50	5.27%
2000	53	4.16%
2001	69	2.80%
2003	135	7.26%

2. Mark-Recapture Population Estimation

A. Summary of Each Season's Cohorts

Table 5 shows the number of turtles within each cohort, and table 6 lists the number of encounters within each cohort. I tested to ensure there was no variation among the cohorts due to lunar cycles, tidal variations, or some other behavioral or environmental factor. I grouped the number of turtles encountered within each cohort over the four years of my analysis. There is no significant difference among the average number of turtles encountered over the four year period for each of the nine cohorts ($p = 0.92$, ANOVA). Similarly, there is no significant difference among the average number of encounters over the four year period for each of the nine cohorts ($p=0.89$, ANOVA).

Table 5: Number of Turtles in Each Cohort

Cohort	1999	2000	2001	2003
1	145	184	253	222
2	153	117	226	205
3	153	142	318	254
4	151	137	333	227
5	178	167	406	243
6	119	205	360	269
7	143	214	374	270
8	147	215	302	201
9	132	184	279	190

Table 6: Number of Encounters in Each Cohort

Cohort	1999	2000	2001	2003
1	160	196	262	228
2	182	122	232	211
3	172	148	333	264
4	171	144	346	238
5	209	178	430	256
6	133	212	376	277
7	154	231	398	286
8	172	230	318	206
9	156	197	287	195

B. Population Estimates

The seasonal nesting population estimates and their 95 percent confidence intervals generated by Program Capture are shown in tables 7 through 10. In 1999, 873 leatherbacks were tagged on Matura Beach. The average value of the cohort population estimates for the 1999 season was 640 nesting females. A total of 873 female leatherbacks were actually encountered on Matura during the 1999 season. Nature Seekers observed 1,271 female leatherbacks in 2000, and the average population estimate was 1,646. Patrollers observed 2,456 turtles in 2001, and the mean population estimate for the nine cohorts was 3,959 nesting females. In 2003, 1,859 leatherbacks were seen, and the average nesting population estimate was 3,610 females.

Table 7: 1999 Population Estimates

Cohort	Population Estimate	95% CI
1	816	515 to 1364
2	487	363 to 687
3	724	487 to 1132
4	640	438 to 985
5	586	441 to 813
6	568	364 to 945
7	1012	594 to 1822
8	498	363 to 719
9	431	312 to 630

Table 8: 2000 Population Estimates

Cohort	Population Estimate	95% CI
1	1653	954 to 2987
2	1296	609 to 2949
3	1537	763 to 3275
4	1733	806 to 3951
5	1357	788 to 2449
6	2821	1447 to 5717
7	1643	1033 to 2713
8	1504	964 to 2437
9	1274	793 to 2137

Table 9: 2001 Population Estimates

Cohort	Population Estimate	95% CI
1	3224	1781 to 6030
2	4613	2088 to 10564
3	3062	1933 to 4981
4	4364	2591 to 7534
5	4153	2747 to 6409
6	4231	2614 to 7012
7	3134	2124 to 4729
8	2986	1857 to 4936
9	5861	2819 to 12547

Table 10: 2003 Population Estimates

Cohort	Population Estimate	95% CI
1	3437	1675 to 7341
2	3114	1518 to 6655
3	4181	2132 to 8480
4	2998	1545 to 6055
5	2268	1337 to 3989
6	5308	2558 to 11363
7	2588	1558 to 4445
8	3837	1612 to 9582
9	4763	1764 to 13472

IV. Discussion

1. Developing a Mark-recapture Model for Estimating Nesting Populations

A. Meeting the Assumptions of the Model

Several features of the leatherback nesting population must be considered to ensure that the assumptions of mark-recapture population models are met. First, marks must not be lost between sampling periods and all marks must be recorded during resampling periods (Ogle, 1996). Leatherbacks exhibit a high rate of tag loss (Philippe, 2001). Tags are frequently lost just after tagging, and this loss must be accounted for in a modeling effort. Double tagging and the use of more archival tag methods such as PIT tags compensate for tag loss, or at least provide an accurate means to estimate this loss.

When researchers in St. Croix, US Virgin Islands, began using PIT tags in addition to their standard flipper tags, population estimates declined by 18.9 percent due to increased tag retention (MacDonald and Dutton, 1998). Nature Seekers double tags each female and uses PIT tags, although budget constraints limit the number of PIT tags available each season. Multiple tags also help make sure that tags are recorded during recaptures and provide a system for checking recording errors.

All animals must have the same probability of capture when estimating population size based on mark-recapture statistics. Female leatherbacks do not nest every year. However, they typically lay six or seven clutches during the seasons in which they do nest. Since the number of turtles nesting varies each year, I focused on estimating a single season population estimate for each year.

Encounter probabilities also vary within a single season. The probability of encountering an individual female leatherback varies based on the time of the year and the number of days since the last encounter of that turtle. Encounter probabilities are greatest during the peak of the nesting season in May and June. Despite the fact that we know some turtles arrive earlier or stay longer at the nesting beach, we cannot currently predict arrival and departure times based on characteristics such as a female's age, her number of previous nesting seasons, or any other factor. Therefore, we have to consider all turtles equally likely to appear at the beginning and end of the season.

The greatest reencounter probabilities were seen 9 and 10 days after a previous nesting event since the average renesting interval for leatherbacks is 9.8 days. In order to address the variability in reencounter probability due to number of days since the last capture, I developed a cohort estimation strategy. Since each turtle had the same likelihood of being recaptured nine days from its initial capture date, I divided each season into nine sampling cycles. Each cohort was composed of the encounters occurring on a nine day cycle.

A final assumption is population closure meaning that the size of the population is not affected by births, death, immigration, or emigration throughout the study (White, et al., 1982). I minimized the influence of births and deaths by estimating single season populations of nesting adult females. Leatherbacks generally nest on the same beach season after season, but some turtles are known to nest on multiple beaches. I examined tag recovery data for Matura turtles nesting in other locations. Between 1999 and 2003, 298 Matura Beach turtles were seen nesting on other beaches in Trinidad. The majority of these nests occurred at Fishing Pond Beach just south of Matura. Only thirteen Matura tagged turtles were recorded nesting on beaches in other countries. This indicates that the population is closed within Trinidad. A closer look at the number of turtles seen nesting at both Matura and another beach in Trinidad shows that fewer than 8% of the turtles each season were recorded at multiple locations. For the purpose of this study, I assumed population closure and restricted my estimates to the Matura Beach nesting population.

B. Sources of Error in Population Models

Three types of error exist in population estimation models: systematic error, random error, and demographic and environmental fluctuations. Random errors due to sampling procedures were minimized by double tagging each turtle, using pit tags when financially possible, and maximizing beach coverage with the limited manpower available. Systematic error was assumed to be low but could have been produced by less than expected philopatry, or the tendency of an animal to return to its birthplace to nest, and nesting activity outside of the survey hours (Kerr, 1998). As previously discussed, we expect females to consistently return to the same nesting beach. Although some females were observed on other beaches, the majority repeatedly nested at Matura. Since no consistent evidence exists for daytime nesting in leatherbacks, conducting only nocturnal sampling should not have increased systematic error.

Variations in the probability of capturing individual animals due to heterogeneity or trap response can lead to deviations from mark-recapture assumptions. Heterogeneity means that capture rates vary by age, sex, social status, or some other factor. Nesting beach population size estimates focus solely on reproductive females, so this source of variability is minimal. Some species exhibit trap responses by either actively avoiding or seeking recapture. Nesting leatherbacks are cautious when leaving the ocean and establishing a nesting site, but tagged animals do not exhibit more or less caution than untagged animals (Pollock, et al., 1990).

C. Model Used for Generating Population Estimates

I used the Darroch time dependent model for closed population estimates within Program Capture to generate my nesting population estimates. This time dependent model assumes all individuals are equally at risk of capture on a particular trapping occasion, but this capture probability can change over time (Otis, et al., 1978). Tagging effort varied within each season due to variation in volunteer effort, changes in the funding available throughout the season, contests and prizes being offered, and the presence of Earthwatch teams. It is also expected that weather affected tagging effort and that tagging and monitoring strategies differed slightly by individual patroller. The model I used allowed for these differences between trapping occasions but considered each turtle at the same risk of being encountered on a particular occasion.

2. Leatherback Nesting Population Estimates

Data from the 2000, 2001, and 2003 seasons yielded mark-recapture nesting beach population estimates averaging 62 percent greater than the minimum number of turtles encountered. This is consistent with the 40 percent beach coverage estimate provided by Nature Seekers at the initiation of this analysis (Eckert, S.A., pers. comm.). The 20 to 24 day average time between encounters of individual leatherbacks (Table 1) also supports the theory that Nature Seekers observes slightly less than half of the nesting events on Matura Beach since leatherbacks are known to nest every nine to ten days.

The average population estimate for 1999 was 640 leatherbacks. This estimate was 26 percent less than the minimum number of turtles encountered during the tagging project that year. Several factors could have led to this inaccuracy. 1999 was the first year of the full season tagging project on Matura Beach. Therefore, the staff was inexperienced and encountered many technical problems.

Dennis Sammy (1999), the president of Nature Seekers, documented several concerns in his project report for the 1999 season. Beach monitors were instructed that doing a good job of tagging a few turtles was more effective than haphazardly tagging as many turtles as possible. Since the monitors were inexperienced, they likely spent a greater amount of time with each turtle during this first season than they would in subsequent years. This large investment in fewer turtles would lead to lower numbers of total encounters as shown in table 1. Sammy reported that many taggers felt tagging while the turtle was covering her nest was difficult due to the power of the leatherback's flippers. In addition, many front flipper tags applied in 1999 caused infections because the tags were not cleaned before insertion (Sammy, 1999). These issues may have influenced the rate at which new turtles were tagged. If multiple leatherbacks were nesting simultaneously, monitors might have focused on recording the presence of previously tagged turtles rather than tagging neophytes. Furthermore, tag loss was greatest during this season due to the inexperience of the taggers, so more time was spent replacing tags in previously encountered turtles. These factors could greatly influence the mark-recapture population estimate. Further research should be done to gage the attitudes of taggers during their first season on the beach.

V. Conclusions and Recommendations for Future Population Models

Developing models to estimate sea turtle populations in situations where saturation tagging is not possible is critical for determining the status of these endangered species. Future research should investigate monitoring strategies to maximize leatherback encounter rates on isolated beaches with limited patrol resources. The short-term intensive saturation tagging strategy demonstrated by Kerr (1998) offers an alternative to full season monitoring in situations where adequate patrol effort is available and beach conditions are suitable. Nature Seekers should also improve their database records by including the results of the leatherback emergence. The current database does not differentiate between false crawls and successful nesting events.

Another improvement would be to develop a better index of tagging effort throughout the season. The only effort data available for this analysis was time card records for the paid beach monitors, but these records did not reflect the amount of volunteer tagging effort present on the beach. The large number of encounters during the

2001 tagging contest shows the importance of recording volunteer effort as well as paid patrol work. Included in the new effort index should be a record of the number of hours spent within each beach zone. Encounter data indicated greater turtle activity within zones eight through thirteen, but this could have been the result of increased monitoring in those areas rather than a truly higher nesting density. If leatherbacks preferentially nest within these zones, patrol patterns should be designed to maximize coverage in this area rather than spreading limited human resources among all the zones. In order to successfully model the nesting population, a consistent monitoring strategy should be followed.

Population closure is a critical assumption in mark-recapture models. Few Matura turtles have been observed nesting in other countries, but efforts to increase leatherback monitoring on neighboring islands should be encouraged. This would provide more conclusive evidence of natal beach homing among leatherbacks. More data should also be gathered on the number of turtles that nest at multiple beaches in Trinidad to determine the true degree of population closure within the country. Monitors on Fishing Pond and Grand Riviere beaches should be given PIT tag readers to increase the chance that a Matura tagged turtle will be recognized on another beach. Tagging projects could also be started on these other beaches so that migration can be monitored in both directions.

Finally, a model should be developed that accounts for daily variation in encounter probabilities based on the date of a turtle's last nesting event and the average number of nests per turtle. In order to generate a single estimate of a season's nesting population using all the available recapture data, a model that accounts for each source of variability in encounter probability must be developed.

Great efforts are being taken to protect the leatherback sea turtle. In order to determine the success or failure of these endeavors, accurate population estimates must be generated. Nesting beaches afford us the opportunity for repeated close contact with these giant turtles, so developing mark-recapture models for nesting population estimation could be critical for understanding the status of this species.

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