APPENDIX 1:

META-ANALYSIS OF POPULATION TRENDS OF LOGGERHEAD AND LEATHERBACK TURTLES

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1 Introduction

Critical conservation decisions often have to be made from widely scattered local data that may show what appears to be contradictory trends. Traditionally, each trend was examined independently to determine if they show statistically significant results. This approach–determining the proportion of studies individually exhibiting statistical significance in the prescribed direction–is known as "vote counting" in the meta-analysis literature, and is inherently flawed (Hedges and Olkin 1985). Hedges and Olkin (1980) showed that as the number of studies becomes large, the proportion of studies yielding significant results is approximately the average power of the test.

Here we suggest an improved approach. Our goal is to obtain the most powerful estimates, and still model the variation among sites.

2 A Mixed Model Approach

We begin with the simplest of models. Let X_{it} be the estimate of abundance of nesting females at each site i in year t. We will examine the simplest possible dynamic model for each site, given that each site began with an initial number of nesting females in the first year of the study, i.e. at $t = 0$ each site had x_{i0} nesting females. If each population is changing at a constant rate over the period of time of the censuses, we have

$$X_{it} = X_{i0}e^{r_i t + \varepsilon_{it}}$$

where r_i is the instantaneous rate of population change, X_{i0} is the initial population size of the ith population, and ε_{it} is the error in the estimate of abundance and deviations from the assumed model (sometimes called "process error").

It is unlikely that all the nest sites will have exactly the same rate of change, so we will investigate a simple mixed effect model where we assume that $r_i \sim N(\mu_r, \sigma_r^2)$, where μ_r is the mean instantaneous rate of change in population size for the nesting sites and σ_r^2 is the variance among populations.

We will investigate two approaches to the above model: (1) we log transform the data and use a linear mixed model and (2) we will use the raw counts and use a generalized linear mixed model. the second approach is more flexible, and can handle years in which no turtles were observed, but the first is easier to implement and understand.

3 A Linear Mixed Model

First, we can log transform the above model. Let $x_{it} = \log X_{it}$, then we have

$$x_{it} = x_{i0} + r_i t + \varepsilon_{it}.$$

Now r_i can be interpreted as a slope, and x_{i0} can be interpreted as an intercept. The initial population number is also observed with error so that it is clearer if we define the true initial log abundance to be a parameter, $\theta_i =$ true x_{i0}, which we will estimate. The above equation becomes

$$x_{it} = \theta_i + r_i t + \varepsilon_{it}.$$

The nesting sites vary in size and suitability for nesting, and these properties can be thought of as intrinsic to each site, and unrelated to any other site. Since the intercept for each nesting site determines the initial density, we treat the intercepts as site-specific fixed effects. The rate of change of the population at each nesting site, however, may reflect larger-scale phenomena such as climate or management policies. Therefore we model the slope for each nesting site as a random effect.

We used restricted maximum likelihood (REML) to fit the linear mixed models. REML can be thought of as an adjustment to the degrees of freedom accounting for the fixed effects, giving unbiased variance estimates (Searle et al. 1992). The likelihood ratio test (lrt) was used to compare the fit of different models.

We estimated the parameters of this model under two different assumptions for ε_{it}. First, we assumed that the variance of ε_{it} is the same for all sites. That is, we assume that $\varepsilon_{it} \sim N(0, \sigma^2)$, where σ^2 is estimated from the data. An alternative approach is to assume that the variances are primarily due to factors unrelated to sample size, and estimate a separate variance, σ_i for each site.

For loggerheads, we were interested in if the population growth rate has changed after the introduction of TEDs in 1989. We thus fit the piecewise linear mixed model:

$$X_{it} = X_{i0} e^{r_i t + r_i^* t^* + \varepsilon_{it}}$$

where $t^* < 0$ if $t < 1990$ and $t^* = t - 1989$ otherwise, and r_i^* is the difference in the instantaneous rate of population change before and after TEDs were introduced.

4 A Generalized Linear Mixed Model

In order to test the robustness of our approach we investigated alternative model formulations. Alternatively, we assumed that the residual variation in the above model was described by a gamma, as opposed to a lognormal, distribution. For this model, we used a generalized linear mixed model with a log link and a gamma error distribution. The variation of r among sites was still considered Gaussian. These parameters were estimated using the generalized linear mixed model methods developed by Wolfinger and O'Connell (1993).

5 Obtaining an overall estimate of population changes

The above model does not provide an estimate of the total population change over time. One approach can be used if trend data is available for all sites, though at some sites very limited data might be available. In this case we can include all reliable data and obtain predictions (BLUP) from a mixed model for each site and year.

6 Data

6.1 Loggerheads

We used data from beach surveys of nesting. We have limited our analysis to beaches where we believe the effort has been relatively constant over time by including only the years where consistent length of beach was surveyed and survey start dates were similar (within a two week time period). However, for Georgia this information was not available and the assumption of consistent effort may not always be true, particularly for the early years. We view this as the greatest uncertainty in the analysis. The loggerhead nesting data has been divided into two groups, the northern subpopulation and the southern subpopulation. The northern subpopulation includes the beaches in North Carolina, South Carolina, Georgia, and northern Florida. We combined results for two different time periods: 1979-1999 and 1989-1999. We believe that the data from the more recent period are more consistent. The following table shows the beaches that are included in the analysis.

Subpopulation	State	Beach	Distance surveyed	Date of first survey
northern	North Carolina	Cape Lookout National Seashore	?	?
northern	North Carolina	Bald Head Island Conservancy	15 miles	5/15
northern	North Carolina	Hammocks Beach State Park	3 miles	5/15
northern	North Carolina	Camp Lejeune Marine Base	6.8 miles	5/24
northern	South Carolina	Cape Island	?	?
northern	Georgia	Blackbeard Island	?	?
northern	Georgia	Cumberland Island	?	?
northern	Georgia	Jekyll Island	?	?
northern	Georgia	Little Cumberland Island	?	?
northern	Georgia	Little St. Simons Island	?	?
northern	Georgia	Tybee Island	?	?
northern	Georgia	Ossabaw Island	?	?
northern	Georgia	Pine Island	?	?
northern	Georgia	Sapelo Island	?	?
northern	Georgia	St. Catherine's Island	?	?
northern	Georgia	Sea Island	?	?
northern	Georgia	St. Simons Island	?	?
northern	Georgia	Wassaw Island	?	?
northern	Florida	Flagler Co.	24.1 km	4/25-5/1
northern	Florida	Washington Oaks	1.1-1.2 km	5/1
northern	Florida	Anastasia SRA	7.2 km	5/1
northern	Florida	Fort Mantanzas NM	11.2-11.3 km	5/14-5/27
northern	Florida	Ponte Vedra S	23.6 km	4/28-5/10
northern	Florida	Guana River SP	6.7-6.8 km	5/1-5/15
northern	Florida	Amelia Island	14.4-14.5 km	5/1
northern	Florida	Ft Clinch SP	3.7 km	5/1
southern	Florida	Hutchinson Island	36.5 km	4/10-4/24
southern	Florida	Broward Co. Beaches	34.7 km	3/1
southern	Florida	J.U. Lloyd SRA	3.9 km	4/20-4/30
southern	Florida	Boca Raton Beaches	8.0 km	3/1
southern	Florida	MacArthur SP	2.9 km	3/1-3/10
southern	Florida	Casey Key	11.8 km	5/1
southern	Florida	Siesta Key	9.0 km	5/1

A negative correlation was found between abundance and date of first nest for Cape Hatteras National Seashore, North Carolina and Pea Island National Wildlife Refuge, North Carolina. These beaches were left out of the analysis. Cape Lookout National Seashore, North Carolina is believed to be standardized after 1990 so this beach was included even though there is no distance surveyed or first date of survey. For one of the Georgia beaches, Little Cumberland Island, there has been a large amount of beach erosion. We decided to keep this beach in the analysis because this represents natural variation among beaches, and the turtles from that beach probably nested elsewhere in the region. A second analysis was performed for the northern subpopulation leaving out the

Georgia beaches because the reliability of that information is not known at this time.

6.2 Leatherbacks

Distance of beach covered and survey start date were known for some of the beaches observed for leatherback nesting. Again, we tried to use only the years with consistent coverage. The data were separated into three areas for analysis because the overall trends differed for these three areas. These areas are: South America, St. Croix (US Virgin Islands), and Florida. For Florida we have limited our analysis to beaches where we believe the effort has been relatively constant over time by including only the years where consistent length of beach was surveyed and survey start dates were similar (within a two week time period). However, for South America and the US Virgin Islands this information was not available and the assumption of consistent effort may not always be true, particularly for the early years. The following table shows the beaches that are included.

Area	Beach	Distance surveyed	Date of first survey
Florida	Hutchinson Island	36.5 km	4/8-4/18
Florida	Jupiter/Juno Beach	9.6 km	2/15-3/1
Florida	Jupiter Island	13.7 km	3/1-3/3
Florida	MacArthur SP	2.9 km	3/1
Florida	Highland Beach	4.8 km	4/1-4/15
Florida	Broward Co. Beaches	34.7 km	3/1
Florida	S Brevard Beaches	40.5 km	4/26-5/8
S. America	Yalimapo, French Guiana	?	?
S. America	Galibi, Suriname	?	?
S. America	Matapica, Suriname	?	?
US Virgin Islands	St. Croix	?	?

7 Results

We fit a variety of models to each data set: with lognormal, gamma, or extra-Poisson variability in the observation error, with separate error variances for each beach, and with and without outliers. We found that there was relatively little difference among these models fits, but that the separate error variance was usually needed. For simplicity we will report the lognormal error with separate error variances as our primary estimates.

7.1 Loggerheads

7.1.1 Georgia

As an example, we first consider the beaches in Georgia individually from 1979-1999. The estimates of the slope if each nesting site is fit individually by OLS regression are:

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Nesting    Parameter      Standard    T for H0:
Site       Estimate          Error   Parameter=0    Prob > |T|
BKB         0.005577    0.01366527         0.408        0.6878
CUM         0.007004    0.01254062         0.559        0.5860
JEK         0.015879    0.01160858         1.368        0.1903
LCI        -0.092834    0.00900179       -10.313        0.0001
LSI         0.041901    0.03072965         1.364        0.2026
OSS         0.017643    0.01747988         1.009        0.3270
PIN        -0.011962    0.03620422        -0.330        0.7473
SAP         0.057755    0.02783523         2.075        0.0622
SCI        -0.011230    0.01948592        -0.576        0.5760
SEA         0.073510    0.04804723         1.530        0.1604
SSI        -0.192613    0.06439019        -2.991        0.0152
TYB        -0.001411    0.08965388        -0.016        0.9878
WAS         0.024396    0.01453494         1.678        0.1096
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Note that there are two nominally significant declines (LCI and SSI), but 8 of the 13 slopes are positive.

We now consider the mixed model results. The estimate for the mean instantaneous rate of change, μ, was -0.003 (s.e. = 0.015). The standard deviation of r among sites, σ_r, was estimated to be 0.04, and the standard deviation of the error, σ, was estimated to be 0.43.

If we allowed separate error variances for each site, μ is estimated to be slightly positive ($\hat{\mu} = 0.002$, s.e. = 0.01), and with less variation among sites ($\hat{\sigma}_r = 0.03$).

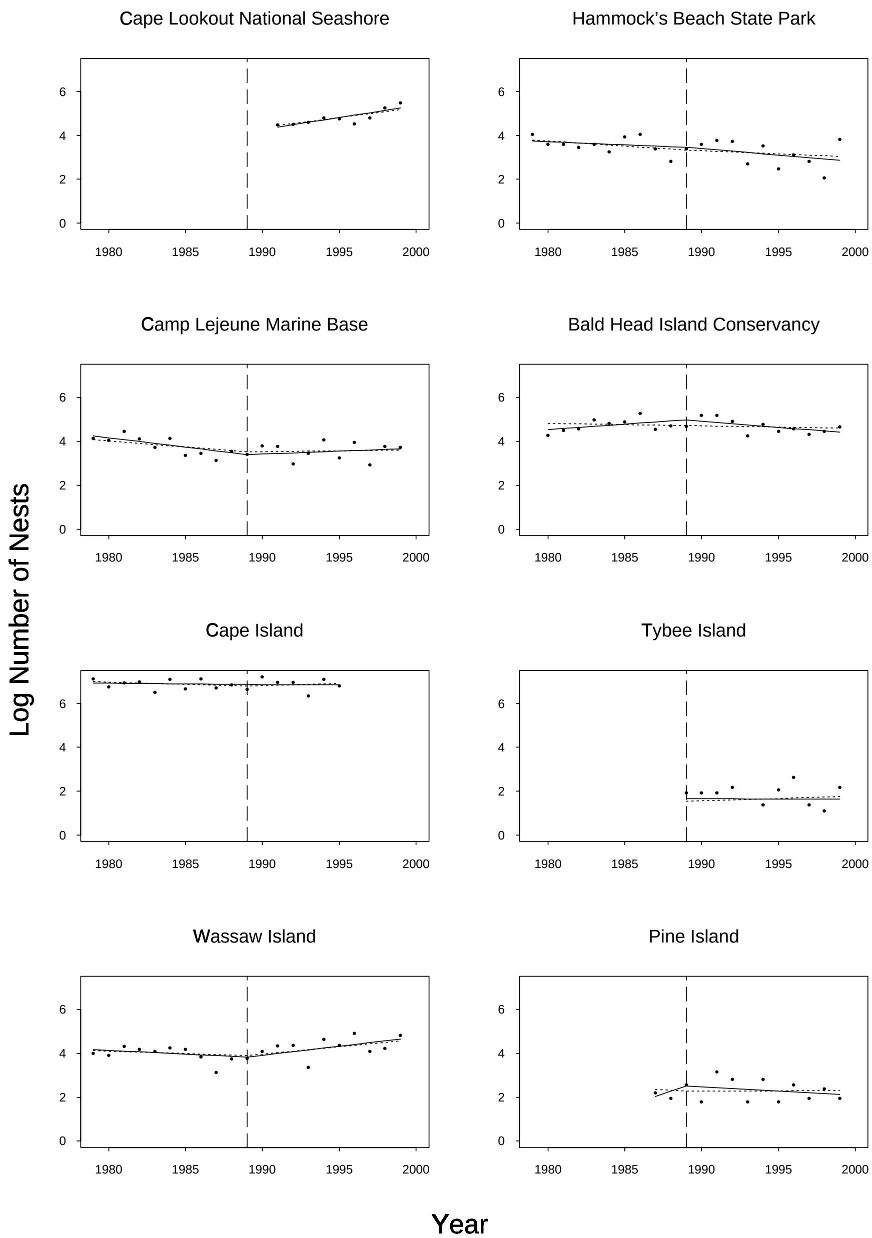
Similar results were obtained for the time period from 1989 to 1999 when the nesting data is believed to be more reliable, i.e. there was no evidence of an overall change in the populations in Georgia.

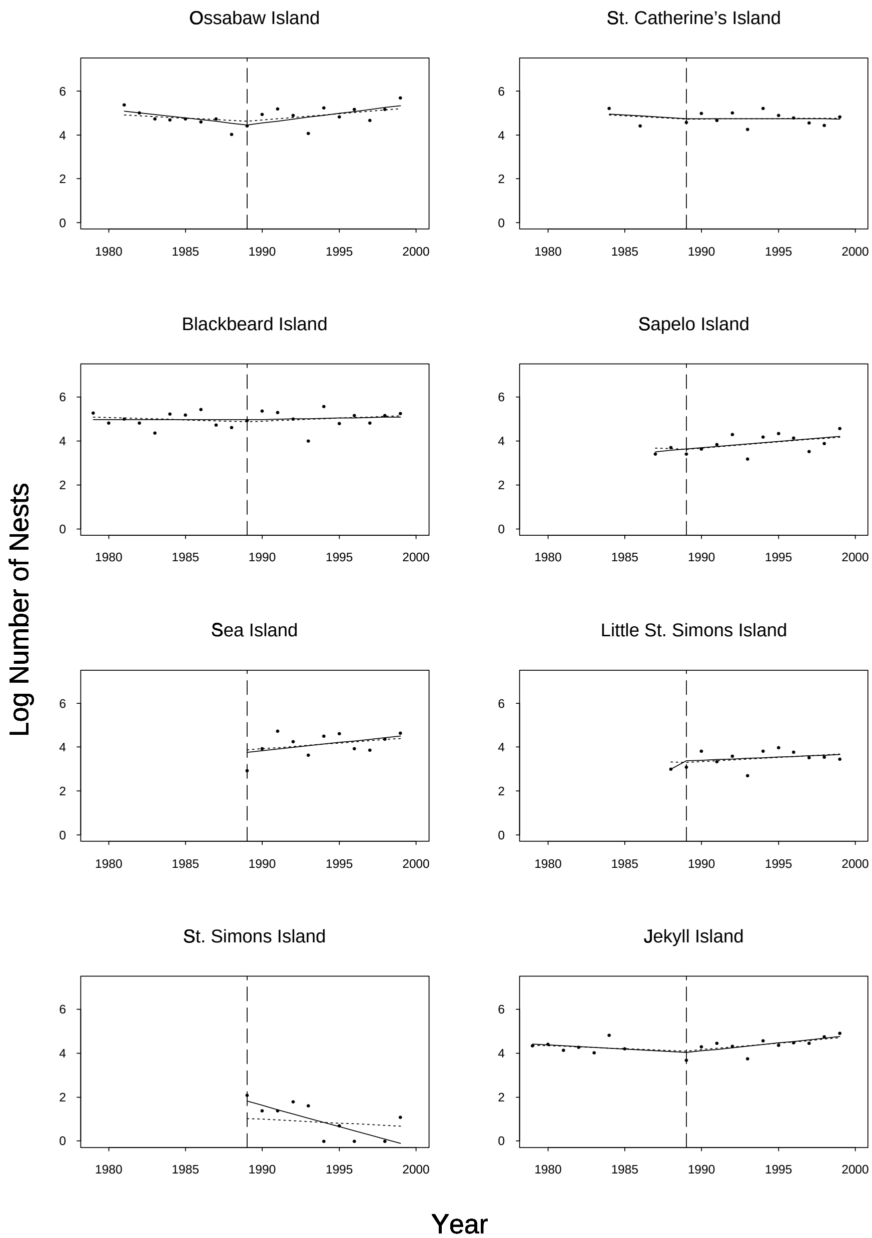
7.1.2 Northern US population

In this analysis we fit the data from 1978-1989 with one “r” and the data after with a second “r” (r^*) using a piecewise linear model. In the results below, the “r” for the early period is estimated, then the change in “r” is added on, all in the same mixed model.

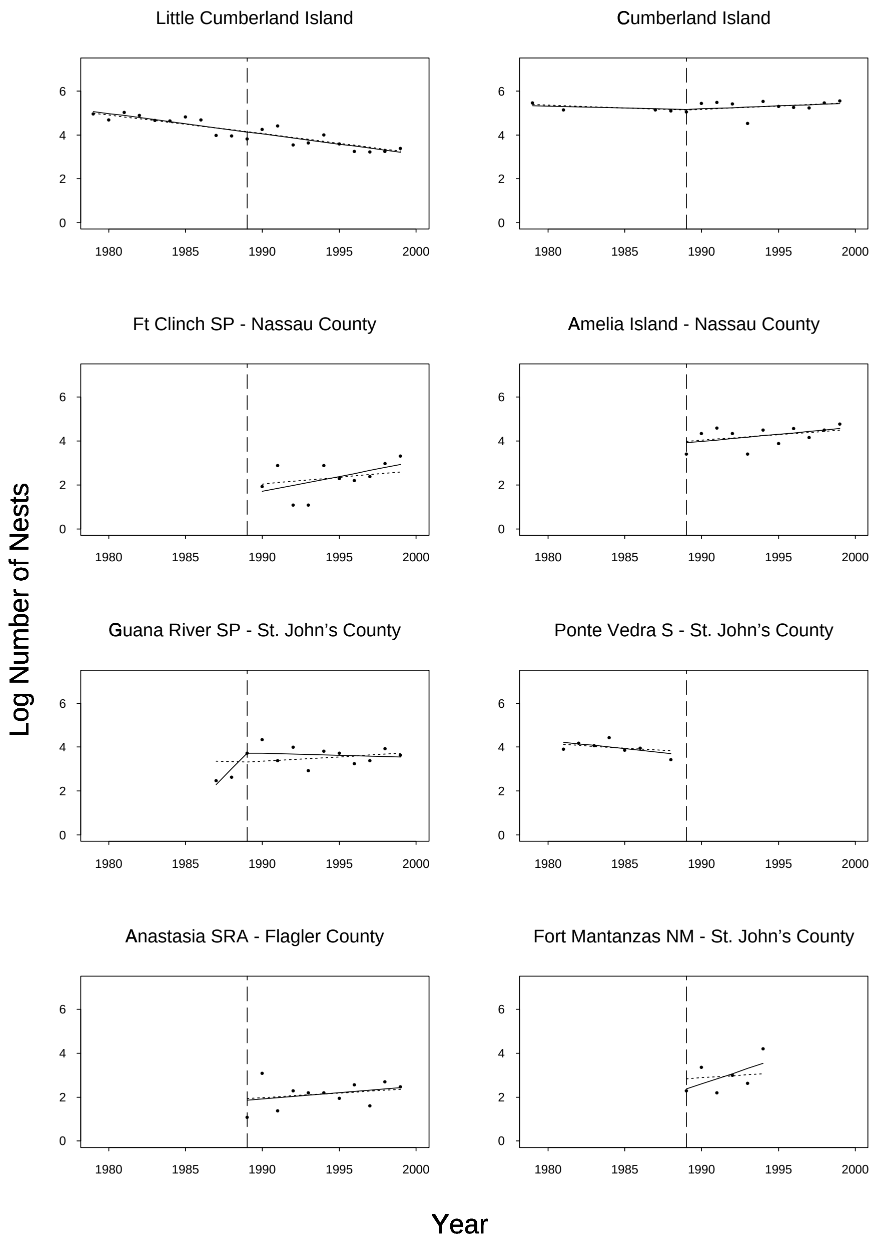
error	separate error variance	year	estimate	se pred	df
lognormal	no	> 1978	$r = -0.026$	0.015	25
lognormal	no	> 1989	$r^* = 0.054$	0.022	18
lognormal	yes	> 1978	$r = -0.030$	0.012	25
lognormal	yes	> 1989	$r^* = 0.059$	0.017	18

The effect of the mixed model analysis for the northern US loggerhead populations is clear when examining the data (Fig. 1). Each point in the plot represents the number of log transformed nests. Note that when there are outliers, the mixed model fits downweight these outliers.





Ossabaw Island
St. Catherine's Island
Blackbeard Island
Sapelo Island
Sea Island
Little St. Simons Island
St. Simons Island
Jekyll Island
Log Number of Nests
Year



Little Cumberland Island
Cumberland Island
Ft Clinch SP - Nassau County
Amelia Island - Nassau County
Guana River SP - St. John's County
Ponte Vedra S - St. John's County
Anastasia SRA - Flagler County
Fort Mantanzas NM - St. John's County
Log Number of Nests
Year
0
2
4
6
1980
1985
1990
1995
2000

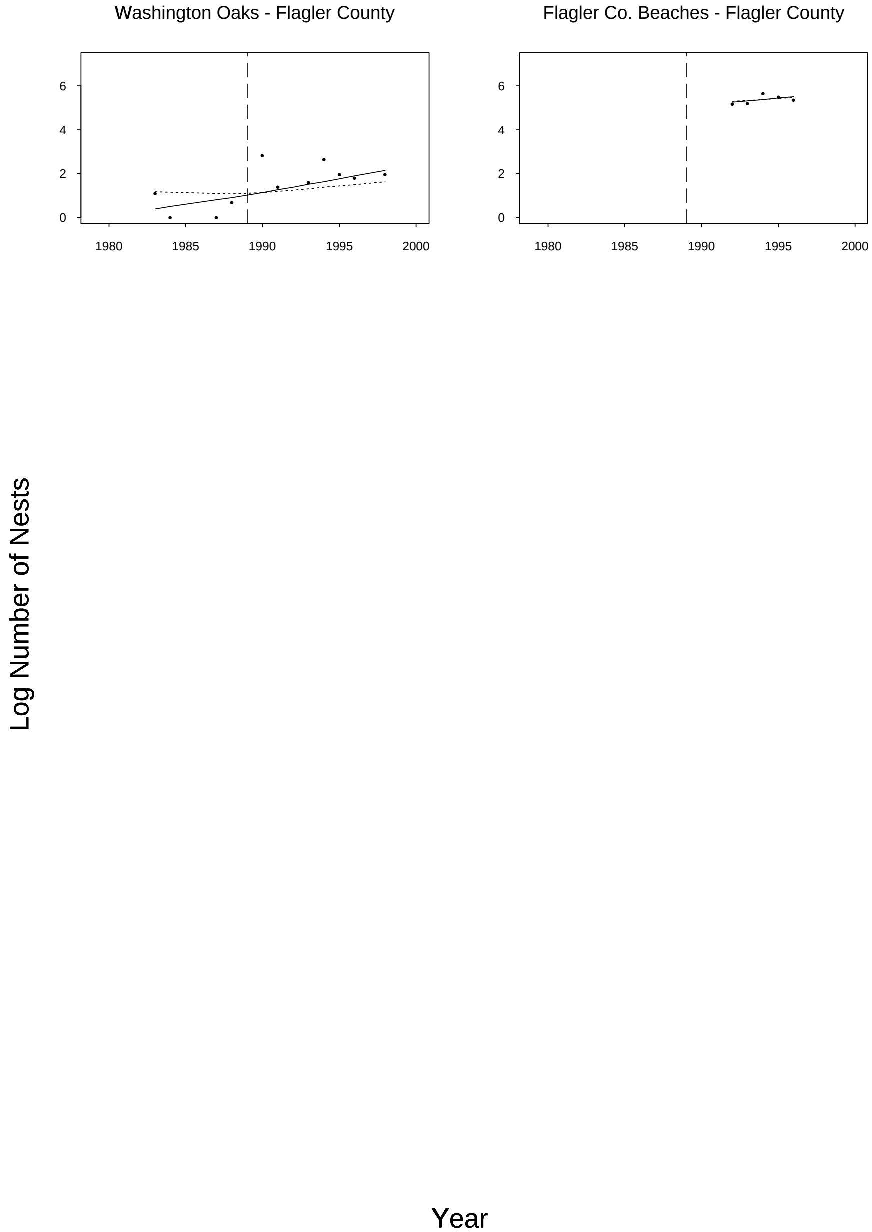


Figure 1: Plots of log transformed nest counts for the beaches in the northern US subpopulation of loggerhead turtles. Each point is an observation, the solid line is the ordinary least squares fit, and the dashed line is the BLUP from the mixed model. The mixed model fits come from a model that assumes a separate error variance for each beach. The vertical dashed line marks the year that TEDs were first employed.

The upshot is: either no change or a decrease from 1978 to 1989 (depending on which model you consider), and a probable increase from 1989 to 1999. The magnitude and statistical significance of the increase depends upon the exact implementation of the model, but the effect is suggestive in all analyses.

7.1.3 Northern US population - Georgia not included

One problem with the analysis of the northern US population is that the reliablity of the data from Georgia is not known. The other sites had both distance of beach surveyed and the start date of the survey, information that was missing from the Georgia data. To assess the robustness of the previous results we fit the same model as before, but this time omitted the Georgia sites from the analysis.

error	separate error variance	year	estimate	se pred	df
lognormal	no	> 1978	$r = -0.002$	0.026	12
lognormal	no	> 1989	$r^* = 0.049$	0.034	7
lognormal	yes	> 1978	$r = -0.011$	0.019	12
lognormal	yes	> 1989	$r^* = 0.048$	0.028	7

When Georgia is left out of the analysis the parameter estimates obtained are similar, resulting in similar trends, but these results are no longer statistically significant.

7.1.4 South Florida Loggerheads

The results for the south Florida loggerheads are:

error	separate error variance	year	estimate	se pred	df
lognormal	no	> 1978	$r = 0.054$	0.022	6
lognormal	no	> 1989	$r^* = -0.011$	0.028	1
lognormal	yes	> 1978	$r = 0.055$	0.014	6
lognormal	yes	> 1989	$r^* = -0.015$	0.021	1

In summary, for south Florida the model with the separate error variances for each beach, the population has been growing with a $\hat{r} = 0.054$ (s.e. 0.022) since 1979. When an additional term is added for the period since 1989, there is not a significant change (r^* is estimated to be -0.011 (s.e. 0.028)). Note that the direction of change is the opposite sign as for the northern population.

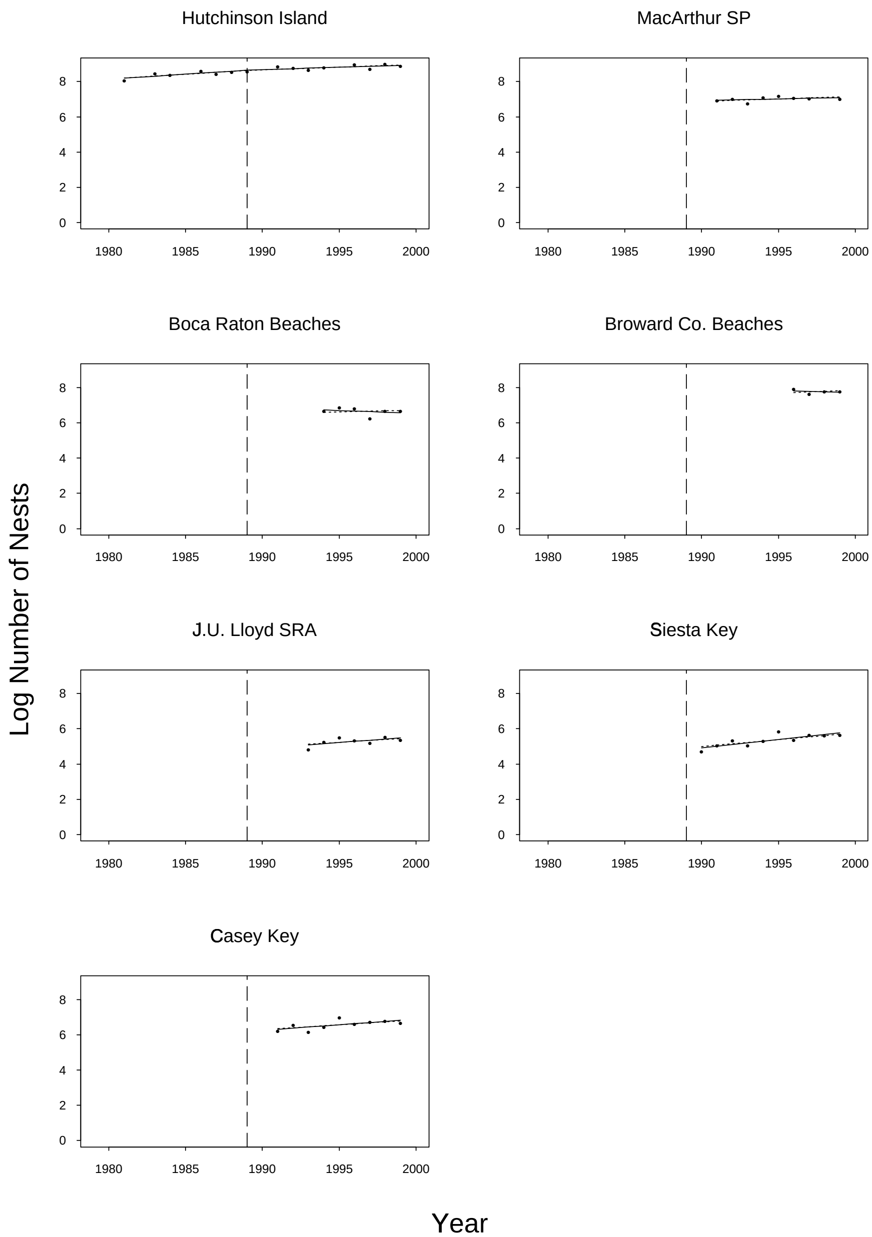


Figure 2: Plots of log transformed nest counts for the beaches in the southern US subpopulation of loggerhead turtles. Each point is an observation, the solid line is the ordinary least squares fit, and the dashed line is the BLUP from the mixed model. The mixed model fits come from a model that assumes a common error variance among beaches. The vertical dashed line marks the year that TEDs were first employed.

We also display the estimated total number for the northern and southern populations of loggerhead for the surveyed beaches (Fig. 3). In these plots, we summed the predicted numbers in the individual regressions and the mixed models estimates to estimate the total number in the areas surveyed.

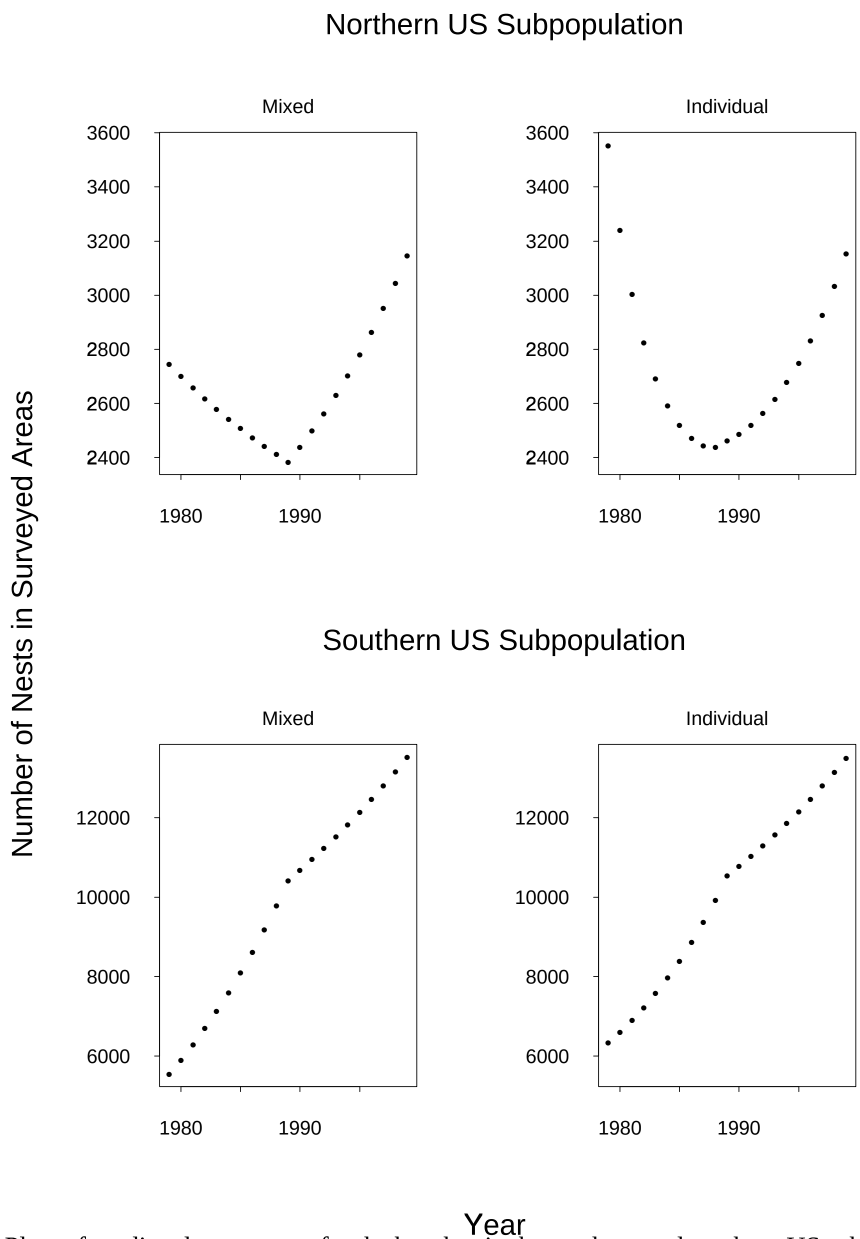


Figure 3: Plots of predicted nest counts for the beaches in the northern and southern US subpopulation of loggerhead turtles. The individual estimates are from the sum of the individual OLS regressions, and the mixed model estimates are from the sum of the Best Linear Unbiased Predictors for each beach.

7.2 Leatherbacks

For leatherbacks we treated the data from the Virgin Islands, South America, and Florida as separate groups, or populations. For the Virgin Islands and Florida we examined data from 1979 on, but used data from 1987 on for South America because of changes in local fishing policy.

For the US Virgin Island site, we carried out a simple linear regression on the log transformed nests to estimate the instantaneous rate of population change. The estimate was 0.078 (s.e.= 0.014). For the Florida sites,

error	separate error variance	estimate	se pred	df
lognormal	no	$r = 0.118$	0.056	6
lognormal	yes	$r = 0.109$	0.019	6
Poisson	no	$r = 0.095$	0.049	6
Poisson	yes	$r = 0.107$	0.059	6
gamma	no	$r = 0.122$	0.053	6
gamma	yes	$r = 0.117$	0.052	6

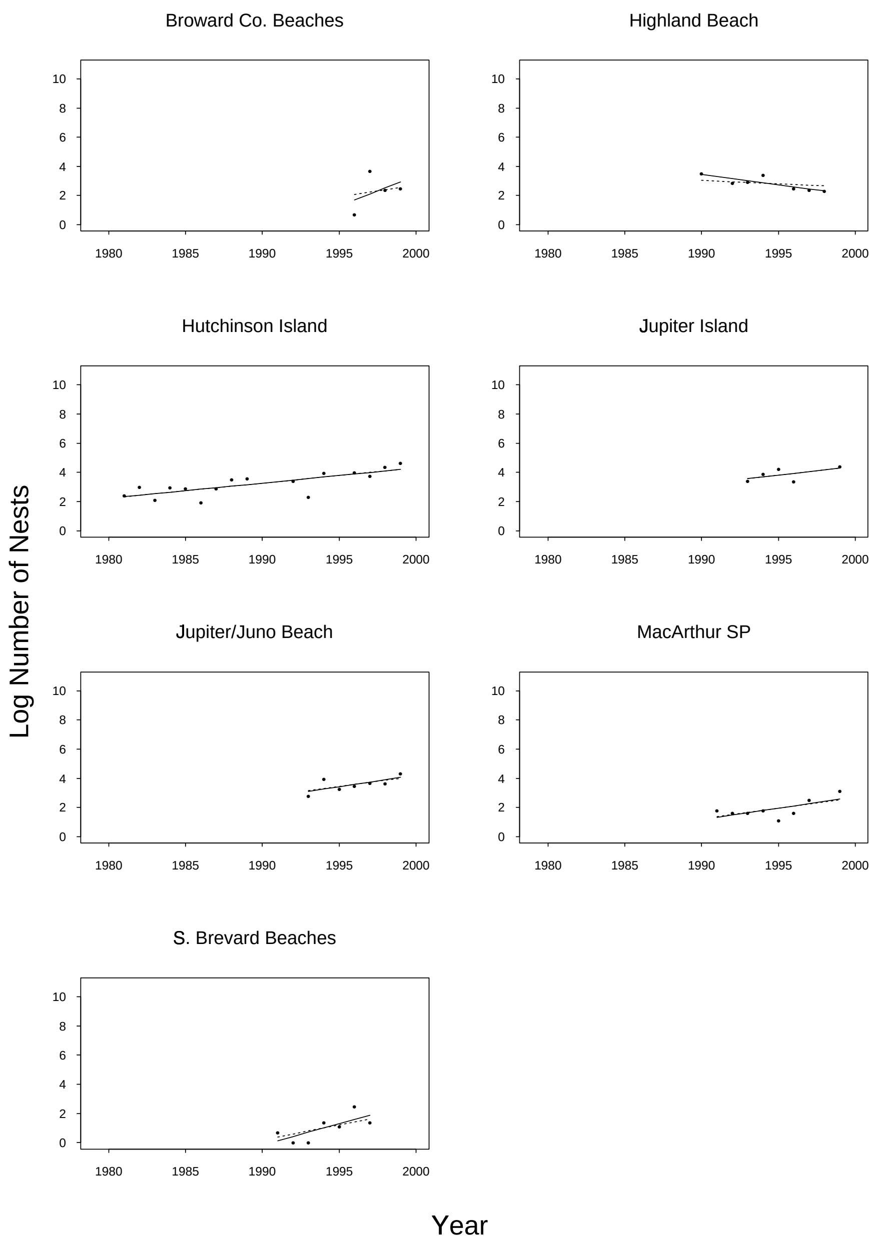


Figure 4: Plots of log transformed nest counts for the beaches in the Florida population of leatherback turtles. Each point is an observation, the solid line is the ordinary least squares fit, and the dashed line is the BLUP from the mixed model. The mixed model fits come from a model that assumes a common error variance among beaches.

For South America,

error	separate error variance	estimate	se pred	df
lognormal	no	$r = -0.190$	0.060	2
lognormal	yes	$r = -0.163$	0.041	2

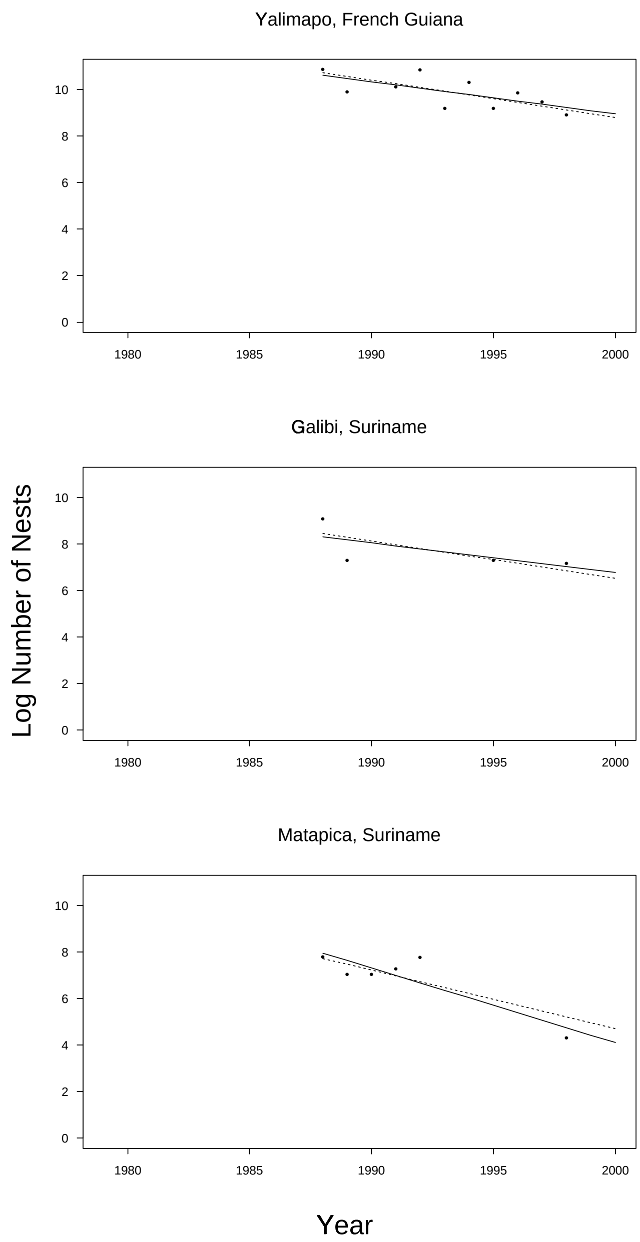


Figure 5: Plots of log transformed nest counts for the beaches in the South American population of leatherback turtles. Each point is an observation, the solid line is the ordinary least squares fit, and the dashed line is the BLUP from the mixed model. The mixed model fits come from a model that assumes a common error variance among beaches.

We also display the estimated total number for the northern and southern populations of loggerhead for the surveyed beaches (Fig. 6). In these plots, we summed the predicted numbers in the individual regressions and the mixed models estimates to estimate the total number in the areas surveyed.

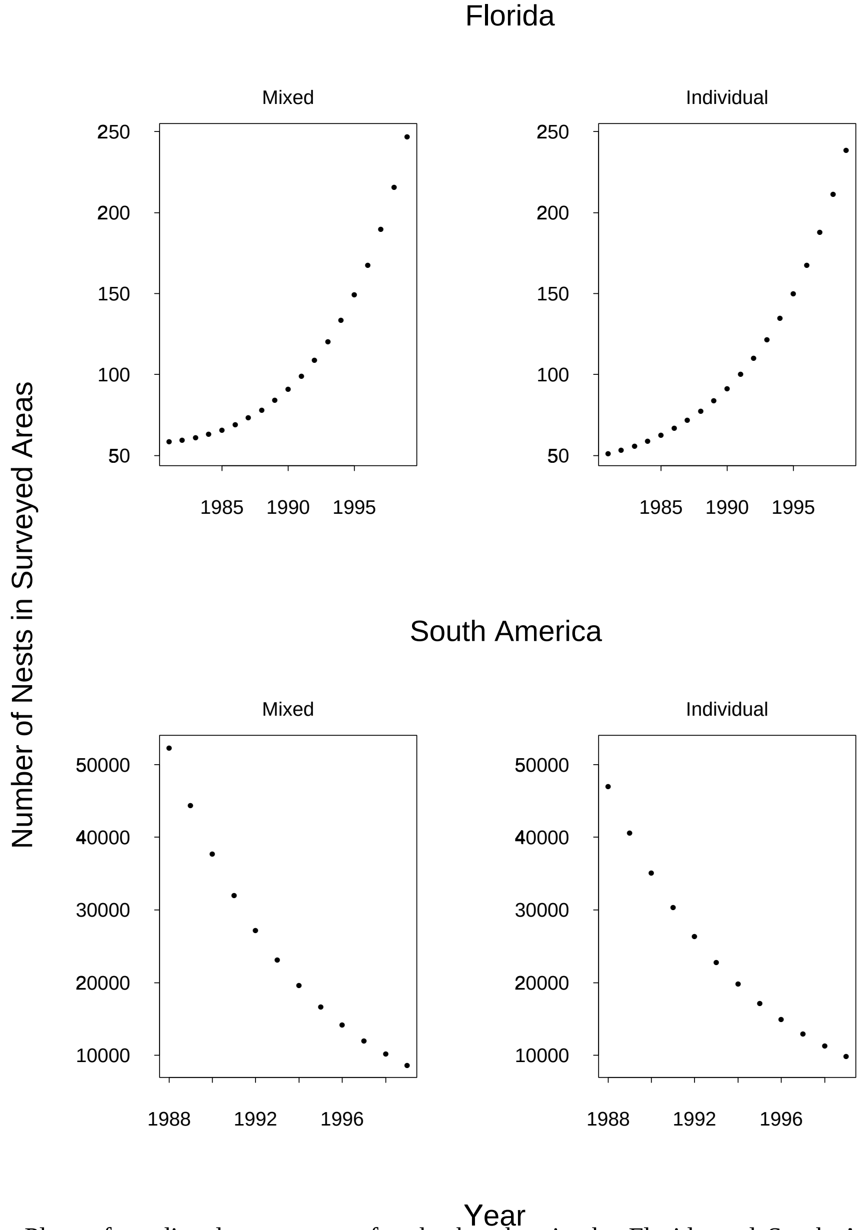


Figure 6: Plots of predicted nest counts for the beaches in the Florida and South America subpopulation of leatherback turtles. The individual estimates are from the sum of the individual OLS regressions, and the mixed model estimates are from the sum of the Best Linear Unbiased Predictors for each beach.

7.3 Limitations of the analysis

This study was limited by the inability to access the raw data to assess day by day counts and effort. Future analyses would be much more reliable if such data was made available.

7.4 Acknowledgements

We would like to acknowledge all the individuals and organizations that collected and contributed data that made this analysis possible. Melissa Snover and Lisa Csuzdi provided the nesting beach data. For Georgia we would like to thank Mark Dodd of the Georgia Department of Natural Resources, Jim Richardson for Little Cumberland Island, Jekyll Island Sea Turtle Project for Jekyll Island, The Lodge on Little St. Simon's Island, Georgia Department of Natural Resources for Sapelo Island and Ossabaw Island, Savanna Coastal refuges and the U.S. Fish and Wildlife Service for Blackbeard Island, the Caretta Research Project and the U.S. Fish and Wildlife Service for Wassaw Island and Pine Island, and the National Park Service for Cumberland Island. For North Carolina we would like to thank Ruth Boettcher of the North Carolina Department of Natural Resources, the North Carolina Wildlife Resources Commission, Sea Turtle Activities at Cape Hatteras National Seashore for Cape Hatteras National Seashore, North Carolina Division of Parks and Recreation and the Department of Environment and Natural Resources for Hammock's Beach State Park, University of North Carolina - Wilmington and the Bald Head Island Conservancy, U.S. Fish and Wildlife Service for Pea Island National Wildlife Refuge, and the Emerald Island Volunteer Program for Bogues Bank. Cape Romain National Wildlife Refuge provided the data for Cape Island. The Florida Fish and Wildlife Commission provided the Florida data. A special thank you to all the volunteers contributing to the nesting beach studies over the years.

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