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Breeding on the edge: Estimating sex ratios of loggerhead turtles *Caretta caretta* at the northern extent of their range.

Project Role:

The majority of my data was collected by 51 sea turtle monitoring programs in each of the 3 states. Most of the data I used was from 2000-2006 for some states and sites data went as far back as the 80s. I received data from each state's natural resources agency, which collates and organizes data every year. I converted data prior to 2000 from SC to electronic format. I spent about 4 months reorganizing and reformatting the data, checking for mistakes and pulling out the information I needed. DuBose Griffin and Matthew Godfrey, both state coordinators, helped me decipher this data.

I coordinated most site visits and did all the sand collection. I programmed and put out all the loggers at each site except two in NC. Staff from each site usually helped me with transport onto the beaches. I also helped with spectroradiometer readings in the lab in Edinburgh. Alasdair Mac Arthur converted the readings into albedo values for each sample because I did not have the software or the expertise that he did. My thesis was edited by Brendan, DuBose and Matthew.

Problems:

The biggest problem I had was making sense of data that wasn't collected by me. Trying to reformat and reorganize it so everything was consistent took a lot of time and effort. I ran into many obstacles of inconsistency and entry errors.

Losing loggers was another problem. It probably would have been better if my supervisor could have come out in the field with me in the beginning. I think I would have labeled them better and been more careful about where I put them with his guidance. I think I underestimated the power of the wind and sea!

I also had some issues with time. It seemed all a bit rushed at the end because my fieldwork ended so late and I think I might feel more confident in my work if I had more than a month to write it up.

Journal: Marine Ecology Progress Series

I chose this journal because it is the leading journal in its field. It covers all aspects of marine ecology, fundamental and applied. I feel my study contains both fundamental and applied aspects of marine ecology. Studying sex ratios is a fundamental part of understanding the total ecology of sea turtles but can also be applied to help conserve and manage the species.

Breeding on the edge: Estimating sex ratios of loggerhead turtles *Caretta caretta* at the northern extent of their range

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Running head: Sex ratios of northerly loggerheads

Journal: Marine Ecology Progress Series

ABSTRACT

Temperature-dependent sex determination (TSD) has been studied in loggerhead sea turtles for a number of decades. Most loggerhead populations have been found to exhibit predominately female biased primary sex ratios. Here we study a sub-population in the North Atlantic which has been thought to have a less skewed sex ratio. Temperature and sand were collected from 51 sites along the southeastern United States in order to explain patterns of sex ratios. Incubation durations were calculated for over 18,000 nests from 2000-2006 and converted to sex ratios. Temperature and therefore incubation duration correlated significantly with latitude. Deviations from this trend were explained by sand albedo. On average sex ratios become gradually less female-biased as latitude increases, with the most northern sites producing male-biased clutches. The overall sex ratio was 53.4% female. Long term trend analysis of sex ratios revealed one site had a significant increase in females from 1980-2006. Northern nesting sites are essential for producing consistent numbers of males in an overall heavily biased population. These males will become increasingly more important if climate change causes southern sites to produce further biased primary sex ratios. Continual protection from harmful anthropogenic influence, especially that which could alter the thermal habitat, must be a high priority for conserving and managing this species.

KEYWORDS: loggerhead turtle, *Caretta caretta*, temperature-dependent sex determination (TSD), incubation duration, latitude, climate change, sand albedo

INTRODUCTION

Temperature-dependent sex determination (TSD)

Sex determination of an individual, and therefore the sex ratio of an entire population, can either be influenced by genetic and/or environmental factors. Temperature is the most studied and most influential environmental factor for differentiating sex in vertebrates (Charnier 1966, Yntema 1979, Yntema & Mrosovsky 1980, Mrosovsky 1988; Ciofi & Swingland 1997, Chevalier et al. 1999, Shine 1999, Godfrey and Mrosovsky 2001, Azuma et al. 2004, Robert et al. 2006). Temperature-dependent sex determination (TSD) often has a specific range of values which produces both sexes at varying percentages and at the pivotal temperature the sex ratio is 1:1. Above and below this range offspring are either all male or all female (Yntema & Mrosovsky 1982, Ciofi & Swingland 1997). Actual patterns and ranges differ for each species: some produce all male at higher temperatures and others all female. These temperatures trigger genes and hormones that cause the differentiation of gonads after an egg has been fertilized (Ciofi & Swingland 1997, Pieau & Dorizzi 2004). The evolution of TSD and its adaptive significance is still not fully understood (Shine 1999, Leimara et al. 2004, Valenzuela 2004).

TSD in reptiles

There is much debate about the evolution of TSD in reptiles, even though they have been studied for over 4 decades (Charnier 1966, Yntema 1979, Yntema & Mrosovsky 1980, Mrosovsky 1988, Bull & Charnov 1989, Ciofi & Swingland 1997, Chevalier et al. 1999, Godfrey et al. 1999, Shine 1999, Robert et al. 2006). It is unclear why some reptiles have genetic sex determination (GSD) while others have environmental sex determination (ESD). The type of sex determination is not strongly associated with evolutionary linkage (Janzen & Krenz 2004). Neither seems to be the ancestral trait; they could have evolved multiple times or have different origins (Ciofi & Swingland 1997). Even the pattern of sexual differentiation response to temperature varies within reptile taxa (Ewert et al. 2004, Harlow

2004). Nest incubation temperatures determine the sex in TSD reptiles. The temperature inside the nest in turn is dependent on several factors, including: nest material/substrate and its subsequent grain size, porosity, water content and albedo; nest location in regards to both depth and linear space; the number of eggs in a clutch which affects the metabolic heating of the nest; and climatic conditions such as air temperature and rainfall (Janzen 1994, Hays et al. 1995, Ackerman 1997, Ciofi & Swingland 1997, Shine 1999, Janzen & Morjan 2001, Hays et al. 2001, Miller et al. 2004).

Loggerhead sea turtles

One of the most heavily studied reptiles with TSD is the loggerhead sea turtle, *Caretta caretta* (Yntema & Mrosovsky 1980, Yntema & Mrosovsky 1982, Limpus et al. 1983, Maxwell et al. 1988, Mrosovsky 1988, Marcovaldi et al. 1997, Hanson et al., 1998, Godley et al. 2001a b, Mrosovsky et al. 2002, Kaska et al. 2006). Loggerhead clutches have a viable thermal range from about 25-35ºC with lower extremes producing all males, upper extremes producing all females and a middle range producing both sexes (Yntema & Mrosovsky 1982, Ackerman 1997). Loggerheads are widely distributed around the world, from tropical to warm temperate waters in the Atlantic, Indian, and Pacific Oceans as well as the Mediterranean and the Caribbean Seas. Despite the large range, loggerheads typically have a pivotal temperature between 28.6 - 29.2 ºC (Limpus et al. 1985, Mrosovsky 1988, Marcovaldi et al. 1997) and pivotal incubation duration—the time period giving an even sex ratio—between 59.3 - 61.7 days (Godfrey & Mrosovsky 1997, Marcovaldi et al. 1997). These slight variances in pivotal temperatures and incubation durations might be due to the limitations of direct sex ratio sampling when creating sex ratio models and/or differences in laboratory conditions (Mrosovsky 1988).

Limitations of sex ratio sampling

Classifying sex in young sea turtles is often difficult because they do not display external dimorphic sexual characteristics nor do they have dimorphic sex chromosomes (Bull 1980, Ewert 1991). Therefore sex is usually assigned by microscopic visualization of the gonads, a technique that unfortunately results in the death of the hatchling. Because hatchlings must be killed, direct sex ratio sampling is limited because loggerheads are a protected species in much of their range. Often the studies relating sex ratio to temperature only include a few clutches (Yntema & Mrosovsky 1982, Limpus 1983, Mrosovsky 1988).

However these models make it possible to estimate sex ratios indirectly on a large scale through sand temperatures (Mrosovsky & Provancha 1992, Hanson et al.1998, Godley et al. 2001b) and even incubation durations (Marcovaldi et al. 1997, Mrosovsky et al. 1999, Godley et al. 2001a). Estimating sex ratio indirectly is less accurate for individual hatchlings, but allows for greater spatial and temporal extent (Mrosovsky et al. 1999). Using incubation durations especially allows for long-term sex ratio estimates because archived nest data can be used. Still, temperatures and incubations from multiple years from only one beach may not give an accurate estimate of an entire population's sex ratio. Information from a variety of nesting beaches as well as long term sex ratio information is preferred as incubating temperatures can change dramatically from beach to beach and from year to year (Mrosovsky et al 1984, Godfrey & Mrosovsky 1999).

Loggerheads in the U.S.A.

Loggerheads in the United States nest along the southern Atlantic coast and are the second largest population of loggerheads in the world (Magnuson et al. 1990, TEWG 1998, TEWG 2000). The majority of the population nests in Florida, however their range extends from Texas through Georgia, the Carolinas, and even Virginia, spanning a multitude of beaches and temperatures. Most of the studies in the past have focused on the turtles nesting in

Florida since it holds the majority of the population. These studies have shown that turtles in Florida are up to 90% female (Mrosovsky & Provancha 1992, Hanson et al. 1998). This is not unique as other populations in the Mediterranean and in Brazil are also predominately female (Marcovaldi et al. 1997, Godley et al. 2001a, b). Protecting male producing beaches is critical for the population's survival (Baptistotte et al. 1999). Initial studies covering some of the most northerly beaches in this population's range, which have cooler temperatures, suggest they have a near balanced sex ratio (Mrosovsky et al. 1984, Mrosovsky 1988, Hawkes et al. 2007). This may indicate that the northern sites have extreme conservation value by virtue of their consistent male production, and thus require special attention. Studies of Brazilian loggerheads have shown that cooler beaches, though smaller in nest numbers, are important for producing males into the population there (Marcovaldi et al. 1997, Baptistotte et al. 1999, Mrosovsky et al. 1999). However, there has not been a large scale study covering the entire extent of northern loggerhead nest sites in the U.S.A.

Climate change

Climate change could have a significant impact on a species that is innately connected with temperatures of its habitat (Janzen 1994, Davenport 1997, Fish et al 2005, Salinger 2005, Hawkes et al. 2007). With increasing temperatures, loggerhead populations that are already skewed, may become entirely female. Some clutches may even extend above thermal limits for successful incubation (Davenport 1997, Matsuzawa et al. 2002). Thus it is important to understand historical and present population trends for the entire population in the face of possible large scale changes to their environment.

In this study we attempt to examine the sex ratios of the entire northern nesting population of loggerhead turtles in the southeastern United States. We will use incubation duration to estimate hatchling sex ratios using long-term data from monitored nesting beaches in

Virginia, North Carolina and South Carolina. It is expected that there will be temporal, latitudinal and sand albedo effects on sex ratio.

MATERIALS AND METHODS

Nesting data

Nesting data were collected by a range of government and non-government agencies over the past few decades by daily nest monitoring programs at 51 beaches from Virginia, North Carolina and South Carolina in the southeastern United States. Sites spanned from 32° 09' N to 37° 56' N latitude. Nesting data were collated and stored by each state's natural resources agency. Incubation duration and hatch success were extracted from these datasets from years which were thought to have complete coverage of each state. When compiling records from all three states, only data from 2000-2006 were used. Incubation duration was recorded as the number of days between egg laying and first emergence of the hatchlings. Because monitoring was mostly carried out in the morning, the date laid and emergence date were scored as the date of the morning after these events occurred the previous night. Several days after the first hatchling emergence, nests were excavated to count the number of egg shells and any eggs or hatchlings, dead or alive, which were left in the nest. Hatch success was calculated as the total number of empty egg shells divided by the total number of eggs laid subtracting any dead hatchlings found for each year for each site. Hatch success was only calculated for nests with clutch and emergence information available. Sex ratios were calculated using published models relating percent female to incubation duration for loggerheads in the U.S.A. (Godley et al. 2001a, Godfrey & Mrosovsky 1997). Sex ratios were only calculated for nests with incubation duration and did not take into account hatch success.

Sand temperature

Twelve of the fifty-one sites were monitored for sand temperature during the 2007 nesting season. Three data loggers were placed at each site. In Virginia and South Carolina Tiny Talk II Gemini data loggers (Chinchester, UK) were used and in North Carolina Hobo data loggers (Hobo u-pendants, Onset computers, Massachusetts, U.S.A) were used. Data loggers registered temperature measurements every four hours. Data loggers were placed in the sand 45 cm deep which is mean nest depth for loggerhead turtles in this area (Hawkes et al. 2007).

Sand temperatures were averaged to give daily mean temperatures for each beach. Some loggers were lost, therefore some beaches did not have all three data sets to average. Because of limitations in field time, temperatures were only collected over the first two months of the four month nesting season. When temperatures were compared only values from overlapping days were used which was from 27 May -27 June and this period constitutes the first third of the nesting season. To give an indication of relative thermal environment at these beaches deviance from the median temperature value (25.8°C) was calculated for each site.

Sand absorption measurements

Sand was collected from the surface of the beach of most sites along the coast and measured for broad-band absorption (α) using a spectroradiometer (FieldSpec FR, Analytical Spectral Devices, Boulder, CO, U.S.A.) which measures the reflectance in 1 nm increments between 350 and 2500 nm of light. We repeated the exact same procedures as in Hays et al. (2001) to obtain albedo (ρ) or reflectance values for each sand sample in the lab. Albedo is the proportion of incoming solar radiation that is reflected back into the atmosphere and is the complementary value to absorption. When albedo is high, absorption is low leading to less heating of the surface from solar energy. Absorption values were obtained by subtracting the albedo values from 100:

$$\alpha_{350\text{–}2500}(\%) = 100 - \rho_{350\text{–}2500}$$

RESULTS

Latitudinal Comparisons

Latitudinal comparisons where made for 47 beaches which had consistent monitoring from 2000-2006 (Figure 1a). Number of nests varied greatly from beach to beach because of differences in length and latitude. Comparing annual number of nests per km shows a large range of nesting densities from less than 1 nest km^{-1} yr^{-1} to over 66 nests km^{-1} yr^{-1}. Larger nesting areas are located in South Carolina, followed by North Carolina, with very low nesting densities in Virginia (Figure 1b).

The mean incubation duration for the entire northerly population from 2000-2006 was 61.2 ± 5.6 days (range= 54.7 - 90 days, n = 47) (Figure 1c). Incubation duration generally increased as latitude increased. The mean site specific sex ratio was 53.4% ± 0.146 female (range= 0 - 77%, n = 47) (Figure 1d) but this proportion decreased with increasing latitude. Mean hatch success rate for the entire study area was 71.1% ± 0.129 (range= 16 - 93%, n = 47) (Figure 1e). There seems to be a peak in hatch success in the middle latitudes, in southern North Carolina and northern South Carolina. Hatch success was lowest in Virginia.

Range of incubation durations and sex ratio

In Virginia incubation durations ranged from 55-97 days and 0-75% female (Figures 2a and b). In North Carolina incubation durations ranged from 43-99 days and 0-95% female (Figures 2c and d). In South Carolina incubation durations ranged from 43-90 days and 0-95% female (Figures 2e and f).

Incubation durations varied considerably by state (Figures 2a, c and e). The majority of nests in Virginia and South Carolina were above and below the pivotal incubation duration respectively (Figures 2a and e). However in North Carolina nests were split almost evenly above and below the pivotal incubation duration (Figure 2c). A complementary pattern was seen in the sex ratios of each state (Figures 2b, d, and f). Given the South Carolina bias in magnitude of nests, the entire population from 2000-2006 had incubation durations below the pivotal incubation period thus making most nests predominantly female (Figures 2g and h).

Total nests and hatchlings

There were approximately 18,000 loggerhead turtle nests monitored in Virginia, North Carolina and South Carolina from 2000-2006, which is ~ 2575 nests annually. Virginia, North Carolina and South Carolina received 0.2%, 26% and 73.8% of the total number of nests laid in this region respectively. There were ~1.2 million hatchlings that emerged from these nests. Average sex ratio was 53% female and 47% male. Nests laid in Virginia and the Carolinas from 2000-2006 account for ~ 4% of the total population in the U.S.A. (Table 1).

Latitude and sand absorptance models

Sand absorptance ($\alpha_{350–2500}$) values ranged from 45.75 - 67.54% (Figure 3). The average raw absorptance value was 56.47 % ± 0.05 (n = 57). Using a general linear model (GLM)-ANOVA to test for significance, temperatures were highly correlated with latitude (F = 45.78, $p < 0.001$) and slightly less correlated with absorption (F = 5.94, $p < 0.05$). The interaction between latitude and absorption did not have a significant affect on temperature (F = 0.09, $p > 0.05$) (Figures 4a and c). GLM-ANOVA analysis also showed correlation between incubation durations and latitude (F = 13.91, $p < 0.001$) and absorption (F = 7.67, $p < 0.01$). The combined interaction between latitude and absorption also had a significant affect on incubation duration (F = 8.12, $p < 0.01$) (Figures 4b and d).

Long term trends in sex ratio

At a number of sites long-term datasets were available going back a few decades which were utilized to examine any temporal trends in sex ratio. There no was trend in sex ratio for most sites except for Bald Head Island (Figure 5). In Bald Head Island, the percentage of females is increasing annually (regression: $F_{1, 24} = 17.6$, $p < 0.001$, $R^2 = 0.44$). Annual fluctuations can be seen in all sites. There seems to be more variation in annual sex ratio in northern sites—Virginia and North Carolina—than sites in South Carolina. There also seems to be an increasing trend from 2000-2006 for most sites.

DISCUSSION

Latitudinal comparisons

Incubation durations and resulting sex ratios followed the predicted patterns of variance with latitude. On average, incubation durations were shorter and the percentage of females greater in lower latitudes compared with higher ones. This pattern is consistent with previous research which showed a higher percentage of males in northern sites compared with sites in Florida (Mrosovsky et al. 1984, Mrosovsky and Provancha 1992, Hawkes et al. 2007).

The pattern in hatch success is interesting because it does not follow other latitudinal trends. The peak in the mid-latitudes may mean optimal temperatures and conditions are met there. Coupled with sex ratio, high hatch success in the mid-latitudes may mean more hatchlings are being produced from nests with even sex ratio. Varying numbers of nests could explain the differences between the states. In Virginia, nests numbers are so low that a few unhatched nests could skew the entire average. In South Carolina, there are so many nests, not all can be monitored on an individual level and many are lost to over wash and predation. Also South Carolina has higher temperatures than the other states and higher temperatures have been shown to increase turtle mortality (Yntema & Mrosovsky 1980). Hatch success is also a challenging measure to consistently evaluate across various sites and years. In addition, this study did not include nests for which clutch size was unknown and then were completely destroyed before inventory could occur. This means that hatch success values given here may be slightly higher than the true values. Also, predation by foxes and raccoons may be a serious issue on some beaches which can further distort hatch success.

Incubation durations and hatch success can also be greatly affected by conservation efforts. Each state has its own regulations for turtle nest monitoring. In South Carolina, for example, eggs can be lost due to probing when initially searching for the nest. This practice is not carried out in Virginia and North Carolina. Also many sites relocate more nests than others due to erosion or interference with human activities. This can skew hatch success and sex ratio because nests are usually moved higher up the beach which can increase the temperatures inside the nest. In some years, as many as 60% of all nests have been relocated in North Carolina and South Carolina. With such large numbers of nests being moved from their original positions, it is likely to change incubation durations but at the same time may ensure more successful nests.

Range of Incubation Durations and Sex Ratios

Ranges of incubation durations and sex ratios for each state were interesting because they showed that all states had at least some nests which produced all males (Figure 2). Some of the highest and lowest incubation durations may not be entirely accurate because they fall outside the normal range of incubation. Even with North Carolina and Virginia producing non-female biased nests, the overall range of nests are predominately female biased because South Carolina accounts for over two-thirds of the total. Although most nests were predominately female, the overall mean sex ratio was relatively even. This mean value is based on averages by site so it does not take into account how many nests are at each site. The ranges of sex ratios shown in Figure 2 are a more accurate description of what is happening with nests in Virginia and the Carolinas.

Total number of nests

Means calculated for each site do not include incubation and hatch success data for every nest observed. Beach patrols occasionally miss some nests both when eggs are laid and hatching. Some sites do not have the capacity to inventory every single nest. Additionally, storms can wipe out a multitude of nests before any inventory can be done. Also, total number of nests and hatchlings shown in this study do not represent every nest and hatchling produced in these areas. There are still some beaches that are not monitored for sea turtle nesting or have not been monitored long enough to include in this study. Most of the missing sites are remote barrier islands which make daily monitoring difficult. Other sites are not monitored simply because turtle activity is too low to warrant daily beach patrols. South Carolina has the most missing number of nests. Based on aerial surveys on average, one-third of nests in South Carolina are not monitored from the ground (DB Griffin, pers. comm.). This is a large number of nests for which incubation duration data is missing which in turn could affect the overall sex ratios calculated here.

Virginia, North Carolina and South Carolina make up a small portion of the of 65,040 loggerhead nests produced on average each year between 2000-2006 in the United States (Florida Fish and Wildlife Conservation Commission 2007, M Dodd, pers. comm.). According to this study, these states account for about 4% of the North Atlantic loggerheads. This number may be the result of a gradual decline of the northern population. Aerial surveys flown by the South Carolina Department of Natural Resources have shown a 3% annual decline (1980 –2007) in nesting numbers for South Carolina (DB Griffin, pers. comm.). However this decline is not confirmed in other states. But if numbers of turtles from these sites are declining, it is further reason to ensure their protection.

Although the amount of males being produced at these sites does not make up for the heavily female-biased sites in Florida these sites are very important for the future survival of this population. Climate change may cause total feminization in sites in Florida which are already predominately female. Northerly sites may become the only places in this population’s habitat range which are able to produce males. Additionally southern turtles may begin to shift their nesting habits north to these sites (Janzen 1994, Davenport 1997, Hays et al. 2003) or they may change their time of year for nesting. Although they may have low nest numbers now, northern loggerhead nest sites may become the primary nesting areas in the future.

Latitude and sand absorption models

Latitude is the primary driver of temperatures and therefore incubation durations. Sand absorption describes the deviance from the expected latitudinal trend. Our sand absorptance values were similar to those sands measured in Hays et al. (2001). There was a temporal mismatch of incubation durations and albedo values which might explain why the combined effect of latitude and absorption on incubation was not more influential than latitude alone. Ideally incubation durations from 2007 should have been compared with sand albedo from 2007. Although it may seem like an outlier, significance was not greatly influenced by the long incubation duration from Assateague Island (90 days) because when tested without it, latitude still had a significant affect on incubation.

Significance values were greater for comparisons with incubation duration than temperature because of a type II statistical error in sample size. If temperature was measured at more sites, the interaction between latitude and absorption would have probably been significant. The latitudinal and absorption trends in temperature are consistent with previous research testing these interactions (Mrosovsky et al. 1984, Mrosovsky et al. 1988, Mrosovsky and Provancha 1992, Hays et al. 1995, Hays et al. 2001, Hawkes et al. 2007). Latitudinal trends in incubation duration for loggerheads in the United States mirror trends found in Brazil (Marcovaldi et al. 1997). Incubation durations have not been compared with absorption as of yet in other studies but should be considered in future research on sex ratios considering its significant effect here.

Long Term trends in Sex Ratio

The absence of a temporal trend in sex ratio for most sites may mean that no significant warming has occurred in the study area so far. Not all regions on the earth are experiencing the same amount of warming (IPCC 2001). It is predicted that extreme latitudes will bear the brunt of climate change, but since the sites from this study are in neither of those ranges it is possible temperatures may not significantly rise here for a long time (Hawkes et al. 2007). However it is possible data from some sites did not go back far enough to notice a trend. Bald Head Island, which had a significant trend, had a data set going back 16 years. This site may be an example of what could be seen at other sites if more data was available. Inter-annual differences in temperature may be the source for the differences in sex ratio from year to year however temperature is obviously not the only factor influencing sex. If that were the case, years of high temperatures would produce relative high percentages of females at all sites. There are clearly site-specific factors which influence the nests at each beach. Then again, close examination of the last 6 years of sex ratios at these sites does show an increase in percent females for 5 out of 6 of the sites. It is not a significant trend yet, but may become one if warming increases over the next few years or decades.

Study limitations

There are several limitations in this study that could have affected some of the results. Every effort was made to standardize data from all three states. Hatch success and incubation duration calculations are standardized in all states, but only for recent years and that does not mean there were no mistakes made when data were entered. Because this study spanned such a large area and time period, data collection and inventory was a collaborative effort and mistakes were obviously inevitable. For example incubation duration can easily be calculated wrong if the date of first emergence is confused with the date of last emergence or if the evening's date is recorded instead of the date observed. However, we assumed that these errors would occur randomly and thus not greatly bias the results in any particular direction.

Sand temperatures were only monitored over the first third of the nesting period due to field time constraints. A greater correlation between sand temperature and latitude as well as albedo would have probably been observed if temperatures were monitored over the entire nesting period. Also some sites did not have three data sets of sand temperatures because loggers were lost. On large beaches with varying sand type and usage, one sample of sand temperatures may not be an accurate depiction of the entire beach. Additionally multiple sand samples from each site could have been collected to capture the entire sand albedo spectrum of these beaches. Although other studies have shown little within beach variation in sand albedo (Hays et al. 2001) renourishment and disposal of sand in the United States happens repeatedly along many public beaches and should be considered when collecting sand for sand spectral analysis.

Beach alterations

Many alterations to a beach can be made which can change its thermal properties including beach renourishment and disposal but also beachfront development, and/or deforestation. Beachfront development often causes coastal squeeze. This leaves less room on the beach for nests and usually shifts nest further towards the sea which is usually detrimental to hatch success (Carthy et al 2003). High-rise development may also alter the thermal characteristics of a beach by artificially shading certain areas (Mrosovsky et al 1995).

Beach renourishment occurs when homeowners want to protect their property from being destroyed by storm surge and erosion—which subsequently will increase with warming temperatures and rising sea levels. They refill beaches which have become narrow, in hopes that their properties will be better protected. The sand is usually dredged from the ocean floor and so it can be different from the original sand on the beach. Most ocean bottom sand is full of shells, coarser, and in some cases darker (Ackerman 1997). This could cause warmer incubation temperatures and therefore make northern beaches produce more females than normal. More research is needed testing differences in sand albedo between natural and renourished sand. Deforestation along beach edges could also cause warmer incubation temperatures by removing the shaded areas that allow for cooler temperatures at the top of the beach (Kamel & Mrosovsky 2006). Beach alterations should therefore be kept to a minimum to ensure they do not amplify the affects of global warming.

Conclusions

Our study shows that many of the northern nesting sites for North American loggerheads produce a considerable amount of male hatchlings even though these sites only make up a small portion of the total population. The consistent production of some males is important for a loggerhead population which is overall heavily female biased (Mrosovsky & Provancha 1992, Marcovaldi et al. 1997, Hanson et al. 1998, Baptistotte et al. 1999, Mrosovsky et al. 1999, Godley et al. 2001a b). With a rise in global temperatures, these sites will only become more important for the production of males in the population.

Our study is useful in that it encompasses multiple sites and multiple years over a continuous latitudinal spread. More studies in the future should attempt to cover such large-scale data sets because they are more accurate in determining the status of a population as a whole. It is clear that northerly nesting sites for these loggerheads should continue to be protected and are of considerable importance for the existence of the population. If there are alterations to these northern sites which can change their thermal properties, these sites may become less capable of ensuring the population's success.

ACKNOWLEDGEMENTS

This research was carried out as part of a master's thesis at the University of Exeter in Cornwall. This work would not have been possible without the collaborative efforts of all involved, especially B. J. Godley, M. H. Godfrey, D. B. Griffin and R. Boettcher. Special thanks to the South Carolina Department of Natural Resources, North Carolina Wildlife Resources Commission, and the Virginia Department of Game and Inland Fisheries for collecting and storing turtle data, S. Murphy, S. Dawsey and C. Chacon for addition data collection, site managers and staff for their assistance with temperature data loggers, A. Broderick for supplying data loggers, A. Mac Arthur for sand spectral analysis and the NERC Field Spectroscopy Facility at the University of Edinburgh. This project was supported by the Natural Environment Research Council and the European Social Fund.

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TABLES

Table 1. Total nest and hatchling data for each state from 2000-2006 monitored beaches

State	Average annual number of nests	Total number of nests	Percent of total nests	Total number of hatchlings	Percent female	Percent male	Percent of total loggerhead population[a]
Virginia	5	38	0.2%	1,366	24.9%	75.1%	0.01%
North Carolina	669	4,683	26.0%	347,812	48.9%	51.1%	1.03%
South Carolina	1,900	13,302	73.8%	867,763	57.0%	43.0%	2.92%
All	2,575	18,023	100%	1,216,941	53.5%	46.5%	3.96%

[a] Based on a mean estimated number of 65,040 loggerhead nests a year in the United States from 2000-2006 (Florida Fish and Wildlife Conservation Commission 2007, M Dodd, pers. comm).

FIGURE LEGENDS

Figure 1: Compared by Latitude a) Map showing range of study. Black dots indicate sites from North to South: Assateague Island, VA; Sandbridge, VA; Back Bay National Wildlife Sanctuary, VA; False Cape SP, VA; Northern Outerbank Beaches, NC; Pea Island National Wildlife Refuge, NC; Cape Hatteras National Seashore, NC; Cape Lookout National Seashore, NC; Fort Macon State Park, NC; Bogue Banks, NC; Bear Island, NC; Onslow Beach, NC; Topsail Island, NC; Figure Eight Island, NC; Wrightsville Beach, NC; Pleasure Island, NC; Fort Fisher State Park, NC; Long Beach/Oak Island, NC; Holden Beach, NC; Ocean Isle, NC; Caswell Beach, NC; Sunset Beach/Bird Island, NC; Bald Head Island, NC; City of Myrtle Beach, SC; Long Bay Estates, SC; Myrtle Beach State Park, SC; Horry County, SC; Huntington Beach State Park, SC; Litchfield, SC; Pawleys Island, SC; DeBordieu, SC; Hobcaw, SC; South Island, SC; Cape/Lighthouse Island, SC; Dewees Island, SC; Isle of Palms/Sullivans Island, SC; Folly Beach, SC; Kiawah, SC; Seabrook, SC; Edingsville, SC; Edisto Beach State Park, SC; Town of Edisto Beach, SC; Harbor Island, SC; Hunting Island State Park, SC; Fripp Island, SC; Pritchards Island, SC; and Hilton Head, SC. b) Mean annual number of nests per kilometer for each site; c) Mean incubation durations for each site; d) Mean sex ratio for each site by latitude; e) Mean hatch success for each site from 2000-2006. Dotted lines indicate average for entire study site.

Figure 2: Range of incubation duration and sex ratios for study areas. a) and b) Virginia 1985-2006; c) and d) North Carolina 1995-2006; e) and f) South Carolina 2000-2006; g) and h) All states 2000-2006. Dotted lines indicate median incubation durations/sex ratios. Dashed lines indicate pivotal incubation which gives 50% of either sex. Sex ratio bars are not continuous but come from incubation/sex ratio model and follow this pattern: 0%, 4.95%, 5.77%, 6.72%, 7.80%, 9.05%, 10.48%, 12.10%, 13.93%, 15.99%, 18.29%, 20.84%, 23.64%, 26.69%, 29.98%, 33.49%, 37.19%, 41.05%, 45.02%, 49.06%, 53.11%, 56.96%, 60.88%, 64.66%, 68.27%, 71.68%, 74.85%, 77.78%, 80.45%, 82.88%, 85.06%, 87.00%,

88.73%, 90.25%, 91.59%, 92.75%, 93.77%, 94.65%, 95.42%, 96.08%, 96.64%, 97.13%, 100%. Sex ratio patterns are clearly different for each state.

Figure3. Distribution of absorption of incident solar radiation by sand samples ($\alpha_{350–2500}$). Average absorption was 56.76 % ± 5.47.

Figure 4: Relationship between a) temperature and latitude b) incubation duration and latitude c) temperature and sand absorption and d) incubation duration and sand absorption. Temperature and sand absorption values were obtained in 2007 and incubation durations were averaged for each site from 2000-2006. There are significant latitudinal trends for both temperature and incubation. Deviations from these trends can be explained by differences in sand absorption.

Figure 5: Annual sex ratios for six sites with long term incubation data: a) Back Bay National Wildlife Refuge, VA (36°40' N 75°54' W); b) Cape Lookout National Seashore, NC (34°49' N 76°21' W); c) Bald Head Island, NC (33°51' N 77°59' W); d) Cape/Lighthouse Island, SC; e) Edisto Beach State Park, SC (32°30' N 80°18' W); f) Hilton Head Island, SC (32°09' N 80°43' W). Dotted lines indicate average sex ratio. No significant long term trend in sex ratio was found for any site except Bald Head Island (regression: $F_{1, 24}$= 17.6, $p<0.001$, R^2=0.44)

Figure 1. a)

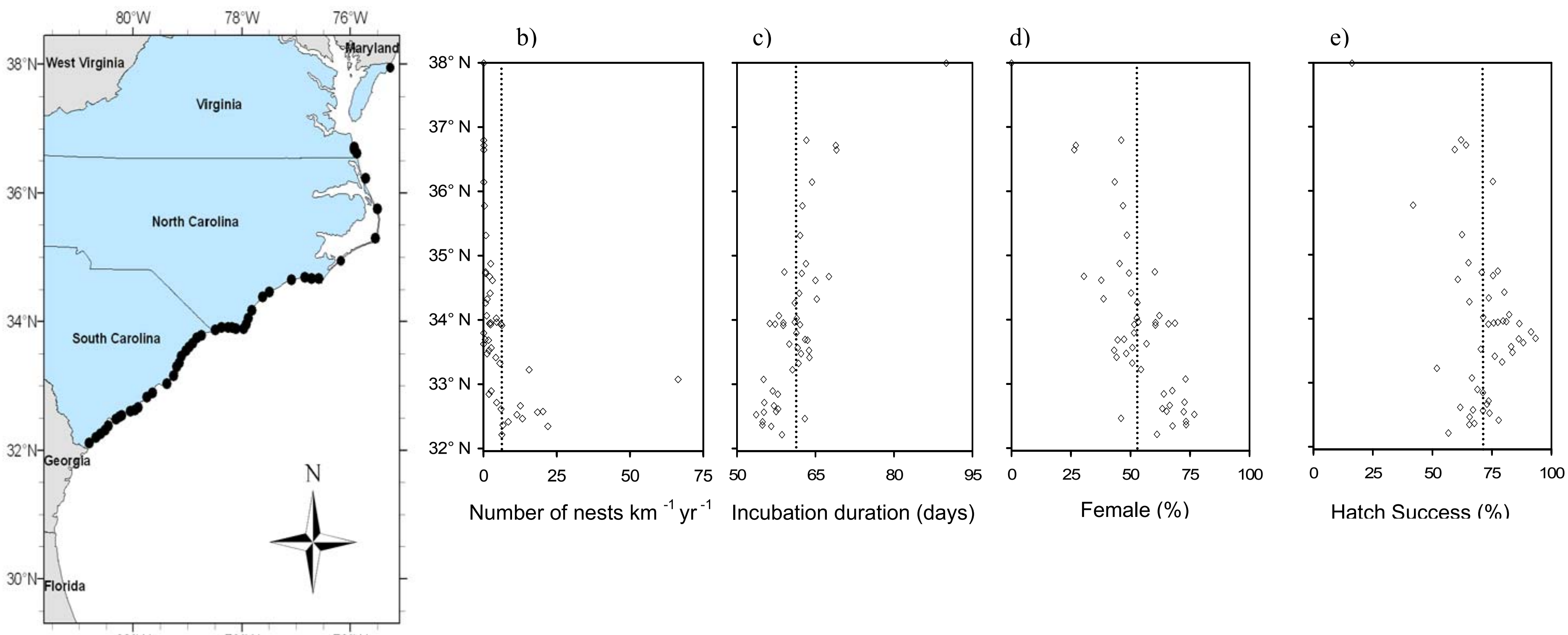

80°W
78°W
76°W
Maryland
West Virginia
Virginia
North Carolina
South Carolina
Georgia
Florida
N
38°N
36°N
34°N
32°N
30°N
b)
c)
d)
e)
38° N
37° N
36° N
35° N
34° N
33° N
32° N
0 25 50 75
Number of nests km $^{-1}$ yr $^{-1}$
50 65 80 95
Incubation duration (days)
0 25 50 75 100
Female (%)
0 25 50 75 100
Hatch Success (%)

Figure 2.

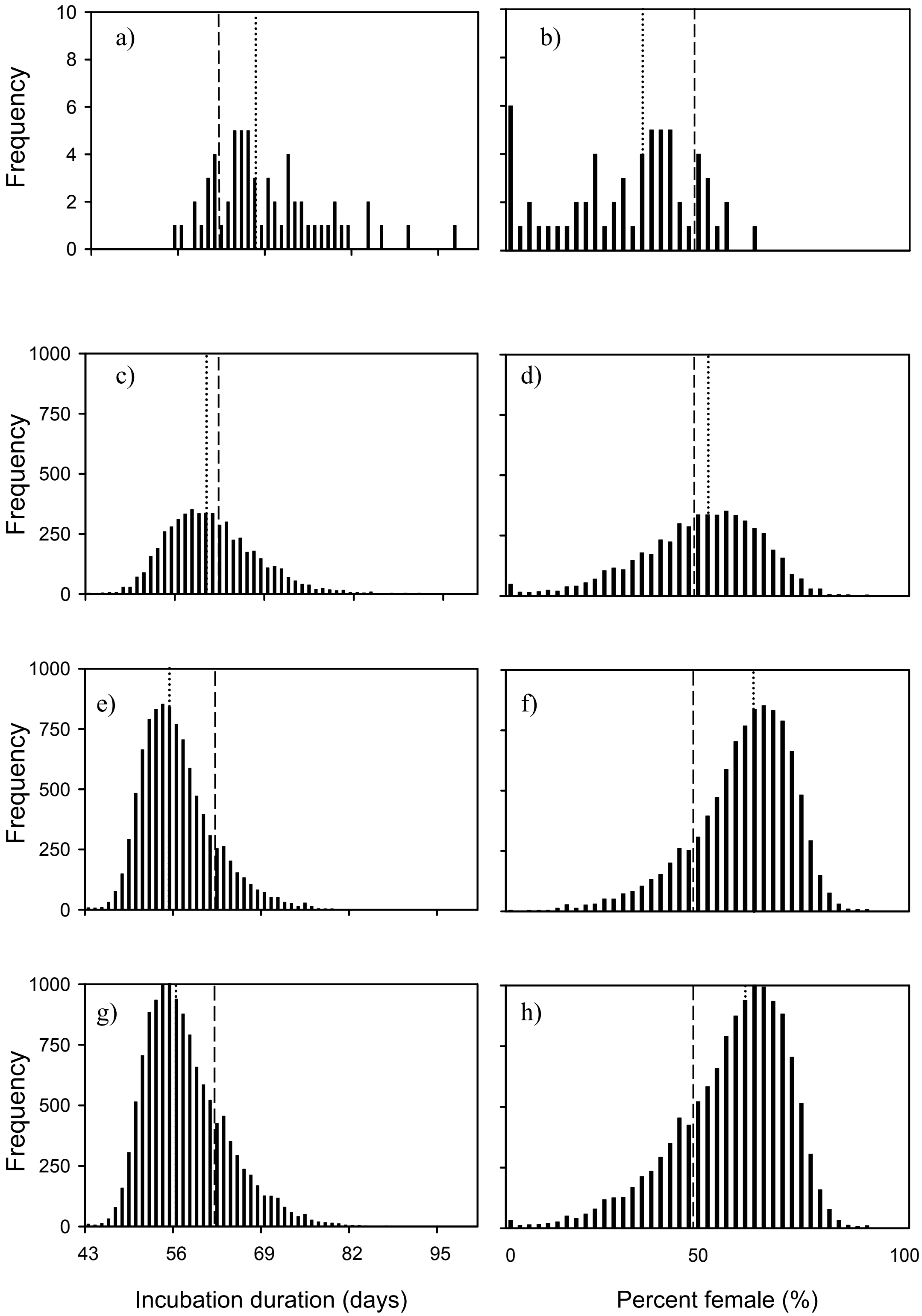

a)
b)
c)
d)
e)
f)
g)
h)
Frequency
0
2
4
6
8
10
250
500
750
1000
43
56
69
82
95
0
50
100
Incubation duration (days)
Percent female (%)

Figure 3.

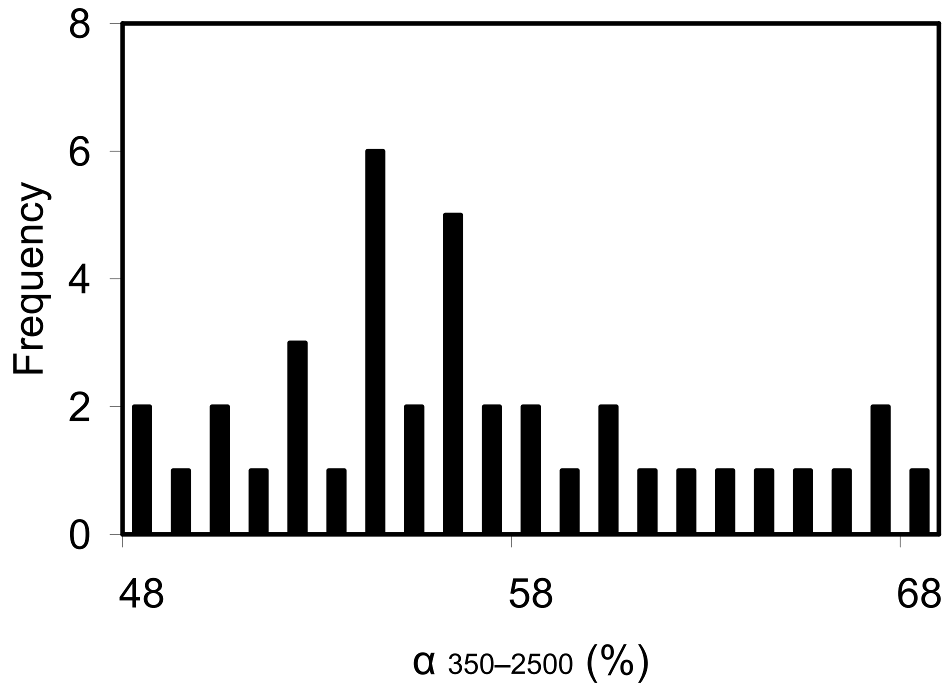


Figure 4.

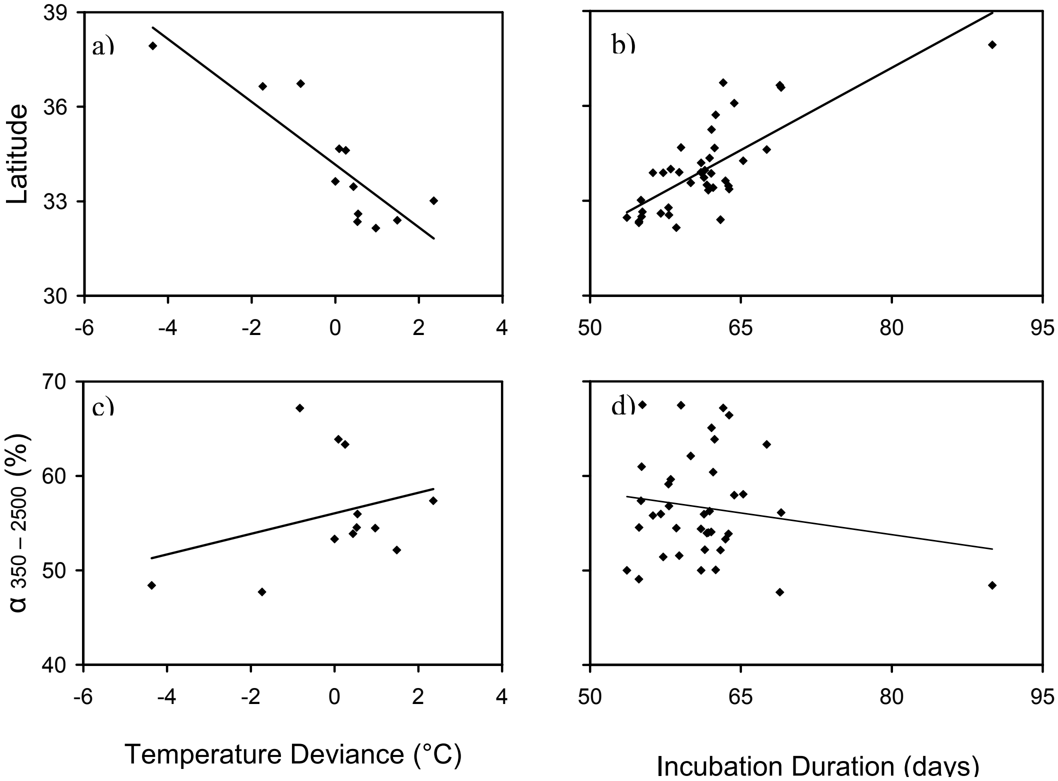
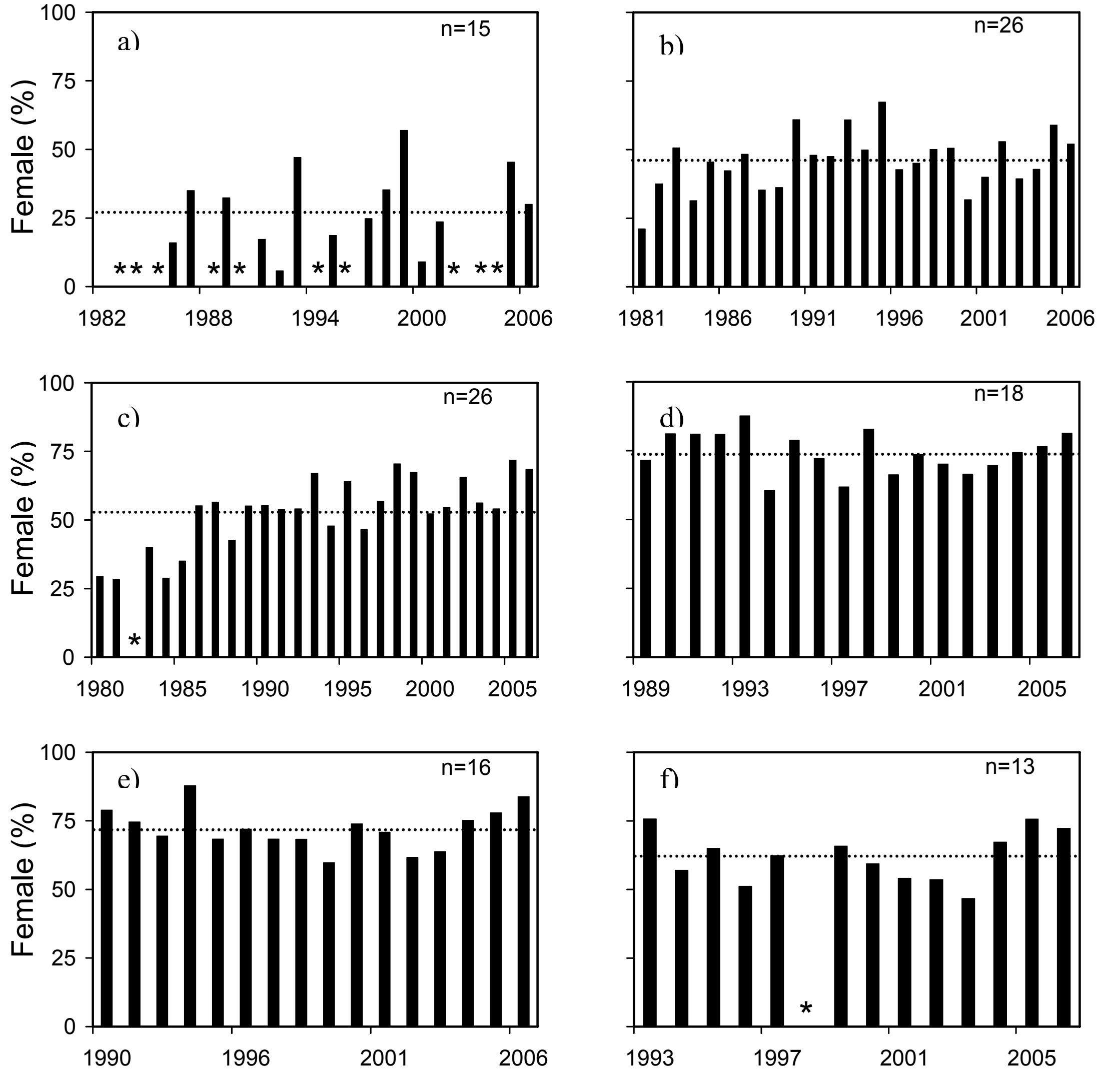

a)
b)
c)
d)
Latitude
α 350 – 2500 (%)
39
36
33
30
70
60
50
40
-6
-4
-2
0
2
4
50
65
80
95
Temperature Deviance (°C)
Incubation Duration (days)

Figure 5.


a)
n=15
b)
n=26
c)
n=26
d)
n=18
e)
n=16
f)
n=13
Female (%)
100
75
50
25
0
1982
1988
1994
2000
2006
1981
1986
1991
1996
2001
2006
1980
1985
1990
1995
2000
2005
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