



Tracking green turtle nesting trends at a remote oceanic rookery

Luciana Medeiros¹ · Milani Chaloupka² · Alan B. Bolten³ · Eduardo M. von Muhlen¹ · Alexsandro Santos¹ · Ana C. J. Marcondes¹ · João C. A. Thomé⁴ · Maria Ângela Marcovaldi¹ · Karen A. Bjorndal³

Received: 9 December 2021 / Accepted: 7 April 2022

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract

Trindade Island, Brazil, is a small, remote volcanic island located 1140 km off the coast of southeastern Brazil. The green turtle (*Chelonia mydas*) nesting aggregation on Trindade is genetically distinct, the largest in the southwest Atlantic, and represents the southern limit of green turtle nesting in the Atlantic. Projeto TAMAR (a Brazilian conservation program) has monitored the nesting aggregation discontinuously since 1982. In 2009, a standardized protocol was established for the two beaches (Andradas and Tartarugas) with the highest nest abundance. Data from December 2009 through April 2017 (except 2013) were used in this study. Annual numbers of tracks left by females that emerged onto the beach vary between 558 and 3317 tracks for Andradas and between 760 and 3559 tracks for Tartarugas. Mean nesting probabilities (probability that an emerging female deposits eggs) for all years were 0.22 (95% HDI (highest posterior density interval)=0.14–0.30) for Andradas and 0.45 (95% HDI=0.37–0.53) for Tartarugas. Nesting probabilities varied among and within years and had a negative relationship with daily track counts. During our study, annual estimates of nests were stable on both Andradas (range 38–2001) and Tartarugas (range 248–2769). Nest abundance estimates between 1991 and 2008 from an earlier study indicated a stable population, extending the duration of apparent stability to 26 years with the caveat that the studies used different estimation methods. This stability is in contrast with the increasing trends for most green turtle nesting aggregations in the Atlantic.

Keywords *Chelonia mydas* · Marine turtle · Nesting probability · Population trend analysis · Sea turtle · Trindade Island, Brazil

Introduction

Knowledge of long-term trends in population size, and demographic rates will help improve predictions of future changes in marine resources in response to climate change. In addition, populations located at the range limits of their distribution are more likely to be affected by and exhibit

the consequences of climate change (Angert 2009; Berggren et al. 2009; Lavergne et al. 2010).

For the preferred approach of ecosystem-wide management of marine systems to succeed (Mills et al. 1993; Costanza et al. 1998; Pikitch et al. 2004; Long et al. 2015), knowledge of stability and trends in abundance of dominant or keystone species is needed. Population assessments of sea turtles have received considerable attention over the past few decades, originally because of their threatened status, but increasingly because of their critical roles as ecosystem engineers, nutrient transporters, and major predators in marine ecosystems (Bjorndal and Jackson 2003; National Research Council 2010; Heithaus 2013).

Sea turtles are difficult to monitor at sea because of their long lifespans and extensive migrations (Bolten 2003; National Research Council 2010). Population assessments are usually conducted at nesting beaches, where females come ashore at night to deposit eggs, but such assessments are challenging because individual turtles usually skip one

Responsible Editor: P. Casale.

✉ Karen A. Bjorndal
bjorndal@ufl.edu

- ¹ Fundação Projeto TAMAR, Mata de São João, Bahia, Brazil
- ² Ecological Modelling Services Pty Ltd and Marine Spatial Ecology Lab, University of Queensland, Brisbane, Australia
- ³ Archie Carr Center for Sea Turtle Research and Department of Biology, University of Florida, Gainesville, FL, USA
- ⁴ Centro TAMAR-ICMBio, Vitoria, ES, Brazil

or more annual nesting seasons and lay a variable number of clutches each season (Dutton et al. 2005; Troëng and Chaloupka 2007; Prince and Chaloupka 2012; Pilcher and Chaloupka 2013). Moreover, indices of population abundance are often based on counts of the tracks left in the sand by nesting turtles as they traverse the beach or visual signs of egg deposition. A serious impediment to using track counts alone as an index of abundance is that not every emergence results in egg deposition.

Nesting probability (the probability that an emerging female will deposit a clutch of eggs) varies among seasons and among beaches for the same rookery (Weishampel et al. 2003; Weber et al. 2014). When nest counts cannot be observed directly, integrating track counts and nesting probability can yield estimates of nest abundance, which is a more reliable assessment metric than track counts alone (National Research Council 2010).

Trindade Island is a remote oceanic island lying 1140 km off the Brazilian coast that supports the largest known green turtle (*Chelonia mydas*) nesting aggregation in the southwest Atlantic (Almeida et al. 2011). Genetic studies revealed that green turtles nesting in Trindade are significantly different (based on mitochondrial haplotype frequencies) from the other two rookeries in Brazil: Atol das Rocas and Fernando de Noronha (Bjorndal et al. 2006; Shamblin et al. 2015) and contribute to mixed stocks in foraging grounds of green turtles at different life stages along the Brazilian coastline (Naro-Maciel et al. 2007; Proietti et al. 2012; Jardim et al. 2016).

Trindade should be considered an important index nesting site for green turtles globally, because it represents the southern-most limit of green turtle nesting in the Atlantic region and is one of few nesting sites in the South Atlantic—a region identified as requiring more attention for sea turtle studies (Rees et al. 2016). The nesting aggregation has been protected from exploitation since 1965, although Trindade has undergone serious habitat degradation.

Projeto TAMAR (a Brazilian conservation program) with the support of the Brazilian Navy has monitored the green turtle nesting aggregation at Trindade since 1982 (Filippini and Bulhões 1988; Moreira et al. 1995; Marcovaldi and Marcovaldi 1999; Almeida et al. 2011). The remote location and challenging logistics have made monitoring difficult. From 1982 to 2009, surveys were conducted during 17 non-consecutive nesting seasons with large temporal and spatial differences in patrol efforts. The types of data collected varied because teams and goals were different among years. Almeida et al. (2011) evaluated the trend in nest numbers and presented biometric data for green turtles nesting on Trindade. Based on these results, Projeto TAMAR developed a revised strategy in 2008 for future research and monitoring with consistent

survey efforts focused on the two beaches with greatest nest abundance—Andradas and Tartarugas.

We estimate the nesting probability and number of nests for the 2 main green turtle nesting beaches at Trindade Island that were monitored from 2009 through 2016. We integrate within-season patterns of nesting probability with spatial and temporal patterns of nest distribution, so that management efforts on Trindade can be focused on areas and times most important to protect and to monitor the green turtle nesting aggregation. Long-term trends are apparent for other Atlantic green turtle rookeries (Mazaris et al. 2017), so we assess the long-term trend in Trindade nest abundance from 1991 through 2016 using previous estimates for the period from 1991 through 2008 (Almeida et al. 2011).

Materials and methods

Study area and history

Trindade Island (20.5° S, 29.3° W) is of volcanic origin and is part of the Vitória–Trindade seamount ridge (Barth 1958; Fig. 1). The island is located 1140 km off the coast of Espírito Santo state, southeastern Brazil, and has an area of about 8 km². Trindade is surrounded by oligotrophic waters under the influence of the warm Brazil Current (Peterson and Stramma 1991) with deep waters ranging from 4000 to 5000 m depth (Barth 1958). Green turtles nest on nine beaches on Trindade (Cabritos, Portugueses, Calheta, Andradas, Tartarugas, Parcel, Túnel, Ponta do Túnel, and Príncipe; Fig. 1) during austral summer, from December to June, with more than 95% of emergences occurring from 1 December to 30 April (Almeida et al. 2011). All beaches are relatively narrow, except Tartarugas beach, and the coastline has a narrow shelf with sedimentary coral reefs (Barth 1958; Leal and Bouchet 1991).

The majority of green turtle nests is deposited on Andradas and Tartarugas beaches (Fig. 2). Andradas beach is approximately 200 m long and 57 m wide. Its sediments are characterized by a granulometry ranging from medium to coarse, with the upper beach also comprising fallen blocks from the erosion of the hills close to the beach. Tartarugas beach is approximately 310 m long and 470 m wide and has the largest sedimentary stock among the island's beaches, with sediments characterized by medium sand granulometry and a vast dune field in the upper portion of the beach. The mineralogy of Andradas and Tartarugas are similar, and these beaches, together with Calhetas beach, constitute the beaches with the highest percentage (50–60%) of biogenic limestone (Pinheiro 2017; Olsen 2020).

Evaluations of population trends should consider the history—both recent and historical—of threats to and protection of the population. On Trindade up until the recent past,

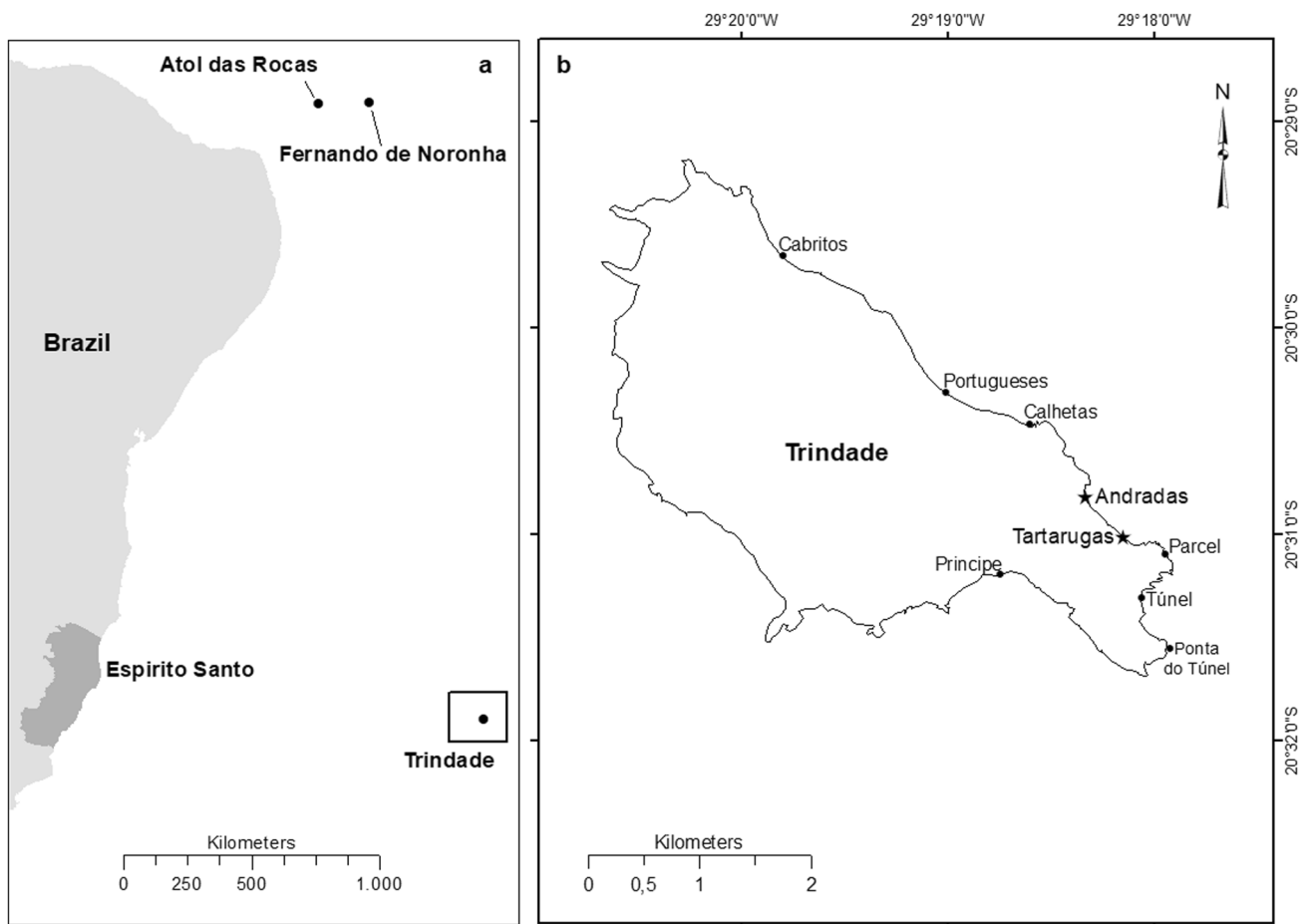
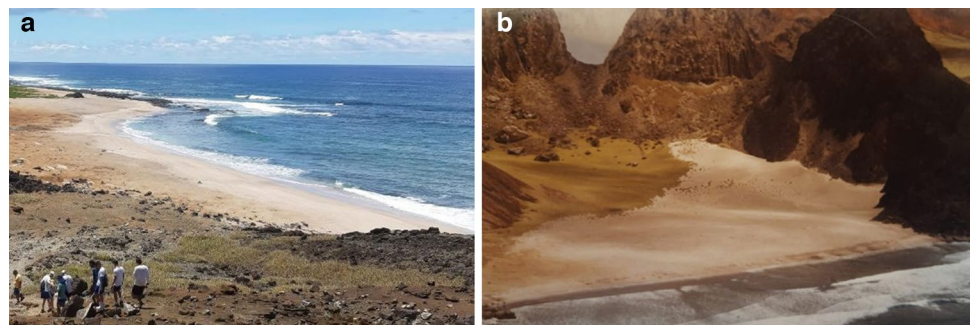


Fig. 1 Map of study area. **a** Green turtle rookeries in the southwestern Atlantic Ocean: Atol das Rocas, Fernando de Noronha, and Trindade Island; **b** study area with the nine nesting beaches on Trindade

Island. The black stars indicate Andradas and Tartarugas beaches, surveyed in the present study, and the black dots indicate the other nesting sites of green turtles on Trindade

Fig. 2 Main nesting beaches. **a** Andradas beach, **b** Tartarugas beach



effects of introduced species on abundance of green turtles nesting on Trindade would have been great and almost certainly continue to the present. The Brazilian Navy has controlled Trindade since 1957. Access to the island is restricted to Navy personnel (~ 35 people), staff of the weather station, and visiting scientific researchers under permits and support from the Navy. The only buildings on the island are the Navy headquarters, the weather station, and a research station.

The Brazilian government, through the Navy, has provided excellent management and protection for the natural resources of Trindade in recent decades in collaboration with the Pro-Trindade Program through the CIRM (Comissão Interministerial para os Recursos do Mar). Sea turtles have been completely protected from any direct human disturbance. However, Trindade has a long history of exploitation and introduction of exotic animals and plants that

caused significant loss of local biodiversity and vegetation cover that resulted in severe habitat changes and soil erosion (Duarte and Horta 2012). In the early and mid-eighteenth century, goats (*Capra hircus*), pigs (*Sus scrofa*), sheep (*Ovis aries*), domestic cats (*Felis catus*), mice (*Mus musculus*), and Guinea fowl (*Numida meleagris*) were introduced and established breeding populations. Donkeys (*Equus asinus*) were introduced in the early twentieth century. The original flora that covered 85% of Trindade decreased to less than 5% as a result (Alves et al. 2011). The Navy eliminated sheep, pigs, and donkeys by 1965, cats in 1998, and goats in 2005 (Alves et al. 2011; Silva and Alves 2011). Vegetation is now recovering. These long-term habitat modifications may have substantially increased sediment transfer from inland areas to the beaches, changing beach composition, particle size and albedo which in turn could affect emergence success and primary sex ratios of sea turtle clutches. Hogs depredated many green turtle nests; Barth (1958) suggested that green turtles would disappear from Trindade unless hog populations were eradicated. Predation by cats, a known predator on green turtle hatchlings on Ascension Island (Mortimer 1981; Glen et al. 2006) may have had an impact on Trindade green turtles.

Large populations of yellow land crabs (*Johngarthia [Gecarcinus] lagostoma*) can be found throughout Trindade, and recovery of vegetation on Trindade may have allowed the crab populations to increase. Although the Brazilian list of threatened species includes the yellow crab as an endemic species of Brazilian islands (MMA 2018), Soto (2009) suggests that the yellow land crab may not be native to Trindade based on an account from 1675 and another from the 1790s that did not record the presence of these crabs. Yellow land crabs reduce hatchling production by preying on green turtle eggs and on hatchlings on route from the nest to the sea (Bellini and Sales 1992; Santos et al. 2016).

Surveys

Each nesting season bridges two calendar years; we use the convention of identifying a season by its first year (e.g., the season beginning in Dec 2009 is referred to as 2009). For this study, during seven non-consecutive nesting seasons from 2009 to 2016 (the season 2013 was not monitored), surveys were conducted on foot on the two major nesting beaches (Andradas and Tartarugas), which comprise about 54% of track counts (Almeida et al. 2011). To detect the first nesting occurrence, morning surveys were conducted daily starting at sunrise in late November. After the first nesting activity was observed, the full survey protocol was initiated with both day and night surveys.

Daily morning surveys were conducted on both beaches between 0600 and 0800 h to record the total number of tracks created during the previous night without determining

whether or not a track resulted in a nest. Tracks were obliterated to avoid including them in subsequent counts. Night surveys were conducted each night from 1800 to 0600 h, alternating between Andradas and Tartarugas beaches, until the end of the nesting season. During each night survey, the beach was patrolled on foot to determine what proportion of tracks resulted in nests for a random sample of tracks (with no set number) and to apply metal tags (Inconel, style 681 National Tag and Band Co.) to the trailing edge of each female's front flippers between the first and second proximal scales. Data from the night patrols were used to determine nesting probability—the probability that an emergence will result in egg deposition—and to convert track counts to nest counts.

In the 2016 season, patrols were shortened to between 0500 and 0600 h for morning surveys and to between 1900 and 0500 h for night surveys. This reduction in survey effort did not affect our estimates of nesting probability, except to decrease sample size, but may have resulted in a slight decrease in track counts, and thus nest abundance, in our last survey year.

Estimation of annual track counts

Numbers of tracks on Andradas and Tartarugas were estimated for each nesting season from 2009 through 2016 except for 2013, following Almeida et al. (2011). Numbers of tracks made on each beach were recorded during each morning survey. The start and end of the nesting season were based on track distribution patterns and set as 15 November and 30 May, or 29 May in leap years. These are the same end points used in Almeida et al. (2011) so our results are comparable. A value of zero tracks was assigned to each end point. We differentially weighted the actual count values (= 1) and the set end points (= 0.1), except the November endpoint of 2014 and both endpoints of 2015 and 2016 were given a weight of 1.0, because no track surveys were conducted near those endpoints. The total number of tracks for each beach in each nesting season was estimated using a generalized additive model (GAM) function, `gam()` of Spotfire S-plus software (version 8.2).

Estimation of nesting probability

Numbers of tracks for each beach in each year were converted to numbers of nests using nesting probabilities generated for each beach in each year. Nesting probability of green turtles on each beach was derived from the 4706 observed emergences that were known to either result in a nest or no nest over seven sampling years (2009–2016, excluding 2013). These binary data (0 = no clutch laid, 1 = clutch laid) for each observed track were sampled from a Bernoulli probability distribution and so was

appropriately modelled using a regression model with Bernoulli likelihood—which is a special case of a binomial likelihood model but with a single trial (Congdon 2003). Modelling the individual nesting probability for each green turtle using a regression model with Bernoulli likelihood supports inclusion of turtle-specific information such as nest history, time of season and nest location (beach). The turtle-specific nesting probability was then estimated within a Bayesian modelling framework using the Stan computation engine (Carpenter et al. 2017) via the brms interface (Bürkner 2017). Specifically, a varying-coefficient generalized additive mixed regression model (GAMM: Fahrmeir and Lang 2001) with Bernoulli likelihood was fitted to the nesting probability data accounting for nonlinear temporal (season) effects for each beach, month within the season of the observation for each beach, and the beach-specific nonlinear density of monthly observed tracks recorded for each season. The unique identity of each tagged turtle was also included as a random effect to account for annual sampling variability due to a range of potentially informative factors, such as different field observers, sampling effort, and season-specific weather conditions impacting sampling. Simpler models without separate beach-specific effects (so no varying-coefficient structure) were fitted for comparison.

All models were implemented using weakly informative regularizing priors (Lemoine 2019) with posterior samples sourced from 4 chains and 5000 iterations after a warmup of 1000 iterations per chain. Therefore, the posterior for each estimate comprised 16,000 samples or draws that were used to derive the quantile-based uncertainty estimates (also known as equal-tailed credible intervals in Bayesian statistics parlance; Kruschke and Liddell 2018). A probability statement about the existence of a particular effect, such as beach-specific effects, can be determined with those 16,000 draws using the probability of direction metric proposed by Makowski et al. (2019). Convergence diagnostics such as effective posterior sample size and the Gelman–Rubin statistic ($R_{hat} < 1.01$) reflected convergence of all Bayesian models used here (Gelman and Hill 2007). Model selection was based on leave-one-out cross-validation metrics to estimate any comparative difference in expected predictive accuracy between the various models fitted (Vehtari et al. 2017). The weight of evidence in favor of one model over any other candidate models was also assessed using Bayesian stacking, which is the Bayesian analogue of model averaging (Yao et al. 2018). Further evaluation of the best-fit-model was then assessed using graphical posterior predictive checks (Gabry et al. 2019). All inference was then made using the best-fit model.

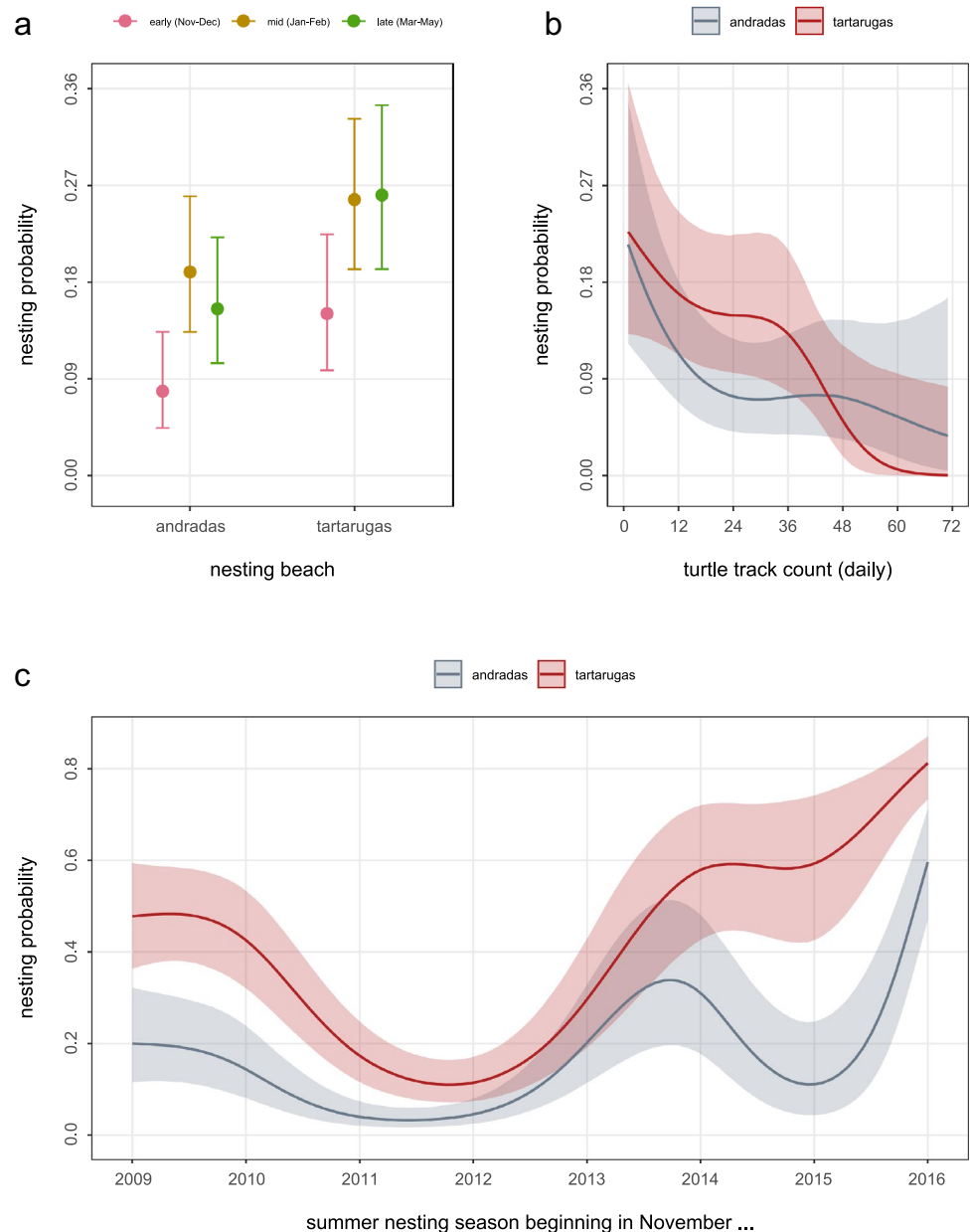
Estimation of annual nest abundance

We used an empirical Bayes approach (Casella 1985; Robinson 2017) based on the estimated nesting probabilities and annual track counts to derive the expected number of nests laid each year on each of the two beaches. Specifically, we estimated the Beta distribution parameters for the beach-specific nesting probabilities (Fig. 3c) using the *fit-distr()* function from the MASS package for R (Venables and Ripley 2002). Using those Beta sampling distribution parameters for each beach, we then derived the mean posterior annual nest abundance and the 95% quantile-based uncertainty intervals (Kruschke and Liddell 2018) for each beach by sampling from a Beta-binomial likelihood (Dorazio et al. 2013; Robinson 2017). Therefore, we derived the expected annual nest count from annual track counts given the annual nesting probability for each beach by simulating from the following two-stage function using 1000 trials: $nests_i \sim \text{Binomial}(N_i, p_j)$, where N_i = annual track counts in each year (i) and $p_j \sim \text{Beta}(a_j, b_j)$ with the parameters (a, b) estimated from the distribution of annual nesting probabilities for each beach (j). Simulations were conducted using R (R Core Team 2020) and summarized using the tidybayes package for R (Kay 2020). We could of course simulate directly using a one-stage beta-binomial likelihood approach but the two-stage formulation outlined above makes the simulation procedure more transparent and intuitive for ecologists while providing the same outcome.

Long-term nest abundance trend

A Gompertz density-dependent population dynamics model (Dennis and Ponciano 2014; Anderson et al. 2017; Muniz Leão et al. 2018) was then fitted within a Bayesian state-space modelling framework (Pedersen et al. 2011) with robust Student-t likelihood (Járez and Steel 2010) to the annual nest abundance estimates using JAGS via the rjags package for R (Plummer 2015, 2016). A state-space model is a hierarchical model that enables the precision (observation component) in the annual nest abundance estimates at the Trindade rookery to be accounted for in the estimation of the long-term trend (process component). It also accounts for any temporal correlation in the annual nest abundance time series and for any missing data (Dennis and Ponciano 2014; Pedersen et al. 2011). A Student-t likelihood is appropriate as it is robust to outliers in the observed time series (Anderson et al. 2017). Density-dependent demographic processes are known for marine turtle populations (Bjorndal et al. 2000), further supporting the use of an explicit population dynamics model to determine any long-term trend in the estimated Trindade nest abundance, which comprises the estimates from Almeida et al. (2011) for 1991–2008 and the current

Fig. 3 Expected beach-specific probability that a green turtle that emerged onto the beach successfully deposited eggs for the nesting seasons from 2009 to 2016, **a** expected intra-seasonal beach-specific nesting probabilities, **b** expected nonlinear beach-specific effect of recorded track density on nesting probability, **c** expected annual trend in the beach-specific green turtle nesting probability. In panel **a** the solid dot = posterior mean estimate, vertical bar = 95% uncertainty interval. Solid curves in panels **b**, **c** show the estimated posterior mean effect with the shaded areas showing the 95% pointwise uncertainty bands



study (2009–2016). Unlike for the current study, there were no precision estimates for the nest abundance estimates for the time series from 1991 to 2008 (Almeida et al. 2011), so the observation process here is unweighted for the entire time series from 1991 to 2016. In addition, of course, the annual nest abundance data series were derived from two different methods, so caution in interpretation of any inferred trend using the combined time series is warranted. An excellent introduction to the use of state-space models for modelling ecological time series data can be found in Auger-Méthé et al. (2021).

Results

Abundance and temporal distributions of the numbers of tracks on Andradas and Tartarugas were estimated for each nesting season from 2009 through 2016 except for 2013 (Figs. S-1, S-2). Beach-specific annual counts of observed tracks and beach-specific annual estimates of total tracks generated by GAM analyses are presented in Table S-1. Number of observed tracks between 15 November and 30 May each year vary from 409 to 1808 on Andradas and

from 536 to 2347 on Tartarugas. Estimated total track counts between 15 November and 30 May each year range from 588 to 3317 for Andradas and from 760 to 3559 for Tartarugas.

For nesting probability, the best-fit model is the varying coefficient GAMM with Bernoulli likelihood and beach-specific nonlinear temporal trends and beach-specific recorded track density effects (difference = -2, SE = 2.9). The weight of evidence is 75% in support of this model compared to a similar model but without nonlinear beach-specific track density effect. However, the summary results are similar irrespective of which model is used to derive any inference, and the posterior predictive check tests are also similar, indicating well-fitting models.

The estimated beach-specific nesting probabilities from the model with beach-specific track density effects are shown in Fig. 3. Nesting probabilities are lower at Andradas than at Tartarugas for all months (Fig. 3a) and generally decline with increasing track density at both beaches (Fig. 3b). Nesting probabilities also fluctuate among years at both beaches but are generally lower for all years at Andradas (Fig. 3c). The overall mean beach-specific nesting probabilities summarized for all years are 0.22 (95% HDI = 0.14–0.30) for Andradas and 0.45 (95% HDI = 0.37–0.53) for Tartarugas. HDI is the highest posterior density interval (Kruschke and Liddell 2018). The probability of direction of a beach-specific effect was 0.99, so we are 99% certain that the overall expected nesting probability is higher at Tartarugas than at Andradas.

The expected numbers of nests laid each season at the 2 nesting beaches are relatively constant from season to season

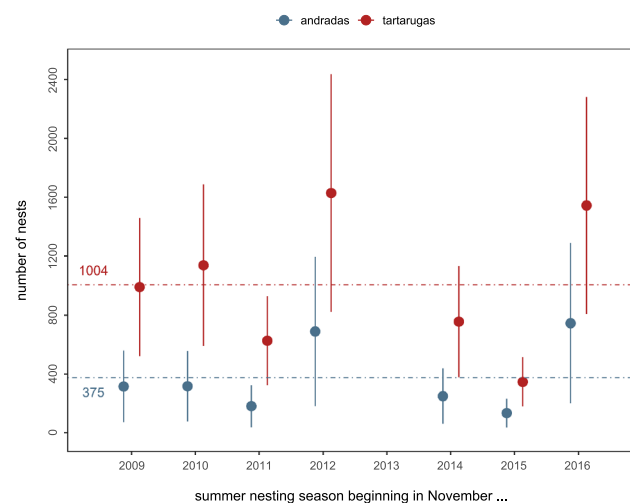


Fig. 4 Expected beach-specific number of nests laid each season. solid dot = posterior mean estimate, vertical bar = ± 1 standard deviation of the posterior samples, dashed horizontal lines show the expected long-term means (375 nests on Andradas, 1004 nests on Tartarugas)

but with significant peaks in the 2012 and 2016 seasons at both beaches (Fig. 4). Significantly more nests are estimated at Tartarugas than Andradas in most seasons, which follows from the higher recorded seasonal track counts and higher estimated nesting probability at Tartarugas (Fig. 3c) used to derive the annual nest counts. On average, about 1000 egg clutches and 400 egg clutches are laid each season at Tartarugas and Andradas, respectively (Fig. 4). There was no meaningful long-term trend in the estimated annual nest abundance since 1991 (Fig. 5), although the trend estimate for the period from 1991 to 2008 is quite imprecise.

Discussion

Patterns of nesting probability

Despite being in close proximity on Trindade (Fig. 1)—only separated by a volcanic rock formation (Castro 2010)—Tartarugas has significantly higher nesting probability within and across nesting seasons than Andradas (Fig. 3a, c). The mean beach-specific nesting probabilities summarized for all years are 0.22 (95% HDI = 0.14–0.30) and 0.45 (95% HDI = 0.37–0.53) for Andradas and Tartarugas, respectively. These values are consistent with the pattern and within the ranges estimated for 4 years between 1999 and 2008 by Almeida et al. (2011): 0.17–0.57 for Andradas and 0.34–0.69 for Tartarugas. The lower nesting probability on Andradas is apparently not the result of the smaller beach area increasing the probability of disturbance from other nesting females,

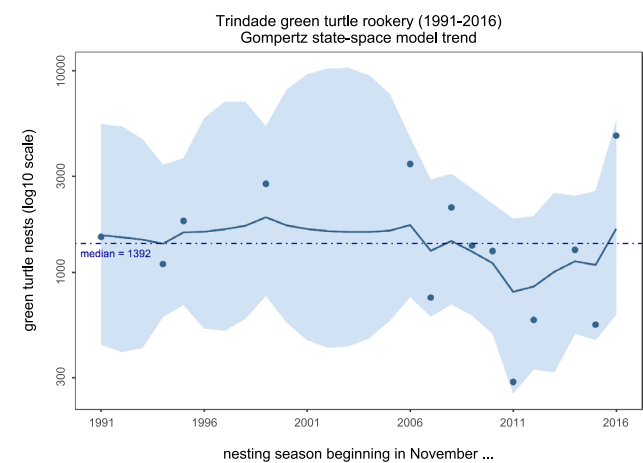


Fig. 5 Estimated nest abundance trend at the Trindade green turtle rookery derived using a density-dependent Gompertz population dynamics model. Solid dots are the annual nest counts derived from the estimated annual nest abundance for this study and Almeida et al. (2011). Solid curve shows the expected model trend fitted to those annual estimates, polygon shows the 95% credible region for that trend. The estimates (solid dots) for 1991–2008 from Almeida et al. (2011) and for 2009–2016 from the current study

because the two beaches have a similar relationship between nesting probability and daily turtle track counts (Fig. 3b). The lower nesting probability on Andradas may be a result of its coarser granulometry compared to that of Tartarugas (Pinheiro 2017; Olsen 2020; Mohd Salleh et al. 2021). On Ascension and Aldabra islands, green turtles have more difficulty digging egg chambers in those covehead beaches that have coarser sand and must make multiple attempts and emerge on successive nights before depositing eggs (Mortimer and Carr 1987; Mortimer 1990; Godley et al. 2001).

Nesting probabilities of green turtles nesting on Andradas are either below or in the low range of values reported for other green turtle nesting aggregations throughout the Atlantic, whereas values for Tartarugas are more similar to those values. Similar to Trindade, green turtles nest on several beaches on Ascension Island. In 2012, nesting probabilities ranged from 0.15 to 0.51 among the beaches with an overall value of 0.34 (0.31–0.37 95% Confidence Interval) for all beaches on Ascension (Weber et al. 2014). In Cuba, nesting probabilities of green turtles at two beaches over 4 years ranged from 0.50 to 0.78 and differed significantly between beaches and among years (Azanza-Ricardo et al. 2003). At Tortuguero, Costa Rica, nesting probability for green turtles ranged from 0.33 to 0.74 among years from 1972 to 2000 (Tiware 2004). Mean annual nesting probability over an 11-year period was 0.48 for green turtles in Florida, USA (Weishampel et al. 2003), and 0.38 from a 5-year study of green turtles on Samandağ Beach, Turkey (Yalçın-Özdilek 2007).

Nesting probability is lower in the first part of the nesting season compared to later in the season on both beaches (Fig. 3a). A similar pattern was reported for green turtles nesting at Ascension Island (Mortimer 1981) and Tortuguero, Costa Rica (Tiware 2004), hawksbills (*Eretmochelys imbricata*) in the Seychelles (Mortimer and Bresson 1999), and loggerheads (*Caretta caretta*) at Mon Repos, Australia (Pfäller et al. 2008). This increase in nesting probability as the season progresses may be a result of renesting turtles becoming more experienced (Pfäller et al. 2008).

Population assessment

Based on beach-specific nest abundance from 2009 to 2016 at Andradas and Tartarugas (Fig. 3), the nesting aggregation appears to be stable. However, as noted repeatedly (e.g., Bjørndal et al. 1999), trends in nest abundance do not always mirror trends in female abundance because of variation in clutch frequency (the number of clutches laid by a female each year). The stable trend in nest abundance for the two beaches has apparently extended over 26 years (1991–2016) (Fig. 5). Tartarugas has significantly higher nest abundance than Andradas (Fig. 3), perhaps because Tartarugas has a

substantially larger area of nesting and a higher probability of nesting compared to those of Andradas (Fig. 2a, b).

The apparent stability of the Trindade nesting aggregations based on annual nest abundance is in contrast to recent reports of other green turtle nesting aggregations globally. Several reports have indicated that populations of green turtles are now recovering in many areas as a result of long-term conservation efforts (Chaloupka et al. 2008; Weber et al. 2014; Mazaris et al. 2017). Why the Trindade aggregation is not increasing is a matter for careful consideration. Given the heavy depredation on nesting females and eggs before 1965 and the ongoing high mortality of green turtles on foraging grounds along the southern coast of Brazil, some of which are known to derive from Trindade (Cantor et al. 2020), it is unlikely that the Trindade aggregation is at carrying capacity. An analysis of carrying capacity and density-dependent population regulation similar to those carried out at the green turtle rookeries in Tortuguero, Costa Rica, and French Frigate Shoals, Hawaii, may yield valuable insights (Tiware et al. 2006, 2010).

Most population assessments have the objective not only to discern the past and current population trends of sea turtle populations, but also to gain some insight into future stability and trends by incorporating demographic parameters, such as recruitment and survival rates (National Research Council 2010). In this regard, nest counts alone may be misleading unless hatchling emergence success (the percentage of eggs in a nest that produce viable hatchlings at the beach surface) or hatchling production are sufficiently high and consistent among years to support adequate recruitment into the breeding population. The green turtle nesting aggregation on Raine Island has provided an excellent example of this issue (Booth and Dunstan 2018).

Nest counts alone, however, will continue to be a common metric because of (1) the decades-long datasets of nest counts that now exist for many nesting aggregations and (2) the logistic constraints of extending the length of monitoring seasons to add hatchling emergence success and/or hatchling production. Monitoring populations over the months-long nesting and hatching seasons is logistically challenging and requires substantial investments of time and funds. Monitoring remote nesting beaches greatly increases these challenges. Subsampling is an important approach to lessen investments of time and funds, but designing such sampling regimes is challenging (National Research Council 2010). Accurate subsamples require an understanding of within and among season variation in nesting (or track counts and nesting probability) and hatchling emergence success to design and interpret sampling regimes.

Survival rates of hatchlings from nest to sea is an aspect of hatchling production that should be considered when estimating recruitment of hatchlings into the ocean. Although mortality during this brief stage can have a substantial effect,

it has rarely been quantified (but see Santidrián-Tomillo et al. 2010; Santos et al. 2016; Erb and Wyneken 2019; Villegas Vindiola 2019) and deserves more attention. Predation on hatchlings by yellow land crabs on Trindade (Bellini and Sales 1992; Santos et al. 2016) should be further quantified.

Stability of nesting aggregations also relies on survival of sea turtles away from the nesting beach. Over the past decades, anthropogenic threats, such as marine pollution (Santos et al. 2015; Rizzi et al. 2019) and bycatch in fisheries (Gallo et al. 2006; Lopez et al. 2015; Monteiro et al. 2016), have had increasing impacts on sea turtle survival on their foraging grounds. Therefore, monitoring foraging aggregations is also necessary to assess stability of reproductive aggregations. Aggregations on foraging grounds comprise individuals from distinct natal origins (mixed stocks; Bjørndal and Bolten 2008; Jensen et al. 2013). Green turtles from Trindade contribute to several foraging aggregations of all life stages along the Brazilian coastline (Naromaciel et al. 2007; Proietti et al. 2012; Jardim et al. 2016). Recently, large-scale surveys of sea turtle carcasses stranded along coastlines of the Brazilian states of Rio de Janeiro, São Paulo, Paraná, and Santa Catarina revealed that large numbers of juvenile green turtles are being removed from populations in the Southwest Atlantic (Cantor et al. 2020; Guimarães et al. 2021), many from bycatch in commercial fisheries. Because of this high mortality of juveniles, some of which would have recruited to the Trindade nesting aggregation, and the late sexual maturity of green turtles (over 40 years; Avens and Snover 2013), the number of nests at Trindade may not remain stable and might decrease in the future.

Future research and management at Trindade

This study has revealed important topics for future research and management on Trindade. Hatchling emergence success should be determined for large samples of nests, including those that fail to produce any hatchlings. In this age of rising sea levels and beach temperatures, monitoring hatchling emergence success and hatchling production should be among the goals for monitoring sea turtle nesting aggregations particularly because of the increased risk of “invisible” nest lost due to drowning by rising groundwater levels and increasing temperatures exceeding lethal levels. Recent reviews of the effects of climate change on sea turtles (Patrício et al. 2021) and research priorities for sea turtles (Hamann et al. 2010; Rees et al. 2016) emphasize the importance of monitoring emergence success and hatchling production.

Survival rates of hatchlings during their movements from nest to surf should also be evaluated, possibly by

assessing the fates of hatchlings by following their tracks from the nests. The extent of variation within and among nesting seasons in nest abundance and nesting probability for Andradas and Tartarugas demonstrates the need to have estimates of these parameters for the other 7 nesting beaches on Trindade. Although Andradas and Tartarugas are the primary nesting beaches, the other 7 beaches had approximately 46% (range: 45–47%) of the track counts in the three years (1999, 2006, 2007) during which all nesting beaches were surveyed (Almeida et al. 2011). Intermittent monitoring of the other 7 beaches could avoid serious errors in prediction of population stability for Trindade and may reveal necessary management actions, such as for extremely low hatchling emergence success on some beaches.

Successful removal of most of the feral species on Trindade by the Navy has greatly improved environmental quality of the entire island of Trindade. Continued efforts are needed to control introduced animals (e.g., mice and, perhaps, yellow land crabs) and support the regrowth of natural vegetation to prevent the transfer of inland sediment onto the nesting beaches. As Soto (2009) emphasized, future studies should focus on whether the yellow land crab is a native or introduced species and on the extent of predation on eggs and hatchlings by yellow land crabs (Santos et al. 2016). If crabs pose a significant threat to hatchling survival, appropriate management actions—which would depend on whether the crabs are native—should be considered.

In 2018, ICMBio, the Federal Agency for Biodiversity, created a marine protected area called Área de Proteção Ambiental de Trindade e Martim Vaz in the area around Trindade. This Conservation Unit will make it possible to increase the number of expeditions to Trindade, expand research actions, and monitor and mitigate impacts such as fisheries.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-022-04054-7>.

Acknowledgements We thank the Brazilian Navy (Marinha do Brasil, 1° Distrito Naval) for providing logistical support for nesting surveys since the 1980s. We thank Bruno Giffoni for his assistance with preparation of the manuscript. We also thank the many volunteers who worked over the years collecting data and made this study possible. We appreciate the efforts of two anonymous reviewers whose comments helped improve the manuscript.

Author contributions All authors contributed to the study conception and design. Material preparation and data collection were performed by LM, EMM, AS, AM, JCAT and MÂM. Data analyses were performed by LM, MC, ABB, AS and KAB. The first draft of the manuscript was written by Luciana Medeiros, and all authors commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

Funding Our study was funded essentially from Visitor Centers and Stores that are part of the circular economy program of Fundação Projeto TAMAR, a private nonprofit organization.

Availability of data and materials The dataset analyzed during the current study is not publicly available because the authors have other manuscripts in progress. However, the data are available from Projeto TAMAR upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval All procedures performed in studies involving animals were in accordance with the ethical standards of the Centro TAMAR-ICMBio and conducted under SISBIO permit 28938–3 from the Brazilian Ministry of the Environment.

References

- Almeida AP, Moreira LMP, Bruno SC, Thomé JCA, Martins AS, Bolten AB, Bjorndal KA (2011) Green turtle nesting on Trindade Island, Brazil: abundance, trends, and biometrics. *Endang Species Res* 14:193–201. <https://doi.org/10.3354/esr00357>
- Alves RJV, da Silva NG, Aguirre-Muñoz A (2011) Return of endemic plant populations on Trindade Island, Brazil, with comments on the fauna. In: Veitch CR, Clout MN, Towns R (eds) *Island invasives: eradication and management*. IUCN, Gland, Switzerland, pp 259–263
- Anderson S, Branch T, Cooper A, Dulvy N (2017) Black-swan events in animal populations. *PNAS* 114:3252–3257
- Angert AL (2009) The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. *PNAS* 106:19693–19698. <https://doi.org/10.1073/pnas.0901652106>
- Auger-Méthé M, Newman K, Cole D, Empacher F, Gryba R, King A, Leos-Barajas V, Mills Flemming J, Nielsen A, Petris G, Thomas L (2021) A guide to state–space modeling of ecological time series. *Ecol Monogr* 91:e01470. <https://doi.org/10.1002/ecm.1470>
- Avens L, Snover ML (2013) Age and age estimation in sea turtles. In: Wyneken J, Lohmann KJ, Musick JA (eds) *The biology of sea turtles*, vol 3. CRC Press, Boca Raton, pp 97–133
- Azanza-Ricardo J, Ibarra ME, Espinosa G, Diaz R, Sanson G (2003) Conducta de anidacione la Tortuga Verde (*Chelonia mydas*) en las playas Antonio y Caleta de los Piojos de la Peninsula de Guanahacabibes, Pinar del Rio, Cuba. *Rev Inv Mar* 24:231–240
- Barth R (1958) Observações biológicas e meteorológicas feitas na Ilha de Trindade. *Mem Inst Oswaldo Cruz* 56:261–279. <https://doi.org/10.1590/S0074-02761958000100013>
- Bellini C, Sales G (1992) Registro de predação de ovos e neonatos de tartaruga marinha aruanã, *Chelonia mydas* em ilhas oceânicas brasileiras. In: Congresso Brasileiro de Zoologia, p 132
- Berggren A, Bjorkman C, Bylund H, Ayres MP (2009) The distribution and abundance of animal populations in a climate of uncertainty. *Oikos* 118:1121–1126. <https://doi.org/10.1111/j.1600-0706.2009.17558.x>
- Bjorndal KA, Bolten AB (2008) Annual variation in source contributions to a mixed stock: implications for quantifying connectivity. *Mol Ecol* 17:2185–2193
- Bjorndal KA, Jackson JBC (2003) Roles of sea turtles in marine ecosystems: reconstructing the past. In: Lutz PL, Musick J, Wyneken J (eds) *Biology of sea turtles*, vol II. CRC Press, Boca Raton, pp 259–273
- Bjorndal KA, Wetherall JA, Bolten AB, Mortimer JA (1999) Twenty-six years of green turtle nesting at Tortuguero, Costa Rica: an encouraging trend. *Conserv Biol* 13:126–134
- Bjorndal KA, Bolten AB, Chaloupka M (2000) Green turtle somatic growth model: evidence for density-dependence. *Ecol Appl* 10:269–282
- Bjorndal KA, Bolten AB, Moreira L, Bellini C, Marcovaldi MA (2006) Population structure and diversity of Brazilian green turtle rookeries based on mitochondrial DNA sequences. *Chelonian Conserv Biol* 5:262–268. [https://doi.org/10.2744/1071-8443\(2006\)5\[262:PSADOB\]2.0.CO;2](https://doi.org/10.2744/1071-8443(2006)5[262:PSADOB]2.0.CO;2)
- Bolten AB (2003) Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz PL, Musick JA, Wyneken J (eds) *The biology of sea turtles*. CRC Press, Boca Raton, pp 243–258
- Booth DT, Dunstan A (2018) A preliminary investigation into the early embryo death syndrome (EEDS) at the world's largest green turtle rookery. *PLoS ONE* 13:e0195462. <https://doi.org/10.1371/journal.pone.0195462>
- Bürkner PC (2017) brms: An R Package for Bayesian multilevel models using Stan. *J Stat Softw* 80:1–28. <https://doi.org/10.18637/jss.v080.i01>
- Cantor M, Barreto AS, Taufer RM, Giffoni B, Castilho PV, Maranhão A, Beatriz C, Kolesnikovas C, Godoy D, Rogério DW, Dick JL, Groch KR, Rosa L, Cremer MJ, Cattani PE, Valle RR, Domit C (2020) High incidence of sea turtle stranding in the southwestern Atlantic Ocean. *ICES J Mar Sci* 77:1864–1878. <https://doi.org/10.1093/icesjms/fsaa073>
- Carpenter B, Gelman A, Hoffman M, Lee D, Goodrich B, Betancourt M, Brubaker M, Guo J, Li P, Riddell A (2017) Stan: a probabilistic programming language. *J Stat Softw* 76:1–32. <https://doi.org/10.18637/jss.v076.i01>
- Casella G (1985) An introduction to Empirical Bayes data analysis. *Am Stat* 39:83–87. <https://doi.org/10.1080/00031305.1985.10479400>
- Castro JWA (2010) Ilhas oceânicas da Trindade e Fernando de Noronha, Brasil: uma visão da Geologia ambiental. *Revista De Gestão Costeira Integrada J Integr Coast Zone Manag* 10:303–319
- Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB, Ehrhart LM, Limpus CJ, Suganuma H, Yamaguchi TSM (2008) Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Glob Ecol Biogeogr* 17:297–304. <https://doi.org/10.1111/j.1466-8238.2007.00367.x>
- Congdon P (2003) *Applied Bayesian modelling*. Wiley, Hoboken
- Costanza R, Andrade F, Antunes P, van den Belt M, Boersma D, Boesch DF et al (1998) Principles for sustainable governance of the oceans. *Science* 281:198–199
- Dennis B, Ponciano J (2014) Density dependent state space model for population abundance data with unequal time intervals. *Ecology* 95:2069–2076
- Dorazio R, Martin J, Edwards H (2013) Estimating abundance while accounting for rarity, correlated behavior, and other sources of variation in counts. *Ecology* 94:1472–1478. <https://doi.org/10.1890/12-1365.1>
- Duarte RH, Horta GCMM (2012) Barth and the Trindade Island, 1957–1959. *Hist Cienc Saude Manguinhos* 19:951–968. <https://doi.org/10.1590/S0104-59702012000300010>
- Dutton D, Dutton P, Chaloupka M, Boulon R (2005) Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biol Conserv* 126:186–194

- Erb V, Wyneken J (2019) Nest-to-surf mortality of loggerhead sea turtle (*Caretta caretta*) hatchlings on Florida's east coast. *Front Mar Sci* 6:271. <https://doi.org/10.3389/fmars.2019.00271>
- Esteban N, Mortimer JA, Hays GC (2017) How numbers of nesting sea turtles can be overestimated by nearly a factor of two. *Proc R Soc B* 284:20162581. <https://doi.org/10.1098/rspb.2016.2581>
- Fahrmeir L, Lang S (2001) Bayesian inference for generalised additive mixed models based on Markov random field priors. *Appl Stat* 50:201–220. <https://doi.org/10.1111/1467-9876.00229>
- Filippini A, Bulhões HA (1988) Estudo da ecologia da tartaruga marinha *Chelonia mydas* Linnaeus, na Ilha da Trindade. *Bras Florest* 65:5–15
- Gabry J, Simpson D, Vehtari A, Betancourt M, Gelman A (2019) Visualization in Bayesian workflow. *J R Soc Ser A* 182:1–14. <https://doi.org/10.1111/rssa.12378>
- Gallo BMG, Macedo S, Giffoni BB, Becker JH, Barata PCR (2006) Sea turtle conservation in Ubatuba, southeastern Brazil, a feeding area with incidental capture in coastal fisheries. *Chelonian Conserv Biol* 5:93–101. [https://doi.org/10.2744/1071-8443\(2006\)5\[93:STCIUSJ\]2.0.CO;2](https://doi.org/10.2744/1071-8443(2006)5[93:STCIUSJ]2.0.CO;2)
- Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York
- Glen F, Broderick AC, Godley BJ, Hays GC (2006) Thermal control of hatchling emergence patterns in marine turtles. *JEMBE* 334:31–42. <https://doi.org/10.1016/j.jembe.2006.01.005>
- Godley BJ, Broderick AC, Hays GC (2001) Nesting of green turtles *Chelonia mydas* at Ascension Island, South Atlantic. *Biol Conserv* 97:151–158. [https://doi.org/10.1016/S0006-3207\(00\)00107-5](https://doi.org/10.1016/S0006-3207(00)00107-5)
- Guimarães SM, de Almeida LG, Nunes LA, Lacerda PD, de Amorim CES, Burato M, Baldassin P, Werneck MR (2021) Distribution and potential causes of sea turtles stranding in the state of Rio de Janeiro, southern Brazil. *Herpetol Conserv Biol* 16:225–237
- Hamann M, Godfrey MH, Seminoff JA, Arthur K, Barata PCR, Bjornald KA, Bolten AB et al (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endang Species Res* 11:245–269. <https://doi.org/10.3354/esr00279>
- Heithaus MR (2013) Predators, prey, and ecological roles of sea turtles. In: Wyneken J, Lohman JK, Musick JA (eds) *Biology of sea turtles*, vol III. CRC Press, Boca Raton, pp 249–285
- Jardim A, López-Mendilaharsu M, Barros F (2016) Demography and foraging ecology of *Chelonia mydas* on tropical shallow reefs in Bahia, Brazil. *J Mar Biol Assoc UK* 96:1295–1304. <https://doi.org/10.1017/S0025315415001629>
- Járez M, Steel M (2010) Model-based clustering of non-Gaussian panel data based on skew-t distributions. *J Business Econ Stat* 28:52–66
- Jensen MP, FitzSimmons NN, Dutton PH (2013) Molecular genetics of sea turtles. In: Wyneken J, Lohmann KJ, Musick JA (eds) *Biology of sea turtles*, vol III. CRC Press, Boca Raton, pp 153–154
- Kay M (2020) tidybayes: tidy data and geoms for Bayesian models. *R Package Version 2(1):1*. <https://doi.org/10.5281/zenodo.1308151>
- Kruschke J, Liddell T (2018) The Bayesian new statistics: hypothesis testing, estimation, meta-analysis, and power analysis from a Bayesian perspective. *Psychon Bull Rev* 25:178–206. <https://doi.org/10.3758/s13423-016-1221-4>
- Lavergne S, Mouquet N, Thuiller W, Ronce O (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annu Rev Ecol Evol Syst* 41:321–350. <https://doi.org/10.1146/annurev-ecolsys-102209-144628>
- Leal JH, Bouchet P (1991) Distribution patterns and dispersal of prosobranch gastropods along a seamount chain in the Atlantic Ocean. *J Mar Biol Assoc UK* 71:11–25. <https://doi.org/10.1017/S0025315400037358>
- Lemoine N (2019) Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos* 128:912–928. <https://doi.org/10.1111/oik.05985>
- Long RD, Charles A, Stephenson RL (2015) Key principles of marine ecosystem-based management. *Mar Policy* 57:53–60. <https://doi.org/10.1016/j.marpol.2015.01.013>
- Lopez GG, de Salies EC, Lara PH, Tognin F, Marcovaldi MA, Serafini TZ (2015) Coastal development at sea turtles nesting ground: Efforts to establish a tool for supporting conservation and coastal management in northeastern Brazil. *Ocean Coast Manag* 116:270–276. <https://doi.org/10.1016/j.ocecoaman.2015.07.027>
- Makowski D, Ben-Shachar M, Lüdtke D (2019) bayestestR: Describing effects and their uncertainty, existence and significance within the Bayesian framework. *J Open Sourc Softw* 4:1541. <https://doi.org/10.21105/joss.01541>
- Marcovaldi MA, Marcovaldi GG (1999) Marine turtles of Brazil: the history and structure of Projeto Tamar-Ibama. *Biol Conserv* 91:35–41. [https://doi.org/10.1016/S0006-3207\(99\)00043-9](https://doi.org/10.1016/S0006-3207(99)00043-9)
- Mazaris AD, Schofield G, Gkazinou C, Almpianidou V, Hays GC (2017) Global sea turtle conservation successes. *Sci Adv* 3:e1600730. <https://doi.org/10.1126/sciadv.1600730>
- Mills LS, Soulé ME, Doak DF (1993) The keystone-species concept in ecology and conservation, management and policy must explicitly consider the complexity of interactions in natural systems. *Bioscience* 43:219–224
- MMA (Ministério do Meio Ambiente) (2018) Lista de espécies da fauna brasileira ameaçadas de extinção. Volume VII Invertebrados. https://www.icmbio.gov.br/portal/images/stories/comunicacao/publicacoes/publicacoes-diversas/livro_vermelho_2018_vol7.pdf
- Mohd Salleh S, Nishizawa H, Anuar Mohd Sah S, Jalal Khan Chowdhury A, Uzair Rusli M (2021) Sand particle size influences nest site selection of green turtles (*Chelonia mydas*) differently in east and west peninsular Malaysia. *Herpetol Conserv Biol* 16:671–680
- Monteiro DS, Estima SC, Gandra TB, Silva AP, Bugoni L, Swimmer Y, Seminoff JA, Secchi ER (2016) Long-term spatial and temporal patterns of sea turtle strandings in southern Brazil. *Mar Biol* 163:247. <https://doi.org/10.1007/s00227-016-3018-4>
- Moreira L, Baptistotte C, Scalfone J, Thomé JC, Almeida AP (1995) Occurrence of *Chelonia mydas* on the Island of Trindade. *Brazil Mar Turtle Newsl* 70:2
- Mortimer JA (1981) Reproductive Ecology of the Green Turtle, *Chelonia mydas*, at Ascension Island. In: Doctoral dissertation, University of Florida
- Mortimer JA (1990) The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtles (*Chelonia mydas*). *Copeia* 1990:802–817. <https://doi.org/10.2307/1446446>
- Mortimer JA, Bresson R (1999) Temporal distribution and periodicity in hawksbill turtles (*Eretmochelys imbricata*) nesting at Cousin Island, Republic of Seychelles, 1971–1997. *Chelonian Conserv Biol* 3:318–325
- Mortimer JA, Carr A (1987) Reproduction and migration of the Ascension Island green turtle (*Chelonia mydas*). *Copeia* 1987:103–112. <https://doi.org/10.2307/1446043>
- Muniz Leão S, Pianka E, Pelegrin N (2018) Is there evidence for population regulation in amphibians and reptiles? *J Herpetol* 52:28–33
- Naro-Maciel E, Becker JH, Lima EHSM, Marcovaldi MA, Desalle R (2007) Testing dispersal hypotheses in foraging green sea turtles (*Chelonia mydas*) of Brazil. *J Hered* 98:29–39. <https://doi.org/10.1093/jhered/esl050>
- National Research Council (2010) Assessment of sea-turtle status and trends: integrating demography and abundance. National Academies Press, Washington, DC
- Olsen, WS. (2020). Os controles geomorfológicos na resposta costeira a elevação do nível do mar nas praias arenosas da Ilha da

- Trindade, Brasil. Masters dissertation. In: Universidade Federal do Rio Grande, p 83
- Patrício AR, Hawkes LA, Monsinjon JR, Godley BJ, Fuentes MMPB (2021) Climate change and marine turtles: recent advances and future directions. *Endang Species Res* 44:363–395. <https://doi.org/10.3354/esr01110>
- Pedersen M, Berg C, Thygesen U, Nielsen A, Madsen H (2011) Estimation methods for nonlinear state-space models in ecology. *Ecol Model* 222:1394–1400
- Peterson RG, Stramma L (1991) Upper-level circulation in the South Atlantic Ocean. *Prog Oceanogr* 26:1–73. [https://doi.org/10.1016/0079-6611\(91\)90006-8](https://doi.org/10.1016/0079-6611(91)90006-8)
- Pfaller JB, Limpus CJ, Bjørndal KA (2008) Nest-site selection in individual loggerhead turtles and consequences for doomed-egg relocation. *Conserv Biol* 23:72–80. <https://doi.org/10.1111/j.1523-1739.2008.01055.x>
- Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO et al (2004) Ecosystem-based fishery management. *Science* 305:346–347
- Pilcher N, Chaloupka M (2013) Using community-based monitoring to estimate demographic parameters for a remote nesting population of the Critically Endangered leatherback turtle. *Endang Species Res* 20:49–57
- Pinheiro YG (2017) Morfodinâmica das praias arenosas e riscos costeiros do setor leste da Ilha da Trindade, ES. Masters dissertation. In: Universidade Federal do Rio Grande, p 134
- Plummer M (2015) JAGS version 4 user manual. https://sourceforge.net/projects/mcmc-jags/files/Manuals/4.x/jags_user_manual.pdf/download
- Plummer M (2016) rjags: Bayesian graphical models using MCMC. R package version 4–6. <https://CRAN.R-project.org/package=rjags>
- Prince R, Chaloupka M (2012) Estimating demographic parameters for a critically endangered marine species with frequent reproductive omission: hawksbill turtles nesting at Varanus Island, Western Australia. *Mar Biol* 159:355–363
- Proietti MC, Reisser JW, Kinan PG, Kerr R, Monteiro DS, Marins LF, Secchi ER (2012) Green turtle (*Chelonia mydas*) mixed stocks in the western South Atlantic, as revealed by mtDNA haplotypes and drifter trajectories. *Mar Ecol Prog Ser* 447:195–209. <https://doi.org/10.3354/meps09477>
- R Core Team (2020) R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria
- Rees AF, Alfaro-Shigueto J, Barata PCR, Bjørndal KA, Bolten AB et al (2016) Are we working towards global research priorities for management and conservation of sea turtles? *Endang Species Res* 31:337–382. <https://doi.org/10.3354/esr00801>
- Rizzi M, Rodrigues FL, Medeiros L, Ortega I, Rodrigues L, Monteiro DS, Kessler F, Proietti MC (2019) Ingestion of plastic marine litter by sea turtles in southern Brazil: abundance, characteristics and potential selectivity. *Mar Pollut Bull* 140:536–548. <https://doi.org/10.1016/j.marpolbul.2019.01.054>
- Robinson D (2017) Introduction to Empirical Bayes: examples from baseball statistics. pp 142. <http://varianceexplained.org/r/empirical-bayes-book>
- Santidrián-Tomillo P, Paladino FV, Sus JS, Spotila JR (2010) Predation of leatherback turtle hatchlings during the crawl to the water. *Chelonian Conserv Biol* 9:18–25. <https://doi.org/10.2744/ccb-0789.1>
- Santos RG, Andrades R, Boldrini MA, Martins AS (2015) Debris ingestion by juvenile marine turtles: an underestimated problem. *Mar Pollut Bull* 93:37–43. <https://doi.org/10.1016/j.marpolbul.2015.02.022>
- Santos RG, Pinheiro HT, Martins AS, Riul P, Bruno SC, Janzen FJ, Ioannou CC (2016) The anti-predator role of within-nest emergence synchrony in sea turtle hatchlings. *Proc R Soc B* 283:20160697. <https://doi.org/10.1098/rspb.2016.0697>
- Shamblin BM, Dutton PH, Bjørndal KA, Bolten AB et al (2015) Deeper mitochondrial sequencing reveals cryptic diversity and structure in Brazilian green turtle rookeries. *Chelonian Conserv Biol* 14:167–172. <https://doi.org/10.2744/CCB-1152.1>
- Silva NGD, Alves RJ (2011) The eradication of feral goats and its impact on plant biodiversity—a milestone in the history of Trindade Island, Brazil. *Rodriguésia* 62:717–719. <https://doi.org/10.1590/2175-7860201162315>
- Soares HC, Gherardi DFM, Pezzi LP, Kayano MT, Paes ET (2014) Patterns of interannual climate variability in large marine ecosystems. *J Mar Syst* 134:57–68. <https://doi.org/10.1016/j.jmarsys.2014.03.004>
- Soto JMR (2009) Ações antrópicas negativas nas ilhas oceânicas brasileiras. In: Mohr LV, Castro JWA, Costa PMS, Alves RJV (eds) Ilhas oceânicas brasileiras: da pesquisa ao manejo. Ministério do Meio Ambiente, Brasília, pp 329–350
- Tiwari M (2004) Density-dependent effects on hatchling production in the green turtle nesting population in Tortuguero, Costa Rica. In: Doctoral dissertation, University of Florida
- Tiwari M, Bjørndal KA, Bolten AB, Bolker BM (2006) Evaluation of density dependent processes and green turtle, *Chelonia mydas*, hatchling production at Tortuguero, Costa Rica. *Mar Ecol Prog Ser* 326:283–293. <https://doi.org/10.3354/meps326283>
- Tiwari M, Balazs GH, Hargrove S (2010) Estimating carrying capacity at the green turtle nesting beach of East Island, French Frigate Shoals. *Mar Ecol Prog Ser* 419:289–294. <https://doi.org/10.3354/meps08833>
- Troëng S, Chaloupka M (2007) Variation in adult annual survival probability and remigration intervals of sea turtles. *Mar Biol* 151:1721–1730
- Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat Comput* 27:1413–1432. <https://doi.org/10.1007/s11222-016-9696-4>
- Venables W, Ripley B (2002) Modern applied statistics with S, 4th edn. Springer, New York
- Villegas Vindiola B (2019) Measuring nest-to-surf mortality of Florida's east and west coast loggerhead sea turtle (*Caretta caretta*) hatchlings. Masters thesis, Florida Atlantic University. <http://fau.digital.flvc.org/islandora/object/fau:41418>
- Weber SB, Weber N, Ellick J, Avery A, Frauenstein R, Godley BJ, Sim J, Williams N, Broderick AC (2014) Recovery of the South Atlantic's largest green turtle nesting population. *Biodivers Conserv* 23:3005–3018. <https://doi.org/10.1007/s10531-014-0759-6>
- Weishampel JF, Bagley DA, Ehrhart LM, Rodenbeck BL (2003) Spatiotemporal patterns of annual sea turtle nesting behaviors along an East Central Florida beach. *Biol Conserv* 110:295–303. [https://doi.org/10.1016/S0006-3207\(02\)00232-X](https://doi.org/10.1016/S0006-3207(02)00232-X)
- Yalçın-Özdilek Ş (2007) Status of sea turtles (*Chelonia mydas* and *Caretta caretta*) on Samandağ Beach, Turkey: a five-year monitoring study. *Ann Zool Fenn* 44:333–347. <https://www.jstor.org/stable/23736926>
- Yao Y, Vehtari A, Simpson D, Gelman A (2018) Using stacking to average Bayesian predictive distributions (with Discussion). *Bayesian Anal* 13:917–1003. <https://doi.org/10.1016/S10.1214/17-BA1091>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Supplementary Material

Tracking nesting trends for green turtles at Trindade Island, Brazil, a remote oceanic rookery

Luciana Medeiros¹, Milani Chaloupka², Alan B. Bolten³, Eduardo M. von Muhlen¹, Alexandro Santos¹, Ana Marcondes¹, João C. A. Thomé⁴, Maria Ângela Marcovaldi¹, Karen A. Bjorndal³

¹ Fundação Projeto TAMAR, Mata de São João, Bahia, Brazil

² Ecological Modelling Services Pty Ltd and Marine Spatial Ecology Lab, University of Queensland, Brisbane, Australia

³ Archie Carr Center for Sea Turtle Research and Department of Biology, University of Florida, Gainesville, Florida, USA

⁴ Centro TAMAR-ICMBio, Vitória, Espírito Santo, Brazil

Corresponding Author: Karen A. Bjorndal; bjorndal@ufl.edu

Table S-1 Annual numbers of observed tracks from morning surveys between 15 November and 30 May each year and estimated annual total track counts between 15 November and 30 May each year from GAM analyses.

Nesting Year	Andradas observed tracks	Tartarugas observed tracks	Andradas estimated track counts	Tartarugas estimated track counts
2009/10	886	1618	1439	2161
2010/11	881	1773	1433	2478
2011/12	513	1354	825	1359
2012/13	1808	2347	3143	3559
2014/15	503	720	1116	1648
2015/16	409	536	588	760
2016/17	1585	1662	3317	3410

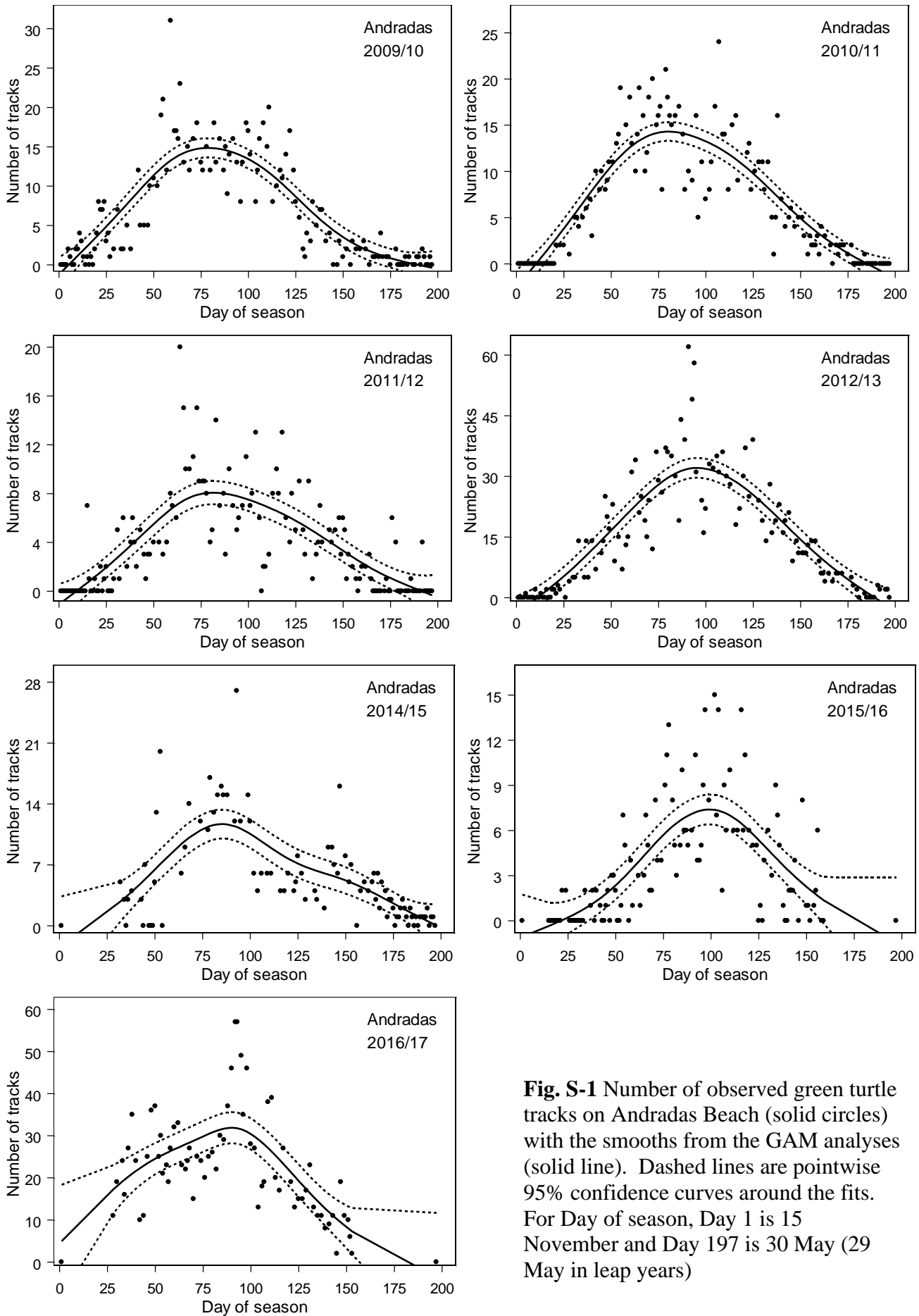


Fig. S-1 Number of observed green turtle tracks on Andradas Beach (solid circles) with the smooths from the GAM analyses (solid line). Dashed lines are pointwise 95% confidence curves around the fits. For Day of season, Day 1 is 15 November and Day 197 is 30 May (29 May in leap years)

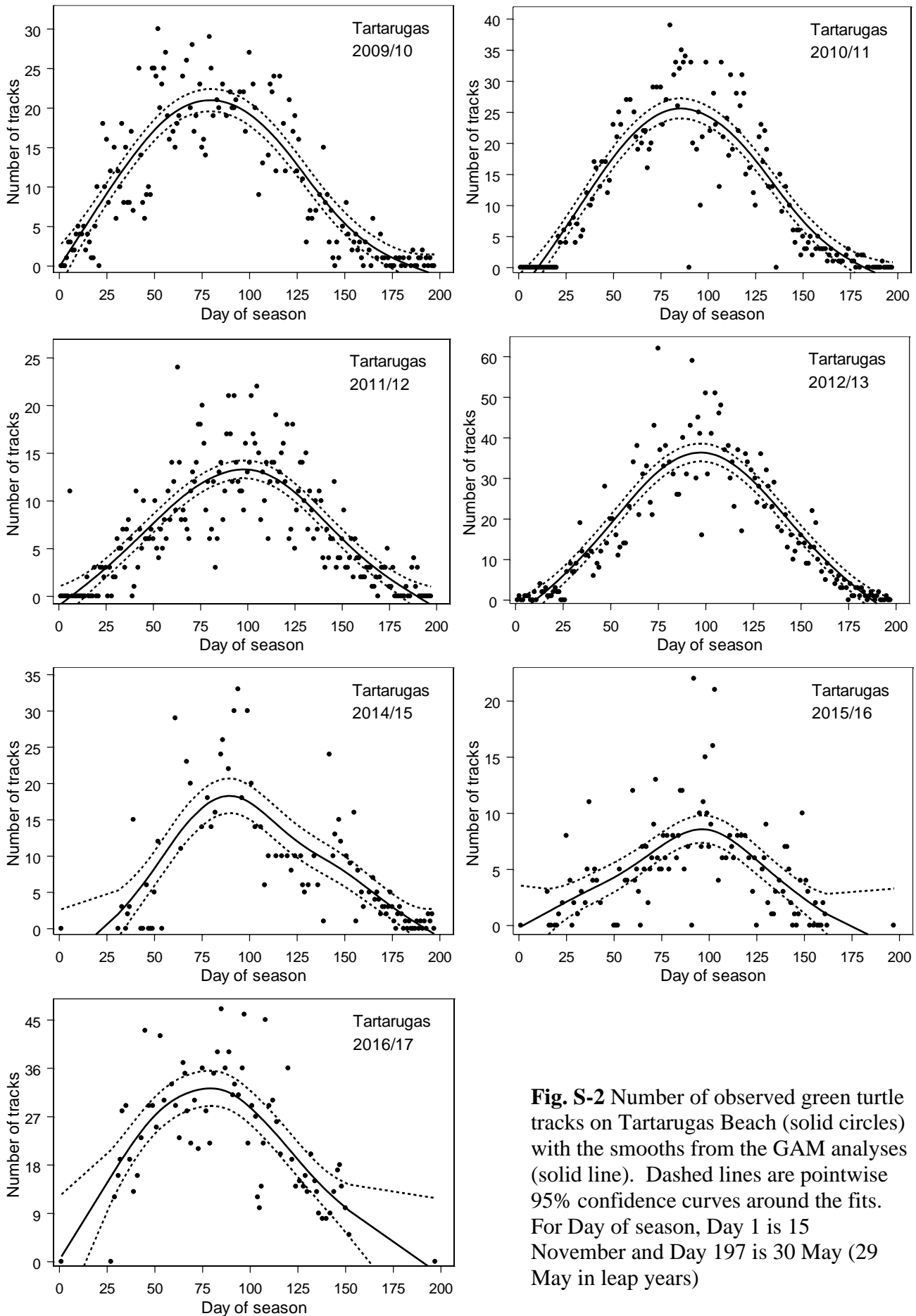


Fig. S-2 Number of observed green turtle tracks on Tartarugas Beach (solid circles) with the smooths from the GAM analyses (solid line). Dashed lines are pointwise 95% confidence curves around the fits. For Day of season, Day 1 is 15 November and Day 197 is 30 May (29 May in leap years)