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Abstract

Marine turtles are intra-seasonal iteroparous animals; they nest from one to up to 14 times during the nesting season, laying up to 180 eggs each time. Their annual reproductive effort can therefore be estimated from clutch size, nesting frequency, and length of the nesting season. Moreover, the estimation of nesting frequency, usually obtained from the internesting period (i.e., the time in days between two nesting events) is essential for assessing the number of females in a population. However, the internesting period is strongly influenced by variation in individual behaviour of the nesting female, including abortion of nesting attempts. It is also affected by imprecise detection of females during beach monitoring, often related with a lack of fidelity to the nesting beach. Using an individual-focused model based on capture-mark-recapture data we were able to statistically characterize the nesting behaviour of the populations of green turtles (*Chelonia mydas*) and olive ridley turtles (*Lepidochelys olivacea*) in São Tomé and Príncipe (Eastern Atlantic). The developed model proposes a novel approach in estimating the internesting period, by including the different factors that lead to the heterogeneity observed in the duration of internesting periods across a single season, corrected for the probability of a female aborting a nesting process. The calculated lengths of the internesting periods for the two species are congruent with previous estimates, validating the model. Furthermore, the inference of the rank of a nest for an individual female is predicted by the model with high accuracy, even when the recapture rate is low and the time between observations is long. A limitation of the model is its inability to estimate the true clutch frequency at the scale of the population but it was not its purpose.

Keywords: *Chelonia mydas*, *Lepidochelys olivacea*, internesting period, iteroparity, nesting abortion, Eastern Atlantic

1. Introduction

Female marine turtles come ashore and nest several times during the nesting season at regular intervals (Miller, 1997). The number of days between consecutive clutches, named hereafter the internesting period, is typical for each species (Alvarado and Murphy, 1999). For instance, leatherback turtles (*Dermochelys coriacea*) have the shortest internesting period, typically lasting only 10 days (Fretey and Girondot, 1988), while for cheloniids this average interval spans from 12 (in green turtles, *Chelonia mydas*) up to 20 days (in olive ridley turtles, *Lepidochelys olivacea*). Several factors are thought to influence this intra-seasonal iteroparity pattern. Marine turtles, as most ectotherms, are mainly capital breeders, storing most of their energy at the foraging sites prior to their reproductive migration (Bonnet et al., 1998; Myers and Hays, 2006); the shorter the nesting season is, the less time females spend away from their foraging sites. On the other hand, when the nesting season encompasses several months, different clutches of a single female will incubate under various temporal conditions. Marine turtles are species with temperature-dependent sex determination in which sex is determined by temperature during the middle-third of the development period of the embryo, and so the distribution of clutches along several months could be also a strategy to ensure that both sexes are produced (Fuentes et al., 2017). Thus, both shorter and longer nesting seasons can be advantageous. Within each nesting season the internesting period (basically the number of days that elapses between 2 clutches (Frazer and Richardson, 1985)) is related to the time that each clutch of eggs takes to develop inside the turtle's body cavity (Miller, 1997; Rostal et al., 1996), and to the size of the cavity itself (Hays, 2001). It would be expected that the longer the internesting periods are, the more time the female has to develop more eggs and increase clutch size, reducing the number of incursions on the beach, where it is particularly vulnerable.

On every monitoring program following individually-marked females, the observed clutch frequency (*OCF*) is simply the number of clutches observed for a single female during the nesting season (Frazer and Richardson, 1985), and it is a key parameter in the estimation of population size (e.g. Broderick et al., 2002). However, the actual number of clutches laid by a female within a season is difficult to estimate due to imperfect capture probability, either because of fieldwork constraints or of the ability of females to choose different nesting beaches in different nesting events (Tucker, 2009, 2010). The regularity of the internesting period (*IP*) has been used to calculate the estimated clutch frequency (*ECF*): $ECF = 1 + (d_2 - d_1)/IP$ with

d_1 representing the ordinal date of first observation of the nesting female in the season, and d_2 the ordinal date of last observation of the nesting female in that same season. *ECF* is thus equal to or higher than *OCF*.

Sound estimates of the interesting period are not easy to obtain for several reasons: (i) some females abort the nesting process upon emergence on the beach, not returning to nest until several days later, (ii) some females may not be detected by patrols while being on the beach, (iii) in most situations, it is not known if the female has indeed laid eggs or if it has aborted the nesting process, and (iv) fidelity to the nesting beach is not perfect. All these different events can co-occur making the estimation of the number of days between two nesting events difficult. For example, when a female leatherback turtle, which typically nests every 10 days (Girondot and Fretey, 1996), is seen for the second time on the beach 30 days after the first visit, it may be interpreted as its third nest after the first observation, or the second nest after the first observation if the turtle has aborted 1 or 2 nesting processes or even the first nest if the nesting process was aborted several times. It could also be the fourth nest if the internesting period of that particular female is unusually short, for example, seven days.

Until now this difficulty has been overlooked and the internesting period has been determined empirically: when a turtle is seen returning before the minimum expected IP (internesting period - for example, seven days), it is considered that the female did not lay a clutch during the first observation. Indeed, six days or less could be not sufficient for ovulation and formation of eggshells (Miller, 1997; Rostal et al., 1996), and thus two separate nesting events cannot take place within that time. If the return interval is longer than maximum expected IP (for example, 18 days), it is considered that the female has deposited one intermediate clutch that has not been observed (Frazer and Richardson, 1985).

The local NGOs Associação Programa Tatô and Fundação Príncipe Trust ensure complete monitoring coverage of all beaches in São Tomé and Príncipe islands, which is complemented by the implementation of a capture-mark-recapture program through the tagging of nesting females, providing the most complete dataset of sea turtle nest distribution in the Gulf of Guinea. These two islands host an important green turtle rookery which is genetically distinct from all others in the Atlantic (Formia et al., 2006; J. Hancock, unpubl. data). The second most common species is the olive ridley turtle, believed to represent a fraction of the major rookery for olive ridley in Central Africa (Girard et al., 2016). Using data obtained during the

monitoring programs of these two species, we propose a novel modelling approach of the internesting period. We combine nesting counts and tagging data obtained at a rookery level to estimate this parameter, while taking into account the potential heterogeneity in the length of internesting periods resulting from female individual behavior, including abortion of the nesting process.

2. Materials and methods

2.1. Data Collection

On São Tomé island, green turtles nest mostly in the southern coast, with most of the nesting activity being concentrated between the beaches of Jalé and Cabana and also Planta; on Príncipe island, this species nests primarily in two beaches, Praia Grande and Infante, with minor nesting occurring in Boi and Ribeira Izé/Mocotó beaches. The olive ridley turtle nests only on the island of São Tomé, mostly in the north of the island, with most nesting activity concentrated along the 9 km stretch of coastline between the beaches of Juventude and Tamarindos. The importance of these beaches for each species were confirmed by early surveys conducted by Graff (1996), and they have been subjected to full monitoring every night from October through February since 2012 (olive ridley) and 2015 (green turtles). Locations are shown in Figure 1.

Monitoring effort during night patrols was standardized at all above mentioned beaches and set to take place each night between 6 p.m. and 5 a.m. by groups of 2 trained assistants, each group covering 1.5 km stretch of contiguous coastline. During each patrol, data on female or track encounters was collected. The monitoring protocols in place in São Tomé and Príncipe require that the investigators walk along the beach just above the high tide line, and carefully check each one way track to confirm the presence of a turtle on the beach, always ensuring that any turtle is approached from behind without using any light. To further minimize interference of the turtle's natural behaviour, no turtles were intercepted on their ascent on the beach, and encountered turtles were approached very carefully if oviposition is not confirmed to have occurred; any tagging and data collection are only performed after successful oviposition, or a turtle has initiated her descent to the surf. Oviposition is always confirmed either by direct observation, or by carefully uncovering the top layer of eggs, never later than 8h after suspected oviposition. If the clutch is not found, the activity is noted as "false crawl" (no body pit or nest chamber) or "attempt" (body pit or abandoned nest chamber present). Flipper tagging was done

to allow individual identification and follow up in consequent nesting events, by placing a pair of Inconel flipper tags (National Band and Tag Co., Style 681) on the trailing edge of each of the fore-flippers after egg laying.

2.2. Data preparation and use

The data collection implemented during the monitoring program allowed the compilation of the dates of the first and all subsequent observations (re-captures) of individual females within each season on each beach. Our dataset comprised of 757 individual green turtle females (n=1738 captures and recaptures) over two seasons (2015-2016 and 2016-2017) and 635 individual olive ridley turtles (n=700 captures and recaptures) over four seasons (2012-2017). A summary of the data used is found on Table 1.

2.3. Model development

A stochastic model was formulated to describe the nesting process after the first observation of a female on a beach (Fig. 2). If the female was unable to nest and aborted, with a probability *pAbort*, then it was expected to return for another nesting attempt after *logN(meanAbort, sdAbort)* days. When it returned to the beach, this female would be seen with a probability *pCapture*. After a successful nest, the female could not return to nest before the minimum interesting period, *minIP* (when used, *minIP* is an integer). Its return occurred after *logN(meanIP, sdIP)* + *(Nclutch – 1)×DeltameanIP* with *Nclutch* being the rank of the nest (i.e., 1st, 2nd, etc.). This female would produce *x* clutches (see below about parametrization of *x*). If it was its last recorded nesting event for the season and it was successful, we considered this observation as the final one. The model is schematized in Fig. 2.

The distribution of the number of clutches per female after its first observation on the beach, *DF* (*CF* is the common acronym for Clutch Frequency, *D* rather than *C* is used in this case to indicate that it is not the true *CF*), can be obtained from a parametric model *logN(meanDF, sdDF).* An alternative parametrization uses *DF.1*, *DF.2*, to *DF.max* (*DF.0* is fixed to 1) and the probability that a female laid *x* clutches after its first observation on the beach is p_x=abs(*DF.x)*/∑abs(*DF.i).* This parametrization has the advantage of not forcing any shape on the distribution of the clutch frequency. It is important to note that *DF* is the

distribution of the number of clutches after the first observation of an individual female on the beach and therefore it is not equal to *CF,* which is the distribution of the number of clutches that a female is laying during a complete nesting season, taking into account that some females are not observed during their first nesting attempt.

This model generated a theoretical distribution of the number of observations for 0 to *maxDays* with *maxDays* being the maximum number of days before a recapture after the first observation. Then a set of expected number of captures C_{day} for days 0 to *m* after the initial capture was obtained (0 indicates that a female was seen twice in the same night, after aborting its first nesting attempt). These values were transformed into probabilities using $p_{day}=C_{day}/\sum C_{day}$ (Fig. 2). The larger the *N*, the closer the distribution of p_m is to the true distribution.

The development and testing of the model was performed with the green turtle data because nesting is concentrated on few individual beaches, which facilitates the full coverage of each beach by the night patrols and thus increasing the chances of observing a turtle. Olive ridley turtles nest sparsely over several kilometres of coast, reducing the chances of encounters by the night patrols; for this reason, observations are much sparser than for green turtles. We used the data collected for this species for testing and validating the model in cases when recapture rates may be lower, resulting in lower quality data. This situation is indeed frequent in marine turtle monitoring programs that suffer constraints in field data collection.

2.3.1. Fitting the parameters of the nesting process

The data obtained from the beach monitoring (Fig. 3) was organized in *k* observations (*i.e.*, *k* individuals) in series of $n_{i.days}$ (*i* is the individual and *days* the number of days after first observation) with 0 (no capture) and 1 (capture). The likelihood of the observation *i* given the outputs p_{day} of the model is based on a multinomial distribution:

$$L_i(N_0 = n_{i.0}, \cdots, N_m = n_{i.m}) = \frac{n_i!}{n_{i.0}! \cdots n_{i.m}!} p_0^{n_{i.0}} \cdots p_m^{n_{i.m}}$$

The log likelihood of all the observations given the model is:

$$log(L) = \sum_{i=1}^{k} log(L_i)$$

with L_i being the likelihood to capture the individual i after $n_{i.0}$ to $n_{i.m}$ days. L is the likelihood of the observations for all the k individuals; in this formula, the organization level is the individual.

An alternative option is to use the daily sum (top of Fig. 3) as the values for n_{days}. In this case, the organization level is the nesting event, but the females with a larger estimated clutch frequency will have a larger impact on global likelihood than the ones with lower estimated clutch frequency. This solution has not been retained here.

The parameters *pCapture* and *pAbort* were fitted as *-logit* of the corresponding probabilities to ensure that they remained estimable at all times without defining constraints during the fit. The parameter values maximizing the likelihood were fitted using the Nelder-Mead followed by Broyden-Fletcher-Goldfarb-Shanno method with R package *optimx* (Nash and Varadhan, 2011). To test the suitability of different models fitted with the same datasets, we used the AIC estimator (Burnham and Anderson, 2002). AIC is a measure of the quality of the fit penalized by the number of parameters used, calculated as $-2\ log(L) + 2\ p$ with p being the number of parameters of the model (Akaike, 1974); models with lower AIC have more chance to better represent the process that generated the data.

The model has been scripted in R language and is available in the R package *phenology* (version 7.1 and above) (Girondot, 2018b).

2.3.2. Stability of likelihood

A stochastic model was used to generate the distribution of p_{day} (see previous section). Thus, from run to run, the values change. We needed to minimize the inter-run variability of the likelihood of data given the model to ensure that a maximum likelihood fit could operate under a realistic computing time. To determine the best combination of the number of replicates and computing time, we ran the model with 10^4 to 10^5 steps (by 10^4 steps), and $2x10^5$ to $2x10^6$ (by 10^5 steps) replicates to study the dispersion of the log likelihood. For this test we used the parameters at maximum likelihood fitted using 10^6 replicates.

2.3.3. Identifiability of the parameters

The Metropolis-Hastings algorithm is a Markov Chain Monte Carlo (MCMC) method for obtaining a sequence of random samples from a probability distribution for which direct sampling is not available or difficult (Chib and Greenberg, 1995). It was used to estimate the posterior distribution for each parameter over 10,000 iterations. This value has been chosen based on the Raftery and Lewis (1992) diagnostic. Maximum likelihood estimates were used as initial parameter values during the MCMC search, using no adaptation iteration. Proposed distributions were adapted after every 500 iterations using the method of Rosenthal (2011) as implemented in the R package *HelpersMG* (Girondot, 2018a). Priors were all obtained from a uniform distribution with limits being always very wide to ensure that a large range of parameter values could be checked (see supplementary material). Convergence was first visually examined to ensure that the time series of the parameters were stationary, and then tested using the Heidelberger and Welch (1983) diagnostic. The standard error of the parameters was estimated after correction for autocorrelation (Roberts, 1996). Results from the MCMC were analyzed using the R package *Coda*, version 0.19-1 (Plummer et al., 2011). Covariations of all parameter pairs were checked visually using bivariate plots and Pearson correlation coefficients.

The comparison between the distribution of priors and posteriors after the Metropolis-Hastings MCMC run show that some parameters cannot be estimated using this model because the posterior distribution is very similar to the prior distribution. The *DF* distribution (*meanDF*, *sdDF* or *DF.x*) as well as the capture and abort probabilities (*pCapture* and *pAbort*) are not identifiable. High values (>9) of the parameter *minIP* can be excluded, but the lowest cannot. Finally, the parameters *meanIP*, *sdIP*, *DeltameanIP*, *meanAbort* and *sdAbort* are identifiable (see supplementary material). The only very strong covariation of parameters is between *meanIP* and *DeltameanIP*: their negative correlation indicates that when *DeltameanIP* tends towards 0, *meanIP* is lower (see supplementary materials).

2.3.4. From estimating the number of days between observations to clutch frequency

By knowing the distribution of the number of days between two clutches or nesting abortions, as well as the probabilities of a turtle aborting a nesting process or being observed (captured), it was possible to relate the number of days between two observations on the beach and the true number of clutches between these two observations. A total of 10^6 simulations were performed using the green turtle fitted parameters. In each simulation, for each turtle captured we recorded

the number of days after its first observation (capture) on the beach and the number of clutches observed being laid by that female up to that day. Consolidating this information on a data frame, we used it to calculate the probability that an observation of a female X days after its first observation was the n^{th} clutch.

2.3.5. Stability of the likelihood

The likelihood calculated with 10^4 iterations was quickly estimated but the inter-run likelihood variability was too high to be used during the fitting process. On the other hand, the calculation of the likelihood with 10^6 iterations took too long to be used routinely. A number of 10^5 iterations was considered an adequate compromise as it provided a correct fit to our data (Fig. 4) and was used thereafter.

3. Results

The distributions of the internesting periods for the two turtle species, considering both nesting seasons (2015-2016 and 2016-2017) and islands (São Tomé and/or Príncipe) are shown in Fig. 5. The mean shortening of the IP along the successive clutches was similar between different datasets, therefore we chose to combine these to have a global estimate for the region with the lowest confidence interval.

3.1. Green turtles

The patterns of the internesting periods observed for either São Tomé or Príncipe green turtles were very similar (Fig. 3). Several peaks were observed, for 12, 24, 36 days after the first observation, and successive peaks were entangled (i.e., the lowest part of one peak distribution overlapped the highest part of the previous one). Other peaks were observed after 40 days, but they were more difficult to discriminate because the dispersion of the peaks for the higher number of days is higher, making the peaks flatter. The number of days between the first and the last observation was highly related to the ordinal date of first observation (linear model, *t*-test, p=0.002); the earlier the turtle was first seen, the longer it was observed on the beach.

The green turtle mean internesting period between the first and the second clutch was estimated at 12.32 days (95% confidence interval from 12.26 to 12.37). The 95% range of all internesting periods was between 10.10 and 15.05 days (Table 2; showing also the values estimated for other populations). The internesting period became shorter as the number of clutches increased (*DeltameanIP* parameters are all negative, supplementary materials). This effect is noticed for each of the 4 datasets, as well as when combined, and the inclusion of the *DeltameanIP* parameter greatly improved the fitting of the model (ΔAIC=19.76, Akaike weight p=0.999). The fitted estimation of the minimal number of days between two clutches was 8.12 days (95% confidence interval from 8.11 to 8.13 days). When a nesting attempt was aborted in our model simulation, the time before the next attempt was on average 1.59 days (95% confidence interval from 1.57 to 1.60) and 95% of the values were between 0.23 to 10.88 days. It should be noted that the upper 95% limit of the confidence interval (10.88 days) was higher than *minIP* (8.12 days), therefore the return to the nesting beach after an abortion event could be confused with a new clutch.

The probability that a female laid a n^{th} clutch when it was recorded X days after its first observation during the season is shown in Fig. 6; Table 3 depicts the probabilities of the various clutch ranks according to the different number of days after the first observation, shown as dotted vertical lines in Fig. 6.

3.2. Olive ridley turtles

The mean internesting period between two successive clutches was estimated at 22.92 days (95% confidence interval ranged from 22.85 to 23.00 days). The 95% range of internesting periods varied between 16.58 and 31.70 days (Table 2, showing also the values estimated for other populations). The change of the internesting period dependent on the progression of clutch rank (*deltaMeanIP* parameter) could not be calculated due to the paucity of recapture data, and *deltaMeanIP* was fixed to 0. The fitted minimum of the minimal number of days between two clutches was 9.16 (95% confidence interval from 8.37 to 9.95 days). When we simulated the abortion of a nesting attempt, the time until the next attempt averaged 3.47 days (95% confidence interval ranged from 3.23 to 3.71 days) and 95% of the values are between 0.54 to 22.21 days. Similarly, to what was observed for green turtles, the upper 95% limit of the confidence interval (23.24 days) is higher than *minIP* (9.16 days), meaning that the return on the beach after an abortion event could be confused with a new clutch.

All the results are presented in supplementary materials with the R scripts used for analysis.

4. Discussion

For decades, the number of nests counted during a nesting season was converted to the number of nesting females using the formula (number of nests)/(clutch frequency) (Gerrodette and Taylor, 1999). The estimation of total number of nests during a nesting season has received general solutions (Girondot, 2010; Girondot, 2017; Girondot and Rizzo, 2015) and it can be considered as being a solved problem for most of the situations. On the other hand a general procedure for the estimation of the number of nests per female (clutch frequency) is still needed (Briane et al., 2007). The most common procedure used the formula $ECF = 1 + (d_2 - d_1)/IP$ with d_1 representing the ordinal date of first observation of the nesting female in the season, and d_2 the ordinal date of last observation of the nesting female in that same season and IP being the internesting period (Frazer and Richardson, 1985). Estimation of mean IP is then done by averaging the number of days between all consecutive nesting attempts. However, the actual number of clutches laid by a female within a season is not known due to imperfect capture probability, either because of fieldwork constraints or of the ability of females to choose different nesting beaches in different nesting events (Tucker, 2009, 2010). Therefore, we can never be sure that two observations of the same nesting female on the beach refer to consecutive nesting events, or if some were missed. In consequence, the quality of the IP estimate is dependent on our ability to count the true number of nests deposited by a female, which may vary from female to female, and is nearly impossible to know. In a general move in ecology from pattern to process (Swihart et al., 2002), the estimate of such an important parameter cannot be based simply on very strong untestable assumptions. This move is particularly relevant for species with a complex life cycle such as marine turtles, for which the interpretation of changes in numbers in terms of population mechanisms is quite challenging.

The identification of a high number of individual females allowed us to observe the typical pattern of succession of peaks at multiples of 12 days which is typical of green turtles (Figure 3). The broadening of the peaks observed in longer returns is likely due to two phenomena: the variability of the internesting periods and the fuzziness resulting from the high rate of nesting abortion classically observed for this species (Mortimer and Portier, 1989). This pattern was less clear for olive ridley turtles and it was impossible to clearly identify peaks within our data

(Figure 3); however, this result is particularly important because it showed that the internesting period can be evaluated even when data are sparse, as for olive ridleys.

The estimation of the internesting interval for both studied species was very reliable according to the diagnostic tools used, showing that the design and implementation of an individual-focused statistical model was successful at producing a robust estimate of the internesting period of female marine turtles. These internesting periods are likely to be dependent on the turtle's physiological reproductive capacity as well as on local external, primarily anthropogenic, factors that may disturb turtles attempting to nest (Tiwari and Bjorndal, 2000). The observation that the nesting season is longer for early nesters has also been noted for leatherback turtles in French Guiana (Fretey and Girondot, 1989). Two non-exclusive explanations were proposed: either the turtles arriving first in the nesting site laid a higher number of clutches or, most likely, the turtles that are seen first later in the season have already nested but were not observed.

Moreover, our model shows an important advance in estimating the rank of a clutch in relation to the date of the first observation of a turtle on the beach (Fig. 6), with a particularly high probability of success when the interval of days is small and close to a multiple of the mean internesting period. For example, for green turtles, when a female is observed on the beach after 12 and 24 days, the probability that these nests correspond to its second and third clutches are respectively 0.997 and 0.992 (Table 3). If the number of days is not a multiple of the internesting period, then the rank of the clutch is uncertain: for an observation 19 days after the previous observation, the probability that it is the second or third clutches are 0.578 and 0.397 respectively (Table 3). When the number of days increase, surprisingly, the determination of the rank of the clutch did not degrade too much. For example, if a female is observed after 100 days, the probability that it is her 10^{th} clutch is 0.71 (Table 3).

Another interesting result from our model, is that we demonstrate that for green turtles, the internesting period declines as clutch rank increases. The inverse relation between internesting period and clutch rank was also demonstrated in loggerhead turtles using data from intensive field work (Limpus, 1985). It is tempting to link this decrease of the internesting period with the lower number of eggs present in the clutches of higher rank as shown in loggerheads (Limpus, 1985), but testing this hypothesis with our dataset was not possible.

5. Conclusion

The use of capture mark recapture (CMR) studies on nesting beaches can be used to estimate the minimum number of reproductive turtles in each season but interpreting the nesting history of a female is a prerequisite to be able to convert an observed total number of clutches into an estimate of the number of females in a population. We consider that up to now, no model is yet able to correctly convert a dataset of observed or estimated clutch frequency (OCF and ECF) into a number of females in a population, as the impracticality of assessing this parameter is directly due to field constraints and to the variability in female behaviour. The common restraints posed by incomplete datasets that include extended time intervals between individual re-observations is solved by our model, which can be used to determine with high probability the rank of an observed clutch since the first observation. Moreover, our model demonstrates the usefulness of CMR datasets in understanding patterns in the individual behaviour of a female on the beach and how these affect the variation in internesting periods for a given population.

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TABLES AND FIGURES

Table 1:

Number of individual green (*Chelonia mydas*) and olive ridley (*Lepidochelys olivacea*) marine turtle females identified and frequency of observations between 2012-2017 in São Tomé and Príncipe islands.

Green turtles *(Chelonia mydas*)

Island	Season	N females	N obs.	Observation Frequencies of individual females								
				1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
São Tomé	**2015-2016**	172	336	88	36	25	16	6	1			
São Tomé	**2016-2017**	109	149	82	17	7	3					
Príncipe	**2015-2016**	355	911	133	75	48	50	27	12	6	1	3
Príncipe	**2016-2017**	121	342	36	24	22	14	16	7	2		

Olive ridley turtles (*Lepidochelys olivacea*)

Island	Season	N females	N obs.	Observation Frequencies of individual females								
				1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
São Tomé	**2012-2013**	56	57	55	1							
São Tomé	**2013-2014**	32	32	32								
São Tomé	**2014-2015**	154	173	135	19							
São Tomé	**2015-2016**	138	153	124	13	1						
São Tomé	**2016-2017**	255	285	226	28	1						

Table 2: Internesting periods in *Chelonia mydas* and *Lepidochelys olivacea*. Min and Max represent the range of IP used to estimate mean and SD. The values in N column has a non-consistent definition across the publications: It can be the number of females, the total number of observations, or the number of observations used to estimate mean and SD. Some values were estimated from published raw data (see notes).

Species	Location	RMU	Mean	SD	Min	Max	N	Reference
Chelonia mydas	São Tomé and Príncipe	Atlantic, East	12.32	1.365	10	15	1842	**This study**
Chelonia mydas	Ascension Island	Atlantic, East	13.9	2.4	7	20	840	Mortimer and Carr (1987)
Chelonia mydas	Alagadi beach, Cyprus	Mediterranean	12.5	1.65	9	19	205	Broderick et al. (2002)
Chelonia mydas	Tortuguero, Caribbean Sea	Atlantic, Northwest	12.1	1.64 [a]	7	18 [d]	4654	Carr et al. (1978)
Chelonia mydas	Tortuguero, Caribbean Sea	Atlantic, Northwest	12.5	2.25 [a]	10 [d]	19 [d]	132	Carr and Giovannoli (1957)
Chelonia mydas	Melbourne Beach, Florida	Atlantic, Northwest	12.9	1.59	10	19	165	Johnson and Ehrhart (1996)
Chelonia mydas	Surinam (1970)	Atlantic, South Caribbean	13.09 [b]	1.26 [a]	11	16	317	Schulz (1975)
Chelonia mydas	Surinam (1971)	Atlantic, South Caribbean	13.27 [c]	1.24 [a]	11	16	601	Schulz (1975)
Chelonia mydas	Tromelin Island (1983-1984)	Indian, Southwest	12.62 [a]	1.92 [a]	8	19	3036	Le Gall et al. (1987)
Chelonia mydas	Tromelin Island (1982-1983)	Indian, Southwest	12.68 [a]	2.04 [a]	8	19	1492	Le Gall et al. (1987)
Chelonia mydas	French Frigate Shoals. Hawaii (1974)	Pacific, North Central	13.2	1.38 [a]	11	18	74	Balazs (1980)
Chelonia mydas	French Frigate Shoals. Hawaii (1975)	Pacific, North Central	13.4	1.35 [a]	11	18	15	Balazs (1980)
Chelonia mydas	Heron Island, Australia	Pacific, Southwest	14.1	1.65	9	21	264	Limpus et al. (1984)
Chelonia mydas	Sarawak, China Sea	Pacific, South Central	10.5	1.33 [a]	8	17	5417	Hendrickson (1958)
Lepidochelys olivacea	São Tomé Island, Central Africa	Atlantic, East	22.92	4.39	16	31	415	**This study**
Lepidochelys olivacea	Orissa, India	Indian Ocean	22.09	0.58	20	25	4411	Tripathy and Pandav (2007)
Lepidochelys olivacea	Mayumba Natl Park, Gabon	Atlantic, East	17.5	4.3	9	25	18	Maxwell et al. (2011)
Lepidochelys olivacea	Sergipe, Brazil	Atlantic, West	22.35	7.01	21.2	23.5	143	Matos et al. (2012)
Lepidochelys olivacea	Playa Grande, Costa Rica	Pacific, East	24.5	7.1	14	50	33	Dornfeld et al. (2014)
Lepidochelys olivacea	El Valle, Colombia	Pacific, East	18.8	4.2	16	25	4	Barrientos-Muñoz et al. (2014)

[a] The value was not calculated in the original publication, [b] The published value was 13.2 days, [c] The published value was 13.4 days, [d] The min and/or max values have been calculated to reflect the published mean value

Table 3:

Clutch rank probability according to an observed internesting period for green turtles (*Chelonia mydas*). The periods considered on the first column are depicted in Figure 6 as dotted lines.

Observed internesting period in days	**Clutch 0**	**Clutch 1**	**Clutch 2**	**Clutch 3**	**Clutch 4**	**Clutch 5**	**Clutch 6**	**Clutch 7**	**Clutch 8**	**Clutch 9**	**Clutch 10**
6	1.000										
10	0.017	0.983									
12	0.003	0.997									
19	0.025	0.578	0.397								
24		0.007	0.992								
30	0.002	0.026	0.658	0.314							
36		0.001	0.015	0.984							
50		0.001	0.003	0.025	0.959	0.013					
100				0.001	0.001	0.019	0.023	0.049	0.193	0.710	0.004

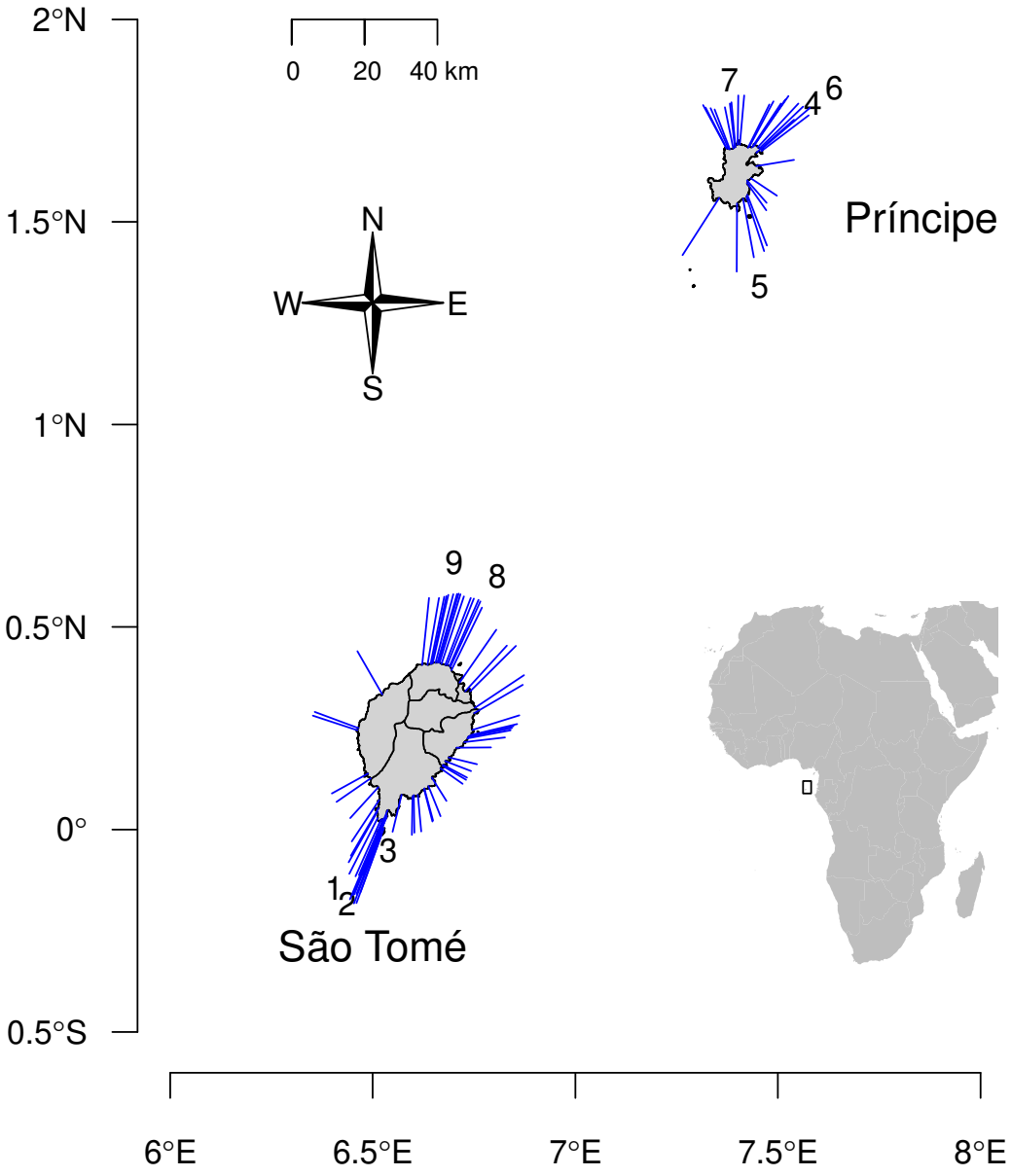

Figure 1: Map of São Tomé and Príncipe. Beaches used by marine turtles are shown with ticks (65 at São Tomé and 29 at Príncipe Island). On São Tomé island, green turtles nest mostly in (1) Jalé, (2) Cabana, (3) Planta; on Príncipe island, this species nests primarily in two beaches, (4) Praia Grande and (5) Infante, with minor nesting occurring in (6) Boi, (7) Ribeira Izé/Mocotó beaches. The olive ridley turtle nests only on the island of São Tomé, mostly in the north of the island, with most nesting activity concentrated along the 9 km stretch of coastline between the beaches of (8) Juventude and (9) Tamarindos.

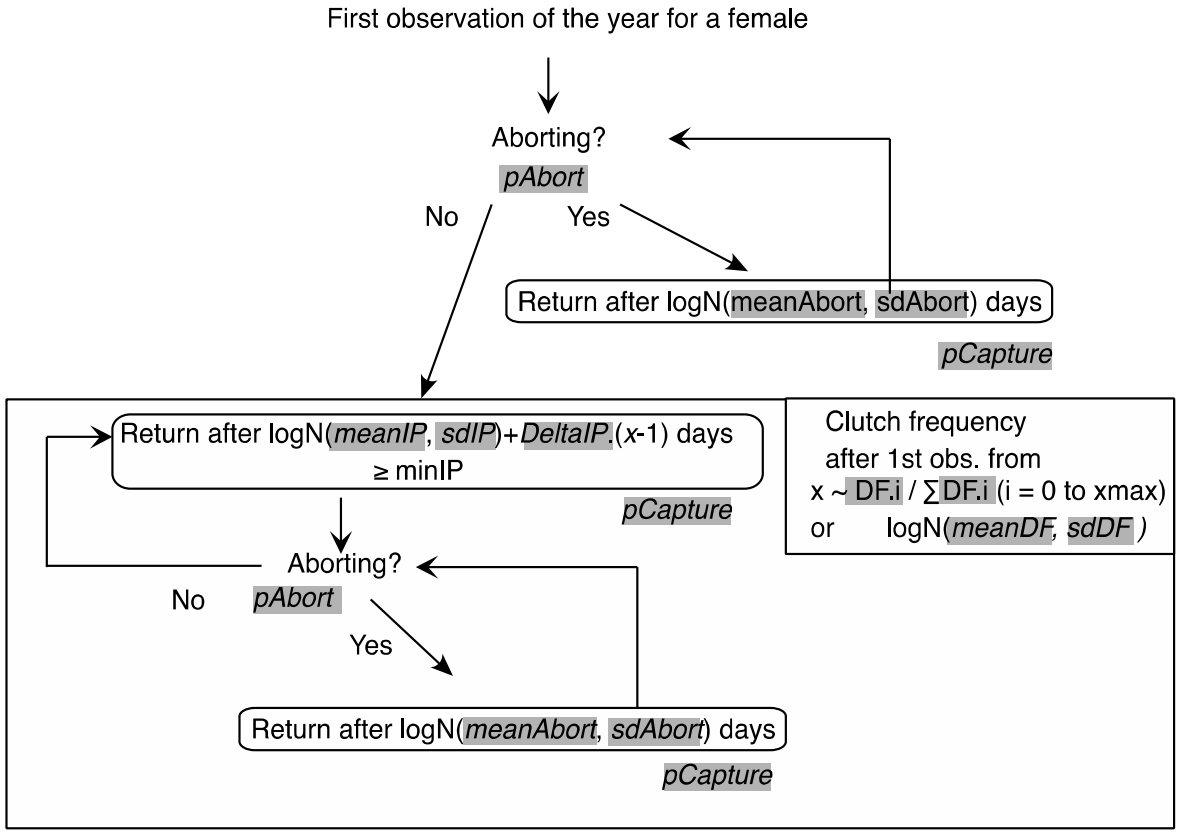

Figure 2: Algorithm of the nesting process of a marine turtle female on a monitored beach (fitted parameters are in grey boxes).

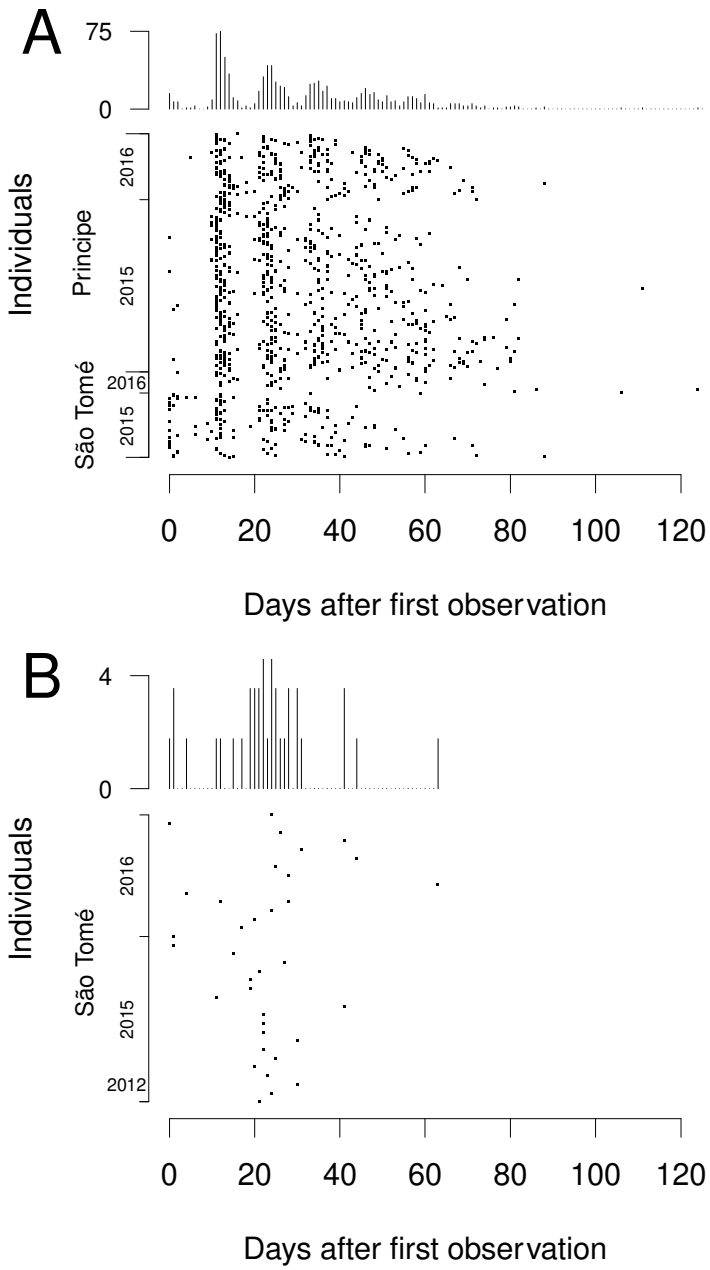

Figure 3.

Distribution of individual daily observations in São Tomé and Príncipe. Rows represent the different captures of a single individual. The sums of all daily observations are depicted at the top of the figure. (A) green turtles (*Chelonia mydas*) and (B) olive ridley turtles (*Lepidochelys olivacea*).

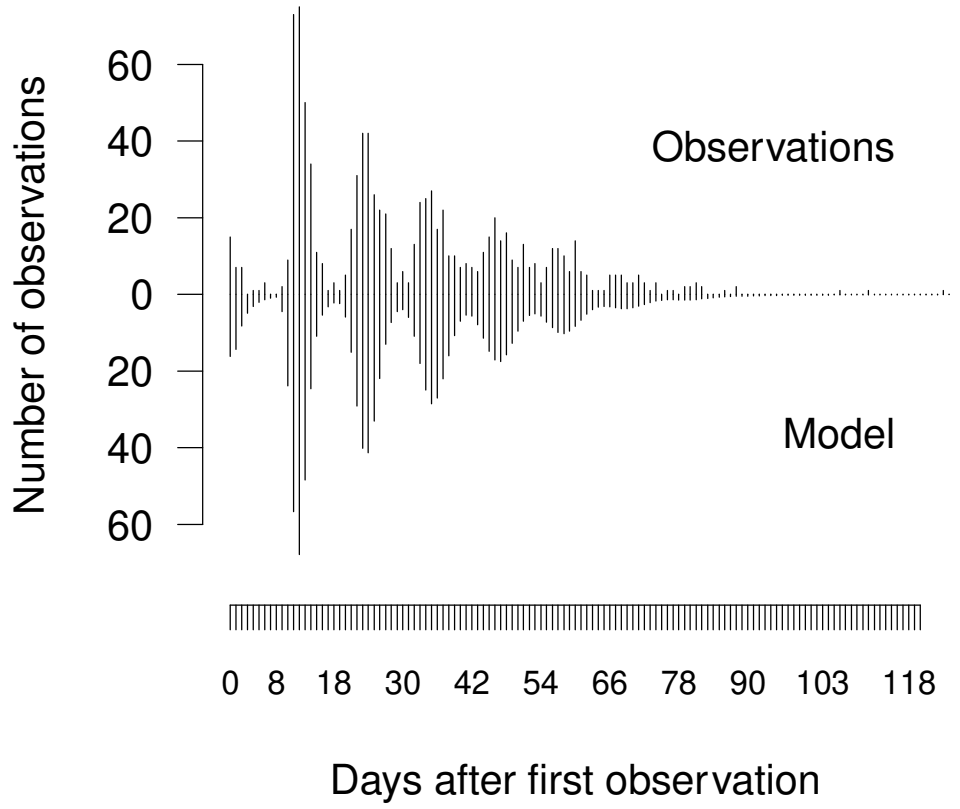

Figure 4:

Comparison between observed (top of fig. 3A) and modelled distribution of the internesting periods for green turtles in São Tomé and Príncipe.

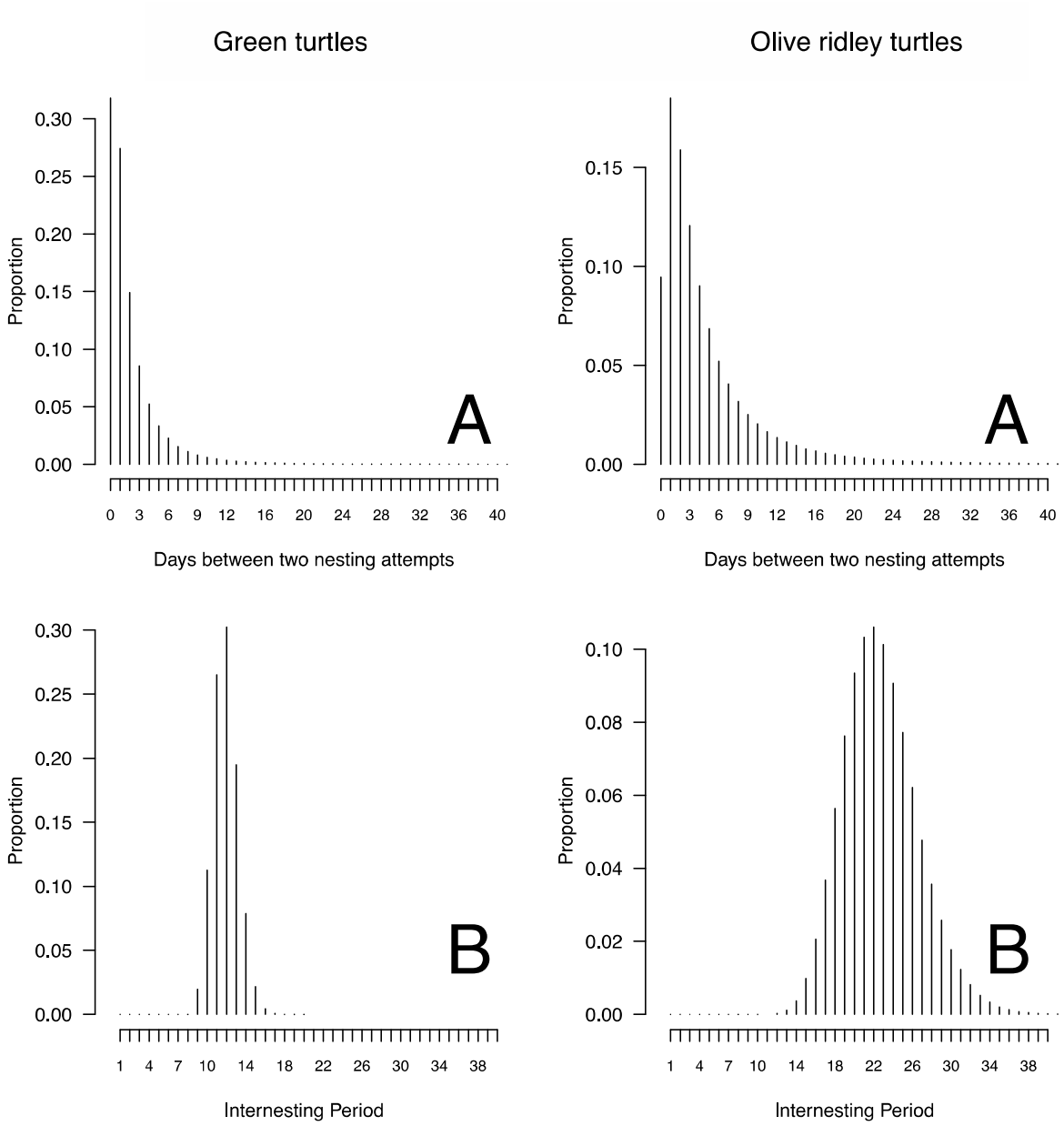

Figure 5:

(A) Distribution of the number of days between two nesting attempts after a nesting abortion, and (B) internesting periods, for green (*Chelonia mydas*) and olive ridley turtles (*Lepidochelys olivacea*).

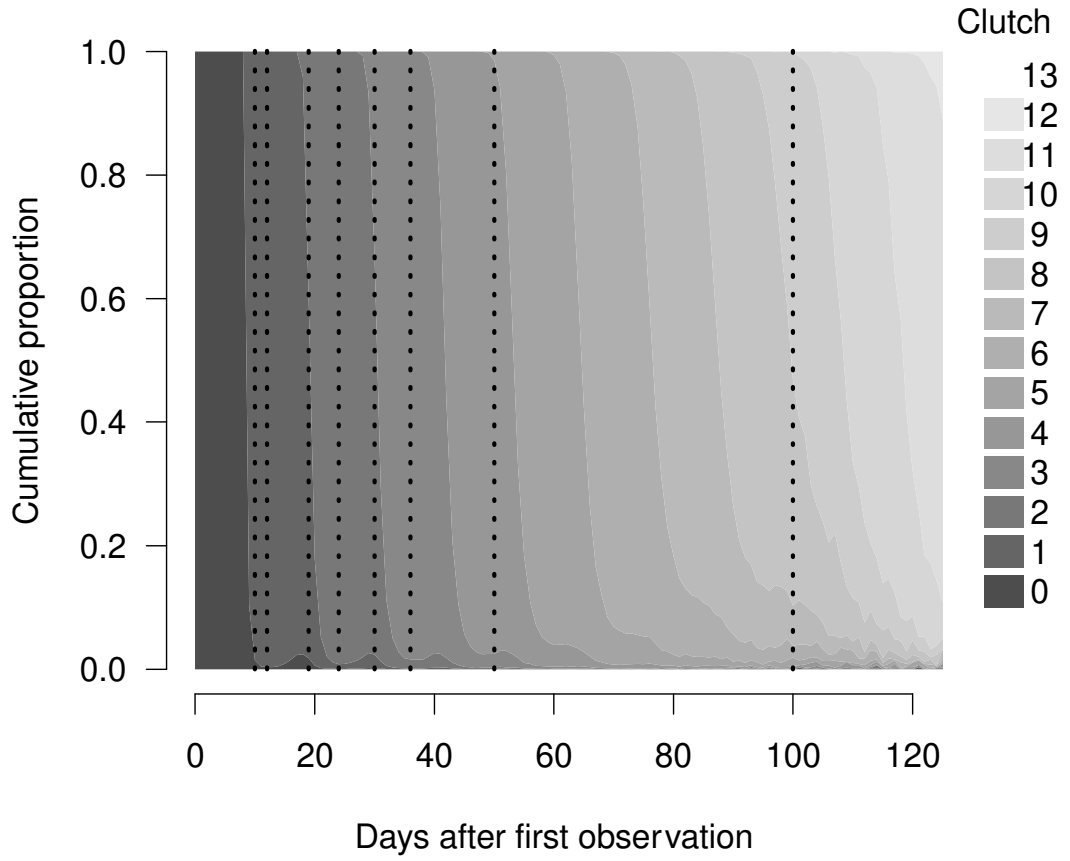

Figure 6:

Probability distribution of the rank of a clutch according to the observed internesting period for green turtles (*Chelonia mydas*) in São Tomé and Príncipe nesting beaches (2015-2017). The values for internesting periods shown as dotted lines are summarized in Table 3.