Factors that Influence Red-billed Tropicbird Survival on Pilot Hill, Sint Eustatius

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Red-billed Tropicbirds breeding on Pilot Hill on the island of Sint Eustatius have been exhibiting an average survival rate of between 30-40%. The influence of nest cavity attributes, environmental covariates, and parent behavior on Red-billed Tropicbird survival were evaluated through nest surveys and camera trap data. Daily survival rate was calculated as a function of selected covariates. Time spent away from the nest by parents and minimum temperature were the most influential factors. Nest attributes and temperature variables did not correlate to survival.

Key words: Daily survival rate, *Phaethon aethereus*, Program MARK, island, incubation

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Introduction

Pelagic seabirds exhibit a set of unique traits such as long lifespans characterized by protracted development and low reproductive rates (Ricklefs, 1990). These traits are believed to be attributes of the seabirds' relationship to the sparse and patchy distribution of their pelagic food supply (Ricklefs, 1990). It is due to this relationship, their tendency to forage at high trophic levels across wide ranges, and their long lifespans that seabirds are known to be good indicators of marine ecosystem health (Furness & Camphuysen, 1997; Paleczny et al.,2015). Although they are good indicators for ecosystem health, this also means that considerable damage or changes to critical ecosystems also stand to negatively impact seabird populations (Furness & Camphuysen, 1997). In the last half-century, seabird populations have deteriorated faster than any other group of birds as they face numerous and varied threats (Croxall et al., 2012). The total population of the world's monitored seabirds has declined by 70% due to direct and indirect human impacts (Paleczny et al., 2015). Marine threats include overfishing and bycatch throughout their lifecycle (Dias et al., 2019; Paleczny et al., 2015; Moss, 2017). Pelagic colonial seabirds are also subject to terrestrial threats during their nesting periods including invasive species, human disturbance, and habitat loss (Paleczny et al., 2015). Overall, increased storm events, changes in food availability, and shifting ecological composition in critical habitats pose serious risks to seabirds (Dias et al., 2019; Paleczny et al., 2015).

Colonial seabirds tend to return to their natal colony year after year and exhibit high fidelity with partners (Morris-Pocock et al., 2012; Moss, 2017; Diop et al., 2018; Boeken, 2012; Madden, 2019; Sherley et al., 2013; Furness & Camphuysen, 1997). High nest site fidelity can facilitate small, genetically isolated colonies with deep evolutionary ties to their habitat, and these seabirds are the most threatened (Croxall et al., 2012; Morris-Pocock, 2012; Nunes, 2018). Seabirds nesting on small, remote islands exhibit sensitivity to their environment via high endemism, genetically separate colonies, and dependence on resource of availability (Morris-Pocock et al., 2012). Small size leaves colonies particularly vulnerable to population decline, as shown in small tropical seabird populations like the Christmas Island Frigatebird and Abbott's Boobies (*Fregata andrewsi; Papasula abbotti*; Morris-Pocock, 2012). The threats small colonies face may be drastically different depending on habitat quality, conservation effort, and invasive species management. For example, colonies of the Red-billed Tropicbird (*Phaethon aethereus*), a pelagic seabird which breeds across a large extant of occurrence, experiences unique reproductive success rates over time and between physically separate colonies (Boeken, 2016; Castillo-Guerrero & Guevara-Medina, 2011; Hernandez-Vazquez et al., 2018; Madden et al. in press a). Two colonies existing on opposite sides of the same small island of Saba exhibited significantly different survival rates of 0% and 74% respectively in the same year (Boeken, 2016). Meanwhile, in Farallon de San Ignacio between the years 2004 and 2007, the nest survival rate was 75% and 35% respectively (Castillo-Guerrero & Guevara-Medina, 2011).

In the Western North Atlantic, there are twenty-one islands with recent population counts, historical evidence, or fossil records of Red-billed Tropicbird presence (Lee & Walsh-McGhee, 2000). Out of the decreasing global population of between 8,000 and 15,000 breeding pairs, 1800 to 3400 breeding pairs reside in the Western North Atlantic (Birdlife, 2021; Lee & Walsh-McGhee, 2000). Most of the population resides on six islands: Saba (35%), Trinidad & Tobago (20%), British Virgin Islands (14%), Saint Martin (7%). The remaining islands hold small, isolated populations of Red-billed Tropicbirds, each totaling less than 5% of the regional population (Lee & Walsh-McGhee). Tropicbirds birds lay a single egg, with the possibility of a second attempt per breeding season (November through May; Castillo-Guerrero & Guevara-Medina, 2011; Boeken, 2016, as cited in Madden, 2019). The parents share incubation duty for approximately 43 days, and then raise the chick to fledging, at about 82 days (Castillo-Guerrero & Guevara-Medina, 2011; Boeken, 2016, as cited in Madden, 2019). Tropicbird chicks are fully reliant on their parents for food and protection from predators in the nest. Red-billed Tropicbirds are top predators, primarily consuming Flying-fish (of the family Exocoetidea), but in years of decreased productivity will also consume an increased proportion of secondary prey such as other pelagic fish and squid (Castillo-Guerrero & Guevara-Medina, 2011).

In a small, but globally significant colony of 300 to 500 pairs breeding in the Boven Important Bird Area of Sint Eustatius, Red-billed Tropicbirds have been experiencing high rates of nest failure in the past decade (Madden, 2019). Tropicbirds on Pilot Hill, monitored between 2013 and 2020, exhibited an egg survival rate of just 39 ± 4% but an 83 ± 5% chick survival rate (Madden et al. in press a). To understand why the Red-billed Tropicbirds of Pilot Hill are experiencing low survival rates in the incubation stage, I hypothesized that the primary threat to the nests was predation by Black Rats (*Rattus rattus*) or cats (*Felis catus)*, because the Caribbean is a region with heavy predation pressure for seabirds (Birdlife, 2021; Boeken 2016; Terpstra, 2015). This hypothesis was also based on the success of predator control in other Red-billed Tropicbird colonies, particularly on the neighboring island of Saba (Terpstra et al., 2015). On Saba, nest survival at one site was shown to improve from 0% to 40% after a moderate, two-season cat removal program (Terpstra et al., 2015). In Puerto Rico, during a control initiative for invasive Black Rats, egg survival increased from 11.5% to 23% to 45.6% over three breeding seasons (Schaffner, 1988).

In addition to predation pressure, there may be other factors at the nest site such as nest attributes, or nest environment covariates that negatively impact the survival of Red-billed Tropicbird nests in the incubation stage on Sint Eustatius (Castillo-Guerrero & Guevara-Medina, 2011). I hypothesized that in addition to threat by predation, the birds may be facing difficulties related to temperature in the nest during the incubation stage, resulting in egg failure. Factors like maximum temperature have been found to significantly influence survival in some seabirds; each increase in the maximum daily temperature of 1℃ resulted in a 40-fold decrease in daily survival rate (DSR) of the Brown Pelican (*Pelecanus occidentalis*; Streker, 2019). Additionally, if temperature-based factors are influential, then exposure to temperature altering factors such as sun and wind may also be important for survival (Hart et al., 2003). These nest attributes can be determined by quantifying sun exposure time and nest orientation.

Finally, the incubation effort by parents may be extremely important both for protection and thermal regulation (Ranconni & Hipfner, 2009). Incubation is an energetically demanding period of avian reproduction, where birds must withstand progressive depletion of energetic reserves by prolonged lack of food (LormÉe et al., 2003; Roncconi & Hipfner, 2009; Sherley et al., 2013). Red-billed Tropicbird eggs rely on parents during incubation for protection and thermal regulation, thus behavioral changes or choices by the parents may impact survival during incubation or increase risk of other factors (Schaffner, 1988). Temperature, predator presence, and parent behavior are all determined using camera traps.

Camera traps are a useful, minimally invasive tool used to obtain precise timing for events such as hatching and predation and avoid personal bias. To investigate these hypotheses, the following research questions were proposed:

1) What predator assemblages are present at the nest site and to what extent are they contributing to predation of Red-billed Tropicbird eggs?

2) Are nest quality and nest environment covariates correlated with reproductive success?

3) Does parental effort influence survival during the incubation stage?

Methods and Materials

Study area

Sint Eustatius is a small (21 km^2) volcanic island in the Carribean; it is a special municipality of the Netherlands. In the northernmost portion of the island exists the Boven Important Bird Area which contains the study colony at Pilot Hill (Geelhoed et al. 2013). Across the island there are numerous Red-billed Tropicbird nest sites, but Pilot Hill (17°29'22'N, 62°59'50'W) is the largest and most accessible (Fig 1). Pilot Hill is an area comprised of rocks and boulders which tumble, erode, and shift on its sandy slopes over time.

Figure 1: Study area outlined in yellow, Pilot Hill, Sint Eustatius in the Caribbean region (Google Earth, 2022).

Weekly nest survey and nest data

Red-billed Tropicbird nests on Pilot Hill have been monitored weekly during the breeding season since 2012; the 2021 to 2022 breeding season surveys followed the same protocol as was previously conducted (Madden, 2019). Breeding season occurs between October and June. The protocol was as follows: nests were historically marked with individual identification numbers and checked approximately every 7 ± 2.06 days. Incubating adults were removed from the nesting cavity by hand and their identification band recorded. Any un-banded individual was given a unique metal identification band on their right leg. Handling of incubating parents did not appear to impact incubating performance, as adults immediately returned to incubating or chick-rearing duty upon release. The orientation of nest openings was determined using Garmin GPSmap 76CSx to measure perpendicular to the primary nest opening. Nest openings were counted, and each nest was ranked on a scale from one to five (1 = inaccessible, 2 = very sheltered, 3 = somewhat sheltered, 4 = very exposed, 5 = unsheltered).

Camera Traps and Photo Processing

Reconyx HC500 Hyperfire trail cameras were deployed inside of occupied Red-billed Tropicbird nesting cavities during the incubation stage over three breeding seasons: 2017 to 2018 (n=13), 2018 to 2019 (n=13), and 2021 to 2022 (n=10). Upon survival or failure of an egg, the camera was moved to a new nest due to the limited number of cameras available (n=6). Cameras were carefully positioned at the edge of nests, so as not to block the nest entrance. Camera traps were set to capture a photo at five-minute intervals and to additionally take a rapid burst of photos when motion was detected. Each photo displays time, date, and temperature in addition to the nest activity in that moment. Batteries and memory cards were replaced during the weekly nest surveys (7 ± 2.06 days).

Analyses, Daily Survival Rate & Program MARK

Photo data included date, time, temperature, adult presence, egg presence, predator presence and identification, adult behavior, and sun exposure. Reconyx camera trap recordings have been compared to a data logger taking temperature measurements at the same time intervals, and the data from both were significantly correlated (> 0.9), rendering the camera trap data accurate enough to use for temperature measurement (Hofmann et al., 2016). Due to differing lengths of camera deployments, adult absence and sun exposure time were taken as a proportion of time, instead of total hours, thus standardizing the data to compare between nests (Castillo-Guerrero & Guevara-Medina, 2011; Rowcliffe et al., 2014). Variables derived from camera trap data include:

- Adult behavior as proportion of time spent incubating, and completely gone from the nest
- Sun exposure was recorded as a binary when egg or adult were in direct sunlight or not, a percentage of total observed time in direct sunlight was calculated.
- Mean temperature in nest
- Mean temperature in nest during day and night (defined between sunrise and sunset)
- Minimum temperature
- Maximum temperature
- Temperature range

In addition to the temperature and behavioral data collected, predator presence and assemblage within nests were determined by recording which predators were documented by camera traps inside nest cavities. Egg mortality attributed to scavenging by predators was determined through photos which show destruction or theft of the egg.

One method for deriving survival rate is to calculate the proportion of all eggs that survived out of all eggs that were detected to determine the apparent hatching success (AHS). However, because successful nests have a higher likelihood of discovery, and nests can be found at different stages of incubation, AHS can be extremely biased (Mayfield, 1975). Instead, Mayfield recommends using the number of total days monitored and nest failures to determine an overall daily survival rate (DSR) that is far more accurate (1975). DSR is the probability any given nest will survive to the next day, based on the data. To determine, for example, the probability of a nest surviving 43 days (the incubation period of Red-billed Tropicbirds), with a DSR of 0.95, the result would be hatching probability = $0.98^{14} = 0.75$. Thus, weekly survey data was used to provide information regarding dates, success, or failure, but Program MARK was used to perform the final analyses using Mayfield's method (1975).

Maximum likelihood was used to estimate DSR using the nest survival model in Program MARK (White & Burnham, 1999). In Rstudio (RStudio, 2020), initial steps included exploring the correlation among individual covariates using Spearman's rank correlation. MARK allows for the modelling of multiple covariates so that competing models can be effectively compared, and the most parsimonious model can give an accurate representation of what factors influence DSR most, as well as an estimate of the DSR. The minimum data requirement for MARK's encounter histories format in nest survival models are the day of the nesting season, the last day the nest was checked when alive, the last day the nest was checked, and the fate of the nest: hereafter called first found, last checked, last found, and fate, respectively. The nesting season days are standardized for each year. The first day of the season is defined as the first day data was recorded. Thus, if a new nest was found a week later, first found would be day seven. The first day was different for each year in this report (October 26, October 29, and October 5).

Data from the camera traps was limited by the small number of cameras, but for nest attribute measurements, cameras were not required. Thus, additional data could be used, and more samples analyzed. I conducted two analyses.

Analysis 1: Exposure and Orientation Data

Measurements of the nest attributes including the exposure ranking, orientation, and number of openings do not require camera data. Thus, more nest survival data could be analyzed to determine any correlation between these variables and survival. To determine whether nest environment covariates influence survival during incubation, the nest exposure data analysis in MARK was performed on four years with reproductive data (n=227)., (2017-2018, 2018-2019, 2019-2020 and 2021-2022; Table 1). The time-specific model performed poorly in previous years (Madden et al., in press a), so the constant nest survival model was used. As with the data obtained from the camera traps, covariates were initially tested for correlation using Spearman's rank correlation in RStudio (Rstudio, 2020), and any non-correlated covariates were used together when attempting to determine the most parsimonious model.

Model	Notation
Single estimate of daily survival	$S_{(*)}$
Year	S_{year}
Season day for nest initiation	S_{Sday}
Season day as quadratic trend	$S_{Sday}{}^2$
Nest exposure ranking	$S_{Exposure}$
Nest orientation	S_{Orien}
Number of openings to nest	$S_{Openings}$

Table 1. Parameters of models using physically measured data to examine daily survival rates (DSR) of Red-billed Tropicbirds during the incubation stage at Pilot Hill, Sint Eustatius between 2017 and 2022.

In both analyses, the most parsimonious model was selected using Akaike's Information Criterion (AIC), which is derived through optimization of Fischer's maximized log-likelihood to compare models to each other (Burnham & Anderson, 2002). Using AIC corrected for small sample size (AICc), the model which most closely describes the data was selected (Burnham & Anderson, 2002). Models with ΔAICc ≤ 2 are supported by the data.

Analysis 2: Camera Trap Data

From the camera data, the fit of 22 a priori models were assessed and ranked using Program MARK. Variables derived from camera data include: nest initiation date (Sday; Julian date), $SDay^2$ (Julian date squared), Year (1=2017-2018, 2= 2018-2019, 3=2021-2022), temperature-based variables (in °C), time spent away from nest (standardized as proportion of time), and sun exposure (also standardized as proportion of time) (Table 2). In addition to these models, combined models of variables which were not found to be correlated in the Spearman's rank correlation were also run and compared. Covariates derived from temperature were not run together in models, as they are derived from the same data.

Model	Notation
Single estimate of daily survival	$S_{(*)}$
Year	S_{year}
Season day for nest initiation	S_{Sday}
Season day as quadratic trend	$S_{Sday}{}^2$
Time spent away from nest	S_{Gone}
Maximum temperature	S_{Max}
Minimum temperature	S_{Min}
Temperature range	S_{Range}
Mean day temperature	S_{Daymn}
Mean night temperature	$S_{Nightmn}$
Overall mean temperature	S_{Mean}
Direct Sun exposure	S_{Sun}

Table 2. Parameters of models using camera trap data to examine daily survival rates (DSR) of Red-billed Tropicbirds during the incubation stage at Pilot Hill, Sint Eustatius between 2017 and 2022.

Results

Predation

In total, for all years, approximately 1.6 million photos were processed. Predator presence was recorded in 80.5% of monitored nest cavities between 2017 and 2022 (Appendix A). 72.2% of all nests had Burrowing Land Crabs (*Gecarcinus ruricola)* in the nests, 16.67% of all nests had Black Rats (*Rattus rattus)*. 13.8% of all nests had both rats and crabs. Rats visited nests when parents were absent 93.33% of all times. Whereas when crabs were present in the nest, they were present alongside incubating parents 68.54% of the time and entered the nest when the egg was unattended 31.46% of the time. Overall, predators were present in nests just 1.09% of the total monitored time (Appendix A). Predators were most often seen in the nest between the hour of zero and five but occurred throughout the day (Fig. 2). Upon initial inspection of the camera trap photos, it appeared that four of the twelve nest failures from monitored nests could be attributed to predation by crabs (n=3) and rats (n=1). However, before being cracked and consumed by predators, the eggs had already been left unattended by parents for an average of 27.64 ± 6.48 hours.

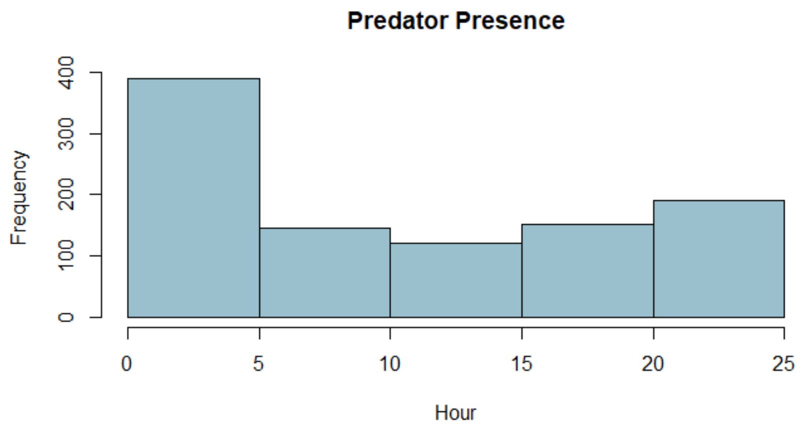

Figure 2. Presence of predators in Red-billed Tropicbird nests on Pilot Hill, Sint Eustatius as frequency of recorded presence by hour using camera traps from 2017 to 2022.

Analysis 1: Exposure and Orientation Data

The most parsimonious models of nest characteristic data did not include any models with nest attributes. The most parsimonious model was the model with year and quadratic trend of season day ($\hat{\beta}_{Year+SDay}{}^{2}$; n=227; Table 3). DSR of 0.21 ± 0.043 was derived from this model which performed 2.99 AIC_c units better than the second-best model. This drastic difference in AICc unit, in addition to the high sample size, indicates that nest orientation, exposure level of nest cavity and number of openings do not influence survival rate of eggs in Red-billed Tropicbirds.

Model Parameter	Φ	SE	Low CI	Upp CI	*k*	∆AICc	AIC_c	w_i
Year + $Sday^2$	0.21	0.043	0.14	0.30	3	0.00	533.98	0.79
Year + Sday	0.21	0.042	0.14	0.30	3	2.99	536.96	0.18
Year	0.21	0.042	0.14	0.30	2	8.71	542.69	0.01
Open + $Sday^2$	0.20	0.040	0.13	0.29	3	9.87	543.85	0.01
Year + Expo	0.21	0.042	0.13	0.30	3	10.68	544.66	0.00

Table 3. Ranking and properties of models that used physical measurement data to examine daily survival rates (DSR) of Red-billed Tropicbirds during the incubation stage at Pilot Hill, Sint Eustatius between 2017 and 2022.

Analysis 2: Camera Trap Data

The most parsimonious model of camera-derived data included time spent away from nest and minimum temperature ($\hat{\beta}_{Gone+Min}$; n=36; Table 4). Any model that contains time spent away from nest is < 2 ∆AIC units. For every increase of 1% in time spent away from nest, the DSR decreased by 0.003% (Fig.3). The DSR estimate across all years provided by the most parsimonious model was 0.32 ± 0.12 ($\hat{\beta}_{Gone+Min}$; n=36; Table 4). This estimate of DSR for any combination of time spent away from nest and minimum temperature in the most parsimonious model is derived by:

$$\frac{\exp \beta0 \ + \ \beta1\,(\text{Gone}) \ + \ \beta2\,(\text{Min})}{1 \ + \ \exp \beta0 \ + \ \beta1\,(\text{Gone}) \ + \ \beta2\,(\text{Min})}$$

Model Parameter	Φ	SE	Low CI	Upp CI	*k*	∆AICc	AIC_c	w_i
Gone + Min	0.32	0.12	0.13	0.60	3	0	102.63	0.15
Gone	0.32	0.12	0.13	0.59	2	0.13	102.76	0.14
Gone + Sun	0.35	0.13	0.14	0.63	3	0.27	102.91	0.13
Gone + Sday	0.33	0.12	0.14	0.61	3	1.04	103.68	0.09
Gone + Range	0.31	0.12	0.13	0.58	3	1.13	103.77	0.09
Gone + Nightmn	0.32	0.13	0.13	0.60	3	1.20	103.84	0.08
Gone + $Sday^2$	0.33	0.13	0.14	0.60	3	1.44	104.07	0.08
Gone + Max	0.31	0.12	0.13	0.58	3	1.85	104.48	0.06
Gone + Mean	0.32	0.13	0.13	0.59	3	1.95	104.59	0.06

Table 4. Ranking and properties of models that used camera trap data to examine daily survival rates (DSR) of Red-billed Tropicbirds during the incubation stage at Pilot Hill, Sint Eustatius between 2017 and 2022.

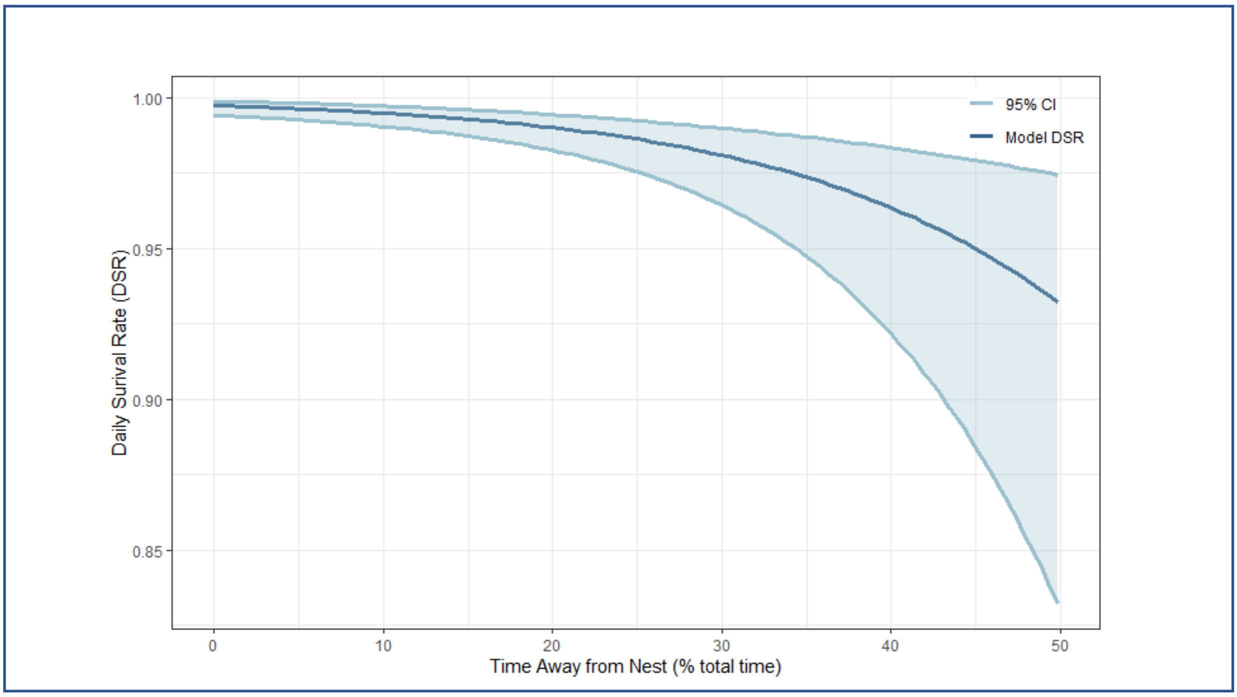

Figure 3. Daily survival rate (DSR) of Red-billed Tropicbirds as a function of proportion of time spent away from nest by parents over total observation period on Pilot Hill from 2017 to 2022.

Parents of successful nests that left their egg unattended did so for 0.78 ± 0.15 hours per absence, and most often between 05:00 and 10:00 h (Fig 4). Parents of failed nests left their egg unattended for 2.52 ± 0.71 hours per absence. The long periods of absence after suspected abandonment would have biased the average period of absence in failed nests, so they were removed from these calculations. The parents of failed nests were also more likely to leave the nest unattended at any point throughout the day, except for between the hours of 20:00 and 24:00 (Fig 4).

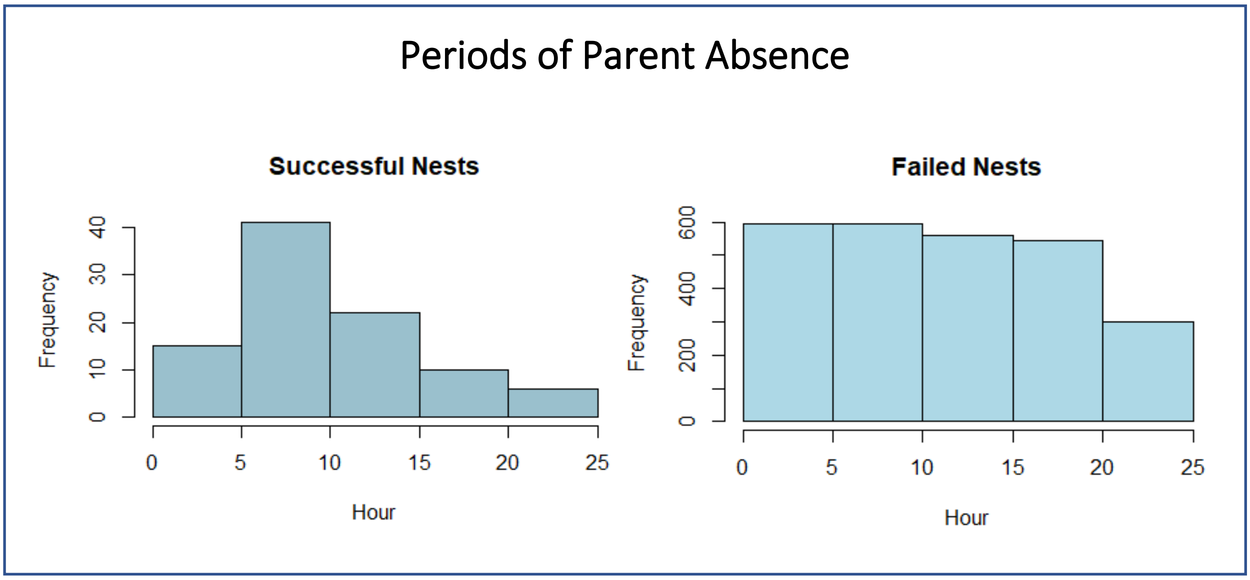

Figure 4: Parental absence from nest in Red-billed Tropicbirds on Pilot Hill, Sint Eustatius as frequency of recorded absence by hour over all camera trap data.

Nests exhibit a larger range of maximum nest temperature than minimum nest temperature. Maximum temperatures ranged from 30 to 46 ℃, whereas minimum temperatures ranged from 20 to 26 ℃. The temperature inside of the nest exhibits a diurnal temperature pattern similar to the external air temperature, but with a delay. Dispite the smaller range, minimum overall tamperature of nest cavities was most influential on daily survival rate of all temperature based covariates, in the top model of the camera data nest survival analysis along with time spent away from nest (Table 4).

Discussion

Predators were present in nests and while the nest was unattended for a long period of time, scavenging of the seemingly abandoned egg could occur. Several nests which were unattended were consumed by crabs or rats, initially indicating that predation may be a primary reason for the extremely low current and historical egg survival rate of tropicbirds at Pilot Hill just 39 ± 4% (Madden et al, in press a). However, in this study, before being predated the eggs had been unattended for over one full day and were already being left unattended for longer periods of time on average (Fig. 4), as opposed to successful nests; this indicates that despite the egg being predated/scavenged, it may be more accurately attributed to parent behavior leading up to the predator interference (Roncconi & Hipfner, 2009). Rats and crabs rarely interacted with parents and were never seen interacting with eggs while parents were present. No cat was detected at any point by camera traps in the Pilot hill colony. On the island of Saba, where cats were a detrimental threat to the breeding tropicbirds, eggs had an 82% probability of hatching compared to Sint Eustatius' 39% (Boeken, 2016; Madden et al, in press a). Rats were never detected predating eggs in the study by Boeken (2016). Meanwhile, the same colony had a 0% probability for chicks to fledge, while Sint Eustatius showed an 83% probability of fledging (Boeken, 2016; Madden et al, in press a). Additionally, there was no significant increase in Red-billed Tropicbird survival during the incubation stage following rat control on Sint Eustatius (Madden pers. comm.). Thus, despite the presence of some nest predators, predation of eggs may not currently be a major risk to the Pilot Hill breeding colony, although it does occur and could evolve into a significant threat in the future.

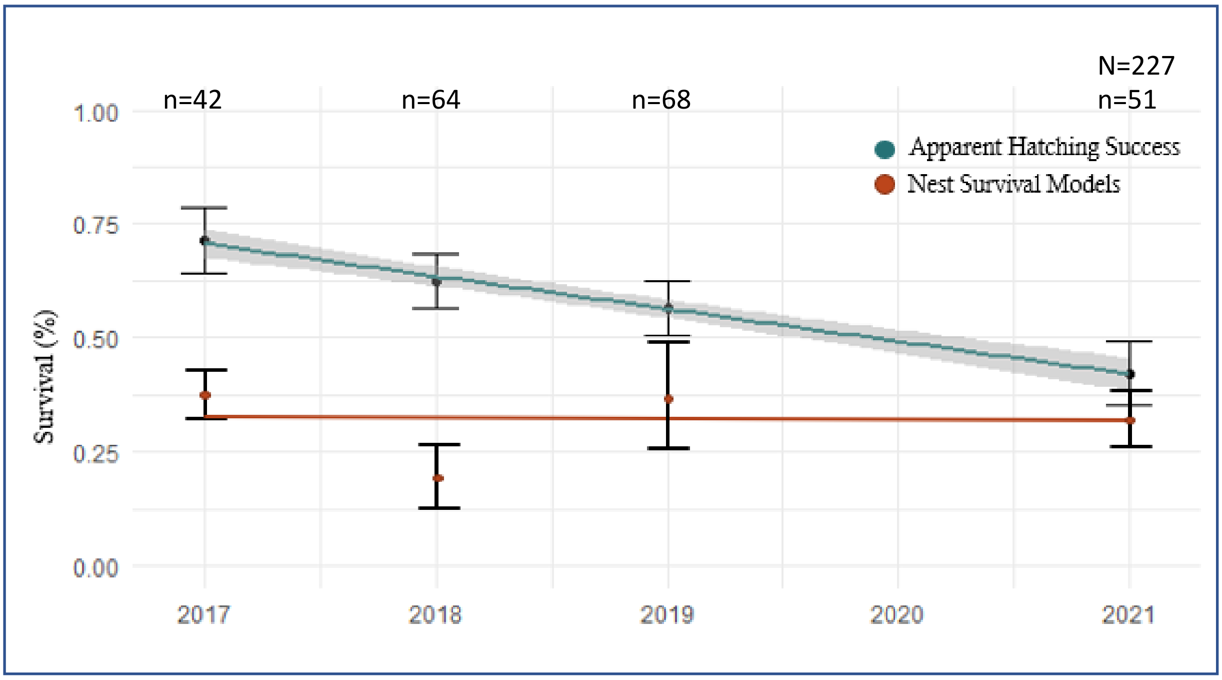

Figure 5: Apparent hatching success Pilot Hill Sint Eustatius 2017 - 2021 versus survival probability estimates using Mayfield's method (1973).

The values for apparent hatching success are very positively biased and thus the pattern of decreasing is inaccurate. Using Mayfield's method, a higher resolution of survival in relation to relevant covariates is determined (1975; Fig 5). According to the first analysis of this study using Mayfield's method, survival during the incubation stage was not significantly influenced by factors within the nest such as temperature, sun exposure, and nest orientation (Table 3; 1975). Every nest attribute covariate, excepting minimum temperature, was not significantly impactful to the survival of the eggs in nests which were monitored with cameras. Red-billed Tropicbird nests do appear to be influenced by the minimum nest temperature reached (Table 4), meaning that ultimately nests which are able to reach the coolest temperature and possibly remain cool for longer periods of time are going to be the most successful. The appearance of the minimum temperature in the top model may indicate a preference for cooler nest temperatures overall, but further research with precise temperature loggers would be necessary to determine this.

In this study, in the second analysis, on camera trap data, it was determined that the time parents spent away from the nest during the incubation stage negatively influenced the survival probability of eggs (Table 4). With this sample size, the precise degree to which the two are linked cannot necessarily be determined with high power, but it certainly indicates that parent absence and egg survival are related. Leading up to failure, Red-billed Tropicbird eggs were unattended for an average 3.5 times longer during each absence than eggs in successful nests. In Red-billed Tropicbirds of the Gulf of California, this type of behavior, decreased nest attendance, was seen more frequently during a period of low productivity than in periods of high productivity (Castillo-Guerrero & Guevara-Medina, 2011).

Reproduction is a complex and energetically expensive process for pelagic seabirds. Parents must manage extensive periods of fasting, particularly in species that avoid leaving the nest unattended, such as the Red-footed Boobies (*Sula sula*) of Europa Island in the

Indian Ocean. The Red-footed Boobies must forage for 11-13 hours per day to have sufficient energy reserves and balance available foraging time with their partner to avoid leaving the nest unattended (LormÉe et al., 2003). In birds that trade-off or coordinate incubating shifts, there is increased time pressure to finish foraging and return to the nest. In the Cassin's Auklet on Triangle Island in British Columbia, eggs were neglected increasingly with high windspeed, when foraging conditions were poor, and foraging parents opted to remain at sea for longer, at which point the incubating parent could decide to leave as well (Roncconi & Hipfner, 2009). Decreased foraging conditions lead to decreased nest attendance, and in the Cassin's Auklet, cumulative days of neglect increased probability of eggs being damaged by predators; invasive Keen's mice (*Peromyscus keeni*) were found to be indicators for incubation consistency (Roncconi & Hipfner, 2009). In this study, eggs which had been unattended for long periods of time (> one day) were ultimately damaged by rats or crabs, and as aforementioned, predators only interacted with unattended eggs, thus, opportunistically.

Many seabirds are detrimentally impacted by poor foraging conditions at sea: decreased prey availability for the temperate African Penguin (*Spheniscus demersus*) around Robben Island over eight years was correlated with decreased survival probability of nest contents (Sherley et al., 2013). Conversely, with increased prey quality and availability, African Penguins showed increased survival (Castillo-Guerrero & Guevara-Medina, 2011; Sherley et al., 2013), while Blue-footed Boobies on El Rancho Island in Mexico were able to lay eggs earlier, lay a larger clutch, and have a higher survival rate in years (Gonzalez-Medina et al., 2018). Long-lived seabirds may opt to leave their nest unattended because they are able to reduce the risk of their own mortality by accepting an increased risk of mortality to their offspring (Martin, 2002). With significant body mass loss, there is also possibility for long-term fitness decrease (Hanssenn et al., 2005). If egg neglect facilitates better exploitation of patchily distributed resources, then the benefits for parents must outweigh the cost of leaving eggs unattended (Murray et al., 1980). This points to a possible trade-off between future reproductive success of the parents and their present effort where parents can invest in future reproduction by reducing nest attentiveness (Martin, 2002). The tropical marine environment is known to be a low-productivity area (Weimerskirch et al., 2004). Red-billed Tropicbirds travel long distances to forage for patchily distributed prey in these nutrient poor tropical waters (Madden et al. in press b). Nest attributes and nest environment covariates had no significant impact on egg survival (Table 3). With tough foraging conditions for Tropicbird parents, and nest attendance (particularly time spent away from nest) appearing as the most influential factor for survival in incubation, conditions away from the nest site may be contributing to the low survival rate of eggs at Pilot Hill. Parents may opt to decrease effort towards their eggs in years with poor foraging conditions in favor of their own survival and future reproductive health (Hanssenn et al., 2005; Martin, 2002).

Dependence on individual stocks or a small selection of stock can leave pelagic seabirds vulnerable to changes in the stock population (Furness & Camphuysen, 1997). Red-billed Tropicbirds' primarily consumed prey is Flying-fish (family Exocoetidae), but in times of low availability, such as the period following El Niño, tropicbirds will also consume an increased amount of secondary prey like pelagic fish and squid (Castillo-Guerrero & Guevara-Medina, 2011). In the Caribbean, the Flying-fish fishery is multilaterally managed, but catch statistics are incomplete and often go underreported (Fanning et al., 2011). Human demand for Flying-fish as bait has increased with the growing use of longline fishing in the lesser Antilles (Fanning et al., 2011). Although the northernmost Caribbean Flying-fish fisheries are less exploited than the southernmost fisheries, the increasing demand for bait through expansion of longline fisheries will contribute to possible expansion of exploited areas (Fanning et al., 2011). Due to the methods of gillnet or pelagic troll fishing an increase in Flying-fish demand will also inevitably lead to an increase of pelagic fish catch overall in the Caribbean (Fanning et al., 2011). In the tropics, where productivity is low and important resources like Flying-fish are patchily distributed, fisheries may exacerbate the existing challenges with resource availability for tropicbirds (Fanning et al., 2011).

Island-based seabird colonies are often genetically isolated and have deep evolutionary ties to their habitat which make them particularly vulnerable to population decline (Croxall et al., 2012; Morris-Pocock, 2012; Nunes, 2018). Red-billed Tropicbirds exhibit high nest fidelity and return to their natal colony which allows for this type of genetic isolation (Madden et al., 2019; Diop et al., 2018). Although the type and degree of threat may vary colony to colony, threats at the nest site include invasive species, human disturbance, and habitat loss. Additionally, climate change increases risks from sea level rise and storm events like hurricanes which can do irreversible damage to small, isolated populations (Croxall et al., 2012; Morris-Pocock, 2012). Some colonies may be more likely to face threats at sea than at the nesting site, such as the colony at Pilot Hill on Sint Eustatius. These threats may include, but are not limited to overfishing, bycatch, changes in food availability, and shifting ecological composition (Dias et al., 2019; Paleczny et al., 2015).

Limitations of this study may include the inability to determine which parent is incubating at a given time. Thus, parent effort could not be determined for individuals, only pairs of parents together. Additionally, the samples size was small for the nest analysis conducted using the camera data (n=36), and between year comparisons were not possible. Temperature data was a measurement of air temperature in the nest. Internal egg temperature may have been a more accurate way to determine if temperature influences egg survival. Additionally, camera traps measure their own internal temperature. Although their measured temperature is closely correlated to external air temperature (Hofmann et al., 2016), factors such as sun exposure may lead to more accurate evening readings and skewed day time readings.

Conclusion

Through camera trap photo analysis, the proportion of time that parents were gone from the nest during the incubation stage significantly influenced DSR for Red-billed Tropicbird eggs at Pilot Hill. When eggs are left unattended for long periods of time, they are at risk of being opportunistically scavenged by crabs and rats (Roncconi & Hipfner, 2009). Individual Red-billed Tropicbird colonies face unique challenges and although these birds are not classified as endangered, their small colony size, site fidelity, and their dependence on conditions at sea leave them particularly vulnerable (Morris-Pocock et al., 2012; Moss, 2017; Diop et al., 2018; Boeken, 2012; Sherley et al., 2013; Furness & Camphuysen, 1997). Small islands support small colonies that can be easily endangered by seemingly typical shifts in population (Morris-Pocock, 2012). The Caribbean is a risk area for hurricanes, which can cause significant damage to small island colonies, and will increase in frequency in coming years (Dias et al., 2019; Paleczny et al., 2015). Protection of Red-billed Tropicbird nesting sites, continued invasive species management, and careful fisheries management are useful tools for protecting birds that are at risk of population decline (Fanning, 2011; Paleczny et al., 2015). Continued population surveys and collection of camera trap data of tropicbird nests at Pilot Hill would contribute to years of historical data and potentially illuminate long-term trends in Red-billed Tropicbird reproduction and survival and influential factors.

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Appendix A:

Year	Nest	Total number of photos	Photos with Crabs	Photos with Rats	Total Predators	Percentage
2021	67	283	0	0	0	0
2021	68	11115	0	0	0	0
2021	80	4072	239	0	239	5.894
2021	93	1144	0	0	0	0
2021	94	8560	8	0	8	0.0935
2021	241	1334	0	2	2	0.1499
2021	505	9034	744	1	745	8.247
2021	522	5704	1	0	1	0.0175
2021	823	2738	2	0	2	0.0730
2021	878	3678	2	0	2	0.0544
2019	62	7944	12	0	12	0.1133
2019	67	9212	2	1	3	0.0003
2019	74	6060	1	0	1	0.0165
2019	80	2752	3	0	3	0.1090
2019	87	6742	11	0	11	0.1632
2019	159	1764	0	0	0	0
2019	508	2052	2	0	2	0.0975
2019	689	3582	1	0	3	0.0838
2019	708	1285	10	0	10	0.7782
2019	801	2014	1	0	1	0.0497
2019	803	2992	4	0	4	0.1337
2019	823	8399	6	0	6	0.0714
2019	873	1488	0	0	0	0
2018	10	5040	1	25	26	0.5357
2018	67	7125	1560	0	1560	21.95
2018	68	12452	0	0	0	0
2018	72	4757	2	0	2	0.0420
2018	84	6692	0	0	0	0
2018	94	8822	0	0	0	0
2018	195	8700	17	0	17	0.2069
2018	787	2762	1	0	1	0.0276
2018	788	6064	1	0	1	0.0165
2018	855	6709	13	0	13	0.0019
2018	870	9267	2	0	2	0.0216
2018	871	4085	7	2	9	0.2203
2018	873	6184	9	0	9	0.1455

Table A1: Predator presence in Red-billed Tropicbird nests of Pilot Hill, Sint Eustatius during the incubation stage between 2017 and 2022.