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Waterbirds

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<https://doi.org/10.1675/063.045.0106>

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# Reproductive Success of Red-Billed Tropicbirds (*Phaethon aethereus*) on St. Eustatius, Caribbean Netherlands

HANNAH MADDEN<sup>1,2\*</sup>, MARDIK LEOPOLD<sup>3</sup>, FRANK RIVERA-MILÁN<sup>4</sup>, KEVIN VERDEL<sup>5</sup>, ÉLINE EGGERMONT<sup>5</sup>  
AND PATRICK JODICE<sup>6</sup>

<sup>1</sup>Marine Animal Ecology Group, Wageningen University, Droevendaalsesteeg 1, 6708 PB, Wageningen, the Netherlands

<sup>2</sup>Caribbean Netherlands Science Institute (CNSI), P.O. Box 65, St. Eustatius, Caribbean Netherlands, NIOZ Royal Netherlands Institute for Sea Research, and Utrecht University, P.O. Box 59, 1790 AB Den Burg, Texel, the Netherlands

<sup>3</sup>Wageningen University, Wageningen The Netherlands

<sup>4</sup>United States Fish and Wildlife Service, Division of Migratory Bird Management, Branch of Assessments and Decision Support, 11510 American Holly Drive, Laurel, Maryland 20708, USA

<sup>5</sup>Utrecht University, Utrecht, The Netherlands

<sup>6</sup>U.S. Geological Survey South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, USA

\*Corresponding author; E-mail: Hannah.madden@cnsi.nl

**Abstract.**—The daily nest-survival rates of Red-billed Tropicbirds (*Phaethon aethereus*) were estimated over six breeding seasons on St. Eustatius in the Caribbean. We analyzed 338 nesting attempts between 2013 and 2020. The daily survival rate (DSR) of tropicbird nests was modeled as a function of nest initiation date, sea surface temperature (SST), elevation, vegetation in front of the nest, and year. Yearly nest survival rates ( $\pm$  SE) of the best fitting models ranged from  $0.21 \pm 0.06$ – $0.74 \pm 0.13$  ( $n = 338$  nests). DSR of the most parsimonious models averaged  $0.39 \pm 0.04$  during the incubation period,  $0.83 \pm 0.05$  during the chick-rearing period, and  $0.30 \pm 0.04$  during the nesting period (incubation through fledging) when data were pooled across all years. Models with linear and quadratic trends of nest initiation date combined with SST and elevation received strong support in the incubation and nesting periods. Nests initiated in peak nesting season, when SSTs were lower, had higher DSR estimates than nests initiated early or late in the season. Compared to studies of the same species from Saba and the Gulf of California, survival probability on St. Eustatius was lower during the incubation stage but higher during the chick-rearing period. Similar to populations in the Gulf of California, tropicbird reproduction differed and laying date varied among years, and survival was influenced by SST. Our results are consistent with a study on White-tailed Tropicbirds (*Phaethon lepturus*) in Bermuda which found that survival was affected by temporal factors rather than physical site characteristics. Our study contributes to a better understanding of the factors that influence Red-billed Tropicbird survival on a small Caribbean island. Received 27 Jan 2021, accepted 7 Nov 2021.

**Key words.**—Daily survival rate, nest initiation, nest survival, *Phaethon aethereus*, program MARK, predation, Red-billed Tropicbird, sea surface temperature, St. Eustatius.

Waterbirds 45(1): 39-50, 2022

Marine birds are among the most threatened avian species worldwide (Croxall *et al.* 2012). Population declines among seabirds are often due to long-term and large-scale environmental changes that can be exacerbated by seabird longevity, large ranges, and foraging patterns (Paleczny *et al.* 2015). Seabirds experience substantial threats, both at their terrestrial nesting sites and their marine foraging areas. These threats include predation of eggs and chicks (Jones *et al.* 2008), overexploitation of food resources (Cury *et al.* 2011; Oppel *et al.* 2015), climate change (Hass *et al.* 2012), pollution (Wilcox

*et al.* 2015), and degradation of nesting areas (Samways *et al.* 2010). Both lethal (e.g., nest predators; Hobson *et al.* 1999) and sub-lethal threats (e.g., nest disturbance by humans; Burger and Gochfeld 1991) can have substantial effects on reproductive success and site fidelity (Blackmer *et al.* 2004). The extent to which seabirds can cope with dynamic marine environments and fluctuations in food availability depends largely on their life-history traits (Crawford *et al.* 2006; Sandvik and Erikstad 2008) including timing of breeding, adult survival, reproductive output, growth rates of chicks, foraging range,

and diet (Weimerskirch 2002). In particular, tropical seabirds live in oligotrophic marine environments where food resources are often scarce and unpredictable (Ballance and Pitman 1999; Weimerskirch 2007). As a result, variations in sea surface temperature (SST) can influence food availability for tropical seabirds, particularly those with long breeding seasons (Barbraud *et al.* 2008; Cubaynes *et al.* 2011).

The Red-billed Tropicbird (*Phaethon aethereus*, hereafter “tropicbird”) is the rarest and most vulnerable seabird in the order Phaethontiformes (Castillo-Guerrero *et al.* 2011). Estimates for the global population of tropicbirds range from 5,000 to 20,000 individuals (BirdLife International 2018). Within the Caribbean region, there are approximately 2,000 nesting pairs, although population size is difficult to assess due to the species’ preference for inaccessible, remote, and scattered nesting sites (Lee and Walsh-McGehee 2000). In the Lesser Antilles, St. Eustatius and Saba together support about 1,300–2,000 pairs (Delnevo 2013). Stonehouse (1962) observed that tropicbirds on Ascension Island in the South Atlantic followed a pattern showing marked peaks and low points of breeding activity, with peaks spaced eleven months apart. This is supported by Boeken (2016) and Sarmiento *et al.* (2014), who documented breeding on Saba in the Lesser Antilles and off the coast of Brazil between October and June. Tropicbirds are the only seabird species known to currently nest on St. Eustatius (Lowrie *et al.* 2012), but no formal studies of their nesting biology on the island have been previously conducted. Tropicbird nesting colonies in the Caribbean experience a variety of threats, including coastal development (Lee and Walsh-McGehee 2000), predation by non-native species (Boeken 2016), and site disturbance from natural causes (Wiley and Wunderle 1993).

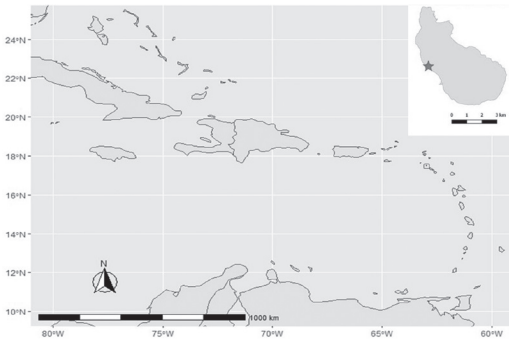
This is the first study of Red-billed Tropicbird reproduction on St. Eustatius. Our objective was to estimate daily survival rates (DSR) of tropicbird nests at the core nesting area on St. Eustatius during breeding seasons from 2013–2020, and to determine

the importance of local and regional environmental variables on survival. Combined with a lack of information about the reproductive success of tropicbirds on St. Eustatius, and given the island’s regional importance for nesting (Delnevo 2013), we sought to identify the main factors influencing their survival of tropicbirds on this island. We hypothesized that differences in DSR estimates between eggs and chicks would exist, with survival being lowest during the incubation period (~43 days) compared to the chick-rearing period (~85 days; Boeken 2016) due to predation on eggs by land crabs (*Gecarcinus ruricola*,) and black rats (*Rattus rattus*). We also hypothesized that DSR estimates of eggs and chicks would increase with time, showing linear or curvilinear relationships with nest initiation date (NID and NID<sup>2</sup>; Ramos *et al.* 2002). A curvilinear relationship would indicate that nest initiation beyond a certain threshold date would result in a decline in DSR. Timing of breeding, and thus nest initiation, may be viewed as a coarse index of food availability; previous studies have demonstrated a causal relationship between timing of breeding and food availability in terns (Safina *et al.* 1988; Ramos *et al.* 2002, Reynolds *et al.* 2014). We predicted that DSR in the incubation period would be linked to sea surface temperature (SST), associated with the effects of food availability (Castillo-Guerrero *et al.* 2011). We expected nests at higher elevations to have higher DSR estimates than those at lower elevations due to decreased predator accessibility (Hervías *et al.* 2013). Lastly, we used year as a covariate to assess interannual variability in nest survival rates.

## METHODS

### Study Area

St. Eustatius (21 km<sup>2</sup>), a special municipality in the Caribbean Netherlands, is a volcanic island that supports two Important Bird Areas (IBA): The Quill IBA to the south and Boven IBA to the north (BirdLife International 2020). Our study took place at Pilot Hill (~1.1 ha; 17.4894°N, 62.9972°W; Fig. 1), which is located inside the boundary of Boven IBA. The study area supports an estimated 30% of known nest sites for tropicbirds on St. Eustatius, and unlike other nesting areas on the island,



**Figure 1.** Map of the Lesser Antilles showing St. Eustatius (black box) and the Pilot Hill study site on St. Eustatius (inset, indicated by a star).

can be accessed for monitoring relatively easily. The terrain consists of rocky slopes and sheer cliffs. Due to the topography and safety concerns, we were only able to monitor nests at elevations < 50 meters above sea level. These nests are located individually along the lower parts of the cliff and are occasionally clumped where large clusters of boulders provide suitable nesting conditions. We estimate that the higher, inaccessible nest cavities on Pilot Hill can reach a maximum elevation of 150 meters.

#### Nest Monitoring

Adult tropicbirds breed annually, laying a single egg in a natural cavity (Castillo-Guerrero *et al.* 2011). Breeding in the Lesser Antilles generally occurs from mid-October to June, with a peak between January and April (Sarmento *et al.* 2014). Similar to other tropical seabirds with asynchronous breeding, nesting can overlap with hurricanes and tropical storms (Nicoll *et al.* 2017). Incubation lasts ~ 43 days, and after hatching the chick remains in the nest for ~ 85 days where it is provisioned by both parents (Boeken 2016). We located nests by opportunistically walking through the nesting area, watching for adults entering or leaving cavities, searching cavities, and by listening for alarm calls of adults and chicks. At discovery, we recorded nest locations with a GPS and affixed a numbered metal tag nearby the cavity.

We monitored 471 nesting attempts between 2013 and 2020, of which 338 were included in our analyses (we excluded nesting attempts for which we did not know the outcome i.e., success/fail). We generally followed nest-monitoring methods described in Brooks *et al.* (2013) and Boeken (2016). Due to difficulties in determining sex among tropicbirds in the field (Nunes *et al.* 2013), adults were not sexed. To estimate DSR of eggs and chicks, we checked all accessible cavities weekly between October and June in 2013–2020, but not in the 2016–2017 season. Chicks were extracted from cavities by hand and subsequently banded at least two weeks post-hatching using individually numbered metal leg bands. In cases where hatch dates were not known and the chicks were inaccessible, we estimated hatch dates

and chick ages based on nesting activity during subsequent visits. Chicks were monitored until they fledged, disappeared, or until the date of the final visit. Any chicks still present with an estimated age of seven or more weeks, or weighing  $\geq 450$  grams, were assumed to have fledged (Mejías *et al.* 2017). Inactive nests, as well as chicks still in the nest on our final visit aged seven weeks or less, or weighing  $\leq 450$  grams, were excluded from the analysis ( $n = 86$ ). This criterion was selected based on previous studies that found chick mortality in the closely-related White-tailed Tropicbird (*Phaethon lepturus*) to be higher among younger chicks (Phillips 1987; Malan *et al.* 2009).

To determine whether predators were responsible for failure at a subset of nest sites, we deployed ten RECONYX cameras during incubation and maintained them until the nest failed or the chick was approximately three weeks post-hatch. Cameras were set to take a photograph every 5 minutes during a 24-hour period, and a series of photographs when triggered by heat or movement. Our decision to move cameras after a chick reached three weeks of age was based primarily on the small number of cameras available ( $n = 10$ ), and the fact that we were primarily interested in determining if predation by rats was occurring during the incubation and early chick-rearing stage. If a nest with a camera was found to be empty (i.e., egg or chick no longer present), we removed the camera and placed it inside another active nest. Nests that were installed with cameras were chosen opportunistically based on a combination of characteristics including accessibility, visibility, and stability. We examined photographs from failed nests to determine if predators were present at or near the failure date. Over the entire nesting period, we also classified nests as having been depredated if we observed an eggshell with bite marks, remains of dead chicks, or predator scat at the nest coincident with egg or chick mortality (e.g., Brooks *et al.* 2013).

#### Daily survival rate (DSR)

For the purpose of this paper, we define “daily survival rate” as the probability that a nest will survive a single day, and “nest survival” as the probability that a nest will be successful. We used maximum likelihood to estimate DSR using the nest survival model as implemented in program MARK (White and Burnham 1999; Dinsmore and Dinsmore 2007; Rotella 2009) and the package *RMark* (Laake 2013) in the R environment (R Core Team 2020). We tested for correlation among individual covariates using the Spearman’s rank correlation. In program MARK we first assessed the fit of models with constant nest survival rate and time-specific nest survival rate. After that initial assessment, we included constant nest survival as the main factor and limited our analyses to a set of 16 *a priori* models that examined the effects of the following covariates: nest initiation date (NID; Julian date to explore a linear relationship with DSR); NID squared (Julian date<sup>2</sup> to explore a curvilinear relationship with DSR); vegetation immediately in front of the nest (0-4; 0 = no vegetation, 4 = nest entrance obscured); elevation of the nest (10-47 m); el-

elevation squared (elevation<sup>2</sup> to explore a curvilinear relationship with DSR); Year (1 = 2013–2014, 2 = 2014–2015, 3 = 2015–2016, 4 = 2017–2018, 5 = 2018–2019, 6 = 2019–2020); sea surface temperature (SST; monthly mean °C at nest fate [success/fail]) measured at monitoring locations within 200 km of the island, downloaded from [https://iridl.ldeo.columbia.edu/maproom/Global/Ocean\\_Temp/Monthly\\_Temp.html](https://iridl.ldeo.columbia.edu/maproom/Global/Ocean_Temp/Monthly_Temp.html); Reynolds *et al.* 2002); and combinations of all categorical and continuous variables that were not correlated (Table 1). DSR was calculated separately for the incubation and chick-rearing stages, and across both stages combined (i.e., overall).

Model selection was based on minimization of Akaike Information Criterion corrected for small sample size (AIC<sub>c</sub>; Burnham and Anderson 2002). Models with ΔAIC<sub>c</sub> ≤ 2 were considered equally supported by the data. We estimated DSR for (1) individual nesting seasons (year 1–6); (2) years pooled for the incubation period; (3) years pooled for the chick-rearing period; and (4) years pooled for the two periods combined (the nesting period). We performed a likelihood ratio test on the most parsimonious models to ensure goodness of fit. We compared DSR of pooled data during the incubation and chick-rearing period with the Z test (Pollock *et al.* 1990).

RESULTS

Nest monitoring

We monitored 471 nesting attempts from 2013 to 2020, based on new and repeat nests in subsequent years. Of the 253 nest attempts that failed among all years, we were

unable to determine the cause of failure of ~79% (Table 2; Tables S1, S2 and S3). Of 161 nests monitored via camera traps, we classified 15 failures (9.3%) as rat predation from nine camera records, and six observations of rat predation via nest monitoring through evidence left by predators.

There was a significant difference in DSR between the incubation and chick-rearing stage, using estimates from the models with the strongest support (all years combined with NID, SST and elevation as covariates) ( $Z = -2.19, P = 0.03$ ). Based on AIC<sub>c</sub>, the time-specific nest survival model performed poorly compared to the constant nest survival model. Thus, we selected the constant nest survival model to explore the influence of our selected independent variables on tropicbird DSR. For incubation and for both stages combined, the most parsimonious models contained the effects of NID, NID<sup>2</sup>, SST, elevation, and elevation<sup>2</sup> (summed  $w_i = 1.00$ ; Table 3). For the chick-rearing period, the most parsimonious models contained the effects of NID, NID<sup>2</sup>, SST, and elevation (summed  $w_i = 1.00$ ; Table 3). The results of these models suggest that nests initiated at the beginning of the year were more likely to succeed as Julian date increased during all stages of the nesting period. When combined with other covariates, the top models

**Table 1. Models examining daily survival rates of Red-billed Tropicbirds (*Phaethon aethereus*) during the incubation and chick-rearing phases and the entire nesting period on St. Eustatius, Caribbean Netherlands, 2013-2020. NID = nest initiation date; SST = sea surface temperature.**

Model	Notation
Single estimate of daily survival	$S^{(y)}$
Effect of year only	$S_{year}$
Effect of elevation only	$S_{elev}$
Effect of vegetation only	$S_{veg}$
Effect of NID only	$S_{NID}$
Effect of SST only	$S_{SST}$
Effect of year + vegetation	$S_{year+veg}$
Effect of NID + a quadratic trend	$S_{NID+NID^2}$
Effect of NID + elevation	$S_{NID+elev}$
Effect of NID + SST	$S_{NID+SST}$
Effect of elevation + a quadratic trend	$S_{elev+elev^2}$
Effect of NID + SST + elevation	$S_{NID+SST+elev}$
Effect of NID + a quadratic trend + SST	$S_{NID+NID^2+SST}$
Effect of NID + a quadratic trend, SST + elevation	$S_{NID+NID^2+SST+elev}$
Effect of NID + SST + elevation + a quadratic trend	$S_{NID+SST+elev+elev^2}$
Effect of NID + a quadratic trend, SST + elevation + a quadratic trend	$S_{NID+NID^2+SST+elev+elev^2}$

**Table 2. Summary of eggs laid/lost, chicks hatched/lost/fledged, apparent hatching success, and apparent breeding success of Red-billed Tropicbirds at the Pilot Hill study area on St. Eustatius, Caribbean Netherlands, 2013-2020. Apparent hatching success is the number of chicks hatched as a proportion of the number of eggs laid. Apparent breeding success is the number of chicks fledged as a proportion of the total eggs laid.**

Season	Total eggs laid	Total eggs lost	Total chicks hatched	Total chicks lost	Total chicks fledged	Apparent hatching success (%)	Apparent breeding success (%)
2013-2014	73	23	50	8	39	64.60	38.80
2014-2015	88	39	49	10	28	57.00	37.80
2015-2016	69	28	41	10	22	59.40	37.30
2017-2018	68	29	54	7	32	57.35	47.01
2018-2019	90	36	54	11	43	60.00	47.78
2019-2020	83	37	46	15	31	55.42	37.35
Total	471	192	279	61	195	58.96	41.01

contained the covariate NID. The influence of vegetation in front of the nest and year on nest survival of tropicbirds was negligible.

DSR estimates derived from the model that received the most support were 0.56  $\pm$  0.12 ( $\pm$  SE) in 2013-2014 ( $_{\text{NID+elev}}$ ;  $n = 82$ ), 0.63  $\pm$  0.134 in 2014-2015 ( $_{\text{NID}}$ ;  $n = 89$ ), 0.74  $\pm$  0.13 in 2015-2016 ( $_{\text{NID+elev}}$ ;  $n = 70$ ), 0.32  $\pm$  0.09 in 2017-2018 ( $_{\text{SST+elev}}$ ;  $n = 59$ ), 0.21  $\pm$  0.06 in 2018-2019 ( $_{\text{NID+NID}^2}$ ;  $n = 74$ ), and 0.38  $\pm$  0.11 in 2019-2020 ( $_{\text{NID+NID}^2+\text{elev}+\text{elev}^2+\text{SST}}$ ;  $n = 62$ ). Overall, when data were pooled across all years, survival probability estimates of the most parsimonious model  $_{\text{NID+NID}^2+\text{elev}+\text{SST}}$  were 0.39  $\pm$  0.04 during the incubation period (Table 3). Models incorporating linear and quadratic trends of NID and SST received substantial support; in the best model were  $_{\text{NID}} = 0.02$  (SE = 0.004, 95% confidence interval (CI) = 0.01, 0.03); and  $_{\text{SST}} = 1.32$  (SE = 0.23, 95% CI = 0.87, 1.77) on a logit scale and these effects were always positive in models with constant survival. Beta parameters for survival in relation to a quadratic trend of NID were inestimable. When the effect of elevation featured in the top models, 95% confidence intervals included zero. There was no evidence of direct effects of year or vegetation in front of the nest on DSR during the incubation period.

The estimate of the average survival probability of the most parsimonious model for the chick-rearing period,  $_{\text{NID+NID}^2+\text{SST}}$  was 0.83  $\pm$  0.05 (Table 3). Models incorporating NID, a quadratic trend of NID and SST received substantial support; in the best model were  $_{\text{NID}}$ : 1.17 (SE = 0.44, 95% CI = 0.30, 2.04);  $_{\text{NID}^2}$ : 0.05 (SE = 0.007, 95% CI = 0.04, 0.07) on a logit scale and these effects were always positive in models with constant survival. Beta parameters for chick survival in relation to SST were inestimable. Models with quadratic and linear trends on DSR received strong support. There was no evidence of direct effects of year or vegetation in front of the nest on DSR during the chick-rearing period.

The estimate of the average survival probability of the most parsimonious model for the nesting period,  $_{\text{NID+NID}^2+\text{elev}+\text{SST}}$  was 0.30  $\pm$  0.04 (Table 3). Models incorporating NID, a quadratic trend of NID and SST received

Table 3. Models used to assess daily survival rate of nests and chicks of Red-billed Tropicbirds on St. Eustatius, Caribbean Netherlands (only the top four models are shown). Estimate ( $\Phi$ ) is average survival probability from 2013-2020, with lower and upper 95% confidence intervals.  $k$  is the number of parameters in the model, and  $w_i$  is the model weight. NID = nest initiation date; SST = sea surface temperature; AICc = Akaike Information Criterion corrected for small sample size.  $\chi^2$  and  $P$  indicate model fit.

Period	Model parameter	$\Phi$	SE	Low CI	Upp CI	k	AICc	$\Delta$ AICc	$w_i$	$\chi^2$	df	P
Incubation	NID+NID <sup>2</sup> +SST+elevation	0.39	0.04	0.31	0.47	5	900.17	0.00	0.70	0.31	1	0.58
Incubation	NID+NID <sup>2</sup> +SST+elevation+elevation <sup>2</sup>	0.39	0.04	0.31	0.47	6	901.87	1.69	0.30	20.68	1	<0.001
Incubation	SST	0.37	0.04	0.29	0.45	2	914.85	14.68	0.00			
Incubation	NID+SST	0.37	0.04	0.29	0.45	2	914.85	14.68	0.00			
Chick-rearing	NID+NID <sup>2</sup> +SST	0.83	0.05	0.71	0.90	4	235.61	0.00	0.63	0.10	1	0.76
Chick-rearing	NID+NID <sup>2</sup> +SST+elevation	0.82	0.05	0.71	0.90	5	237.52	1.90	0.24	0.12	1	0.94
Chick-rearing	NID+NID <sup>2</sup> +SST+elevation+elevation <sup>2</sup>	0.83	0.05	0.71	0.90	6	239.49	3.88	0.09			
Chick-rearing	NID+NID <sup>2</sup>	0.80	0.05	0.69	0.88	3	241.30	5.69	0.04			
Nesting	NID+NID <sup>2</sup> +SST+elevation	0.30	0.04	0.23	0.38	5	1006.40	0.00	0.62	0.02	1	0.89
Nesting	NID+NID <sup>2</sup> +SST+elevation+elevation <sup>2</sup>	0.30	0.04	0.23	0.38	6	1008.39	1.98	0.23	5.68	1	0.02
Nesting	NID+NID <sup>2</sup> +SST	0.30	0.04	0.23	0.38	4	1010.08	3.68	0.10			
Nesting	NID+NID <sup>2</sup>	0.30	0.04	0.23	0.38	3	1011.29	4.89	0.05			

substantial support; in the best model were  $\text{NID}$ : 0.04 (SE = 0.004, 95% CI = 0.03, 0.05); and  $\text{SST}$ : 0.44 (SE = 0.22, 95% CI = 0.02, 0.86) on a logit scale and these effects were always positive in models with constant survival. The slope estimate for elevation was negative ( $\beta_{\text{elev}} = -0.03$ , 1 SE = 0.01, 95% CI = -0.05, -0.01) on a logit scale. Beta parameters for nest survival in relation to a quadratic trend of NID were inestimable. There was no evidence of direct effects of year or vegetation in front of the nest on DSR during the nesting period.

## DISCUSSION

We present the first estimates of DSR for tropicbird eggs, chicks, and nests from the main nesting area on St. Eustatius. Our results suggest that temporal factors are strong predictors of tropicbird survival, whereas the nest-site characteristics derived from our study had an apparently negligible effect. NID was the most important covariate for DSR in all stages of the nesting period, suggesting that survival was best explained by a linear (NID) and non-linear time trend (NID<sup>2</sup>). For the time trend, our models predicted that survival probability increased when nests were initiated between October and April, and subsequently decreased when nests were initiated after April, congruent with observations by Castillo-Guerrero *et al.* (2011) of tropicbird nesting patterns from the Gulf of California. Our results are similar to those from other studies of tropical and subtropical seabirds that demonstrated an increase in survival rates as the nesting season progressed (e.g., Ramos 2001; Monticelli and Ramos 2012). In contrast, Mejías *et al.* (2017) documented a decline in White-tailed Tropicbird chick survival as the nesting season progressed. White-tailed Tropicbirds on Bermuda and Culebra, Puerto Rico nest primarily between May and October (Madeiros n.d., Schaffner 1988), whereas Red-billed Tropicbirds on St. Eustatius nest primarily between October and June. Thus, the difference in chick survival may be explained by the fact that tropicbird nesting

on Bermuda and Puerto Rico coincides with the North Atlantic hurricane season, with September being the peak month of hurricane activity (Elsner *et al.* 1999).

We found that elevation did not affect nest survival rates. However, the restricted elevational range of accessible nests at the site likely limited our ability to accurately detect an effect. Nevertheless, nests at low elevations may be more prone to human disturbance or damage during extreme weather than those at high elevations (Dobson and Madeiros 2009). Other studies (e.g., Hervías *et al.* 2013) have demonstrated a positive correlation with elevation on nest survival rates, whereby nests at higher elevations were less likely to be predated by cats. This may be less relevant for rats and crabs (Sarmiento *et al.* 2014). A study on Bermuda found that White-tailed Tropicbirds preferred nesting in cavities on steeper cliffs with smaller entrances, and that clutch survival declined in cavities with shallower cavity depths and larger entrance heights (Mejías *et al.* 2017). We recognize the possibility that weekly rather than more frequent monitoring at Pilot Hill and the limited number of camera traps may have inhibited detection of predation on tropicbird survival on St. Eustatius.

On nearby Saba, Boeken (2016) recorded 100% mortality of chicks at one nest site in the 2011–2012 breeding season due to cat predation. Subsequently Terpstra *et al.* (2015) removed feral cats from two of Saba's tropicbird nest sites in 2013–2014; however, the results of their study were inconclusive as monitoring ceased before the end of the nesting season. Nevertheless, five chicks were killed by cats; the cause of mortality of other chicks could not be determined (Terpstra *et al.* 2015). The proximity of Saba's "Great Level" nest site to the local landfill was identified as a major contributor to the presence of cats (Boeken 2016). The lack of cats observed at Pilot Hill suggests that cat predation may not be a significant factor affecting tropicbird survival on St. Eustatius. Despite documenting 15 rat predation events, we were unable to quantify the impact of rats (or predation in general) on tropicbird survival over the study period. Campbell (1991),



van Halewijn and Norton (1984) and Schaffner (1988) posit that the larger size of tropicbirds and their aggressiveness at the nest (compared to other smaller ground-nesting seabirds) reduces their vulnerability to rats. Nevertheless, we strongly suggest that the effects of invasive rodents on tropicbird survival be investigated further. Numerous studies (e.g., Daltry *et al.* 2012; Dunlop *et al.* 2015; Le Corre *et al.* 2015; Graham *et al.* 2018) endorse or demonstrate the positive effects of rat-free seabird habitats, and Schaffner (1988) suggested that the majority of depredation of White-tailed Tropicbird eggs on Culebra was due to black rats.

In some marine birds, NID has been linked to sea surface temperature (Ramos *et al.* 2002; Smithers *et al.* 2003; Jaquemet *et al.* 2007), likely linked to food availability (Vlietstra 2005; Frederiksen *et al.* 2006; Tomita *et al.* 2009). In oligotrophic tropical waters, zooplankton and fish abundance are often positively correlated with chlorophyll abundance (Piontkovski and Williams 1995), leading to an increase in prey availability for tropical seabirds in more productive waters (Monticelli *et al.* 2007). The ability of tropicbirds to cope with unpredictable food resources and dynamic marine environments may be related to their life history traits (asynchronous breeding, slow growing chicks, diet and foraging areas; Feare 1981; Catry *et al.* 2009). For example, Red-tailed Tropicbirds (*P. rubricauda*) nesting on Aldabra and Europa Islands in the western Indian Ocean bred when SSTs were higher ( $> 27^{\circ}\text{C}$ ; Prys-Jones and Peet 1980; Le Corre 2001), apparently linked to an increase in food availability during that time period (Le Corre *et al.* 2003). Conversely, Red-billed Tropicbirds at Farallón de San Ignacio, Mexico, initiated breeding with lower ( $< 27^{\circ}\text{C}$ ) SST, which in that system marks the onset of seasonal upwellings (Castillo-Guerrero *et al.* 2011). Whilst these patterns contrast with each other, tropicbird productivity is likely influenced by seasonal marine environmental changes at a regional scale that ultimately increase prey availability. Our results are congruent with those described by Castillo-Guerrero *et al.* (2011), where trop-

icbirds selected NID to maximize nesting success by choosing not to lay eggs too early (October–December) or late (April–June) in the season. Consequently, tropicbirds on St. Eustatius may delay NID to optimize foraging availability, which is linked to higher SSTs and, thus, food availability (Ramos *et al.* 2002; Smithers *et al.* 2003; Vlietstra 2005; Frederiksen *et al.* 2006; Jaquemet *et al.* 2007; Tomita *et al.* 2009).

The western cliffs of St. Eustatius provide an important nesting habitat for tropicbirds in the Caribbean and globally. Pilot Hill is privately owned by GTI Statia and the site can only be accessed with their permission, thus nesting tropicbirds are rarely disturbed by humans. The relative accessibility of the study area allows researchers to continue fieldwork and build upon existing data to form a long-term monitoring program. We cannot confirm whether the same variables assessed in this study affect tropicbird survival at higher elevations on Pilot Hill or elsewhere on St. Eustatius. However, we recognize that nest cavities at lower elevations and closer to inhabited areas may be more accessible to potential nest predators such as cats, but not rats (Mejías *et al.* 2017). In contrast to Saba, the landfill is located on the eastern coast of St. Eustatius; in recent years a recycling facility and incinerator were installed and the previous landfill – which often spilled onto Zeelandia beach on the Atlantic coast – was reclaimed and is no longer in use (BES Reporter 2016). Whilst feral cats are present on St. Eustatius, their populations have not been quantified.

As with most cavity-nesting seabirds, tropicbirds exhibit relatively high nest site and mate fidelity (Madden 2019), potentially making them prone to low survival rates if poor nesting conditions exist (e.g., nest predators, food availability). Within the study area and period, however, temporal (NID) and oceanographic (SST) rather than habitat-related factors were the strongest predictors of tropicbird survival. GPS tracking provides an excellent opportunity to identify behavioral responses of seabirds to the marine environment and food resources (Weimerskirch *et al.* 2005). Determining im-

portant marine habitats and distributional trends for tropical seabird species whose populations have not previously been studied can reveal crucial information related to population ecology and conservation (Thiers *et al.* 2014). With this in mind, we suggest that systematic, long-term nest monitoring combined with parallel studies such as invasive species control and GPS tracking may help conservationists better understand the threats faced by tropicbirds at and away from the nest site.

## ACKNOWLEDGMENTS

We are grateful to two anonymous reviewers whose feedback improved the quality of this manuscript. We thank management of GTI Statia for granting access to the Pilot Hill nesting area and for funding camera traps. We are also grateful to staff, volunteers and interns of St. Eustatius National Parks Foundation and CNSI who assisted with fieldwork. Finally, we thank Adrian Delnevo for providing training, Rochelle Streker for assistance with RMark, and Fred Schaffner and Yvan Satge for providing comments on an earlier draft of this manuscript. Leg bands were funded by the Dutch Caribbean Nature Alliance, Naturalis Biodiversity Center, and the Caribbean Netherlands Science Institute. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. All capture and handling procedures were reviewed and approved by the Netherlands Banding Station (Vogeltrekstation). All research was carried out under Dutch permits, including the Netherlands Banding Station (Vogeltrekstation) Permit #B97. Our methods meet all ethical guidelines for the use of wild birds in research, as stipulated by the standards and policies of the Netherlands.

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