Breeding ecology, population size and nest site preferences of Red-billed Tropicbirds at St Helena, South Atlantic Ocean

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Abstract

We describe the population size and breeding ecology of the Red-billed Tropicbird, *Phaethon aethereus*, a poorly studied pantropical seabird, at St Helena, South Atlantic. The population size of 81-246 pairs and 272-564 individuals identifies the study population as the largest colony of Red-billed Tropicbirds in the South Atlantic, but also an internationally important part of the global population. We estimated the survival from laying to fledging of 158 nests between 2004-2017 at only 33%, among the lowest values reported globally for the species. Most nest failures occurred during incubation, with predation identified as the predominant cause of fledging failure. Intervals between breeding attempts were longer after successful nesting attempts than failed attempts. Previous breeding interval and nest cavity fidelity further influenced the interval between breeding attempts, while presence of replacement clutches did not. Multiple nest site and cavity characteristics were important predictors of cavity use, nest site selection and productivity. Management options for reducing mammalian predators to ensure the long-term viability of this important population at St Helena are discussed.

Keywords: *Phaethon aethereus*; breeding success; breeding periodicity; habitat preferences; seabird; conservation management.

Introduction

Red-billed Tropicbirds have a pantropical distribution across the Atlantic, Pacific and Indian Oceans (Orta 1992). Despite evidence of a decreasing population trend, the species has a global conservation status of 'least concern' with an estimated population size of 8,000-15,000 pairs (BirdLife International 2020b). Populations in the western and eastern Atlantic have been studied (Lee and Walsh-McGehee 2000; Diop *et al.* 2019), however there is little information on the species' abundance in the south Atlantic. The breeding range in the south Atlantic is known to extend from Fernando de Noronha and Abrolhos archipelagos in the south western Atlantic, to Ascension Island and St Helena in the central south Atlantic (Vilina *et al.* 1994). Population estimates for this area are, however, either data deficient (Mancini *et al.* 2016), outdated (Stonehouse 1962), or as in the case of St Helena completely absent. Estimation of the population size and breeding productivity of the Red-billed Tropicbird population on St Helena is therefore important for its management, conservation and protection.

For seabirds, cavity nesting can provide shelter from harsh environmental conditions, supplying a more favourable microclimate for incubation and chick rearing (Mallory and Forbes 2011). Cavities can also provide concealment and protection from predators (Rendell and Robertson 1989; Holway 1991). Red-billed Tropicbirds breed annually, laying a single egg in a cavity, but the influence of the physical nest site and cavity characteristics on tropicbird nest site and cavity choice has been little studied (Mejías *et al.* 2017b).

The primary objective of this study was to compile and update information on the St Helena Red-billed Tropicbird population, to estimate the number of breeding pairs and individuals We also examined key aspects of the species breeding ecology, breeding cycle and periodicity. Lastly, we investigated any influence of nest site and cavity characteristics on cavity occupancy, nest site selection, and reproductive performance, hypothesising that 1) less exposed and more sheltered cavities have higher nest success than those exposed to harsh environmental conditions, 2) cavities that are easy to approach and take off from (as tropicbirds are ungainly on their feet due to short tarsi), would influence occupancy, and 3) nest sites that offer a wide field of view, allowing defence against predators or competing tropicbirds would be preferred.

Methods

Study area and monitoring sites

St Helena, a UK overseas territory in the central South Atlantic (15° 57' S, 5° 42' W) is an isolated subtropical oceanic island of approximately 122 km^2 (Figure 1). We studied seven Red-billed Tropicbird colonies on St Helena for population size estimation. Nest monitoring was conducted on Egg Island, a small offshore islet free from mammalian predators, in addition to two mainland monitoring sites; Ladder Hill and the Firing Butts.

Colony surveys

Monthly colony surveys were conducted (Table 1) by a minimum of two people using a telescope and/or binoculars. Each surveyor estimated incubating adults, nesting adults, nestlings, adults on territories not actively nesting and adults roosting. The average of the two counts from each surveyor was used in analyses. Scan counts were completed from a boat or set observation points on land. Egg Island and Thompson Valley Island were visited monthly between 2005-2007 to conduct scan and ground counts. Ground counts were conducted on foot by slowly walking around each island searching all accessible cavities for nesting attempts. Population size was estimated as the combined numbers of breeding pairs, and mature individuals observed during each monthly survey, from a combination of historic and recent colony surveys as well as recent personal observations (see Table 1). For details on the colony surveys and population estimation, see Appendix S1 (Supporting Online Information).

Breeding phenology and cycle interval

We determined breeding periodicity on Egg Island by summarising monthly totals of adults incubating an egg or chick present between 2004-2007. Nesting activity at Ladder Hill and the Firing Butts was monitored daily from August to December 2013-2017 (see Supporting Online Information Table S1). Breeding cycle interval was estimated as the time period in days between the first day of incubation during one breeding period, to the next recorded breeding attempt in a subsequent breeding period. Where the first day of incubation was not directly observed, it was estimated from hatching or fledging assuming a 43 day incubation period (Stonehouse 1962) and an 85 day chick rearing phase (Harris 1969).

Nest Monitoring

Twenty eight mainland nest cavities were marked, and monitored daily via direct observation and infra-red motion sensor cameras positioned near the entrance of cavities (see Supporting Online Information Table S1). Cameras captured two pictures consecutively after each trigger, with an interval of five seconds between triggers. Egg Island was visited a minimum of once every four weeks during the monitoring period. Adults were caught by hand and fitted with a standard alphanumeric metal ring, in addition, any breeding adults were marked on their head with a non-toxic ink dye following British Trust for Ornithology (BTO) guidelines (licence S5526), enabling individual identification of pairs. Each nest in a cavity was given a unique nest identification number to enable estimation of the nesting cycle (incubation and chick rearing duration), nest success and productivity. Replacement clutches were identified, and the replacement interval calculated from the last date that the original failed nesting attempt was active, to the first day of incubation in the subsequent nesting attempt during the same breeding period. Feather samples were also taken from breeding adults for molecular sexing (using primers 2550F/2718R), following standard protocol described in Fridolfsson & Ellegren (1999). Causes of breeding failure were defined into six categories, adapted from Vanderwerf *et al.* (2014) (Supporting Online Information Table S2), based on evidence from visual inspection and/or nest camera trap images.

Nest site and cavity characteristics

Nest site and cavity characteristics were measured using a set of 11 descriptors plus an additional two descriptors (slope and aspect) for the surrounding 5x5 meter area (Supporting Online Information Table S3) adapted from Einoder *et al.* (2014). A "nest site" was defined as the location where the singular egg was laid by the female, and the "cavity" as the enclosed area around this "nest site". Cavities could contain multiple nest sites. We recorded the type of cavity (e.g. open, overhang, crevice or tube), number of entrances, and the orientation of the entrance to the nearest degree measured with a handheld GPS. Physical characteristics (± 1cm) included depth, entrance height and width, measured using a tape measure. Volume was estimated based on WxHxD, measured from the mid-point of the nest bowl. We also recorded "slope" (whether the nest bowl was flat or had a moderate or steep slope), "substrate" (rock, gravel or soil; present or absent), and whether predators could have access to the monitoring area (mainland: true, offshore: false). To avoid disturbance, cavity characteristics were measured either before the cavity was actively used for nesting, or after fledging when it was empty. Analysis of nest site and cavity characteristics are detailed in Supporting Online Information Table S4.

Statistical analysis

All statistical analyses were carried out in R v 4.1.2 (R Development Core Team 2021) see Appendix S2 (Supporting Online Information) for detailed description. All Generalised linear mixed models (GLMMs, see Supporting Online Information Table S5 for details) were implemented in the *lme4* package (Bates *et al.* 2015), and likelihood ratio tests (LRTs) following Lewis *et al.* (2011) in the *lmtest* package (Zeileis and Hothorn 2002). Significant effects ($P < 0.05$) were plotted using the *ggplot2* (Wickham 2016), *ggpubr* (Kassambara 2020) and *hrbrtheme* (Rudis 2020) R packages.

Results

Population size and breeding phenology

We observed a total of 81-246 breeding pairs and 272-564 mature individuals on St Helena per each (monthly) survey during the study period (Table 1).

Fifty-one nests with eggs and 18 chicks were monitored on Egg Island (Supporting Online Information Figure S1). Red-billed Tropicbirds were observed breeding in every month of the year, with a peak in egg laying from July to January. The highest average number of eggs laid occurred in September, and the lowest in March and April. The number of chicks observed peaked from October-April, with the highest average number of chicks occurring in February and the lowest from May-September.

Breeding cycles and intervals

Mean incubation period was 42.9 days (range 37-46 days, n = 31), and mean chick rearing period was 92.6 days (range 89-103 days, n = 13), giving a mean breeding cycle of 135.5 days (range 126-149 days). The overall average breeding cycle interval identified between 2013-2017 from 50 individuals, over five breeding periods was 416±177 days (range 222-1433 days, n = 91, Supporting Online Information Figure S2), 87% of which bred in consecutive breeding periods with a mean interval of 357±50 days (range 222-465 days, n = 79).

There were significant differences in breeding cycle interval between consecutive breeding periods (LRT; χ_3^2 = 11.807, P = 0.008, n = 79), but not between sexes (LRT; χ_1^2 = 0.077, P = 0.782, n = 90). The length of the breeding cycle interval between 2016-2017 was on average 44 days shorter than between 2013-2014 (2016-2017: mean 324 days, range 277-352 days, n = 12; 2013-2014: mean 368 days, range 222-465 days, n = 24) reflecting initial breeding outcomes (in the later period (2016-2017), all initial breeding attempts failed, whereas in the earlier period (2013-2014) some chicks fledged, see Supporting Online Information Table S7).

After accounting for repeated measures of an individual's breeding cycle interval, initial breeding outcome and nest site cavity fidelity explained the most variation in breeding cycle interval length (Supporting Online Information Table S6). Breeding cycle interval was significantly longer when the initial breeding attempt was successful (β = 0.075±0.035 SE, R^{2m} = 0.111, R^{2c} = 0.404, t = 2.125, P = 0.034, n = 70). Adults that initially successfully fledged a chick took an average of 41 days longer to nest in the following breeding period (mean 391±57 days, range 313-465 days, n = 18) compared with adults that initially failed to breed (mean 350±40 days, range 222-415 days, n = 52, Supporting Online Information Figure S3). There was no significant difference in the breeding cycle interval between individuals which initially failed to breed and laid a replacement clutch, and those which did not lay a replacement clutch after initial breeding failure (LRT χ_1^2 = 1.371, P = 0.242, n = 66).

After accounting for the outcome of the initial breeding attempt and repeated measures of individuals, an individual's breeding cycle interval was not significantly influenced by the outcome of the previous breeding cycle's breeding attempt (LRT; χ_1^2 = 3.548, P = 0.060, n = 30), but was negatively influenced by the length of the previous breeding cycle interval; the longer the previous breeding cycle interval, the shorter the breeding cycle interval in the following breeding period (β = -0.142 ± 0.014; LRT; χ_1^2 = 38.706, P < 0.001, n = 33).

Productivity

Altogether 158 nests were monitored 2004-2017, showing a hatching success of 63%, fledging success of 52%, and overall productivity of 33%. Hatching success on the mainland (64%) was marginally higher than offshore (61%) on Egg Island, LRT; χ_1^2 = 0.305, P = 0.581, n = 135), with no significant difference between years (2013-2017; LRT; χ_1^2 = 0.002, P = 0.961, n = 107). Fledging success was substantially higher offshore on Egg Island (77%) than on mainland St Helena (41%, LRT; χ_1^2 = 4.910, P = 0.027, n = 99), and ranged from 20% in 2016 to as high as 89% in 2017 (LRT; χ_1^2 = 26.638, P < 0.001, n = 84), driven by large between-year variations in daily chick survival (Supporting Online Information Table S7).

Causes of failure

We identified the cause of 88% of breeding failures during the study (Table 2), with 53% of failures occurring during incubation; predominantly abandonment (42%), and 47% during chick rearing; mostly predation (58%). Of 26 known nest predation events, 42% (11) were caused by feral or domestic cats (*Felis silvestris catus*), 8% (2) were caused by domestic dogs (*Canis familiaris*), 4% (1) were caused by rat, however predators remained unidentified for 12 events. Out of nine identified instances where fights with interlopers caused indirect disturbance leading to nest failure, seven involved other Red-billed Tropicbirds competing for nesting cavities (resulting in five broken eggs, one abandoned egg, and one neglected chick). Two free roaming domestic dogs caused significant disturbance to two breeding pairs, leading them to abandon their incubation.

Incidence of replacement clutches

We identified 13 replacement clutches 2013-2017, laid after initial breeding failure, with an average interval of 42±9 days (range: 27-53 days). Six replacement clutches (46%) were laid after loss of an egg, whereas seven replacement clutches (54%) were laid after loss of a chick. Ten pairs were identified as the same combination of individuals as in the first nesting attempt (i.e. confirmed mate fidelity), while the identity of one or both partners in three additional re-nesting attempts remained unverified. Ten pairs (77%) used the same nesting cavity to lay a replacement clutch, whereas three pairs (23%) chose a different cavity despite their previous nesting cavities being vacant at the time of laying the replacement clutch. Two of those three pairs were individuals breeding with the same partner, and the third could not be verified.

Nest site and cavity characteristics

Our full dataset comprised 125 breeding attempts in 46 nest sites from 41 cavities 2013-2017. A maximum of eight individuals were identified using a given cavity within one year. Most nest sites were located on flat or low slopes, and none recorded on steep slopes. After accounting for repeated observations each year and of each cavity, the model that best explained whether a chamber was occupied or not by Red-billed Tropicbirds in a given year (Table 3), included the type of cavity, the number of entrances to the cavity, the size of the tunnel to the nest site, the volume of the nest chamber, the slope of the nest bowl and the aspect of the site. The best model suggested that more enclosed cavities (such as tubes), exhibiting fewer entrances, smaller tunnels, larger chamber volumes, and nest bowls with a flat slope were more likely to be used (R^{2m} = 0.269, R^{2c} = 0.407, n = 136, Table 3). Likewise, the model that best explained nest occurrence in any given year included the cavity type, the number of entrances to the cavity, the width of the cavity entrance as well as some influence of tunnel size. Specifically, nest occurrence on mainland St Helena was positively related to enclosed cavities with a single wide entrance (R^{2c} = 0.133, R^{2m} = 0.300, n = 136, Table 3).

Soil in the nest site and the slope of the site around the cavity were important characteristics determining hatching success . The presence of soil (Supporting Online Information Figure S4) and flatter slope around the site, although slope was not significant in itself, increased the likelihood an egg would hatch (R^{2m} = 0.050, R^{2c} = 0.052, *n* = 125, Table 3). The nest bowl slope was a key component in predicting fledging success, suggesting higher fledging probability in flat nest bowls, along with potential, albeit non-significant influence of cavity orientation and tunnel size (R^{2m} = 0.223, R^{2c} = 0.364, *n* = 81, Table 3, Supporting Online Information, Figure S4).

Discussion

Our findings show that the population of Red-billed Tropicbirds on St Helena is regionally and globally important for the persistence and conservation of the species. However, the low observed breeding productivity, and threats we here identified in this population are cause for concern, and shared with *Phaethon sp*. populations elsewhere (Castillo-Guerrero *et al.* 2011; Sommerfeld *et al.* 2015; Madden 2020).

Population estimates

This study is the first to quantify the number of breeding pairs and mature individuals of Red-billed Tropicbirds on St Helena. The minimum of 32-246 pairs and 106-564 mature individuals observed in the monthly surveys is likely to be an underestimate, however it suggests that the St Helena population probably is the largest colony in the South Atlantic, compared to an estimated 10 individuals on Fernando de Noronha, 538 individuals in the Abrolhos Archipelago (Mancini *et al.* 2016) and 50-100 pairs on Ascension Island (Stonehouse 1962). St Helena harbours at least 1% of the global population of Red-billed Tropicbirds, and at least 35% of the South Atlantic population. These population estimates exceed the Important Bird Area (IBA) threshold (BirdLife International 2020a), making St Helena's population a "regionally important congregation" of Red-billed Tropicbirds in the South Atlantic (criterion B3a), and an internationally important part of the global population (≥1%; criterion A4).

Breeding phenology and cycle interval

From colony surveys we found Red-billed Tropicbirds breeding throughout the year on St Helena, with a peak in egg laying in September similar to that described from the Galápagos (Snow 1965) and nearby Ascension Island (Stonehouse 1962). This phenology differs from populations in Senegal (Diop *et al.* 2019), the Cape Verde archipelago and Mexican breeding colonies (e.g. Clarion Island (González-Zamora *et al.* 2017), San Jorge Island (Mellink and Palacios 1993) and Farallon de San Ignacio (Castillo-Guerrero *et al.* 2011)), which have differing seasonal patterns in productivity ranging from October to June. Variation in annual cycles across populations is likely due to oceanographic conditions and food availability (Weimerskirch 2007; Diop *et al.* 2019).

Individual Red-billed Tropicbirds on St Helena typically had a consistent annual breeding cycle, supporting previous suggestions by Stonehouse (1962), Snow (1965) and Harris (1969). However some individuals were recorded as absent in one cycle period, but appearing in subsequent cycle periods, suggesting that individuals may skip a breeding cycle under certain conditions (Ashmole 1965; Chastel 1995; Jouventin and Dobson 2002; Dawson 2008). The breeding periodicity of successful breeders was ca. ~ one month longer than that of failed breeders, reinforcing the theory that a major driver of breeding phenology in Red-billed Tropicbirds is linked to breeding outcome (see Stonehouse 1962; Snow 1965; Harris 1969; Prys-Jones and Peet 1980). In addition, we provide evidence that an individual's breeding phenology in a given year is also influenced by time since the last breeding attempt (previous breeding interval) and by nest site fidelity. Our findings suggest that the shorter breeding periodicity observed in repeated unsuccessful breeders may not be sustainable over multiple breeding cycles, hence the negative influence of previous breeding interval on periodicity.

Reproductive success

Hatching success was similar across our monitoring sites and years. In contrast, estimates of fledging success showed considerable spatial and temporal variation, with lower success at sites with mammalian predators being present. On Egg Island, a site with no mammalian predation, breeding success was 47%, whereas at the mammal-impacted sites on mainland St Helena breeding success was only 26%. We observed substantially higher fledging success in 2017, possibly due to climatic and/or food availability fluctuations (Schreiber 1994; Blight *et al.* 2010). As a consequence, resulting variation in breeding success among years was primarily driven by chick survival, consistent with previous studies and between different sites within the same locality (Snow 1965; Harris 1969; Hernández-Vázquez *et al.* 2018; Diop *et al.* 2019),

St Helena's hatching success of 63% is low compared with 75% in the Gulf of California, Mexico (Castillo-Guerrero *et al.* 2011), but higher than on St Eustatius (Caribbean; 59.6%; Madden 2017). St Helena's fledging success (52%) is lower than in both Mexico and St Eustatius (both 78%). The majority of other Red-billed Tropicbird population studies report much greater overall breeding success than at St Helena (33%), for example on St Eustatius (48.4% Madden (2017)) and Saba (65%, Boeken (2016)) in the Caribbean, Ascension Island, South Atlantic (52%, Stonehouse (1962)), and Senegal (average 55.1%, Diop *et al.* (2019)). However, Snow (1965) reported even lower breeding success (32%) on the Caribbean island of Daphne. However, this still places St Helena as having the lowest breeding success rates reported globally for the species.

Causes of breeding failure

Agonistic interactions between adult tropicbirds are not unusual (Schaffner 1991). Nevertheless, conspecific egg predation was not detected during the study period, although it is known to occur by competing adult Red-billed Tropicbirds in Saba (Terpstra *et al.* 2015). Similarly, egg predation by rats *Rattus norvegicus* is known to occur to Red-billed Tropicbird eggs in St Eustatius (Madden and Ellis 2013). On St Helena in 2018, despite the presence of an actively incubating adult, one egg was observed being depredated by a rat from nest camera images (Beard *et al.* unpubl.). Crabs are also a known common cause of nesting failure e.g. in White-tailed Tropicbirds *Phaethon lepturus* in Puerto Rico (Schaffner 1991), and Brown Noddies *Anous stoildus* on Egg Island, St Helena (Rowlands *et al.* 1998). More research on these potential threats and the effectiveness of nest defence behaviours is required to better understand the consequences of predation on Red-billed Tropicbirds.

The devastating negative effects of introduced mammalian predators on small oceanic islands have been well documented e.g. Courchamp *et al.* 2003, Hilton and Cuthbert 2010. Feral and domestic cats are known predators of two petrel species occurring on the mainland of St Helena (Beard 2016), so it is not surprising that chick predation was the main cause of fledging failure in this present study.

Camera images (Beard *et al.* unpubl.) showed that two domestic dogs caused four breeding failures; two directly through chick predation and two indirectly through disturbance. Given the more remote location of other Red-billed Tropicbird colonies around St Helena, the close proximity of our monitoring sites to human habitation and the fact that only domestic (not feral) dogs were observed in the colony, the impact of dogs on the entire St Helena population is likely less severe than our results suggest.

There were no incidences of swamping of nests by ants causing breeding failure, unlike observations for other tropicbird populations (e.g. Mejías *et al.* 2017b; Luna *et al.* 2018), and other bird species on St Helena (e.g. Burns *et al.* 2013). Likewise, there were no observed negative effects of litter e.g. through entanglement or ingestion (Hyrenbach *et al.* 2013; Vanderwerf and Young 2014) despite part of the mainland monitoring sites encompassing a disused refuse dump.

Replacement clutches

Many bird species will attempt to lay a second clutch within the same breeding period if the first nesting attempt fails. Whether tropicbirds lay a replacement clutch is often dependent on the stage of failure and/or date that the first attempt failed (Sommerfeld *et al.* 2015). Since environmental conditions tend to deteriorate during most seabird breeding seasons (Hamer *et al.* 2002), increased energetic costs can render late-season clutches unsustainable (Mejías *et al.* 2017a). Our findings suggest that, at St Helena this does not translate into lower likelihoods of late-season re-nesting attempts: pairs that laid replacement clutches were observed in relatively equal stages of initial breeding failure (incubation: 46%, chick rearing: 56%). The observed incidence of replacement clutches was relatively low; only 14% of pairs that initially failed subsequently laid a replacement clutch, compared to 53.1% reported from Red-billed Tropicbirds in the Caribbean (Madden 2020). Red-billed Tropicbirds at St Helena are able to breed in every month of the year. It is therefore possible that they abstain from immediately laying a replacement clutch, and return to the colony earlier in the following breeding period to initiate a new breeding attempt, despite evidence that laying replacement clutches did not significantly influence periodicity.

Habitat preferences

This study has identified the type of cavity and the number of entrances as important predictors of cavity occupancy and nest occurrence, but not of reproductive performance. Adult Red-billed Tropicbirds favoured using enclosed cavities, with fewer entrances, such as a tube type, compared with more open cavity types. The nest chamber volume was the most important predictor in the final model of cavity occupancy, while the number of entrances was the most significant predictor of nest site selection. Inside the nest, the presence of soil rather than harder materials such as rough volcanic rock positively influenced hatching success, likely reflecting lower risk of egg damage. The slope of the nest bowl also influenced cavity occupancy and fledging outcome: flatter nest bowls likely help to keep the egg and/or chick in the nest site when adults arrive and leave.

Management implications

The high level of chick predation by mammalian predators identified as the main cause of fledging failure is a cause of concern for the long-term viability of the "Ladder Hill" IBA colony of Red-billed Tropicbirds. The observed high fidelity to nest sites and cavities, continued poor breeding success and disturbance from mammalian predators will likely lead to a reduction in colony size and range, possibly reducing the colony to inaccessible cliff areas. Stricter controls on free-roaming cats and dogs in residential areas near the colony, backed up by suitable legislation, along with improved compliance with existing regulations such as registering, neutering and micro chipping all owned pets (Jensen and Thomsen 2022), in conjunction with an education and public awareness campaign, would help to reduce the number of cats and dogs foraging within the IBA. Expansion of the existing feral cat control programme for the St Helena Plover IBAs should also include the Ladder Hill IBA, along with a feasibility study on constructing an exclusion area around the IBA. Installation of artificial nest chamber "igloos" (Medeiros 2008) on accessible offshore islets such as Egg Island could be an important tool to increase cavity availability in predator free areas.

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Tables

Table 1. Historical and recent estimation of numbers of breeding pairs and observed mature individual Red-billed Tropicbirds from colonies on St Helena. Values are the range of total numbers counted at each monthly survey instance. *n* = number of monthly colony counts conducted.

Colony	Monitoring period	Method	*n*	Breeding pairs	Individuals
Great Stone Top	July 2013-June 2017	Scan count$_a$	47$_b$	17-78	34-156
Blue Point	July 2013-June 2017	Scan count$_a$	48	7-48	14-96
Shore Island	July 2013-June 2017	Scan count$_a$	48	0-1	2-4
Speery Island	July 2005-June 2007	Scan count$_c$	24	8-26	16-52
Egg Island	July 2005-June 2007 & July 2013-June 2017	Ground count and recent observation	24*	5-7	8-14
Thompson's Valley Island	July 2005-June 2007	Ground count	24	0-1	1-2
Ruperts Valley to Breakneck Valley	July 2005-June 2007 & July 2013-June 2017	Scan count$_c$ and recent observation	24*	44-85	197-240

$_a$ observation from land, $_b$ one monthly survey absent due to poor weather conditions, $_c$ observation from boat, * excluding recent observations

Table 2. Causes of Red-billed Tropicbird nest failures on St Helena (mainland only) 2013-2017.

Cause	Number		Percentage
	Incubation	Chick Rearing	
Predation	0	26	27%
Abandoned	21	1	23%
Broken egg	19	-	20%
Unknown	7	4	12%
Neglect/exposure	0	8	8%
Starvation	-	6	6%
Failed to hatch	3	-	3%
Total	50	45	100

Table 3. Significance and variable importance from generalised linear mixed model (GLMM) selection of specific nest site and cavity characteristics with cavity occupancy, nest site selection and reproductive performance of Red-billed Tropicbirds at St Helena 2013-2017. Cavity identification and year were included as random effects in all models to control for repeated measures.

a) Cavity occupancy [a]				
Predictors	estimate	std error	*z*	*P* value
Cavity type	0.266	0.091	2.908	**0.004**
Aspect	0.176	0.103	1.704	0.088
Number of entrances	-0.418	0.130	-3.227	**0.001**
Tunnel size	-1.195	0.079	-2.472	**0.013**
Volume	0.240	0.071	1.080	**0.001**
Nest bowl slope	0.457	0.152	3.007	**0.003**
b) Nest occurrence [b]				
Cavity type	0.403	0.178	2.256	**0.024**
Number of entrances	-0.559	0.191	-2.928	**0.003**
Width	0.766	0.351	2.185	**0.029**
Tunnel size	-0.626	0.340	-1.839	0.066
c) Hatching Success [c]				
Slope	-0.314	0.039	-1.538	0.124
Soil	0.614	0.286	2.146	**0.032**
d) Fledging success [d]				
Nest bowl slope	-2.029	0.843	-2.407	**0.016**
Orientation	-0.377	0.208	-1.808	0.071
Tunnel size	0.683	0.403	1.694	0.090

[a] Poisson error distribution and sqrt link function, *n* = 136
[b] Binomial error distribution and probit link function, *n* = 136
[c] Binomial error distribution and cloglog link function, *n* = 125
[d] Binomial error distribution and cloglog link function, *n* = 81

Figures

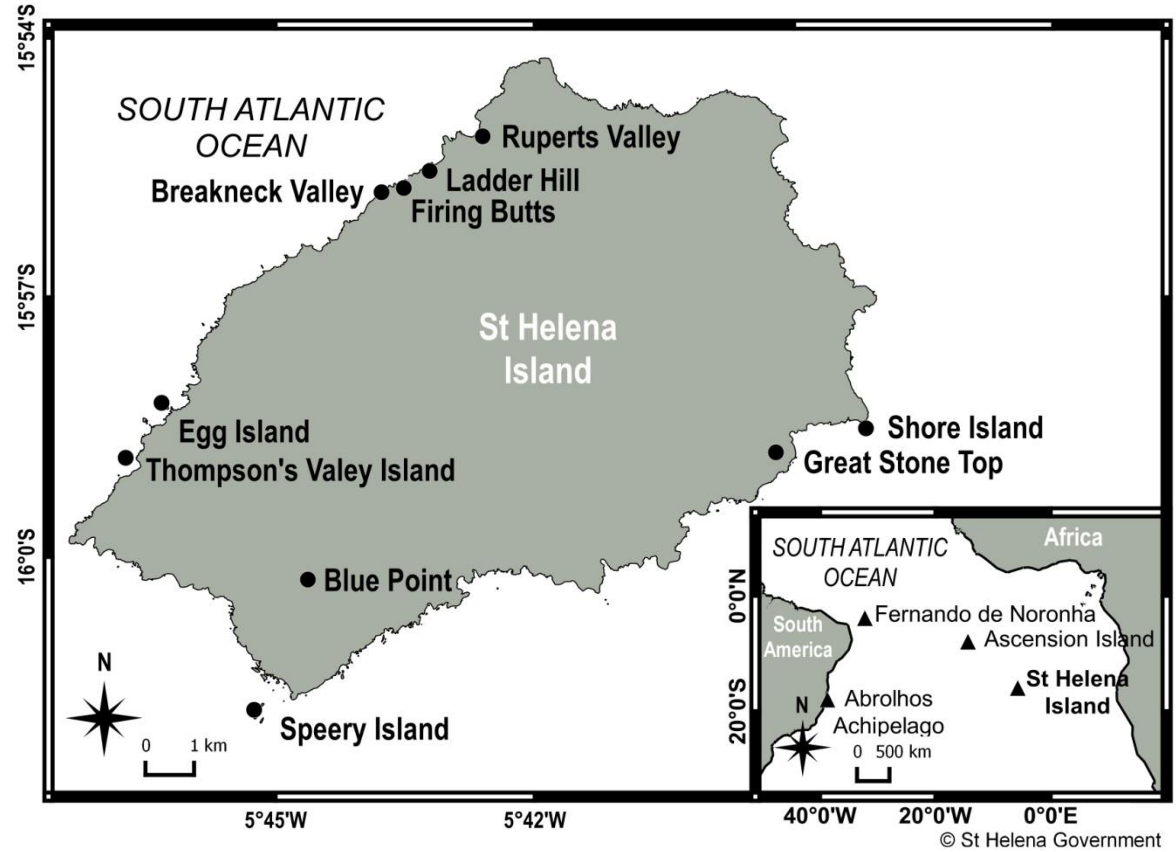

Figure 1. Map showing the location of Red-billed Tropicbird (*Phaethon aethereus)* monitoring sites at St Helena in the South Atlantic Ocean (insert).

Supporting Online Information

Appendix S1: Details of the colony survey protocols and population size estimation methods.

During colony surveys breeding activity and presence of nesting tropicbirds in cavities was often given away by fresh guano deposits, protruding tail streamers and the sound of adults and/or chicks calling. Estimation of the numbers of breeding pairs and mature individuals were derived from a combination of historic and recent colony surveys as well as recent personal observations (See Table 1 for details). Adults observed in flight during colony counts were excluded. Breeding pairs were a sum of observed incubating adults (adults confirmed with an egg or chick), apparently incubating adults (adults observed sitting in a nest scrape but with no confirmed visual of an egg or chick) and nests with nestlings, assuming that each nest was attended by two adults. Adults occupying territories (adults occupying a nesting cavity but no evidence of nesting, e.g. guano covered scrape, egg or chick), adults observed roosting (birds present on the colony but not associated with a nesting cavity) and breeding pairs (assuming two adults to each nest) were pooled to provide numbers of observed individuals. Results are presented as the range of values (minima and maxima) in a month observed during the monitoring period.

Appendix S2: Additional description of statistical analyses used to determine breeding cycle interval, reproductive success and nest site and cavity characteristics.

Breeding cycle interval

We used GLMMs to assess whether the interval between breeding cycles varied between sexes or consecutive breeding periods (e.g. consecutive: 2014 to 2015; non-consecutive: 2014 to 2016). Given the high level of between-season mate fidelity, nest site fidelity and their observed positive effect on breeding success in tropicbirds (Sommerfeld *et al.* 2015), and the potential effect of breeding success on breeding cycle interval (Snow 1965; Harris 1969; Prys-Jones and Peet 1980), we tested whether the interval between breeding attempts varied by 1) initial breeding outcome, 2) partner fidelity, 3) cavity fidelity, 4) initial breeding outcome and partner fidelity, 5) initial breeding outcome and cavity fidelity or, 6) initial breeding outcome, cavity fidelity and partner fidelity or, 7) partner fidelity and cavity fidelity. We excluded any individuals of unknown sex, and those that did not breed in consecutive breeding periods and/or where the breeding outcome or partner fidelity were unknown. We used a model selection approach using Akaike's information criterion adjusted for small sample size (AICc) to identify the most parsimonious model (Burnham and Anderson 2002).

We used GLMMs to assess whether the decision to lay a replacement clutch following initial breeding failure additionally affected the breeding cycle interval, using only data from individuals that initially failed to breed. Individuals which had multiple consecutive breeding cycle intervals were also investigated further, to assess any effect of a) the previous breeding cycle interval and b) the previous breeding outcome on breeding cycle interval. We used a LRT as described above, excluding any cycles that had unknown initial breeding outcomes and/or unknown previous breeding outcomes.

Reproductive success

We excluded 54 of 212 nesting attempts where the fate of the egg or chick could not be ascertained. Estimates of hatching success (proportion of chicks hatched from eggs laid), fledging success (the proportion of chicks fledged from eggs hatched), and productivity (proportion of chicks fledged from eggs laid) were calculated assuming a 43 day incubation period and 85 day chick rearing period, respectively (Stonehouse 1962; Harris 1969). Daily nest survival rates were calculated using Mayfield (1975), and standard errors following Johnson (1979). Differences in breeding performance between the mainland and offshore monitoring sites were assessed by pooling historical and recent nest data. We tested for differences between years in hatching and fledging success, assessed over 5 years (2013-2017), as well as comparing mainland and offshore (Egg Island) monitoring sites using logistic exposure GLMMs (Shaffer 2004), and LRTs to compare candidate models to a null model (Lewis *et al.* 2011).

Nest site and cavity characteristics

We used GLMMs to firstly examine whether occupancy of a cavity (number of individuals identified using each cavity per year) and nest occurrence (coded as 1 for presence of at least one nest per cavity per year, or 0 for absence of any nest) on the mainland monitoring sites varied with cavity characteristics. Then we used GLMMs to investigate whether reproductive performance varied with cavity characteristics, including known replacement clutches and both mainland and Egg Island breeding attempts. Nesting attempts with either unknown outcomes and/or cavity characteristic data were excluded. For each response, we tested all possible model combinations using the 'dredge' function in R package *MuMIn* (Barton 2020). We used a model selection approach using AICc's to identify the most parsimonious model. All candidate models were ranked based on their delta AIC value. We report models with a delta AIC ≤ 1 (Semmens *et al.* 2009).

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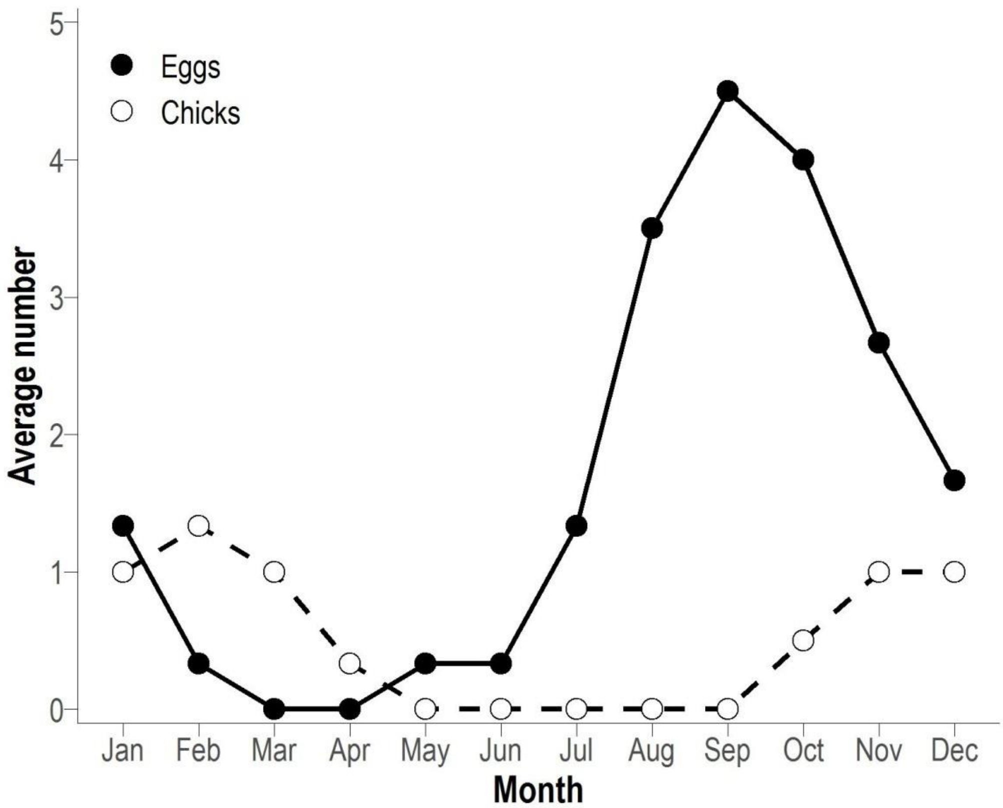

Figure S1. Breeding phenology of Red-billed Tropicbirds on Egg Island, St Helena from October 2004 to August 2007.

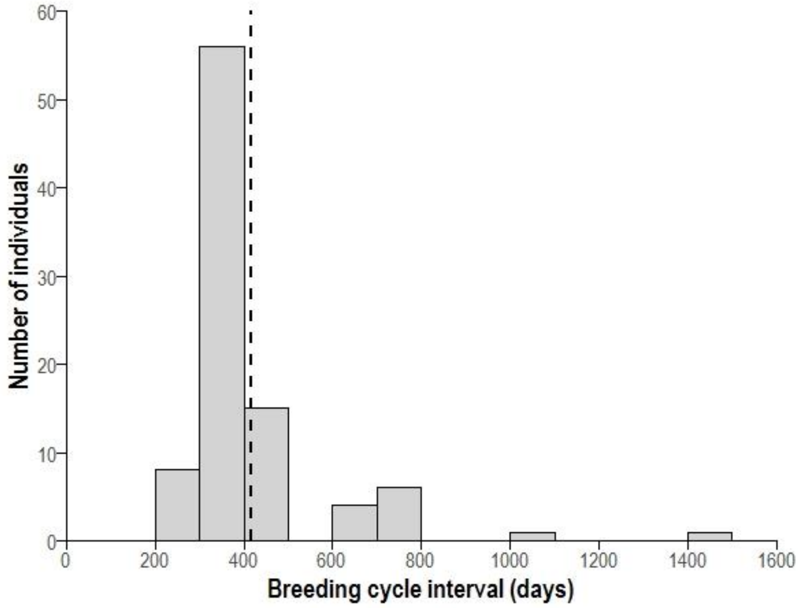

Figure S2. Frequency distribution of breeding cycle intervals of individual Red-billed Tropicbirds 2013-2017 (n = 91), based on recapture of individuals whilst breeding and estimation of laying dates. Dashed black line represents the mean (416±176 days SD).

Figure S3. Breeding cycle interval (duration of time between nesting attempts in different breeding periods) for successful and unsuccessful nesting attempts of Red-billed Tropicbirds in St Helena between 2013-2017. Unsuccessful = the interval between the date when the prior nest failed and the first egg date of the subsequent breeding attempt. Successful = the interval between the date when the prior nest successfully fledged a chick and the first egg date of the subsequent breeding attempt.

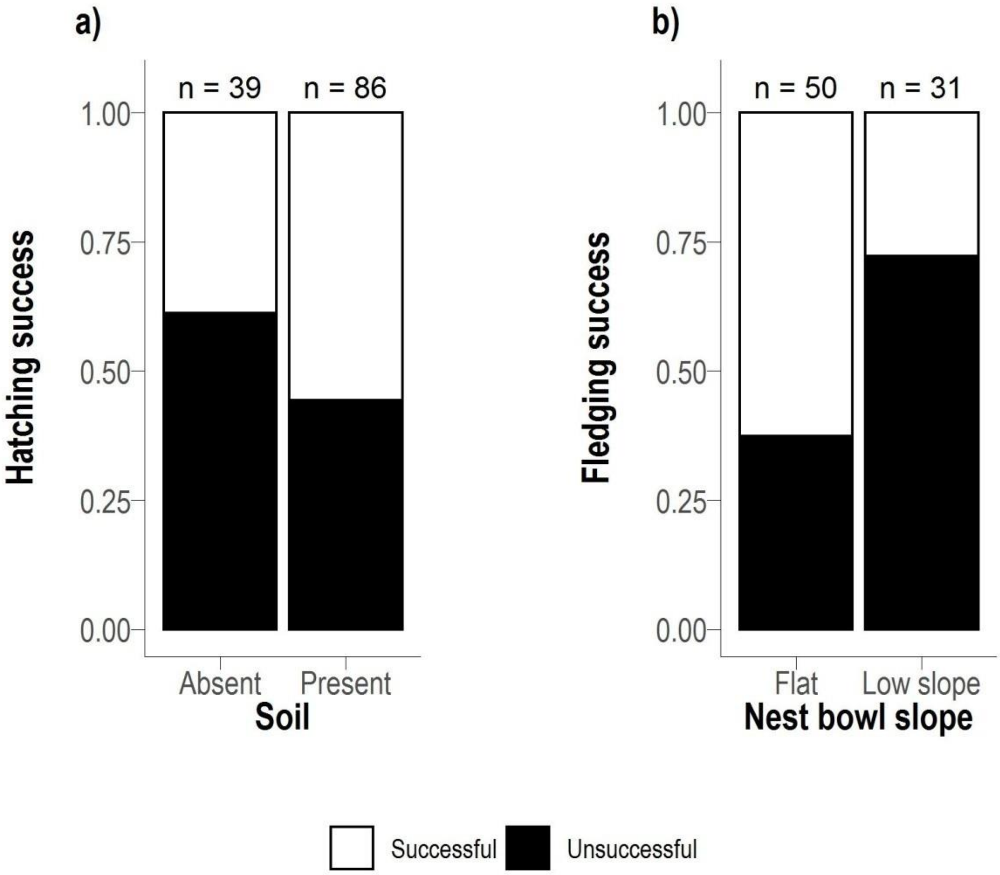

Figure S4. Stacked bar charts showing the proportion of successful and unsuccessful nests in a) soil substrate and b) each nest bowl slope. In successful breeding attempts - white and unsuccessful breeding attempts - black.

Table S1. Summary of cavity and nest monitoring of mainland St Helena Red-billed Tropicbirds, 2013-2017.

Year	Number of cavities monitored	Total number of nests monitored	Minimum visual inspection	Number of cavities, cameras used	Camera deployment details
2013	24	29	daily	0	Not available
2014	28	24	daily	10	4 nests from incubation, 7 from chick rearing
2015	28	24	daily	11	5 nests from incubation, 6 from chick rearing
2016	28	16	Mondays, Wednesdays, Fridays	24	All active nesting attempts (13 cavities) plus 11 frequently used cavities.
2017	27	16	Mondays, Wednesdays, Fridays	25	Installed outside frequently used cavities for complete monitoring period

Table S2. Categories of breeding failure based on the following evidence from visual inspection and/or camera trap images.

Category	Evidence
broken egg	occurring earlier than the expected hatch date based on the mean incubation period (43 days) and not indicative of predation
abandonment	intact egg incubated less than 43 days
failed to hatch	egg incubated longer than 43 days and failed to hatch
predation	remains of an egg or chick with evidence of predation, e.g. bite marks, blood, tissue, feather remains
starvation	where the carcass of a large chick was found
neglect/exposure	carcass of a small chick found with no signs of predation
unknown	egg or chick missing with no evidence of cause

Table S3. Variables recorded for each cavity including characteristics of the surrounding site, cavity entrance and nest site.

Variable	Description
Site	
Slope	F= flat (0°); LS= low slope (1°-5°); MS = moderate slope (5°-20°), steep slope (20°-45°)
Aspect	North = 314°-45°, East = 46°-135°, South = 136°-225°, West = 226°-315°
Cavity type	Open (1), overhang (2), crevice (3) and tube (4)
Cavity entrance	
Number of entrances	1 or >1
Orientation	Mid-point of the nest entrance (degrees)
Height	Maximum height of cavity at entrance (cm)
Width	Maximum width of cavity at entrance (cm)
Nest site	
Min tunnel size	Height x width at narrowest point (cm^2)
Depth	Maximum length, outside edge of entrance to centre point of nest bowl (cm)
Chamber volume	Maximum height x depth x width from the mid-point of the nest bowl

	(cm^2)
Nest bowl slope	Flat = 0°, Moderate slope = 1°-5°, steep slope = 5°-10°
Substrate	Rock, (present (1) or absent (0)); Gravel, (present (1) or absent (0)); Soil, (present (1) or absent (0))
Predator access	Yes (1), No (0)

Table S4. Explanatory variables tested for effects on cavity occupancy, nest occurrence, hatching success and fledging success. Predicted increase (↑) and decrease (↓) of response variables for the appropriate independent variables are shown. Independent variables that were not tested towards a specific dependant variable are denoted with (X), presence (1) or absence (0).

Explanatory variable	Cavity occupancy	Nesting occurrence	Hatching success	Fledging success
Site				
Slope	↑ with slope	↑ with slope	↑ with slope	↑ with slope
Aspect	↓ with angle	↓ with angle	↓ with angle	↓ with angle
Cavity type	↓ with type	↓ with type	↓ with type (exposure)	↓ with type
Cavity entrance				
No. of entrances	↓ with >1	↓ with >1	↓ with >1	↓ with >1
Orientation	↓ with direct sun	↓ with direct sun	↓ with direct sun	↓ with direct sun
Height	↓ with height	↓ with height	↓ with height	↓ with height
Width	↓ with width	↓ with width	↓ with width	↓ with width
Nest site				
Min. tunnel size	↑ with size	↑ with size	↑ with size	↑ with size
Depth	↑ with depth	↑ with depth	↑ with depth	↑ with depth
Chamber volume	↑ with volume	↑ with volume	↑ with volume	↑ with volume
Nest bowl slope	↓ with slope	↓ with slope	↓ with slope	↓ with slope
Substrate; Rock	X	X	↓ with (1)	X
Gravel	X	X	↓ with (1)	X

Soil	X	X	↑ with (1)	X
Predator access	X	X	↑ with (1)	↑ with (1)

Table S5. Description of all generalised linear mixed models (GLMMs). n = sample size. AICc = Second-order Akaike Information Criterion. LRT = Likelihood ratio test.

Dependant and independent variables tested	Error distribution	Link function	Random effects	Fixed effect	Assessment method	*n*
Breeding cycle interval						
Breeding cycle interval = Sex	gamma	log	individual identity	-	LRT	90
Breeding cycle interval = Breeding period	gamma	log	individual identity	-	LRT	79
Breeding cycle interval = initial breeding outcome	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = partner fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = cavity fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval =initial breeding outcome and partner fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = initial breeding outcome and cavity fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = initial breeding outcome + cavity fidelity and partner fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = partner fidelity and cavity fidelity	gamma	log	individual identity	-	AICc	70
Breeding cycle interval = initial breeding outcome+ partner fidelity + cavity fidelity + initial breeding outcome and partner fidelity + initial breeding outcome and cavity fidelity + initial breeding outcome + cavity fidelity and partner fidelity + partner fidelity and cavity	gamma	log	individual identity	-	AICc	70

fidelity						
Breeding cycle interval = Previous breeding cycle interval	gamma	log	individual identity	Breeding outcome	LRT	33
Breeding cycle interval = Previous breeding outcome	gamma	log	individual identity	Breeding outcome	LRT	30
Breeding cycle interval = Replacement clutch	gamma	log	individual identity	-	LRT	66
Productivity						
Hatching success = Location	binomial	Logistic exposure	Cavity identity	-	LRT	135
Hatching success = Year	binomial	Logistic exposure	Cavity identity	-	LRT	107
Fledging success = Location	binomial	Logistic exposure	Cavity identity	-	LRT	99
Fledging success = Year	binomial	Logistic exposure	Cavity identity	-	LRT	84
Nest site and cavity characteristics						
Adult occupancy = Slope + Aspect + Cavity type + Number of entrances + Orientation + Height + Width + Minimum tunnel size + Depth + Chamber volume + Nest bowl slope	Poisson	Square root	cavity identification and year	-	AICc via dredge	136
Nest occurrence = Slope + Aspect + Cavity type + Number of entrances + Orientation + Height + Width + Minimum tunnel size +	binomial	probit	cavity identification and	-	AICc via dredge	136

Depth + Chamber volume + Nest bowl slope			year			
Hatching success = Slope + Aspect + Cavity type + Number of entrances + Orientation + Height + Width + Minimum tunnel size + Depth + Chamber volume + Nest bowl slope + Substrate + Predator access	binomial	cloglog	cavity identification and year	-	AICc via dredge	125
Fledging success = Slope + Aspect + Cavity type + Number of entrances + Orientation + Height + Width + Minimum tunnel size + Depth + Chamber volume + Nest bowl slope + Predator access	binomial	cloglog	cavity identification and year	-	AICc via dredge	81

Table S6. Model selection table evaluating the effect of initial breeding outcome, cavity fidelity and partner fidelity on the breeding cycle interval of Red-billed Tropicbirds 2013-2017 (*n* = 70). *k*: number of estimable parameters; AICc: Akaike's information criterion; Delta AICc: difference in AICc units to the most parsimonious model; wAICc: relative weight of evidence for each model.

Model	k	AICc	Delta AIC	wAICc
Initial breeding outcome + Cavity fidelity	5	733.713	0.000	0.303
Initial breeding outcome	4	733.967	0.254	0.266
Initial breeding outcome + Partner fidelity	5	735.584	1.871	0.119
Initial breeding outcome + Partner fidelity + Cavity fidelity	6	735.795	2.082	0.107
Cavity fidelity	4	735.799	2.086	0.107
Cavity fidelity + Partner fidelity	5	737.063	3.350	0.057
Partner fidelity	4	738.874	5.161	0.023
Null	3	739.235	5.522	0.019

Table S7. Summary of Red-billed Tropicbirds nests monitored on St Helena, 2013-2017. Mayfield daily nest and chick survival estimates (± 1 standard error). Hatching success is the proportion of chicks hatched from eggs laid, fledging success is the proportion of chicks fledged from eggs hatched and productivity is the proportion of chicks fledged from eggs laid.

	Monitoring period					
	2013	2014	2015	2016	2017	Sum
Total eggs laid	27	30	24	22	25	128
Daily nest survival	0.989±0.004	0.984±0.005	0.987±0.005	0.978±0.006	0.990±0.004	
Total chicks hatched	20	19	16	10	19	84
Hatching success (%)	74	63	67	45	76	
Daily chick survival	0.978±0.006	0.986±0.005	0.979±0.006	0.974±0.009	0.998±0.001	
Total chicks fledged	5	9	5	2	17	38
Fledging success (%)	25	47	31	20	89	
Productivity (%)	19	30	21	9	68	