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Mestrado em Biologia da Conservação

Dissertação

Breeding of White-tailed Tropicbird on São Tomé Island: Distribution, phenology, population estimates, nest characteristics and threats.

Gustavo Orselli Marino

Orientador(es)	Ricardo Faustino de Lima Pedro Filipe Pereira

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Abstract

The White-tailed Tropicbird (*Phaethon lepturus* - WTTB) is an understudied seabird in the Gulf of Guinea, with limited information available about its breeding ecology in the oceanic island of São Tomé. This study combined questionnaires targeted at local communities, point counts, and active nest search to assess distribution, phenology, population size, nest site characteristics, and threats to the breeding populations of WTTB in São Tomé. Nesting was confirmed in previously reported areas, validated suspected breeding sites, and discovered a new important breeding location at Homem de Capa, the most numerous aggregation on the main island. The most important breeding location for São Tomé was on the Sete Pedras Islets. Out of 135 nests that were located and georeferenced and breeding pairs observed, 2,358 to 9,430 breeding pairs are estimated for São Tomé and surrounding islets, just during the small dry season. These figures suggest that São Tomé supports the largest populations for the tropical Atlantic subspecies *Phaethon lepturus ascensionis*. Considering that the species appears to breed year-round in the region, this population is likely to be much larger. A total of 70 nests were characterized: 18 on islets, 38 on cliffs, and 14 in trees. Islet and cliff nests were usually in basaltic cavities with minimal to no vegetation cover, whereas tree nests were almost always found in large coral trees (*Erythrina* sp.), at a mean height of 16.3 meters. Using binomial Generalized Linear Models, distance to the coast was found to be clearly the most relevant variable to explain the occurrence of tree nests, and that these were positively correlated. The breeding pairs face the highest pressure from overfishing, bycatch, marine debris and ghost fishing gear, followed by invasive species, human persecution, oils spills and tropical storms. Additionally, tree breeding pairs are threatened by deforestation and agricultural expansion. These findings provide the most comprehensive baseline for long-term monitoring of WTTB in São Tomé, laying out a solid base for future studies. It also emphasizes the need to improve the formal protection of the species on the island, namely on the Sete Pedras Islet and on the coastal cliffs of the Santa Catarina Tunnel. Finally, it is vital to mitigate the impacts of people and introduced species throughout São Tomé to ensure a long-lasting positive conservation status of the WTTB on the island.

Fatores ecológicos de seleção do local de nidificação em *Phaethon lepturus* na Ilha de São Tomé: Integrando caraterísticas da paisagem, morfologia do ninho e pressões humanas

Resumo

O Concozuco (*Phaethon lepturus*) é uma ave marinha que se reproduz nas ilhas oceânicas do Golfo da Guiné, mas a sua ecologia reprodutiva na região permanece mal conhecida. Combinando questionários direcionados às comunidades, contagens em pontos de observação e busca ativa de ninhos, este estudo avalia distribuição, fenologia, tamanho populacional, características dos locais de nidificação e ameaças às populações reprodutoras da espécie na ilha de São Tomé.

Através de busca ativa, a distribuição do Concozuco foi confirmada por quase toda a ilha de São Tomé e nos principais ilhéus circundantes. Foi confirmada a nidificação em áreas onde esta já havia sido confirmada ou onde apenas haviam suspeitas. Através de 169 questionários, foram identificadas 64 potenciais áreas de ocorrência e 39 possíveis locais de nidificação. Foram localizados e georreferenciados 135 ninhos na ilha de São Tomé e nos ilhéus circundantes e descobertos novos locais de reprodução. As concentrações mais importantes de ninhos em falésias foram encontradas no Homem de Capa e nas falésia próximas ao túnel de Santa Catarina, no distrito de Lembá, no Noroeste da ilha, sendo que a maior concentração da ilha principal se encontra em Homem de Capa, no sul de São Tomé. Nos ilhéus os maiores números de ninhos foram encontrados nas Rolas e em Sete Pedras. Os ninhos em árvores foram localizados principalmente em plantações sombreadas de cacau, no Nordeste da ilha. A fenologia foi inferida com base nos questionários. As respostas sugerem que a abundância da espécie ao longo do ano aumenta durante as estações secas, e em particular durante a época seca principal (junho a agosto), embora 81% dos entrevistados relatem observações ao longo de todo o ano. Estimativa populacional foi obtida através da identificação de ninhos ativos e observação de pares reprodutores em pontos de observação. Extrapolando estes resultados para toda a ilha, tendo em consideração o tipo de ninho e tipo do uso do solo, estima-se existirem entre 2,358 e 9,430 pares reprodutores de Concozuco em

São Tomé durante o mês de fevereiro, com 90% dos pares reproduzindo em árvores. Esta população reprodutora poderá ser uma de importância global para a espécie (entre 0.6% e 2.4% da população global) e é certamente a mais numerosa da subespécie de Concozuco (*Phaethon lepturus ascensionis*) do Atlântico tropical. Se se tiver em conta que nesta região a espécie aparenta reproduzir-se ao longo de todo o ano, e que estas estimativas se cingiram a um curto período do ano que nem sequer será o maior pico de atividade reprodutora da espécie na ilha, é bem possível que a importância desta população seja ainda maior.

De todos os ninhos encontrados, foram caracterizados 70 ninhos: 18 em ilhéus, 38 em falésias e 14 em árvores. Nos ilhéus e nas falésias costeiras, a maioria dos ninhos estava em cavidades com pouca ou nenhuma cobertura vegetal, e estabilidade da rocha era variável com a maioria das rochas classificadas como estáveis ou em erosão. Os ninhos em árvores foram sempre encontrados em grandes árvores vivas, quase sempre em cavidades de eritrineiras (*Erythrina* sp.), e em média a 16.3 m do solo. Num geral, ninhos em ilhéus encontravam-se em alturas mais baixas e variáveis enquanto ninhos na ilha principal eram localizados a alturas mais elevadas. Com recurso a Modelos Lineares Generalizados, analisou-se qual a variável ambiental que melhor explica a presença de ninhos em árvores. Verificou-se que a distância à costa era a variável que melhor explicava a ocorrência de ninhos em árvores. Este resultado sugere que a espécie, quando nidifica em árvores, tende a afastar-se da costa. Durante o ciclo reprodutor, os pares são expostos a diversas ameaças. Os indivíduos que se reproduzem nos ilhéus são suscetíveis a ameaças de maior intensidade, do que as populações que nidificam em falésias costeiras ou em árvores. A perda de presas devido à sobrepesca e a captura acidental de Concozucos no mar e detritos marinhos em forma de plásticos ou material de pesca parece constituir a ameaça mais grave e imediata para todos os pares reprodutores. Nos ilhéus, outro impacto significativo são as tempestades tropicais, enquanto a espécie ser percecionada como competição pelos pescadores, a sua caça e espécies invasoras têm impacto médio sobre a espécie. Para os pares que reproduzem em falésias costeiras e árvores, a caça e as espécies invasoras têm impactos significativos. Além do mais, a expansão e desenvolvimento urbano e explorações agrícolas também afetam consideravelmente os nidificantes em árvores.

Este estudo estabelece uma base sólida para a monitorização do Concozuco em São Tomé a longo prazo, bem como de outros estudos com este foco. Identificámos a necessidade de atribuir proteção formal a alguns dos locais de nidificação mais importantes para a espécie em São Tomé, tais como as Sete Pedras, ilhéu Santana e as falésias costeiras junto ao túnel de Santa Catarina. Finalmente, é vital mitigar os impactos antropogénicos e de espécies introduzidas através da educação ambiental e da sensibilização das populações locais para garantir um bom estado de conservação da espécie em São Tomé a longo prazo.

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General introduction

Seabirds

As top predators, seabirds play a fundamental role in ocean ecosystems, and can be used as indicators of marine environmental health (Furness & Camphuysen 1997). Their high position in the food chains allows them to regulate fish and invertebrate populations, while contributing to nutrient cycling between marine and terrestrial ecosystems (Young & Balance 2023). Adapted to a highly specialized and dynamic environment, seabirds have evolved traits such as long-distance flight capabilities, exceptional navigation, and colonial breeding behaviour, often on remote islands that provide refuge from terrestrial predators and human disturbance (Schreiber & Burger, 2001; Young & Balance 2023).

However, seabirds are among the most threatened groups of birds globally, facing pressures from overfishing, pollution, introduced invasive species, and climate change, which can affect food availability and nesting sites (Dias et al., 2019; Philips et al., 2023). When seabirds return to land to breed, they often congregate in dense colonies, making them particularly vulnerable to environmental hazards and predation (Grémillet et al., 2018). However, this also creates an opportunity for studying seabirds, as it is often less expensive or intrusive to monitor their populations across large geographic scales during this phase of the life cycle (Johnson & Krohn, 2001). Understanding their ecology during this critical period is also essential for developing effective conservation strategies and ensuring the maintenance of ecological balance within marine ecosystems.

White-tailed Tropicbirds

Tropicbird species belong to and are the only extant representatives of the order Phaethontiformes (Flores et al., 2017). This order currently consists of a single family, Phaethontidae, which encompasses three very closely related species, all in the genus *Phaethon* Linnaeus, 1758: White-tailed Tropicbird *Phaethon lepturus* Daudin, 1802 (hereafter WTTB), Red-billed Tropicbird, *Phaethon aethereus* Linnaeus, 1758, and Red-tailed Tropicbird, *Phaethon rubricauda* Boddaert, 1783 (Orta, 1992). This genus has a pantropical distribution, being widely distributed throughout all tropical and subtropical oceans (Flores et al., 2017).

Tropicbirds are medium sized with mainly white plumage and long tail streamers (Nelson, 2005). All three species have a pantropical distribution, being widely distributed across tropical and subtropical oceans (Flores et al., 2017). *P. lepturus* and *P. aethereus* can be found throughout the Pacific, Atlantic, and Indian oceans, whilst *P. rubricauda* is restricted to the Pacific and Indian Oceans (Egerton et al., 2022). Most of the life cycle is spent in the pelagic zone, where they feed on fish and invertebrates only returning to remote islands and islets to breed. This genus is known to nest mostly in cavities on the ground or in cliffs, or on the ground under structures that offer adequate shade (del Hoyo et al., 1992). The smallest species, the WTTB is the only one that nests on trees (Nelson, 2005). The WTTB can occur in sympatry with the two larger species, occasionally sharing potential breeding grounds (del Hoyo et al., 1992). In contrast, the other two species only overlap in the Central Indian Ocean (Winkler et al., 2020). Tropicbirds are monogamous and, due to their tropical and sub-tropical distribution, reduced fluctuations in food availability are linked to their protracted breeding seasons, even though phenology changes from place to place (Winkler et al., 2020). Of three extant tropicbird species, the WTTB is the most widespread and abundant. Mostly based on morphological traits, six subspecies are currently recognized: three in the Indian Ocean, two in the Atlantic, and one in the Pacific (Corre & Cebc, 1999). Despite this, a genetic study suggested that all but one (*P. l. europae*) of the Indo-pacific subspecies were genetically indistinguishable, suggesting that they should not be considered distinct subspecies (Humeau et al., 2020).

The breeding season of the WTTB exhibits considerable variability, depending on location (Burt et al., 2021; del Hoyo et al., 1992; Nelson, 2005), and being influenced by oceanographic events that affect food availability. At lower latitudes, breeding populations tend to exhibit less obvious seasonal peaks, becoming more seasonal at higher latitudes (Lee & Walsh-McGee, 1998). Despite regional variations, it has been shown that in some locations, egg laying usually does not take place during the wetter seasons (Phillips, 1987). Inter- and intra-specific competition can also lead to more protracted breeding strategies (del Hoyo et al., 1992), namely it has been shown that young adult birds might only establish their nesting location after older and more dominant birds vacate their nests (Lee & Walsh-McGehee, 1998).

WTTB utilizes remote islands and islets to breed, where they are known to nest in cavities of cliffs and trees (Baker, 1951), or on the ground under vegetation or structures that provide adequate shade cover (del Hoyo et al., 1992). This species displays high nest site fidelity (e.g. Leal et al., 2016; Phillips, 1987). In some areas, individuals exhibit a strong tendency for reusing nests (Stonehouse, 1962), especially when nesting options are limited (Lee & Walsh-McGee, 1998). The nest comprises of bare substrate, as parents do not utilize any nesting materials (Schaffner, 1991). The species tends to prefer nest sites that are easily approached in flight, likely stemming from their clumsy nature on land, as they struggle to walk or navigate through dense growth (Catry et al., 2009; Mejías et al., 2017). Breeding success is dependent on adequate shade and shelter from rain, and high sun exposure reduces egg viability, prompting adults to abandon the nests (Nelson, 2005). Tropicbirds are particularly sensitive to heat, since they cannot use gular-fluttering to cool down (Stonehouse, 1962). In addition, nest concealment is vital to avoid predation and guaranteeing egg and chick survival, as this is one of the most important causes of reproductive failure (e.g. Mejías et al., 2017; Philips, 1987).

Despite being globally classified as “Least Concern”, WTTB populations have been decreasing worldwide (BirdLife International, 2020). Extreme weather events like hurricanes can cause severe mortality, killing both chicks and adults and destroying nesting sites (Lee & Walsh-McGehee, 2000). The loss of nesting habitat due to human encroachment can also cause significant declines of WTTB populations (Stoke, 1988; Wingate, 1988). In the early 1970s, oil pollution posed a major threat but declined after stricter dumping regulations (Lee & Walsh-McGehee, 2000). Nest predation also has noticeable effects on global populations. Predators include native species, such as land crabs (Burt et al., 2021), as well as introduced species, such as rats and feral cats (Raine et al., 2020). Human predation remains an important global threat too (del Hoyo et al., 1992).

São Tomé Island

The Democratic Republic of São Tomé and Príncipe, in the Gulf of Guinea (central Africa), is *ca.* 250 km west of Gabon. It comprises the main islands of Príncipe (139 km^2) and São Tomé (857 km^2), which lie 150 km apart, and several small islets. These are oceanic islands of volcanic origin, which have never been connected to the continent (Ceríaco et al., 2022).

Rising sharply 3,000 m from the bottom of the ocean, the island of São Tomé is characterized by an irregular topography (Ceríaco et al., 2022). The central area is mountainous and deeply dissected by river gorges and waterfalls. The land mass abruptly ends near the coast in the northwest, where it also reaches its highest point at 2,024m, Pico de São Tomé. The northeast of the island has gentler slopes (Jones et al., 1991).

São Tomé has a warm and humid equatorial climate, with average annual temperatures ranging between 22ºC and 33ºC. The mountainous topography acts as a barrier to the predominant moisture rich southwestern winds, resulting in regular heavy rainfall in the south and southwest (Dauby et al., 2022). Consequently, annual rainfall here can exceed 7,000 mm per year, while in the north and northeast, it does not surpass 2,000 mm. Some areas in the extreme northeast reach as low as 600 mm (Jones et al., 1991). The proximity to the Equator leads to two dry seasons interrupted by rainy periods. The most significant dry season, known as *gravana*, stretches from May to September, being more pronounced at lower altitudes in the drier north of the island. From December to February occurs a shorter and less impactful dry period, known as *gravanito* (Vaz & Oliveira, 2007).

The topography and climate of São Tomé have shaped the vegetation. Although originally the island was entirely covered by forest, currently native forest only persists in some areas. Montane and mist forests occur above 800m, restricted to the rugged high-altitude areas of the centre and southwest of the island (Vaz & Oliveira 2007). Native lowland rainforest, although being largely replaced by shade forest, still occurs in the centre and southwest of the island (Dauby et al., 2022). Considering precipitation levels, the north of the island most likely used to be covered by dry woodland, but remnants of this vegetation only persist in scattered patches on gullies

(Jones et al., 1991). Notwithstanding, only a smaller fraction of the island is no longer forested. Examples of these include the fire-prone savannas in the north, the horticultural fields on the gentler slopped areas of the north and northeast, the coastal coconut groves, and the oil palm monoculture in the south (Dauby et al., 2022).

There are several islets scattered around São Tomé. The largest are Ilhéu das Cabras to the northeast, Ilhéu Santana to the east, Sete Pedras to the southeast, and Ilhéu das Rolas to the south. All but Rolas are uninhabited by humans. Ilhéu das Cabras is mainly covered by dry scrubland, while coconut palms cover most of Ilhéu Santana and Ilhéu das Rolas. These islets have an abundance of crevices that hold very significant populations of crabs. Sete Pedras is a conglomerate of approximately 15 small islets, almost all of which are unvegetated. It hosts the most important and diverse assemblage of breeding seabirds in São Tomé. In the country, it is second only to Tinhosas (Valle et al., 2016), which is the most important site for seabirds in the eastern tropical Atlantic (Jones & Tye, 2006). Three seabird species occur as regular breeders on Sete Pedras: *Anous stolidus*, *Phaethon lepturus*, and *Sula leucogaster* (Melo et al., 2022). Ilhéu das Rolas, the largest of the islets next to São Tomé (ca. 2 km²), is also the only one with a permanent human population of about 76 people (INESTP, 2012a). The islet is vegetated and features numerous crevices on its southern cliffs. It holds extensive coconut plantations, and some pockets of secondary forest and of small-scale agriculture. It hosts populations of introduced rats, dogs, pigs, and cats (Monteiro et al., 1997).

The subspecies of WTTB that occurs in São Tomé, *Phaethon lepturus ascensionis*, encompasses all populations in the tropical Atlantic Ocean (del Hoyo et al., 1992). It has few breeding colonies and a small effective population size, estimated to have 1250 to 2660 breeding pairs (Ashmole et al., 1994; Bollen et al., 2018; Leal et al., 2016; Monteiro et al., 1997; Stonehouse, 1962). The main ones are on the Brazilian archipelagos of Fernando de Noronha and Abrolhos, on Ascension and St. Helena Islands, in the British Overseas Territory of Saint Helena, Ascension and Tristan da Cunha, and in São Tomé and Príncipe (Bollen et al., 2018; Leal et al., 2016; Stonehouse, 1962). The population is in decline and has been considered Endangered (Humeau et al., 2020). In São Tomé, WTTB nest throughout the year (Monteiro et al., 1997), with breeding activity peaking during the dry seasons (Rocha, 2022). The

WTTB is the only confirmed breeding seabird on the main island of São Tomé (Monteiro et al., 1997), nesting primarily in coastal cliff cavities (Jones & Tye, 2006) but also further inland, where it has been observed nesting on cliffs (Jones & Tye, 1988) and in tree cavities at elevations up to 1,050 m (Atkinson et al., 1994; Naurois, 1973). The only available population estimate (Monteiro et al., 1997), reports 100 to 210 breeding pairs on the surrounding islets. It also mentions several mainland breeding sites without specifying the number of pair. These include the cliffs of Santa Catarina and Ribeira Palma, and the valleys of Abade, Iô Grande, and Contador. In São Tomé, nests of this species have been recorded within crevices and on shaded or exposed ledges of rocky islets and cliffs, as well as on the ground in dense grass tunnels (Nadler, 1993) and in large hollow rainforest trees (Naurois, 1973). Introduced mammals such as rodents, the Mona monkey (*Cercopithecus mona*), the African civet (*Civettictis civetta*), the Least weasel (*Mustela nivalis*), and domestic and feral cats, dogs, and pigs pose significant predation risks to nesting birds (Jones & Tye, 2006; Monteiro et al., 1997). Native species can also negatively affect breeding success, notably large land crabs like *Johngarthia weileri*, which have been observed preying on chicks in accessible nests (Rocha, 2022). In addition, human harvesting persists, as WTTBs are occasionally captured for their meat, particularly by young boys (Monteiro et al., 1997; R. de Lima, pers. comm.).

Thesis scope

This thesis aims to contribute for a better understanding of the breeding ecology of the WTTB in São Tomé. It is divided in two chapters: Chapter one assesses the distribution, phenology and population size of WTTB on the island discriminated by nest type: Islet, cliff and tree. Chapter two characterizes these nest types, including an assessment of threats.

Unless stated otherwise, all data used in this thesis were collected by Gustavo Marino. Field work was conducted from late September to mid-October of 2024 and from mid-January to late February of 2025. It had the support of Gabriel Oquiongo, a Santomean with extensive experience supporting research, specifically with avifauna and questionnaires. As a side result of this field work, the possible breeding of Red-billed Tropicbird in the South of São Tomé was recorded and published in the scientific journal Marine Ornithology (Annex 1).

Chapter I: Distribution, phenology and population size estimates of breeding White-tailed Tropicbird *Phaethon lepturus ascensionis* in São Tomé Island

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Abstract

The White-tailed Tropicbird (*Phaethon lepturus ascensionis*) breeds on all oceanic islands of the Gulf of Guinea, but little is known about its breeding ecology. This study combined active nest searches, observation point counts, and questionnaires to assess distribution, phenology, and breeding population size of this species in São Tomé Island and nearby islets. We confirmed nesting in sites where it had been previously confirmed or only suspected, but we also identified new locations, including the largest aggregation on the main island. Breeding seems to occur throughout the year, presenting peaks during the dry seasons. We recorded 135 nests, leading to estimates of 2,358 to 9,430 breeding pairs that suggest São Tomé harbours the largest breeding population of the subspecies, and an important global population for the species, possibly representing 0.6% to 2.4% of the global population. It also highlights the relevance of tree nesting in this population, which is a rare feature for the species and unique for the subspecies. These findings provide a valuable baseline for long-term monitoring, namely in terms of methods that can be used. They also show that important nesting sites, such as Sete Pedras, Ilhéu de Santana and the Santa Catarina cliffs are not within protected areas, suggesting that they might be vulnerable to human developments, namely since the species is also not protected in São Tomé and Príncipe.

Key Words: Distribution, phenology, population size, white-tailed tropicbird, São Tomé and Príncipe

Introduction

Tropicbirds (order Phaethontiformes) are mid-sized seabirds with a pantropical distribution, being widespread throughout tropical and subtropical regions (Flores et al., 2017). These birds spend most of their life feeding in pelagic zones, only returning to oceanic islands to breed (Orta, 1992; Nelson, 2005a). This order has one family, Phaethontidae, which encompasses a single genus *Phaethon* Linnaeus, 1758 with three closely related species: White-tailed Tropicbird *Phaethon lepturus* Daudin, 1802 (hereafter WTTB), Red-billed Tropicbird, *Phaethon aethereus* Linnaeus, 1758, and Red-tailed Tropicbird, *Phaethon rubricauda* Boddaert, 1783 (Orta, 1992). In the Gulf of Guinea, both WTTBs and Red-billed Tropicbirds have been recorded. However, WTTB is the only regular breeding species, and it occurs on all oceanic islands of the Gulf of Guinea (de Lima & Melo, 2021). The WTTB populations in São Tomé and Príncipe belong to *Phaethon lepturus ascensionis*, one of the six WTTB subspecies currently recognized. This subspecies is a distinctive conservation unit that occurs across the southern Atlantic Ocean, having a small effective population size and only a few known breeding colonies, it has been considered Endangered especially due to invasive animal species (Humeau et al., 2020).

WTTBs tend to display a seasonal breeding at higher latitudes, with peaks varying from site to site (e.g., Burt et al., 2021; Raine et al. 2020), and continuous or protracted breeding at lower latitudes (e.g., Orta, 1992). The date and the extension of the WTTB breeding season exhibits considerable variability, with weather patterns appearing to exert a strong influence in the reproduction cycle (Burt et al., 2021; Catry et al., 2009; Nelson, 2005a; Ramos et al., 2005). In the Seychelles, WTTB nests throughout the year but tends to avoid the monsoon season or laying eggs during the wettest months (Phillips, 1987). Accordingly, in São Tomé and Príncipe nests can also be found throughout the year, but peak abundance of breeding pairs seems to coincide with the dry season, and particularly with the small dry season between December and January (Rocha, 2022).

São Tomé and Príncipe supports the largest concentration of breeding seabirds in the eastern tropical Atlantic Ocean (Monteiro et al., 1997), hosting internationally significant breeding seabird populations (Jones & Tye, 2006). Notwithstanding, its seabird communities remain poorly studied when compared to its endemic-rich forest avifauna (de Lima & Melo, 2021). The focus of recent studies has been on Tinhosas (e.g., Bollen et al., 2018), a Ramsar site that is undoubtedly the most important seabird colony in the region. Other breeding populations in the country have not been surveyed for almost three decades (Monteiro et al., 1997). This means that most populations of breeding seabirds are not being monitored, as is the case for the WTTB, namely since Tinhosas is not a relevant breeding location for the species in the country (Bollen et al., 2018). The best known WTTB population in the region is the one in Príncipe Island, since it was the only one targeted by a species-specific study (Rocha, 2022), which estimated 100 to 150 breeding pairs. These numbers represent an apparent increase from the late 1990s (Monteiro et al., 1997) and even from January 2017 (Bollen et al., 208), when this population was estimated at 41 to 82, and at 50 to 100 breeding pairs, respectively. Changes in the distribution were also noticeable, since they were confirmed breeding in more locations in 2017 when compared to the 1990s. It is nevertheless unclear each of these changes are real or can be attributed to changes in effort, methodology or observers. In São Tomé, the WTTB is the only confirmed breeding seabird for the main island (Monteiro et al., 1997), nesting in coastal cliff cavities (Jones & Tye, 2006) as well as being seen further inland, nesting in cliffs (Jones & Tye, 1988) or travelling up to 1,050 m (Atkinson et al., 1994) to nest in tree cavities (Naurois, 1973). The only population size estimate dates back from the 1990s and it mentions 100 to 210 breeding pairs on the islets (0-10 for Cabras, 40-80 for Santana, 30-60 for Sete Pedras, uncertain for Quixibá, and 30-60 for Rolas) and an undisclosed number of breeding pairs on several locations on the main island, namely on the cliffs of Santa Catarina and Ribeira Palma, and on the Abade, Iô Grande and Contador river valleys (Monteiro et al., 1997). More recently also, Gabado has also been mentioned as a possible nesting location (Lo Cascio, 2021).

The main objective of this study is to improve our knowledge about the breeding populations of WTTB on São Tomé Island. Specifically, we: (1) assessed distribution across the main island and surrounding islets; (2) collected information on phenology; and (3) estimated the size of the breeding population during the smaller dry season.

Methods

Study Area

São Tomé is an 857 km² volcanic island located 255 km off the West coast of the African continent (Ceríaco et al., 2022). It reaches up to 2,024 m a.s.l. and is surrounded by several islets, the largest of which is Ilhéu das Rolas, located to the south and intersected by the Equator. Other important islets include Cabras (to the northeast), Santana (to the east) and Sete Pedras (a conglomerate of rocky outcrops to the southeast), all of which have been identified as potential or confirmed breeding sites for the WTTB (Monteiro et al., 1997). The average annual temperature ranges between 22ºC and 33ºC, depending mostly on altitude, while annual rainfall varies from 7,000 mm in the Southwest to below 600 mm in the Northeast (Ceríaco et al., 2022). The climate is tropical, having a main dry season between May and September, the *gravana*, and a smaller one between December and February, the *gravanito* (Ceríaco et al., 2022).

A preliminary visit of two weeks took place from late September to mid-October 2024, at the beginning of the rainy season, but most fieldwork was done from mid-January to late February 2025, coinciding with the short dry season.

Distribution

The distribution of the breeding population of WTTB was assessed using questionnaires and active search during both visits, as well as data obtained at observation points during the 2025 visit. Data from the International Waterbird Counts (IWC) from 2020 to 2025 (de Lima et al., 2025) were also used. All occasional observations of WTTB were also registered. Both occasional and systematic records of adults and nests were georeferenced and then used to build distribution maps.

The questionnaires (S1, section B) were used to gather information on locations of potential nesting sites, to help maximize the detection of adults and nests. In São Tomé, the coastal guard divides the coast into 11 sections, each being assigned to a distinct *chefe de praia*. These are focal points, identified amongst the residents of each area to become responsible for a stretch of coast. Since these are often knowledgeable about marine species, we applied questionnaires to the *chefes de praia*. However, we were only able to apply nine of these questionnaires, seven to *chefes de praia* and two to replacements in four of the remaining sections, one to a fisherman and another one to a community leader (Fig. 1). For the remaining two sections, the *chefe de praia* was unwilling to collaborate on one, while the other one was currently not attributed, and we could not find a suitable replacement on either of these. We also applied questionnaires in communities, and decided to focus on the non-urban, since urban dwellers on the island are known to be less knowledgeable about biodiversity (Panisi et al., 2022). To do so, we started by identifying all non-urban communities in São Tomé that had at least 200 inhabitants (INESTP, 2012b), which has been considered a minimum population size to ensure a robust sampling (Panisi et al., 2024). Then, we randomly selected two settlements in each district, except for Água Grande, which is fully urban (Fig. 1), and, in each of these settlements, we contacted a representative to help us choose 16 individuals aged 14 years or older to participate in the study. Preference was also given to male participants, since they are more likely to have occupations that put them in touch with the target species, and have been shown to be more knowledgeable about biodiversity (Panisi et al., 2022). Before starting the questionnaires, all participants were informed about the context and goals of the study, and it was explained that their participation was voluntary and unpaid, and that they could interrupt it at any point. After agreeing to participate, we applied the questionnaire, which was made extremely short to ensure a willingly engagement. All resulting 169 questionnaires were completed to the end.

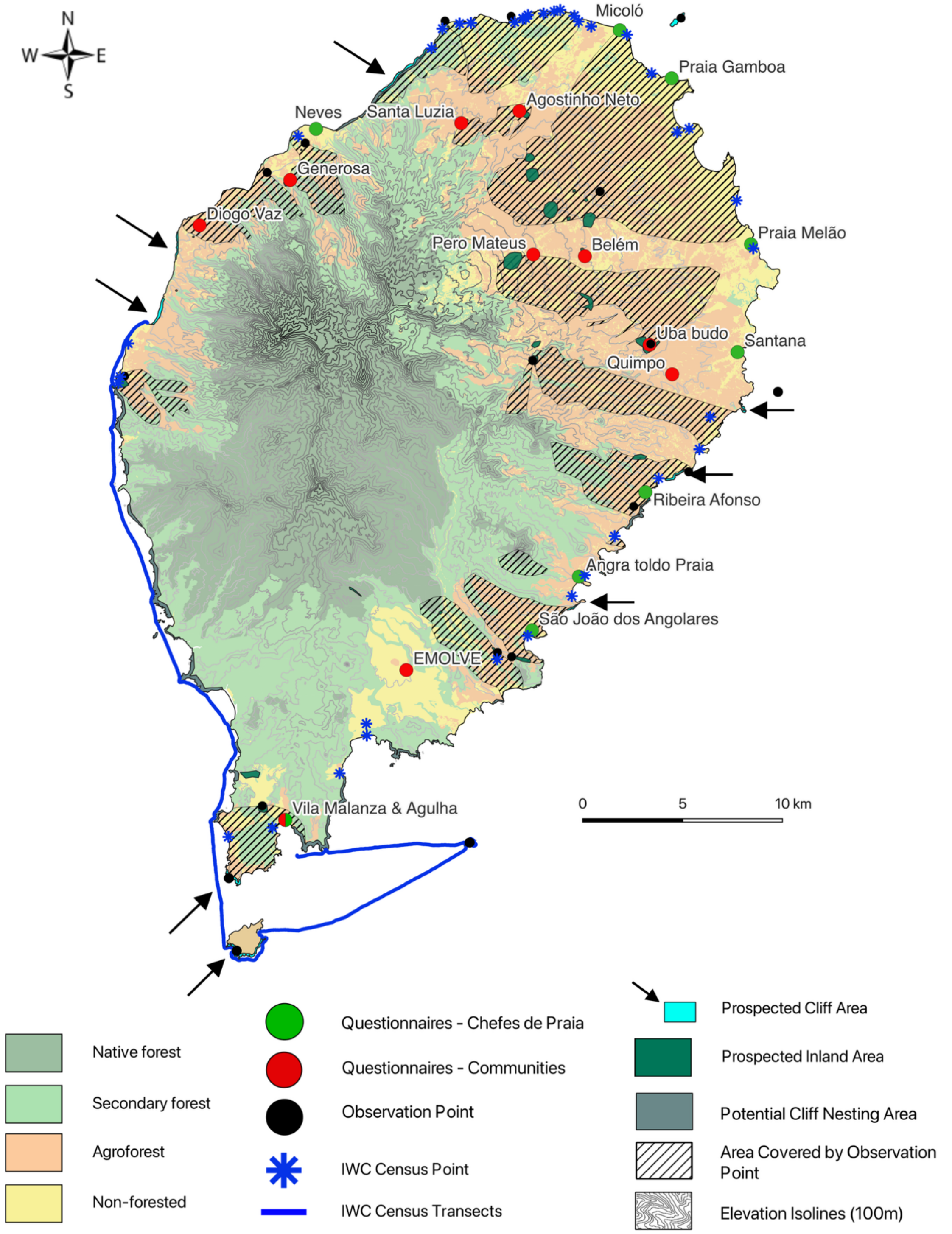

Figure 1 – Sampling locations in São Tomé Island. Questionnaires were applied to *chefes de praia* or substitutes (n = 9) and to people in non-urban communities (n = 10). Observation points were split between the main island (n = 14) and main islets (n = 4). IWC point counts (n = 35) and boat transect are also represented (de Lima et al., 2025). The background map shows 100 m elevation isolines (Salgueiro & Carvalho 2001) and main land use types (Soares et al., 2020).

Eighteen observation points were established (Fig.1) and surveyed once for 1-hour by two experienced observers (Gustavo Marino and Gabriel Oquiongo) to identify adults flying over to their nests, using binoculars. These were strategically placed, mostly on high points or on valley chokepoints, to maximize the coverage of the island. They were identified using a detailed map of the island (Marques, 1961), previous bibliographic information (Monteiro et al., 1997) and personal knowledge of topography and accessibility (Ricardo de Lima, pers. comm.). Eleven points were chosen to survey adults flying inland, presumably to tree nests, while three focused on potential locations of nests on coastal cliffs and the remaining four were placed on the main islets around São Tomé.

Active nest searches focused on areas identified in the bibliography (Monteiro et al., 1997) or during the questionnaires and observation points. Targeted areas were searched once by two observers with varying durations influenced by time of arrival and location. We considered an active nest location to be confirmed when an adult was observed inside the nest or entering a cavity and remaining there for at least five minutes, allowing us to distinguish active nests from sites being prospected by adults. Additionally, nest locations that were reported to us were classified as probable active nest locations only when the observations referred to adults entering and exiting the cavity more than once in less than 24 hours. Nests were classified in three main types: tree, coastal cliffs and islets (Monteiro et al., 1997). Tree nests were surveyed by car or on foot depending on accessibility. Voluntary assistance from occasional informants also played a key role in locating active tree nests, particularly in agroforests. Nests on coastal cliffs were prospected by land whenever possible, and by boat in the less accessible portions of the island. These searches focused on areas with coastal cliffs, which were first identified using detailed maps of the island (Marques, 1961) and satellite imagery (Google Earth, 2025), and then on the ground, to confirm their potential for WTTB nesting. The four main islets around São Tomé Island (Cabras, Santana, Sete Pedras and Rolas) were accessed by boat and areas with potential for WTTB nesting were surveyed on foot or by observation from strategic viewpoints. Nests found in Ilhéu das Rolas were subsequently classified as cliff nests, since they were more like those than to the nests found on smaller islets.

The IWC has been taking place in São Tomé once a year since 2020 (de Lima et al., 2025). During these counts, areas that are accessible by car are surveyed once employing 10-minute counts in 35 points, while less accessible coastal areas and islets are sampled along a boat transect divided in 9 sections. Binoculars are used on all locations, while telescopes are only used during the point counts.

Phenology

The questionnaires gathered information about the phenology of WTTB in São Tomé Island. We asked specifically if there were seasonal changes in the number of adults and nests and, if so, when were the months that these occurred. We inferred phenology based on the results of the questionnaires, complemented by our direct observations of breeding and breeding behaviour collected during the two periods spent on the field.

Breeding Population Size

Breeding population estimates were derived from the number of adults observed in flight from the observation points, combined with the number of nests found through both the observation points and active searches in 2025. In each observation point, 1-hour counts were conducted simultaneously by two experienced observers (Gustavo Marino and Gabriel Oquiongo) in fifteen of the eighteen observation points used to assess the species distribution (Fig. 1). Three of the eighteen points (Homem de Capa, Sete Pedras and Ilhéu Santana) were not considered in this sampling effort, since they were only implemented later on, as observation points for nest counts. Twelve observation points were situated inland at high elevations or at valley chokepoints, normally at the entrance of river valleys, based on the assumption that WTTBs use them as flyways between inland and the coast (Atkinson et al.,1994). The remaining three were in islets (Rolas and Cabras) and on a coastal cliff near the end of a valley.

The observers recorded the number of individuals flying inland (“Entries”) seawards (“Exits”), or with no distinct direction (“No clear direction”). Since WTTBs are pelagic and only come to land to breed (Lee & Walsh-McGee, 1998), and assuming that individuals with defined linear flight paths (“Entries” and “Exits”) were flying to their nest and that the same individual would not do the same route in less than one hour, the number of breeding pairs was inferred by grouping into pairs the number of individuals registered at each observation point. When the count provided odd numbers, the total was rounded up to the nearest even number. Counts were performed during peak activity periods, namely early in the morning (Schaffner, 1990) or midday, as indicated by locals, and confirmed during fieldwork.

Nests were identified through observation points and active searches, and subsequently categorized into three types: islet, coastal cliff and tree (Monteiro et al., 1997). Each confirmed nest was assumed to represent one breeding pair. Islet nest estimates were based on the proportion of the area that was prospected, whereas for coastal cliff nests, estimates were based on the proportion of the cliff length with nesting potential that was prospected. For tree nests, estimates were derived from observation points and active inland searches. The counts from the observation points and systematic ground searches, provided estimates of breeding pairs for a given area. For areas covered by both methods, the highest estimate was the one taken into consideration. The total number of tree nests obtained by combining all methods, was grouped by land use. Then, it was extrapolated to the entire island, for each land-use type, by multiplying the number of nests by the total area (Soares et al., 2020) and dividing it by the prospected area.

To account for detectability, estimates assumed three scenarios of nest detection: 100%, 50%, and 25%. The sum of estimates obtained for each nest category provided the breeding population size estimate for São Tomé and nearby islets during the small dry season.

Results

Distribution

Excluding remote areas, which were clearly under sampled (Fig. 1), the presence and breeding of WTTB was confirmed across São Tomé and main satellite islets (Fig. 2 & 3).

From the questionnaires, we identified 64 potential areas where WTTB occurred and 39 potential active nest sites (Fig. 2). Six of the potential WTTB areas and five of the potential active nest sites were not mapped because their names could not be traced back. Out of 169 questionnaires, only 16% and 36%, respectively, did not provide areas where adults and nests of WTTB could be found. Participants clearly tended to specify areas next to where they lived or that they frequently visited (Fig. 2).

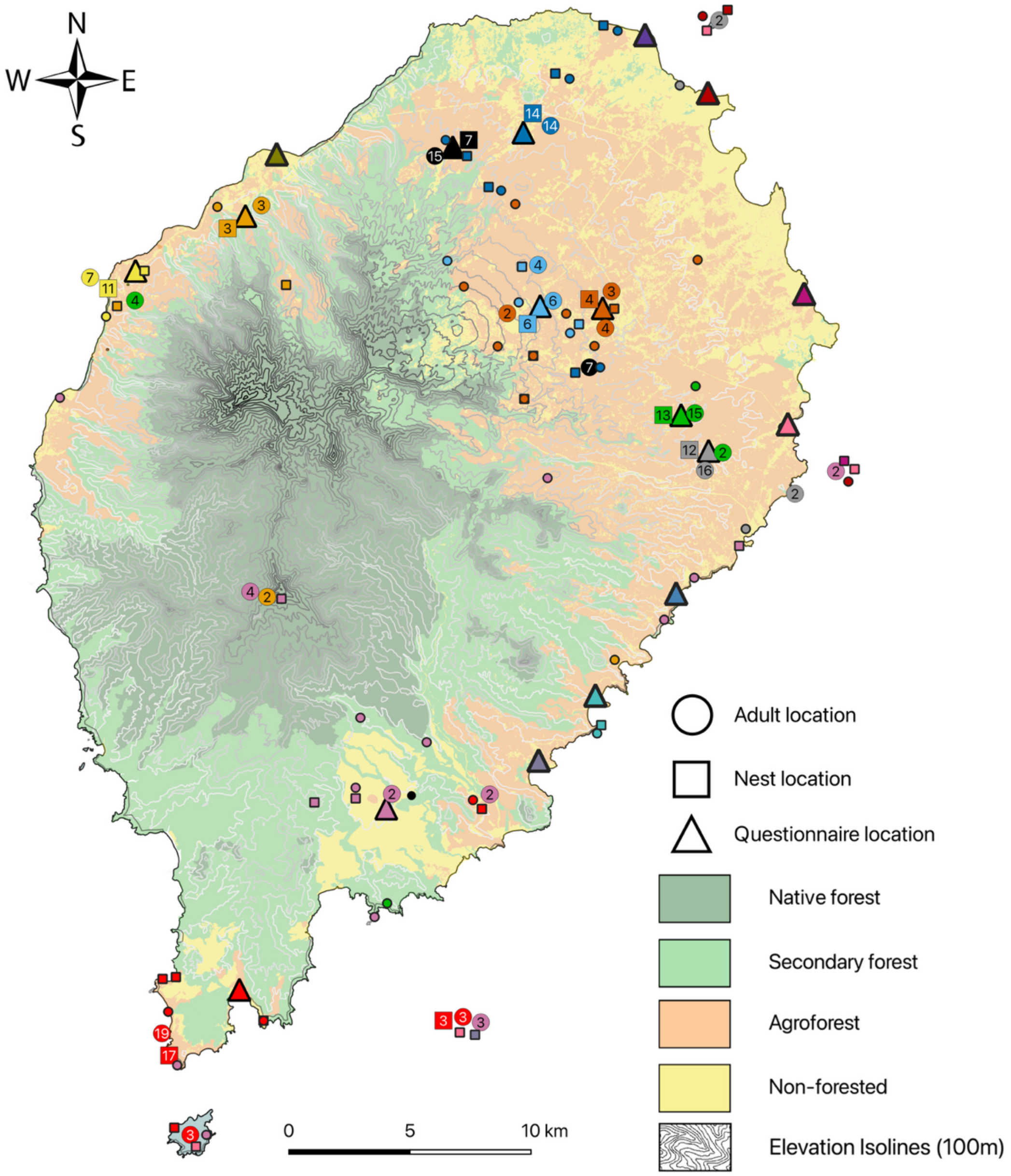

Figure 2 - Potential distribution of White-tailed tropicbirds on São Tomé Island, including locations of adults and nests obtained from the questionnaires. Symbols are colour-coded to distinguish locations mentioned for questionnaires in each community (n=10), while over imposed numbers show the number of times each location was mentioned in each community, if larger than one. The background map shows 100 m elevation isolines (Salgueiro & Carvalho 2001) and main land use types (Soares et al., 2020).

Despite variable abundance, the species was spotted in all 18 observation points (Fig. 3). Out of the 34 potential active nest locations obtained through the questionnaires that were mapped, only 9 were confirmed, while 17 additional nesting sites were found even though they had not been mentioned during the questionnaires. Nests on coastal cliffs were mostly found in the south and northwest. High concentrations of nests were also found in the two southernmost islets, Rolas and Sete Pedras, while most nests on trees were confirmed in cocoa shaded plantations at the base of the mountain slopes in the northeast of the island.

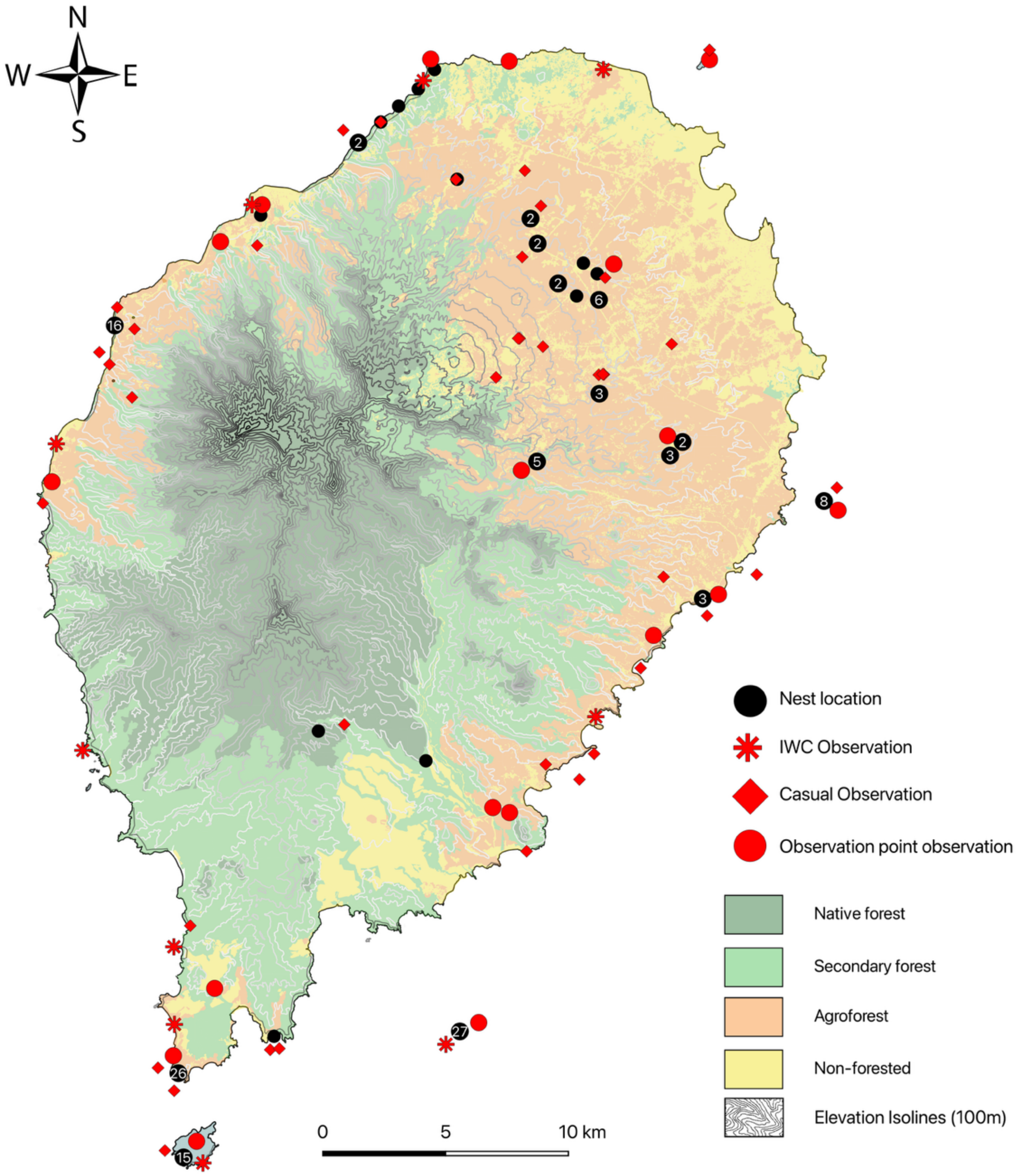

Figure 3 - Confirmed distribution of White-tailed tropicbirds on São Tomé Island, including adult (red symbols) and nest locations (black circles). The IWC observations were compiled between 2020 and 2025 (de Lima et al., 2025), while all others refer to observations made during 2024-25. Black circles with over imposed numbers show the number of nests in each location if nest number larger than one. Nest locations resulted from active searches. The background map shows 100 m elevation isolines (Salgueiro & Carvalho 2001) and main land use types (Soares et al., 2020).

Since 2020, WTTBs have been observed in 16 point counts, and 9 sections of the boat transect during the IWC (Table 1). The highest frequency of WTTB has been on Sete Pedras and Rolas, where they have been observed every year, followed by Cantador River and Jalé where they have been observed in 4 years. During the 2025 IWC, WTTBs were observed in 5 point counts and in 5 boat transect sections.

Table 1 - WTTBs registered during the IWC between 2020 and 2025 (de Lima et al., 2025), shown by location and year. Shades of green correspond to 10-minute point count locations and shades of blue correspond to section of the boat transect.

Location	2020	2021	2022	2023	2024	2025	*Frequency*
Rio do Ouro (Fernão Dias)	2	0	2	0	0	2	3
Small lagoon in Praia do Governador	0	0	1	0	0	0	1
Praia das Conchas	0	1	0	0	0	0	1
Lagoa Azul	0	0	0	0	0	2	1
Praia da Mutamba	0	0	0	0	1	0	1
Contador River	0	0	3	2	0	1	3
Lembá River	0	0	0	0	4	0	1
Cantador River	1	2	0	0	2	2	4
Abade River Bridge	0	0	0	1	3	0	2
Praia Plano	0	0	0	0	3	0	1
Praia das Sete Ondas	0	0	0	2	0	0	1
Praia da Colónia Açoriana	0	2	0	0	0	0	1
Praia de Angra Toldo	0	2	1	0	0	1	3
Yô Grande River Bridge	0	0	0	0	2	0	1
Praia Grande	0	0	0	2	0	0	1
Frequency	2	4	4	4	6	5	
Abundance	3	7	7	7	15	8	
Porto Alegre	1	0	0	0	0	0	1
Sete Pedras	1	4	9	7	7	11	6
Ilhéu das Rolas	1	2	3	4	8	5	6
Jalé	0	3	4	7	12	8	5
Mussacavú	0	0	0	0	0	1	1
Jou	1	0	0	0	0	0	1
São Miguel	0	2	0	0	3	0	2
Bindá	0	0	0	0	6	2	2
Santa Catarina	0	0	3	0	0	0	1
Frequency	4	4	4	3	5	5	
Abundance	4	11	19	18	36	27	

Phenology

According to the questionnaires, perceived yearly changes in the abundance of WTTBs were strongly associated with the small and main dry seasons, both for adults and nests (Fig. 4): Reported abundance being the highest during the main dry season (June to August) and showing another noticeable increase during the shorter dry season (January and February). In addition, 130 respondents claimed to see WTTBs year-round, while 34 replied to see them only in some periods and 5 did not answer.

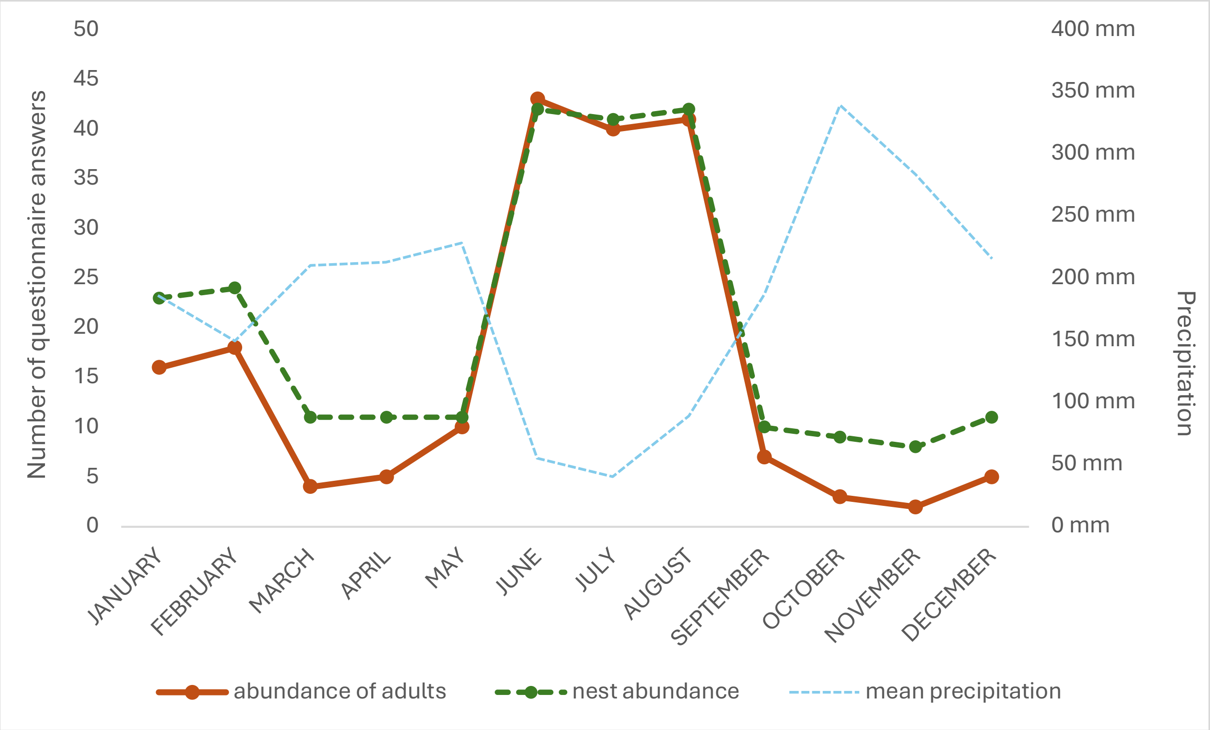

Figure 4 - Perceived seasonal changes in abundance throughout the year, based on questionnaire responses. Mean precipitation obtained from 1991-2020 climatology period (Climate Change Knowledge Portal, n.d.)

Breeding Population Size

We estimated that there were around 4,715 breeding pairs in São Tomé and associated islets during the small dry season of 2025, likely ranging between 2,358 and 9,430 breeding pairs (Fig. 5 & 6, Table 2). Out of these, 4,200 (2,100 – 8,400) correspond to tree nests, 378 (189 - 756) to coastal cliff nests, and 137 (69 - 274) to islet nests.

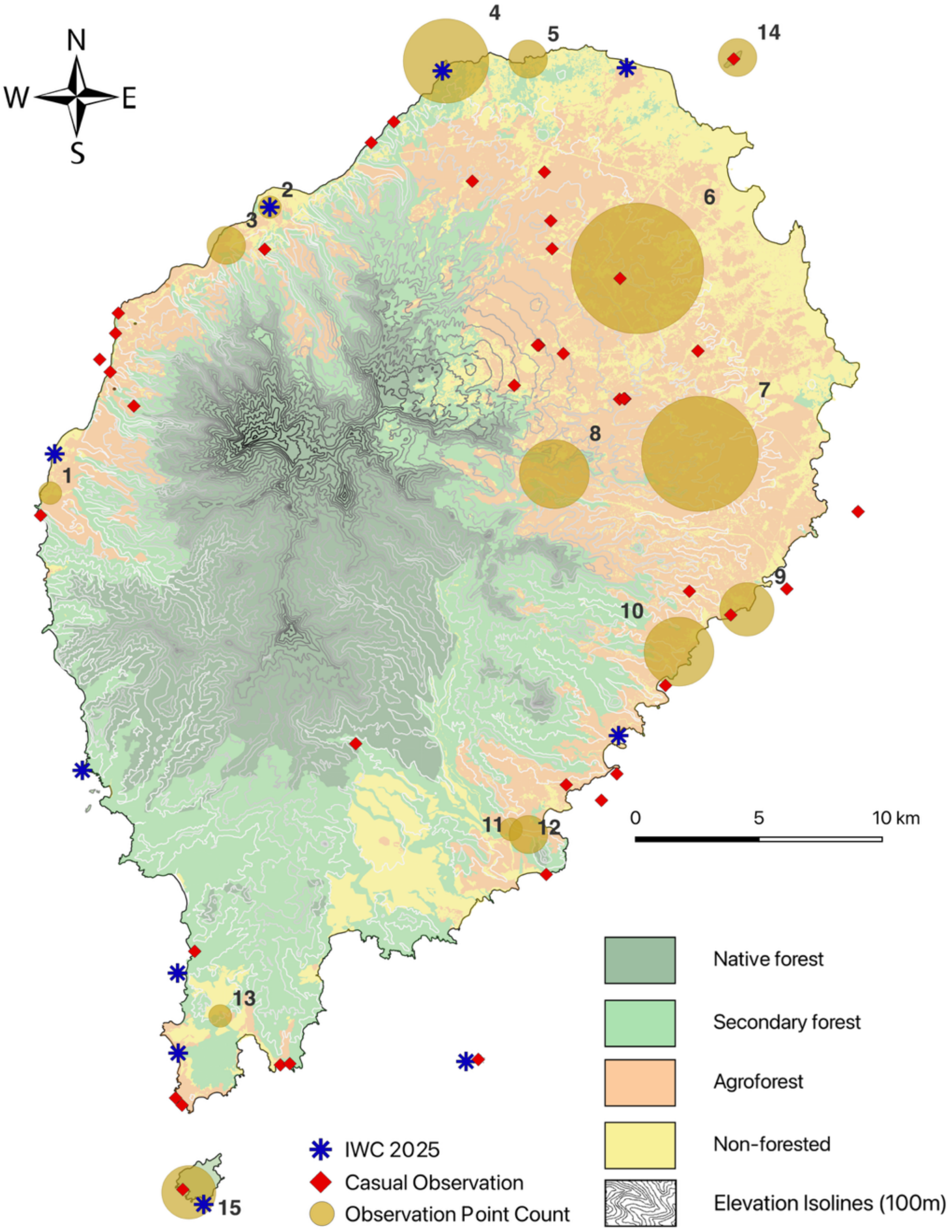

Figure 5 - Number of White-tailed Tropicbirds counted during 1-hour observation points across São Tomé Island – represented by the size of the numbered yellow circles (Table 3 provides exact numbers for each location, following the numbers shown here). Location of IWC and casual observations of WTTBs are also shown. The background map shows 100 m elevation isolines (Salgueiro & Carvalho 2001) and main land use types (Soares et al., 2020).

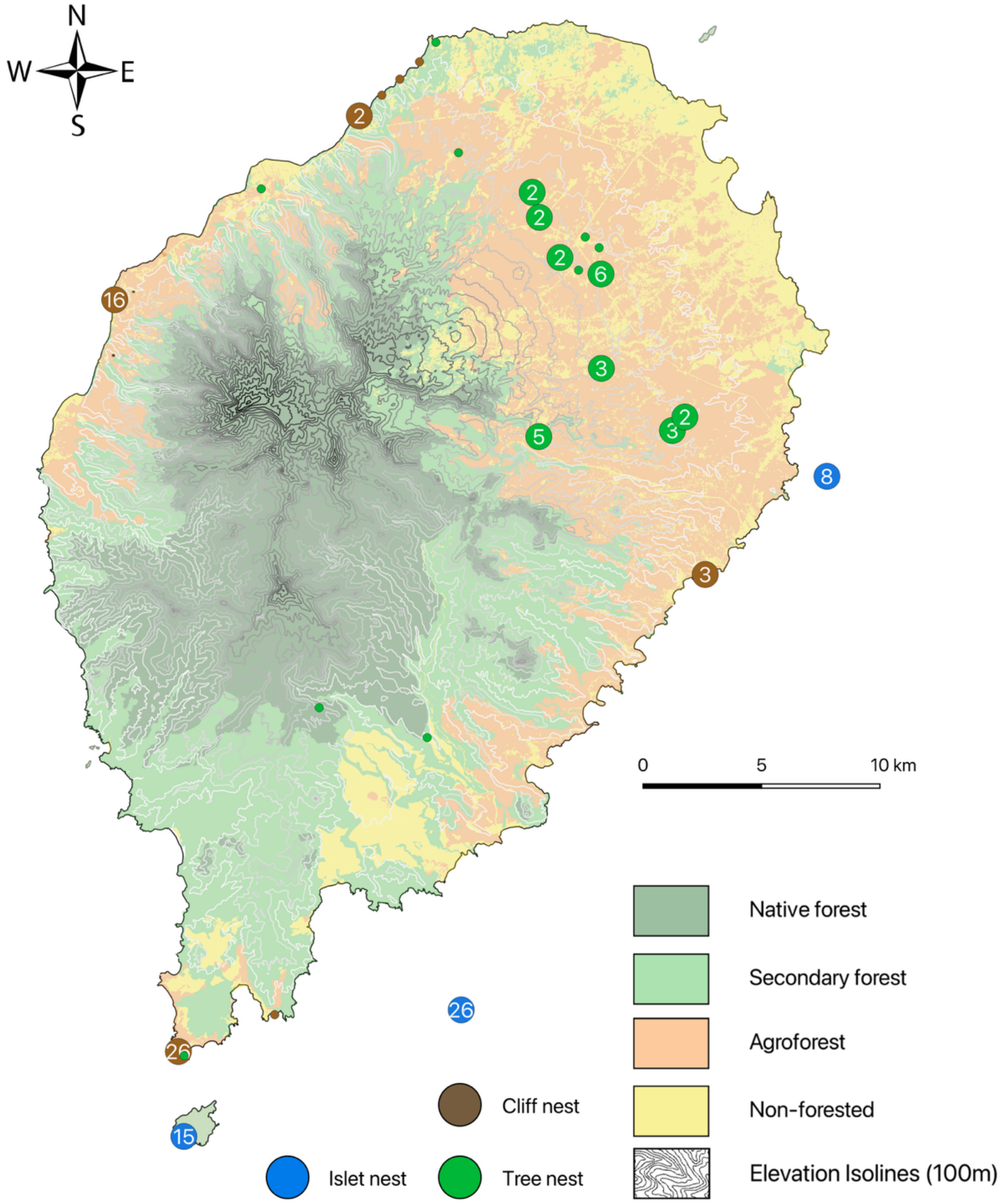

Figure 6 - Number of White-tailed Tropicbirds nests confirmed in São Tomé Island and associated islets during the active nest searches. Colour distinguishes nest category (see Table 2 for additional information). Solid circle represents one nest and circles with numbers represent the sum of nests in given location. The background map shows 100 m elevation isolines and main land use types (Soares et al., 2020).

Table 2 - Nest estimates for the prospected areas and the extrapolated for the total available area, under three detection (D) scenarios: 100%, 50%, and 25%. Full detection (D =100%) for the prospected forested areas corresponds to the sum of nests found by active prospection, direct count of adults from observation points or the largest value when both methods were applied (nests uncovered by active prospection in areas encompassed by observation points were extrapolated to the total area of the observation points).

Location	Prospected	D= 100%	D = 50%	D= 25%	Total availability	D= 100%	D= 50%	D= 25%
Forests	37.1 km²	81	162	324	446.95 km²	978	1956	3912
Agroforests	110.23 km²	929	1858	3716	133.03 km²	1122	2244	4488
Coastal Cliffs	15.71 km	51	102	204	58.19 km	189	378	756
Ilhéu das Cabras	0.14 km²	0	2	2	0.17 km²	2	4	8
Ilhéu Santana	0.02 km²	8	16	32	0.04 km²	16	32	64
Sete Pedras	0.01 km²	27	54	108	0.01 km²	34	68	135
Ilhéu das Rolas	3.42 km	15	30	60	3.80 km	17	33	67
Total	-	1111	2224	4446	-	2358	4715	9430

Around 210 km², corresponding to approximately 25% of the island, was prospected using the 1-hour observation points. These points resulted in approximately 197 breeding pairs (Table 3). Active inland search covered approximately 4.17 km², resulting in the identification of 34 tree nests.

Table 3 – Number of adults registered during the 15 observation points, and extrapolated number of breeding pairs. These were divided into three classes according to their behaviour: Entries - individuals flying inland; Exists – individuals flying seawards; No clear direction – individuals with no distinct directions, normally engaging in circular flight. The number of breeding pairs was extrapolated by rounding up to closest even number, the number of entries or exists, whichever was largest (highlighted in green). Numeration of the observation points is identical to that used in figure 5.

Observation Points	Start of observation	Entries	Exits	No clear direction	Extrapolated number of breeding pairs
1 - Lembá	08h00	8	0	0	4
2 - Ponta Figo	08h40	9	2	0	5
3 - Monte Forte	10h00	16	4	0	8
4 - Lagoa Azul	08h30	43	5	0	22
5 - Morro Peixe	07h30	12	0	2	6
6 - Gratidão	08h00	78	7	0	39
7 - Uba Budo	14h30	64	0	0	32
8 - Abade	09h30	38	33	0	19
9 - Sete ventos	09h00	25	5	0	13
10 - Caridade	13h00	27	34	34	17
11 - Fraternidade	10h50	14	1	0	7
12 - Fraternidade EN2	09h15	10	1	0	5
13 - Alto Douro	07h00	1	0	0	1
14 - Ilhéu das Cabras	05h50	14	4	4	7
15 - Ilhéu das Rolas	06h15	23	9	0	12
Total		382	105	40	197

From all prospected areas, Ilhéu das Cabras was the one where no nest was found. In this case, we considered that it could still host two nests, since two pairs of WTTB were observed in circular flight over the islet during our visit. Potential nest numbers for the prospected areas were estimated to be around 2,224, ranging between 1,111 and 4,446 nests (Table 2). Extrapolating these for the whole study area, the potential number of nests was estimated at 4,715, ranging from 2,358 to 9,430 (Table 2).

Discussion

This study allowed to determine that WTTB nesting is widespread throughout São Tomé. Breeding is reported to occur all year, despite seasonal peaks during both dry seasons. In addition, population size is much larger than previously thought, potentially classifying as being of global importance for the conservation of the species.

Distribution

Our efforts showed that the WTTB, despite variable abundances, occurred throughout São Tomé. Normally, being easily observed in the main island and on the four targeted islets. In the main island, our findings indicate inland nests are more abundant and widespread than previously reported by a previous study which limited tree nests to river valleys (Monteiro et al., 1997). This ample distribution was expected since WTTB are known to travel far inland to breed (Nelson 2005b; Raine et al., 2019) and have been previously documented at high altitudes in São Tomé (Atkinson et al., 1994). We were able to uncover multiple tree nests in cocoa shade plantations spread throughout the island, highlighting it as an important breeding habitat. In addition, similar to previous studies (e.g. Monteiro et al., 1997; Jones & Tye, 2006), our observations resulted in higher concentrations of individuals observed in flight in the north and northeast, as well as in some coastal locations of the south and west. This tendency can be mainly attributed to the fact that these locations harbour higher concentrations of tree and cliff nests. We also observed this species in all four islets with higher concentration of individuals being observed in Sete Pedras and Ilhéu das Rolas, highlighting both these locations as important breeding grounds for WTTB. Overall, our observations on distribution are in alignment with previous reports by other authors, which also described a relative ample distribution. Notwithstanding, our results complements lacking information of inland distribution for the species as previous studies focused more in the coastal and offshore habitats.

Nests were uncovered in multiple locations throughout the study area. In alignment with previous studies (Bannerman, 1915; Naurois, 1973; Monteiro et al., 1997), we found active nests in Ilhéu Santana, Sete Pedras and Ilhéu das Rolas, confirming the species still breeds in these islets. We also confirmed nesting along the northwestern coastal cliffs, including the area of Santa Catarina Tunnel, as well as on the cliffs of Ribeira Funda, corroborating previous suspicions (Monteiro et al., 1997). Tree nests were also confirmed for the first time in the valleys of the Abade, Ió Grande, and Contador rivers, as previously suggested (Monteiro et al., 1997). Our study also uncovered multiple new nest locations (S1, section A). Many inland nests were in previously unreported sites spread through the island, with the most significant abundance in the north, near Ubabudo and Vista Alegre. Our efforts also rendered new cliff nest locations in the northwest, east and south of the island, with the southern locations hosting the most significant nest abundances. Despite observing four adults in circular flight, we could not confirm active nesting in Ilhéu das Cabras, an islet where WTTB was previously reported as abundant and as a breeding species (Bocage, 1889; Frade, 1959; Naurois, 1973). In spite of these historical reports, our result is in alignment with those of the expedition in 1996 and 1997 (Monteiro et al., 1997) which also failed to confirm breeding at this location, hinting that WTTB might no longer breed there. Due to the remoteness of the southwest and lack of adequate observations, this area was under sampled. Notwithstanding, we recognize the high potential for nesting, since the morphology of some cliffs and the presence of large trees and islets in the region suggest it might hold a significant number of breeding pairs. In particular for tree breeding pairs shown by this study to be much more widespread if adequate nesting conditions are present. This area has high potential as it is isolated and is covered in forest with mature trees possibly offering adequate nesting conditions far from human interference. Furthermore, Quixibá, in the southeast (Monteiro et al., 1997) and Gabado in the southwest (Lo Cascio, 2021), are both islets where WTTB nesting has been suggested based on the observations of adults but never confirmed. Future efforts should target these under sampled locations, prioritizing the cliffs and forests of the southwest and include visits to prospect both islets suggested as potential breeding grounds.

Overall, the questionnaires indicated that the species occurs throughout the island, including in habitats far from the sea and less common for seabirds. This suggests that the questionnaires were useful in gathering preliminary information on the species' distribution and in guiding subsequent prospection efforts. It is worth noting, however questionnaires provided an insight of the occurrence of this species in locations that were not prospected, this information tends to be biased. This is due to answers tended to geographically fall close to the inquired communities (Fig. 2), or in locations that are more intuitively associated with it, often giving vague answers such as “beach” or naming their own community. While these responses can serve as a valuable starting point for field prospecting, they may not necessarily reflect the areas where the species is most frequent. This was evidenced for the southwest, as this was the only region where the questionnaires did not indicate the presence of WTTB, because none were applied in that region and the respondents did not frequent that area. During field work, there was an evident contrast of knowledge regarding this species between inland and coastal communities. Each community type harbours different insights in conformity with their geographical location, with coastal communities possessing more information of coastal and offshore habitat distribution and severely lacking any knowledge of inland distribution. The opposite was observed for inland communities, confirming that the distance from different habitat types, influenced and conditioned their overall knowledge on the WTTB. Since communities were randomly selected, most ended up being inland, as stated this influenced the distribution obtained from the questionnaires. We suggest that future studies distinguish these two types of communities, using stratified sampling to randomly select within “inland” and “coastal” communities. This will improve the distribution of the sampling effort and provide a better representation of distinct across the island.

Phenology

From 169 questionnaires, 77% hinted at the year-round presence of the WTTB in São Tomé. They also indicated an increased abundance during the main dry season (June to September) and another noticeable increase during the shorter dry season (December to February). Our field observations were consistent with this variability, as WTTBs were recorded in smaller numbers and in fewer locations in October 2024 compared to February 2025. In October, most birds were engaging in courtship and nest-site prospection, they were found in smaller numbers, and no adults were recorded entering cavities. While in February, levels of courtship and nest prospecting were markedly higher. In addition, our second visit uncovered active nests throughout the whole island highlighting the increase in cavity occupancy and breeding. Furthermore, two brooding adults and a fledgling were photographed in separate nests in Ilhéu Santana on the 21st of August 2025 (Ricardo de Lima, pers. comm.). This is in alignment with observations made in Príncipe (da Rocha, 2022), where peak in abundance of mating pairs coincided with the dry season. In São Tomé, adults have been recorded in Sete Pedras during August and September (Atkinson et al., 1994), suggesting breeding in this location during these months. Seasonal fluctuations had also been recorded for the species on the island (Monteiro et al., 1997), possibly linked to nesting location. In visits that occurred in January and July there was an evident and significant increase in adults, nests and chicks observed in Sete Pedras comparatively to the visit in March, with highest WTTB activity registered for July. This is similar to their visit to Rolas, where no activity was registered in March but was registered in July. Interestingly, the survey of Ilhéu Santana in March of the same year uncovered a high concentration of adult and some immatures but July rendered no activity. Similarly, WTTB were observed in coastal cliffs in March. These results in addition to ours, suggest possible seasonal fluctuations linked to the dry seasons that differ between specific regions. This is likely due to individual breeding phenology possibly varying from year to year, most notably influenced by environmental factors such as food availability, climatic patterns, nest site competition as well as the time since the last breeding attempt (Stonehouse, 1962). The questionnaires, our observations and bibliographic information support that WTTB breeds all year in São Tomé and Príncipe (Bollen et al., 2018) with spatial variation, even though it might have some abundance peaks. Consubspecific populations near the Equator, namely in Abrolhos Island, Brazil (Leal et al., 2016), and in Ascension's Boatswain Bird Island (Stonehouse, 1962), also display a protracted reproductive strategy.

The results obtained regarding the phenology of the WTTB in São Tomé are based mainly on questionnaire data supplemented by observations in the field. So, while they may provide an indication of potential trends, they cannot be considered fully reliable, especially since the WTTB might exhibit local variation in nesting peaks. Inland, cliff, and islet nesting pairs may also respond to different seasonal cues, and local communities often reported subtle differences in timing and abundance despite strong indications that breeding occurs predominantly during the main dry season.

Breeding population size

During field work, 135 (Table A1) nests were georeferenced: 50 of these were on three of the four islets we searched, and Sete Pedras clearly supported the largest aggregation; 34 were on trees, mostly in agroforests of the north and northwest; and 51 were on coastal cliffs, concentrated near the Santa Catarina Tunnel and at the previously unreported site of Homem de Capa, which hosted the largest concentration of active nests in the main island.

The only previous estimate was regarding the number of pairs breeding on islets, which rendered between 100 and 210 breeding pairs (Monteiro et al., 1997). When comparing our estimate results to this earlier estimate, they partially overlap which might suggest stable colony sizes over time. Unlike the estimates from the ’97 expedition, which indicated Ilhéu Santana as the largest concentration of breeding WTTB, our results suggest otherwise. We found Sete Pedras to be the largest and most important offshore breeding area for WTTB in São Tomé, followed by Rolas and only then, Ilhéu Santana. Furthermore, our estimates suggest that the number of pairs breeding on islets as the smallest of the three analysed breeding types.

No previous attempts were made to estimate the number of pairs breeding on the main island, so this study represents the first attempt to do so. Our extrapolations suggest that cliff breeding represents the second most numerous breeding type for the WTTB in São Tomé, ranging from 189 to 756 pairs. Cliff nests represent a relevant portion of the breeding pairs in São Tomé, significantly outnumbering islet nests. Notwithstanding, islet and cliff nests fall short of the number of tree breeding pairs, which represent roughly 90% of the WTTB breeding pairs in São Tomé.

The adaptation to breed on trees can be partially due to pressures of ground predators, such as rats, cats, and crabs, which often devastate seabird colonies on oceanic islands (Burger & Gochfeld, 1991; Igual et al., 2006). Historically, WTTB were reported nesting on the ground at bases of trees or under vegetation in the main island (Jones & Tye 2006) but they no longer do this. By occupying arboreal cavities or bifurcations, WTTB effectively exploit vertical space, gaining a form of “predator refuge” that may enhance adult survival and breeding success in predator-invaded environments. In addition, tree breeding may represent an adaptive response to mitigate competitive pressures for nesting cavities in coastal and offshore habitats, where suitable sites are limited. By expanding into inland forested areas, individuals can reduce intraspecific and interspecific competition while maintaining access to sheltered nesting sites. Similar adaptive shifts in nesting habitat have been observed in other seabird populations facing limited coastal nesting opportunities (Burger & Gochfeld, 1991). The fact that the largest portion of the WTTB population on São Tomé Island breeds in trees makes them highly dependent on the availability of large cavity-bearing trees, such as *Erythrina* species. Consequently, the protection of forested habitats, especially shaded plantations, and the maintenance of mature trees suitable for nesting are crucial for ensuring the long-term persistence of the species on São Tomé. Although tree breeding is expected in areas with adequate forest cover, like Príncipe and Annobón Islands, São Tomé is the only proven location for tree breeding for this subspecies. These results suggest that forested habitats, especially agroforests, may play a more important role in harbouring breeding pairs than previously recognized. However, islets and coastal cliffs, remain key reproductive strongholds for the species, sustaining relative high concentrations of breeding pairs.

The results attained with this study encompass only the short dry season. It is evident that the actual breeding population will most likely be much larger than we report, especially taking into consideration that the WTTB breeds year-round, and that the largest peak is expected to occur during the main dry season. Thus, São Tomé might be the largest and most important colony of WTTB in the Atlantic. In the Western North Atlantic population only around 5,000 pairs are estimated to occur (Lee & Walsh-McGee, 2000). In Ascension Island, in Southern Atlantic, estimates range between 1,050 (Stonehouse 1962) and 2,200 pairs (Ashmole et al. 1994). Our estimates suggest that just the population that breeds in the small dry season in São Tomé could be twice the size of the Western North Atlantic global population or, more conservatively, half of that population. Our estimates suggest São Tomé holds 0.6% to 2.4% of the global population of the species, potentially classifying it as a globally important site for WTTB conservation, according to RAMSAR (Ramsar Convention Secretariat, 1971) and KBA criteria (Key Biodiversity Areas Partnership, n.d.).

Considering the size of São Tomé Island and its rugged terrain, it is hard to estimate what proportion of the tree nests might have been found. Furthermore, coastal cliffs with breeding pairs, had high concentrations of adults in flight. This was most prominent in Sete Ventos and Homem de Capa, where observations of high abundance of adults flying suggest larger colony sizes than what we were able to confirm as some individuals possibly were still in pairing and courtship, not yet having claimed a nesting cavity. Furthermore, other coastal cliff locations may potentially host nests. We suspect the coastal cliff of Ponta Baleia to harbour a much larger number of breeding pairs in contrast to only our one nest identified. Through observations of many individuals seen flying inland in addition to anecdotal reports by locals from Generosa, we suspect that the river valley of Contador River, characterized by steep cliffs, might host a significant number of breeding pairs since this area hosts ideal conditions for nesting WTTB. Our study resulted in nest numbers through different scenarios defining a baseline for future population estimates. Our extrapolations resulted in broader ranges of potential breeding numbers. These results varied significantly across habitats, with the highest potential nest numbers projected for inland nests, located in forests and agroforests, followed by coastal cliffs and finally the islets.

Our estimates highlight the challenges and uncertainties involving seabird census work and estimates in rugged, forested and offshore islet habitats. Tree breeding pairs estimates were problematic due to the topographic characteristics of the island interior. The rugged and densely vegetated terrain made it difficult to find nests and count birds. As for cliff and islet nesting pairs of WTTBs, accessing colonies presented itself a prominent obstacle. Determining the optimal timing of the year and of day to conduct surveys also played a significant role in exacerbating the difficulty in the population estimates. Estimating seabird populations, especially for species that breed year-round, is particularly challenging due to their continuous reproductive cycles, variable breeding events, and large interannual fluctuations, which can obscure true population dynamics and reduce the accuracy of population estimates (Frederiksen et al., 2025).

These estimates, however, must be interpreted with caution. Firstly, they assume that nest densities in the prospected areas are representative of the total available habitat. This assumption introduces uncertainty, particularly in forested habitats, where nest distribution may be highly uneven and estimates assume that tree nesting density in the prospected areas is representative of the entire potential inland breeding range. Since estimates were derived from nests recorded in prospected areas, rather than from standardized random transects, they may be biased and not portray the true reality of the Island interior. Secondly, WTTB often reuses existing nests or usurp those of conspecifics rather than seeking out new cavities (Schaffner, 1991). As a result, the number of nest numbers are most likely lower than the number of available cavities, meaning our extrapolations may overestimate actual breeding pairs. Thirdly, detection probability is variable across different habitats. Forested areas tended to have WTTB breeding in isolated nests spread throughout the region and not in colonies, this likely lead to greater under-detection than the small islets, where nest concentration and optimal breeding habitat were condensed in a small area. Additionally, results from viewpoints were likely influenced by topography, visibility, and time of day, with higher aggregations observed in the gentler slopes in the north and northwest compared to the rugged south, where the rugged terrain limited visibility.

Final remarks

This is the first study characterizing nesting of WTTB in São Tomé Island, laying a basis for future studies such as annual population size census in main breeding points, to build a robust foundation for future conservation plans.

WTTB in São Tomé face a diverse range of pressures that vary between cliff, islet, or tree nests. Overfishing, bycatch, invasive species, native predators, nest harvesting, and hunting impact all nesting types; however, islet nests appear to be the most vulnerable, particularly to marine debris and tropical storms. Cliff and tree nests are primarily affected by habitat degradation and loss. The threats identified in São Tomé largely mirror those reported for seabird populations worldwide (Lee & Walsh-McGehee, 2000; Dias et al., 2019). The increased vulnerability of islet breeding pairs highlights the need of implementing conservation measures in this nesting habitat, namely by offering them legal protection, since both Sete Pedras and Ilhéu de Santana remain outside the national network of protected areas (de Lima et al. 2022). This would not only benefit WTTB but other breeding seabirds (Jones & Tye 2006). Regulating human access, controlling invasive species and mitigating pollution are also imperative for WTTB conservation. Control of invasive mammals through trapping and baiting in the islets, mainly Ilhéu das Rolas which hosts a population of rats and cats that pose the most immediate threat to WTTB in that location. We reinforce that invasive species control is vital for the perpetuity of not only WTTB but the majority of seabirds. Nests on coastal cliffs also require protection from invasive predators, such as rats, and habitat disturbance, namely deriving from tourism and coastal development. We appeal to better coastal planning in areas with cliffs used for breeding exist. We suggest leaving a buffer between constructions and breeding sites in the attempt to not disrupt breeding cycles with human perturbations. Tree nests need mostly protection from habitat loss due to expansion of anthropogenic activities. Since tree breeding WTTB mainly rely on cavities in large trees, adequate forestry management is essential for the preservation of mature trees.

We suggest the designation of the key breeding areas such as Sete Pedras, Rolas, Santa Catarina and Homem de Capa as protected zones. In addition, we advise the implementation of regular annual monitoring programs to track population trends, breeding success, and emerging threats. We recommend the promotion of environmental education to reduce human disturbance, egg harvesting, and habitat loss. Together, these actions would provide a foundation for the long-term preservation of São Tomé’s unique seabird populations. These measures will not only safe-guard the survival of the species in São Tomé, but would also benefit other nesting seabirds, as they share the same coastal breeding locations and face similar threats.

Supplementary materials 1

Section A - Nest category and locations

Table A 1 - Number of nests confirmed in São Tomé Island and the four main Islets during observation points and active nest searches (Figure 6).

Location	Nests found (N_f)	Nest location
Abade	5	Tree
Dona Eugénia	1	Tree
CIAT - Potô	2	Tree
Monte Carmo	1	Tree
Monte Macaco	2	Tree
Morro Peixe	1	Tree
Ototó	1	Tree
Santa Fé	3	Tree
Santa Luzia	1	Tree
Santa Margarida	3	Tree
Uba Budo	5	Tree
Vila Madalena	2	Tree
Vista Alegre	5	Tree
Homem de Capa	1	Tree
Ponta Figo	1	Tree
Sete Ventos	3	Cliff
Buraco Pablo & surrounding	6	Cliff
Homem de Capa	20	Cliff
Ponta Baleia	1	Cliff
Ribeira Funda	5	Cliff
Santa Catarina Tunnel	16	Cliff
Ilhéu das Rolas	15	Islet
Ilhéu Santana	8	Islet
Sete Pedras	27	Islet
Ilhéu das Cabras	0	Islet
Total Tree nests	34	
Total Cliff nests	51	
Total Islet nests	50	
Total	135	

Section B - Questionnaires

Gustavo Marino

Concozuco *Phaethon lepturus*
Inquérito

Enunciado:
Olá!
O meu nome é Gustavo, sou da Universidade de Évora e estou a fazer um estudo sobre uma ave que existe aqui em São Tomé. Posso fazer-lhe algumas perguntas? As respostas que me der vão ser usadas para os meus estudos e podem vir a ser partilhadas em apresentações públicas ou publicações. Só participa se quiser e ninguém mais vai saber quem respondeu, vão ser anónimas e nenhuma das informações pessoais vai ser divulgada.

Pode ajudar-me com este estudo?

Dados do participante

Nome:____

Contacto:______________________________________

Nome da comunidade:_____________________________

Género: ☐ M ☐ F

Idade:________

Ocupação:______________________________________

Identificação da espécie

Conhece esta espécie? ☐ sim ☐ não

Qual o nome?____

Distribuição

Em que zona posso ver esta espécie?__________________________
____

Onde faz o ninho/cria?_____________________________________
____

Há algum sítio aqui perto onde tem ninho? Onde?______________
____

Sazonalidade

Tem o ano todo? ☐ sim ☐ não ☐ n/a

Se não, quando é que aparece?_______________________________
____

Em que altura do ano é que tem mais?_________________________
____

Em que meses do ano é que cria?_____________________________
____

Ameaças

- **5 Biological resource use**

Já comeu esta espécie? ☐ sim ☐ não ☐ n/a

Ainda come está espécie? ☐ sim ☐ não ☐ n/a

Já apanhou alguma vez esta espécie? ☐ sim ☐ não ☐ n/a

Ainda apanha? ☐ sim ☐ não ☐ n/a

Quantas vezes (por ano) é que apanha esta espécie?
____
____

Como é que apanha esta espécie?__________________________
____

Apanha adultos ou crias (bebes)? ☐ Adulto ☐ Cria ☐ n/a

Algum animal ataca esta espécie? ☐ sim ☐ não ☐ n/a

Se sim, qual?____

Alguma outra coisa que ameaça a vida desta espécie? ☐ sim ☐ não ☐ n/a

Se sim, qual é?______________________________________
____

As ações das pessoas é boa ou má para o concozuco? ☐ boa ☐ má ☐ n/a

Como é que é boa/má?____
____

Há 10 anos havia mais ou menos?______________________________
____

Notas:____

Section C - Observation point field sheet

Concozuco - *Phaethon lepturus*

Pontos de observação

Observador:____

Código: E – entrada S – saída

Comportamento: VP – Voo de passagem EN – Entrando em ninho
VC – Voo circular

Data/local/tempo de observação:

#	Código	Quantidade	Comportamento	Notas

CHAPTER II: Nesting Habitat and Threats to Breeding White-tailed Tropicbird *Phaethon lepturus ascensionis* in São Tomé Island

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Abstract

In São Tomé, the White-tailed Tropicbird (*Phaethon lepturus ascensionis*) breeds on a multitude of habitats. To gain a better understanding of the nesting ecology of the species, this study characterized 18 nests on islets, 38 on cliffs, and 14 on trees in forested areas. It also assessed threats and environmental drivers of tree nest selection at the landscape level. Islet and cliff nests were mainly in cavities with little to no vegetation, while tree nests were found, on average, 9 m above the ground in large coral trees (*Erythrina* sp.). Distance to the coast was the most relevant environmental variable to explain nest presence, showing a positive correlation indicating that pairs tended to avoid the coast when nesting in trees. All breeding pairs are highly affected by overfishing and bycatch followed by invasive species, egg harvesting, and oil spills. Islet nests revealed the highest levels of threat, additionally being highly impacted by tropical storms. Furthermore, cliff nests are impacted by coastal development and tree nests are threatened by deforestation, agriculture, and urban development. These results highlight the need to protect forests, regulate fishing, control invasive species and mitigate human disturbance to safeguard the White-tailed Tropicbird in São Tomé.

Key Words: Breeding, habitat selection, threats, tropicbird, São Tomé and Príncipe

Introduction

Understanding why a species selects its habitat is vital for conservation. For seabirds nesting on oceanic islands, this is critical as these species are often prone to threats during this phase of their life cycle (Dias et al., 2019). Seabirds are one of the most threatened avifaunal groups (BirdLife International, 2018). The combination of high nest density in colonies and limited mobility on the ground make pelagic birds prone to predation (Croxall et al., 2012), rendering the reproductive period the most vulnerable of their life cycle (Leal et al., 2016). Information on habitat selection and threats during breeding is thus vital for conservation planning (Sutherland et al., 2004).

The White-tailed Tropicbird (*Phaethon lepturus*, hereafter WTTB) is a long-lived, pelagic seabird that breeds in isolated tropical islands (Orta, 1992; Nelson, 2005).The WTTB is highly plastic when it comes to nest site selection, using a wide variety of nesting sites, that differ in the type of structures and on the location (Lee & Walsh-McGee, 1998). It can be loosely colonial, or form small to medium-sized colonies, of up to 1,000 pairs (Nelson, 2005). Nests are bare substrate, as parents do not bring materials to the nest (Schaffner, 1991). Nests can be in caves and in rock crevices on inaccessible cliffs, on shallow depressions in the sand beneath boulders or ledges, or on trees or in tree hollows, being the only tropicbird species to exhibits tree nesting behaviour (Lee & Walsh-McGee, 1998). Nest-site selection in this species has been suggested to rely primarily on concealment and protection rather than the specific choice of rock or vegetation type (Lee & Walsh-McGee, 1998). Accordingly, breeding success is highly dependent on shade and shelter from rain and sun exposure (Nelson, 2005), and on concealment from predators (Mejías et al., 2017).

São Tomé, a volcanic island 255 km off the west coast of Africa (Ceríaco et al., 2022), seems to hold a rather significant population of WTTB. The first human settlement on the island was established in the late fifteenth century, when it was found by Portuguese sailors (Muñoz-Torrent et al., 2022). Like in many oceanic islands, human colonization has led to habitat modification, hunting and the introduction of species that might pose a significant risk to native biodiversity. The introduction of mammalian species such as the Mona Monkey (*Cercopithecus mona*), African Civet (*Civettictis civetta*), Least Weasel (*Mustela nivalis*), several species of rodent, as well as domestic and feral cats, dogs, and pigs, have been identified as serious potential threats to native biodiversity (Dutton, 1994). These animals can easily access nests on the ground and, in some cases, even high up in trees or cliffs, thus posing a significant risk to breeding success. Native species can also threaten breeding seabirds. Such is the case of large land crabs (e.g., *Johngarthia weileri*) that can predate chicks in accessible nests, possibly affecting fledgling success (Rocha, 2022). In addition to these pressures, WTTB also face human harvesting, as its meat is often consumed on the island, and particularly at risk from adventurous kids (Ricardo de Lima, pers. comms.). Although WTTB is currently “Least Concern” on the IUCN Red List, the species is believed to be declining, mainly due to predation by invasive alien species at its nesting sites (IUCN, 2025).

The WTTB subspecies found in São Tomé, *Phaethon lepturus ascensionis*, has been reported nesting in crevices and on exposed or shaded ledges in rocky islets and coastal cliffs. In addition, pairs in São Tomé have been reported nesting on the ground in thick grass tunnels (Nadler, 1993) and in large hollow trees in the rainforest (Naurois, 1973), some being recorded relatively far from the coast and up to 1,050 m (Atkinson et al., 1994). Despite the recognized importance of this population, detailed information on its nesting ecology is missing, hindering its conservation. Thus, the main objective of this study is to improve our knowledge about the nesting habitat of WTTB on São Tomé Island. Specifically, we assessed: (1) nest-site characteristics; (2) the threats and stressors affecting this breeding population; and (3) site selection of tree nests at landscape level.

Methods

Study area

São Tomé is an 857 km^2 volcanic island (Ceríaco et al., 2022). Rising up to 2,024 m a.s.l at Pico de São Tomé, this profoundly eroded volcanic landscape hosts vertical slopes, tight ridges and extensive talus deposits (Ceríaco et al., 2022). The topography of the island is characterized by a basalt platform sloped towards the sea in the north-east and a steep mountain range with deep river gorges and volcanic peaks and plugs in the centre and south-west (Jones et al., 1991). São Tomé is surrounded by various islets, the largest of which is Ilhéu das Rolas, located to the south and intersected by the Equator. Other important islets include Cabras (to the northeast), Santana (to the east) and Sete Pedras (a conglomerate of rocky outcrops to the southeast), all of which have been identified as potential or confirmed breeding sites for the WTTB (Monteiro et al., 1997).

A preliminary visit of two weeks took place from late September to mid-October, but most fieldwork was done from mid-January to late February, coinciding with the small dry season that occurs between December and February that has been described as a peak of abundance of breeding pairs on Príncipe Island (Rocha, 2022).

Nest site characterization

Field measurements

Nests were identified by active search in target areas mentioned in past studies (e.g., Monteiro et al., 1997) and in areas with high WTTB abundance identified during observation points or from questionnaires (detailed in Chapter I) .

Nests were considered active when an adult was observed or remained inside a cavity for more than five minutes, thus distinguishing active nests from sites being prospected. This interval was chosen based on our observations during fieldwork. Nests resulting from anecdotal reports but that were not visually confirmed as active, were also considered for this study if the report referred to adults entering and exiting the cavity more than once in less than 24 hours. Identified nests were georeferenced using a GPS and photographed using a Canon 80d with a 75-300 mm f/4-5,6 II lens.

Each nest was classified in three main types: islet, coastal cliff or tree (Monteiro et al., 1997). Due to the morphological characteristics of Ilhéu das Rolas southern cliff, all nests located there were classified as coastal cliff nests. Variables measured for each nest location included nest height from water or ground level; cavity orientation; and the presence of any disturbance or threat. For nests located on cliffs and on islets (Table 4), additional variables included: rock stability; nest type (cavity or exposed); vegetation cover surrounding the nest; distance to the nearest neighbouring nest; and cliff height. For tree nests (Table 5), we recorded: tree condition (alive or dead); tree species; diameter at breast height (DBH), nest type (cavity or branch bifurcation); total tree height; height of first branching; epiphyte cover surrounding the nest; and canopy cover percentage.

Table 4 - Variables used to characterize coastal cliff and islet nests, including measurement method (description), variable type and units used.

Variables	Description	Type	Units
Rock type	Obtained from Geological Chart (Munhá et al., 2006)	Categorical	Subaerial or submarine flows of alkaline basalts. Phonolitic/trachyphonolitic flows. With or without interbedded lahar deposits or fluvial gravel beds. Subaerial or submarine mantle basalts
Rock stability	Estimate of rock stability by attributing a stability condition class	Categorical	1 – Stable 2 – Eroding 3 – Crumbling
Nest type	Determined by direct observation if crevice or is exposed	Categorical	CA - Cavity EX - Exposed
Distance to nearest nest	Estimate of distance to nearest nest by attributing a distance class during field observation	Categorical	1 - <2m 2 - 2m/5m 3 - >5m
Vegetation cover	Estimate of vegetation cover around the nest by attributing a cover class estimate by direct field observation	Categorical	1 – None 2 -Sparse 3 – Moderate
Orientation	Use of digital compass	Categorical	N,S,W,E
Height of cliff/rock face	Field estimate and when possible, calculated with the angle obtained with a manual hypsometer and applying the formula height = base length / cos (angle)	Continuous	Meters
Height of nest	Field estimate and when possible, calculated with the angle obtained with a manual hypsometer and applying the formula height = base length / cos (angle)	Continuous	Meters

Table 5 - Variables used to characterize tree nests, including measurement method (description), variable type and units used.

Variables	Description	Type	Units
Species	Identified by two experienced observers in the field following the WCPV and APG IV taxonomy (POWO 2025)	Categorical	ID down to species level when possible
Tree status	Defined by observer by direct observation	Categorical	1 – Alive 2 – Dead
Nest type	Determined by direct observation if cavity or bifurcation	Categorical	CA – Cavity BI – Bifurcation
Epiphyte density	Estimate of epiphyte density in the trunk and branches of the tree done by the observer	Categorical	1 – None 2 – Sparse 3 – Moderate 4 – Dense
Orientation	Measured using digital compass	Categorical	N,S,W,E
Height of the tree	Field estimate and when possible, calculated with the angle obtained with a manual hypsometer and applying the formula height = base length / cos (angle)	Continuous	Meters
Height of first branching	Field estimate and when possible, calculated with the angle obtained with a manual hypsometer and applying the formula height = base length / cos (angle)	Continuous	Meters
Height of Nest	Field estimate and when possible, calculated with the angle obtained with a manual hypsometer and applying the formula height = base length / cos (angle)	Continuous	Meters
Diameter (DBH)	Calculated by dividing by π the circumference of the tree at breast height measured with a tape measure (± 1 cm)	Continuous	Meters
Canopy cover	Average of four measurements of canopy cover percentage taken with a convex densiometer, in the direction of the main cardinal points from the sampling point.	Continuous	Percent of canopy cover (%)

Threats

Information regarding threats faced by the different breeding pair types of WTTB was obtained using questionnaires (chapter 1, S1, section B) and annotations of field work observations. All observed direct threats and stressors that are impacting, have impacted or may impact White-tailed Tropicbirds were registered and compiled (S2, section C). Questionnaires were used to collect information on biological resource use, such as the consumption of WTTBs, capture rates and methods, as well as the developmental stages of targeted individuals. In addition, the impact of invasive and other problematic species such as potential predators, was also inquired.

Landscape-level measurements

To assess site selection for 34 tree nests at landscape level, we generated 34 random points inside the prospected areas, while ensuring a minimum distance of 10 m between each point to emulate natural distances between large trees.

Nest and random locations were characterized using QGIS (QGIS Development Team 2025a) and a data set on altitude, slope, ruggedness, topographic position index, mean annual precipitation, land use, distance to coast and orientation (Soares et al., 2020 - Table 6). The variable altitude was derived from a 90 meters resolution Digital Elevation Model (DEM) and slope, ruggedness, topographic position index (TPI) being calculated from the DEM raster (Soares et al., 2020). Mean annual precipitation was obtained by digitizing the island's mean annual precipitation map in millimetres (Soares et al., 2020). We extracted information on altitude, slope, ruggedness, topographic position index and mean annual precipitation by using the QGIS plugin "sample raster values" (QGIS Development Team 2025b) and intersecting our nest and random points with each raster. Land use information, based on visual interpretation of 2014 satellite images (Soares et al., 2020) was obtained by intersecting the land use shapefile with the point shapefile. Distance to the coast was calculated by using the function "v.distance" from the plugin GRASS GIS Processing Provider v. 2.12.99 (GRASS Development Team 2025) to determine the minimal linear distance in meters between the points and the nearest point on the coast line. Orientation was obtained from the elevation DEM by generating an aspect map using the "Raster Analysis – Aspect" QGIS GDAL algorithm provider (QGIS Development

Team 2025c). Aspect represents the compass direction that each slope faces, expressed as an azimuth in degrees from north, with pixel values ranging from 0° to 360°.

Table 6 - Variables used to characterize tree nest locations and random points at the landscape level, including measurement method (description), variable type and units used.

Variables	Description	Type	Units
Altitude	Digital Elevation Model based on NASA's NASA Global DEM (NASADEM) with 90 meters of horizontal resolution with an error of 1.5m	Continuous	Meters
Distance to Coast	Minimum linear distance from each pixel to the nearest point on the coastline	Continuous	Meters
Slope	Slope calculated from the Digital Elevation Model	Continuous	Decimal degrees
Ruggedness	Ruggedness calculated from the Digital Elevation Model	Continuous	-
Mean Annual precipitation	Vectorised map obtained from a map with 30 years compiled data throughout the island, later smoothed with a circular filter of 20 pixels radius (Soares et al., 2020)	Continuous	Millimetres
Orientation	Orientation calculated from the Digital Elevation Model	Continuous	Decimal degrees
Topographic Position Index (TPI)	Index representing the position of each pixel regarding the mean elevation of a neighbourhood within a 0.05º radius (Soares et al., 2020)	Categorical	Class 1- Flat Plain Areas Class 2 – Valleys Class 3 - Middle Slope Class 4 - Upper Slope Class 5 - Ridges
Land use	Land-use map derived from satellite imagery, field data, the 1970 historical land-use map, and a military map (Soares et al., 2020).	Categorical	Class 1 – Native forest Class 2 – Secondary forest Class 3 – Shade plantation Class 4 – Non-forested areas

Data analysis

All statistical analysis were made using R v. 4.5.1 GUI 1.82 High Sierra build in RStudio v. 2025.09.0+387 (R Development Core Team, 2025).

To model nest presence, we considered the following environmental variables: altitude, distance to the coast, slope, ruggedness, mean annual precipitation, orientation, topographic position index (TPI), and land use (Table 6).

Exploratory analysis

We conducted an exploratory analysis to assess the distribution and relationships among the explanatory variables. Categorical variables (orientation, land use and topography) were converted to factors. Multicollinearity was evaluated using Spearman’s rank correlation coefficient. Correlations were visualized in a correlogram. All variables were retained for subsequent analyses. To inspect variability and identify potential outliers, boxplots were produced for each environmental variable using the “ggplot2” package (Wickham, 2025). Although some variables showed skewed distributions, no extreme outliers were detected, and therefore none removed.

Statistical modelling

Nest presence was analysed using binomial generalized linear models (GLMs). An initial full model including all explanatory variables was fitted, after which collinear variables were removed based on VIF results. The final model was then used as the basis for model selection.

All possible combinations of the remaining explanatory variables without interactions, were generated and ranked using Akaike’s Information Criterion corrected for small sample size (AICc), using the “dredge” function from the “MuMIn” package (Barton, 2025). Variables associated with nest presence were identified using model averaging across the subset of models with ΔAICc < 2.

Threats

We applied the IUCN Threats Classification Scheme (IUCN, 2022) to each WTTB nesting type in São Tomé. Each relevant threat was categorized according to timing, as either “Only in the past and unlikely to return,” “In the past but now suspended and likely to return,” “Ongoing,” or “Only in the future.”, according to the standard time frame of three generations or ten years, whichever is longer, and up to a maximum of 100 years. Impact was also ascertained by determining scope (whole, majority or minority) and severity (very rapid, rapid, slow, fluctuating or negligible declines). The severity was assessed within the scope of each given threat. Each threat was classified using the IUCN Threat Impact Scoring System (Version 1.0), which applies additive scores and defined thresholds under the IUCN Threat Classification Scheme (IUCN, 2022).

Results

Nest site characterization

Islets

Eight islet nests were identified and characterized in Ilhéu Santana and ten at Sete Pedras. All islets are composed of alkaline basalt formed by subaerial flow. Five nests in Ilhéu Santana (e.g. Section E, Fig. D1) and one in Sete Pedras (Fig. D2) were Stable (class 1), while the remaining three in Ilhéu Santana and eight in Sete Pedras (e.g. Fig. D3, Fig. D4, Fig. D5) were Eroding (class 2), and one in Sete Pedras was Crumbling (class 3) (Fig. 7A). One nest in Ilhéu Santana was Exposed (Fig. D6), while all others were in cavities (Fig. 7B). Two nests in Ilhéu Santana, and four in Sete Pedras were between 2 and 5 m to the closest nest (class 2) while the remaining were more than 5 m away from the nearest nest (class 3) (Fig. 7C). In Sete Pedras, no nest had vegetation cover (class 1), while in Ilhéu Santana three had no vegetation cover, two had sparse vegetation cover (class 2), and three had moderate vegetation cover (class 3) (Fig. 7D). In Ilhéu Santana, two nests were facing north-east, one east, one south-east and four south. In Sete Pedras, three nests were facing north, one north-west, two south, and four south-west. Rock height ranged from 6 to 40 m with a mean of 26 m, while nest height ranged from 4 to 25 m with a mean of 13 m (Fig. 8). Rock height in Ilhéu Santana ranged from 25 to 40 m with a mean of 30.6 m and in Sete Pedras it ranged from around 4 m to 25 m with a mean of 22.6 m. Nest height in Ilhéu

Santana ranged from around 5 to 20 m with a mean of 15.0 m and in Sete Pedras it ranged from around 4 m (Fig. D2) to 25 m with a mean of 11.9 m.

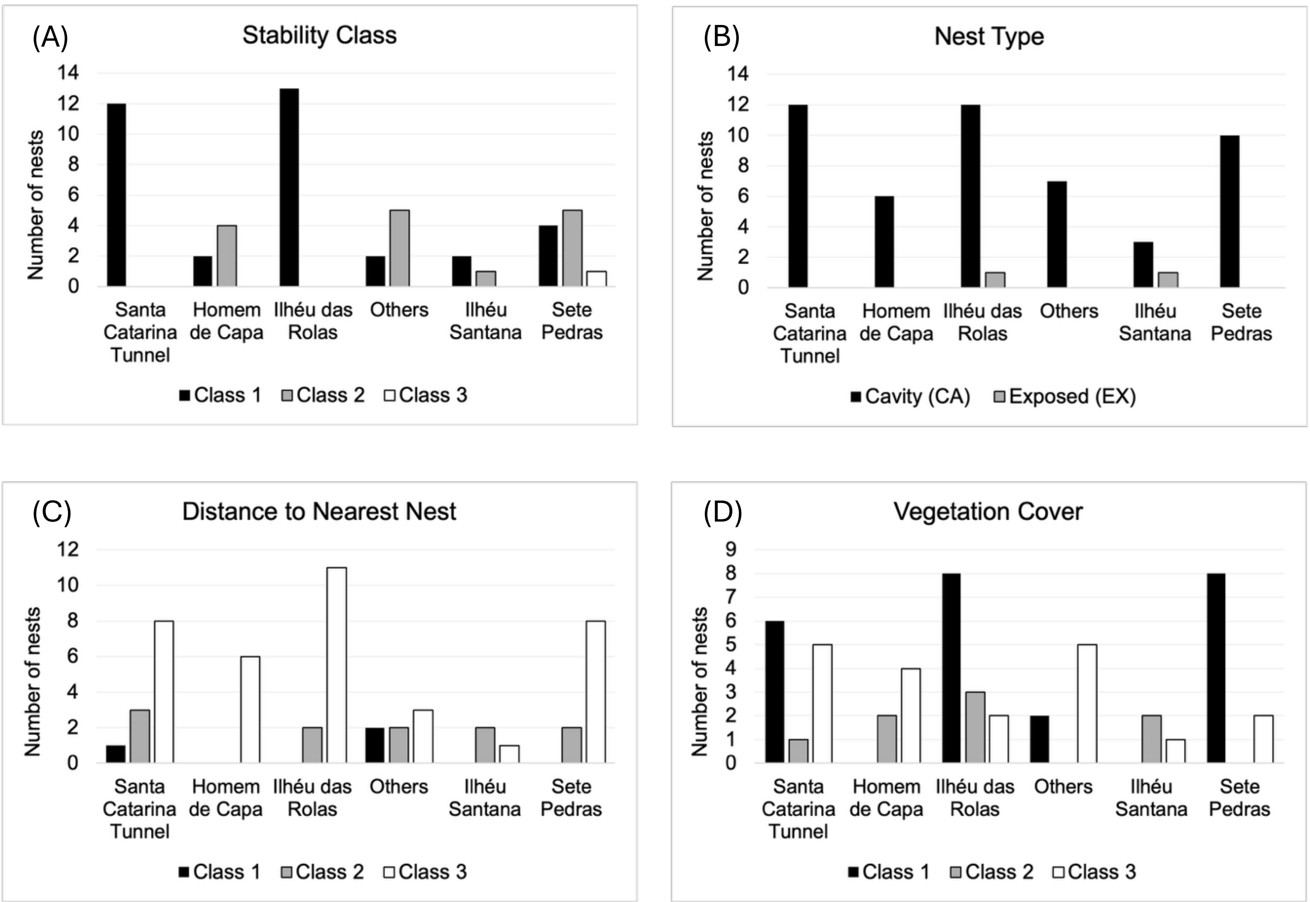


Figure 7 - Characteristics of nests on cliffs and islets around São Tomé Island: (A) Stability class of the rock face: class 1 – Stable; class 2 – Eroding; class 3 - Crumbling. (B) Nest type: Cavity (CA) and Exposed (EX). (C) Distance to the nearest nest: class 1 – less than 2 meters; class 2 – between 2 and 5 meters; class 3 – more than 5 meters. (D) Vegetation cover of the entrance of the nest or the nest: class 1 – None; class 2 – Sparse; class 3 – Moderate. n=80.

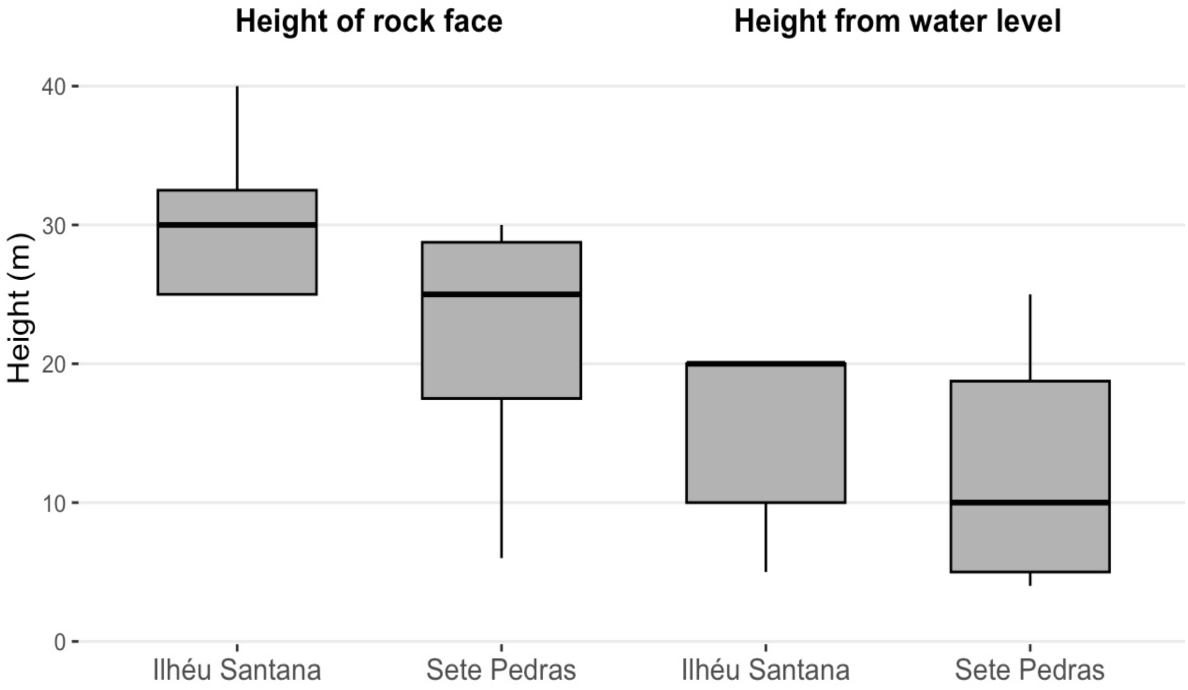


Figure 8 - Height above water level of the rock face and of the nests on islets around São Tomé Island. n=80

Coastal Cliffs

Twelve nests were identified and characterized in the cliffs close to Santa Catarina tunnel, five in Homem de Capa, thirteen in Ilhéu das Rolas, three in an unnamed small beach close to Buraco Pablo (hereafter BP beach), four in Buraco Pablo and one Sete Ventos (the last three locations referred as “Others” in Fig. 7). Buraco Pablo (e.g. Fig. D7) and BP beach are composed of block-and-ash-flow while the remaining locations are composed of alkaline basalt formed by subaerial flow, with Santa Catarina tunnel presenting lahar deposits intercalated in the basaltic lavas (e.g. Fig. D8). All nests in Santa Catarina tunnel (e.g. Fig. D9), BP beach (e.g. Fig. D10, Fig. D11), Ilhéu das Rolas (e.g. Fig. D12, Fig. D13) and one in Homem de Capa were Stable (class 1) and the remaining Eroding (class 2; Fig. 7A; e.g. Fig. D14, Fig. D15). One nest in Ilhéu das Rolas was Exposed (Fig. 7B) while all others were in cavities. One nest in Santa Catarina tunnel and two in Buraco Pablo (Fig. D16) were less than 2 m (class 1) to the closest nest while three in Santa Catarina tunnel, two in PB beach and two nests in Ilhéu das Rolas were between 2 and 5 m to the closest nest (class

2). The remaining were more than 5 m away from the nearest nest (class 3) (Fig. 7C). Six nests in Santa Catarina tunnel, two in PB beach and eight nests in Ilhéu das Rolas had no vegetation cover (class 1). One nest in Santa Catarina tunnel, two in Homem de Capa and three nests in Ilhéu das Rolas had Sparse (class 2) vegetation, while remaining nests had Moderate (class 3; e.g. Fig. D17, Fig. D18) vegetation cover (Fig. 7D). In Santa Catarina tunnel, one nest was facing north and three facing south. PB beach had one facing north and two facing northwest. In Ilhéu das Rolas two were facing south and one facing south-east. One nest in Homem de Capa was facing northwest, two nests facing west and two facing southeast. Buraco Pablo had two nests facing southeast, one facing south and one west. The nest located in Sete Ventos faced northeast. The cliffs ranged from 12.9 meters to 60 meters with a mean of 32.6 meters (Fig. 9A). Nest heights ranged from 2 meters to 40 meters with a mean of 19.4 meters (Fig. 9B). Cliff and nest height in Santa Catarina tunnel ranged from around 35 m to 50 m with a mean of 44.1 m and ranged from around 19 m to 35 m with a mean of 25.0 m respectively. Cliff and nest height in Homem de Capa ranged from around 13 m to 25 m with a mean of 19.7 m and ranged from around 6 m to 20 m with a mean of 14.4 m respectively. Cliff and nest height in Ilhéu das Rolas ranged from around 20 m to 40 m with a mean of 31.2 m and ranged from around 10 m to 25 m with a mean of 17.7 m respectively. Cliff and nest height of Others ranged from around 20 m to 60 m with a mean of 27.4 m and ranged from around 2 m to 40 m with a mean of 17.3 m respectively.

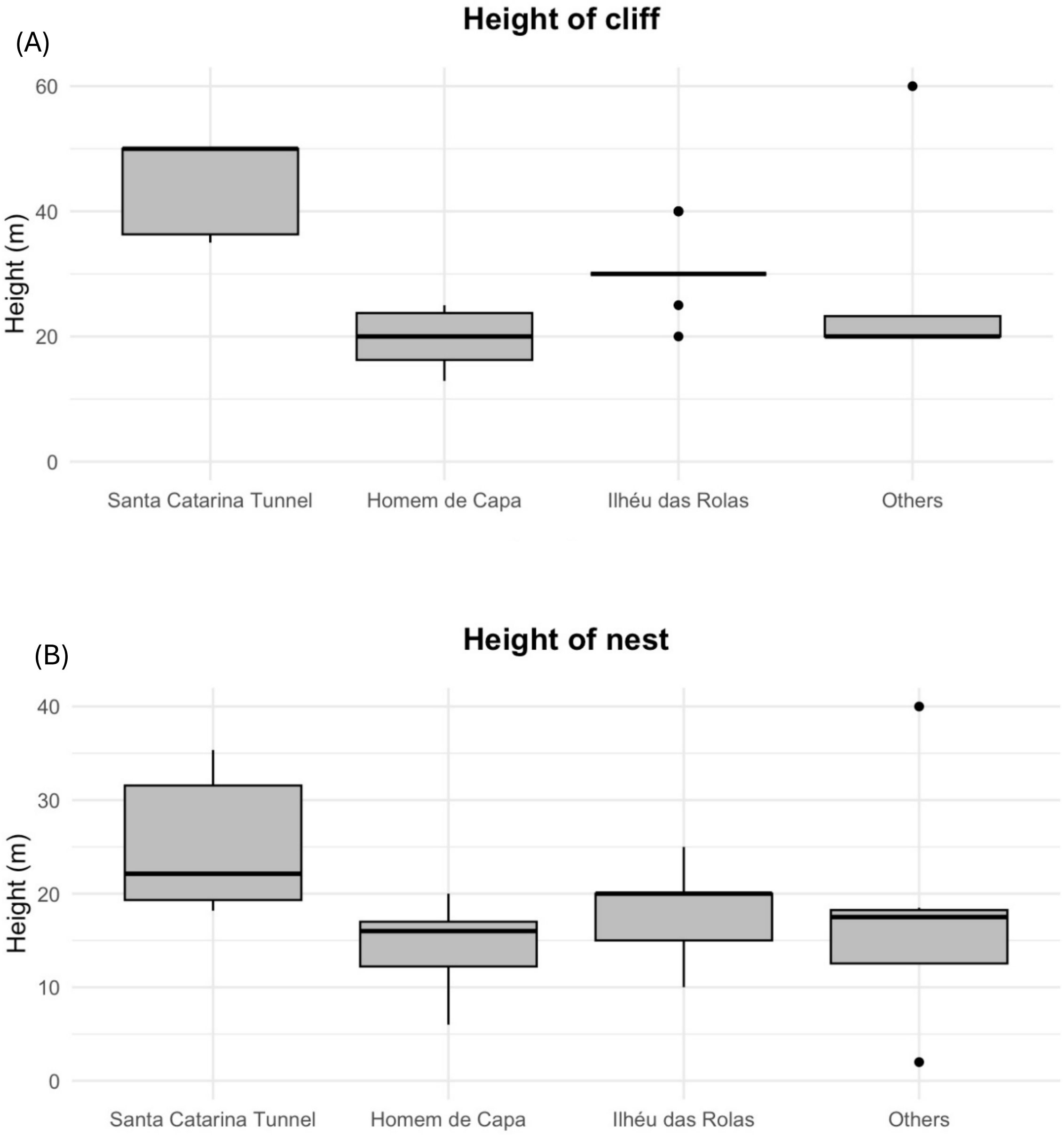


Figure 9 - (A) Box-plot of the height in meters of the cliffs with nests and (B) the height of the nests from ground level. “Others” refer to BP beach, Buraco Pablo and Sete Ventos. n=38.

Tree

Two nests were characterized in Potó, two in Santa Margarida, two in Monte Macaco, two in Santa Fé, five in Vista Alegre and one Santa Luzia. One nest in Santa Margarida was on a strangler fig (*Ficus* sp.), remaining nests were on coral trees (*Erythrina* sp.), namely *E. fusca* and *E. poeppigiana*. All nests were in living trees. One nest in Potó (Fig. D19) and one Santa Margarida were in bifurcations while all others were in cavities (e.g. Fig. D20, Fig. D22). One nest in Potó had dense epiphyte cover (class 4) (Fig. D19), all others had no (class 1) or sparse vegetation cover (class 2) (Fig. 10, e.g. Fig. D22). Nest orientation varied, from north (n=3), northeast (n=3), east (n=1), south (n=2), southwest (n=3) to northwest (n=1 – we were unable to determine the orientation of one). Tree height ranged from around 20 m to 62 m with a mean of 33.9 m (Fig. 11A). Height of first branching ranged from around 4 m to 20 m with a mean of 12.5 m (Fig. 11B). Nest heights ranged from around 9 m to 23 m with a mean of 16.3 m (Fig. 11C). Diameter at breast height (DBH) ranged from around 3 m to 22 m with a mean of 5.4 m (Fig. 11D).

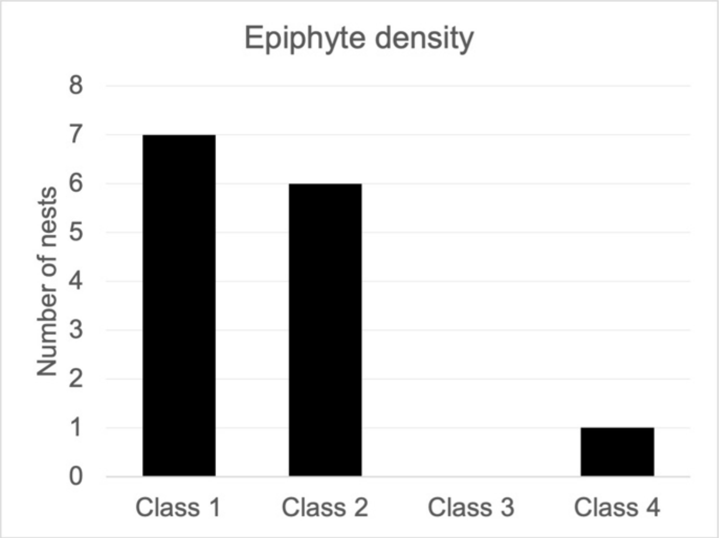


Figure 10 - Characteristics of tree nests in São Tomé: Epiphyte density on the tree: class 1 – None; class 2 – Sparse; class 3 – Moderate; class 4 – Dense. n=14

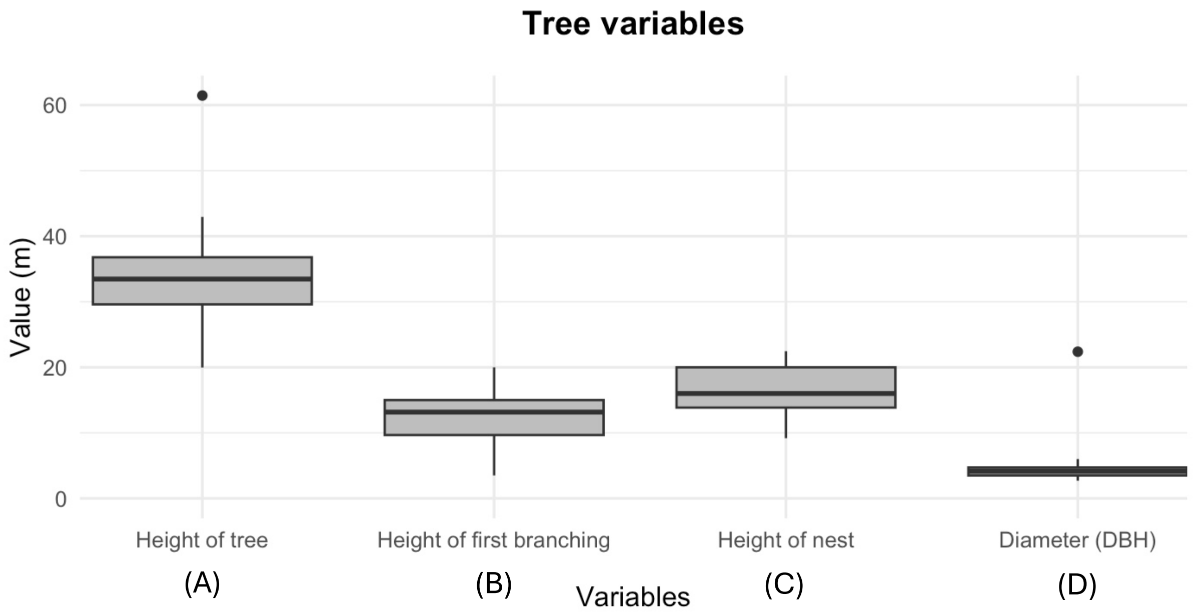


Figure 11 - Box-plot of the (A) height in meters of the trees with nests; (B) height of the first branching; (C) height of the nests from ground level; and (D) diameter at breast height (DBH) in meters. n=14.

Landscape variables

A total of 68 locations were analysed, comprising of 34 nest locations and 34 random points representing available nesting trees. Exploratory analysis revealed strong correlations ($|\rho| \geq 0.7$) between altitude and ruggedness with other topographic variables (Fig. 2A1). Based on these results, and further confirmed by VIF values, altitude and ruggedness were excluded from further analyses to reduce multicollinearity.

Out of all models, six were the best fit for explaining the variables under study (ΔAICc < 2; Table 7). The best-ranked model (AICc = 76.9, $\omega = 0.297$) included distance to coast as the sole explanatory variable, which had a positive effect on nest presence, indicating it was the most important predictor in this analysis. Distance to coast was included in all top-ranked models, whereas land use, orientation, rainfall, slope and TPI appeared less consistently across models (Table 7).

Table 7 - Summary table of the top six models (out of 256) that explain nest presence as a function of the environmental variables under study, obtained using the dredge function and ranked by AICc. The table shows the AICc differences from the best model (Δ) and the Akaike weight (ω) for each model.

Distance	Land use	Orientation	Rainfall	Slope	TPI	AICc	Δ	ω
0.0004611						76.9	0	0.297
0.0004733	0.4536					77.9	1.02	0.178
0. 0004509			-0.0002341			78.1	1.23	0.160
0. 0004517				-0.02996		78.3	1.45	0.144
0.0004741		0.1496		-		78.8	1.93	0.113
0.0004621					-0.09972	78.9	2.06	0.106

Applying “model averaging” across all models generated by the “dredge” function showed as well that the only variable predicting tree nests is distance to coast, with a relative importance of 1.0 (Table 8). All remaining variables showed low relative importance (< 0.25), suggesting weak or no support for their effects on nest presence, with TPI not being included in the model.

Table 8 – Relative importance, model-averaged coefficients, and adjusted standard errors of the explanatory variables predicting nest presence, based on model averaging across all best models.

	Relative variable importance	Model-averaged coefficient	Adjusted standard deviation
Distance to coast	1.00	0.0004618515	0.0001183
Landuse	0.20	0.04535577296	0.2654
Rainfall	0.18	-0.0002340515	0.000137
Slope	0.16	-0.0299637914	0.01821
Orientation	0.13	0.1496016304	0.1173

Threats

Ten threats were identified for the islet breeding pairs (Table 9 and B1). As medium impact we listed direct persecution, egg harvesting, hunting for consumption, the presence of invasive species and leakage from fuel tanks or boat sinking, while loss of prey due to overfishing and bycatch of individuals; marine debris and ghost fishing gear; and tropical storms had high impact.

Table 9 - Threats to islet nesting pairs during the breeding**.** Impact score of threats following the IUCN Threat Classification Scheme. These threats are evaluated based on their timing (past, ongoing, or future), scope (proportion of the population affected), severity (intensity of impact), and associated stress (e.g., habitat loss, reduced breeding success). Impact colour coding: Red – High impact; Orange – medium impact; Yellow – Low impact; Blue – Negligible or No impact.

ISLET NEST THREATS			**SCORE**
3. Energy production & mining	3.1. Oil & gas drilling - offshore drilling		1
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.1. Intentional Use: subsistence/small scale- Egg harvesting, hunting for consumption	7
		5.4.4. Unintentional effects: large scale – Loss of prey species due to overfishing, bycatch	9
		5.4.5. Persecution/control– Species perceived as competition	7
6. Human intrusions & disturbance	6.1. Recreational activities - recreational fishing		6
8. Invasive & other problematic species, genes & diseases	8.1. Problematic invasive species	8.1.2. Named species – *Rattus rattus, Rattus norvegicus*	7
	8.2. Problematic native species	8.2.2. Named species - *Johngarthia weileri, Cardisoma armatum, Milvus migrans parasitus, Tyto alba thomensis*	5
9. Pollution	9.2. Industrial & military effluents	9.2.1. Oil spills – leakage from fuel tanks, boat sinking	6
	9.4. Garbage & solid waste - Marine debris and ghost fishing gear		9
11. Climate change & severe weather	11.4. Storms & flooding - Tropical storms		8

Eleven threats were identified for the coastal cliff breeding pairs (Table 10 and Table B2). Egg harvesting, hunting for consumption, the presence of invasive species and leakage from fuel tanks or boat sinking, marine debris and ghost fishing gear; and Tropical storms were found to have medium impact. Loss of prey species due to overfishing, bycatch of individuals, marine debris and ghost fishing gear have a high impact.

Table 10 - Threats to coastal cliff nesting pairs during the breeding**.** Impact score of threats following the IUCN Threat Classification Scheme. These threats are evaluated based on their timing (past, ongoing, or future), scope (proportion of the population affected), severity (intensity of impact), and associated stress (e.g., habitat loss, reduced breeding success). Score colour coding in the end of the table. Impact colour coding: Red – High impact; Orange – medium impact; Yellow – Low impact; Blue – Negligible or No impact

COASTAL CLIFF NEST THREATS			SCORE
1. Residential & commercial development	1.3. Tourism & recreation areas – coastal tourist resorts		5
3. Energy production & mining	3.1. Oil & gas drilling - offshore drilling		1
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.1. Intentional Use: subsistence/small scale- Egg harvesting, hunting for consumption	7
		5.4.4. Unintentional effects: large scale – Loss of prey species due to overfishing, bycatch	9
		5.4.5. Persecution/control– Species perceived as competition	4
6. Human intrusions & disturbance	6.1. Recreational activities - recreational fishing		4
8. Invasive & other problematic species, genes & diseases	8.1. Problematic invasive species	8.1.2. Named species – *Rattus rattus, Rattus norvegicus, Cercopithecus mona, Civettictis civetta, Mustela nivalis, Felis catus*	7
	8.2. Problematic native species	8.2.2. Named species - *Johngarthia weileri, Cardisoma armatum, Milvus migrans parasitus, Tyto alba thomensis*	5
9. Pollution	9.2. Industrial & military effluents	9.2.1. Oil spills – leakage from fuel tanks, boat sinking	6
	9.4. Garbage & solid waste - Marine debris and ghost fishing gear		9
11. Climate change & severe weather	11.4. Storms & flooding - Tropical storms		7

Thirteen threats were identified for the tree breeding pairs (Table 11 and Table B3). Villages, egg harvesting, hunting for consumption, the presence of invasive species and marine debris and ghost fishing gear were found to have medium impact. Loss of prey species due to overfishing, bycatch of individuals, marine debris and ghost fishing gear have a high impact.

Table 11 - Threats to tree nesting pairs during the breeding. Impact score of threats following the IUCN Threat Classification Scheme. These threats are evaluated based on their timing (past, ongoing, or future), scope (proportion of the population affected), severity (intensity of impact), and associated stress (e.g., habitat loss, reduced breeding success). Impact colour coding: Red – High impact; Orange – medium impact; Yellow – Low impact; Blue – Negligible or No impact

TREE NEST THREATS			SCORE
1. Residential & commercial development	1.1. Housing & urban areas - Villages		7
2. Agriculture & aquaculture	2.1. Annual & perennial non-timber crops	2.1.2. Small-holder farming - Horticulture, small scale agroforestry systems	5
		2.1.3 Agro-industry farming - Oil palm plantation, cocoa plantation, coffee plantation	5
3. Energy production & mining	3.1. Oil & gas drilling - offshore drilling		1
4. Transportation & service corridors	4.1. Roads & railroads - Primitive roads, logging roads, secondary roads		5
5. Biological resource use	5.3. Logging & wood harvesting	5.3.3. Unintentional effects: subsistence/small scale – Falling of trees with cavities	5
	5.4. Fishing & Harvesting Aquatic Resources	5.4.1. Intentional Use: subsistence/small scale – Egg harvesting, hunting for consumption	6
		5.4.4. Unintentional effects: large scale – Loss of prey species due to overfishing, bycatch	9
8. Invasive & other problematic species, genes & diseases	8.1. Problematic invasive species	8.1.2. Named species – *Cercopithecus mona, Rattus rattus, Rattus norvegicus, Mustela nivalis, Felis catus*	6
	8.2. Problematic native species	8.2.2. Named species - *Milvus migrans parasitus, Tyto alba thomensis*	4
9. Pollution	9.2. Industrial & military effluents	9.2.1. Oil spills – leakage from fuel tanks, boat sinking	6
	9.4. Garbage & solid waste– Marine debris and ghost fishing gear		9
11. Climate change & severe weather	11.4. Storms & flooding- Tropical storms		4

Discussion

The three nest types were associated with cavities with sparse to no vegetation cover. Some threats were common to all nest types, but some were type- specific, and threat levels also varied between nest type. Nevertheless, our results indicate that islet nests are the most threatened.

Nest site characterization

All nest types were found in cavities typically with sparse to no vegetation. These results match previous studies that indicate a preference by WTTB for nesting in sheltered locations (e.g. Philips, 1985; Schaffner, 1991). Cavities provide the eggs and chicks protection against environmental extremes, such as severe rain or excess sun exposure (Philips, 1985). This is essential since high sun exposure has been shown to be one of the main environmental factors that limits breeding success the most, leading to embryonic death or nest abandonment by heat-stressed adults (Prys-Jones & Peet, 1980; Nelson, 2005), since tropicbirds are unable to gular-flutter to thermoregulate (Stonehouse, 1962). In addition to providing protection from environmental factors, nesting in cavities also reduces predation risk by providing concealment. Studies have found that breeding success increases in cavities were introduced predators occur (Mejías et al., 2017). Cavity nesting makes the WTTB less accessible to large predators and enable progenitors to fight off smaller ones, such as rats or land crabs (Igual et al., 2006). Historically, WTTB in São Tomé were documented nesting exposed on the ground (Nadler, 1993), reinforcing that the present preference for cavity nesting is likely driven by predation pressures. In addition, the sparse vegetation cover at the entrances of the nests matches what is described for other locations (e.g. Stonehouse, 1962; Schaffner, 1991; Raine et al., 2020). Less vegetation cover may provide better visibility for incubating adults, allowing them to detect threats earlier and reduce predation risk. Rat predation has been showed to increase with vegetation cover in shearwater nests (Igual et al., 2006). Additionally, the absence of vegetation facilitates the approach in flight, as the WTTB is clumsy on land due to its short tarsi. Easier flight access likely makes less vegetated cavities preferable (Catry et al., 2009). In contrast, in Round Island (Indian Ocean), dense vegetation around the entrance is often used to conceal the nest (Burger & Gochfeld, 1991). These differences evidence the plasticity of nest site selection in WTTB, suggesting a focus on concealment and protection over substrate type.

The rocky substrate of the islet and cliff locations, formed by basaltic and block-and-ash flows, are rich in cavities (Munhá et al., 2006), which are suitable for WTTB nesting. In addition, WTTB tendo to display site fidelity (Phillips, 1987; Leal et al., 2016) and depending on the location, the breeding pairs frequently reuse nests (Stonehouse, 1962), especially in areas with limited nest options in relation to the breeding population (Lee & Walsh-McGee, 1998). Such fidelity may explain part of our findings. Because exposed nests are more susceptible to environmental conditions and experience higher predation rates, individuals nesting in cavities generally achieve greater reproductive success (Mejías et al., 2017). Consequently, these birds are more likely to return to the same cavity in subsequent breeding seasons, whereas individuals nesting in exposed location that experience nest failure are more inclined to relocate and attempt nesting elsewhere.

Nest height differed between sites: islet breeders used variable heights, while mainland nests were higher, likely due to stronger predation pressures. Similar to our results, previous studies indicated that WTTB prefer to nest in higher and steeper cliffs (Burger & Gochfeld, 1991), which are more secluded and are less accessible to land predators (Mejías et al., 2017). Tree nests showed similar patterns likely in response to similar pressures.

Islet and cliff nests displayed large variability in rock stability, vegetation cover, and orientation. Cliff sites offered greater elevation and stability than islets. Rock stability of cliff nests was higher than that of islet nests likely due to islets being exposed to more intense adverse weather due to their location. Exposed nests occurred only on remote islets, where fewer predators and disturbances make such sites viable for this type of nest (Mejías et al., 2017).

WTTB is the only species of the genus to nest in tree hollows, likely in response to predation by ground predators and competitive pressures associated with nest site availability. For this subspecies, confined to the south Atlantic, reports of it nesting in trees are limited only to São Tomé (e.g. Naurois 1973; Monteiro et al., 1997). This study is the first attempt of a comprehensive characterization of tree nesting in WTTB. Almost all of these were characterized in cocoa shade plantations, except for two in and around communities. Since shade plantations are composed of large shading trees interspaced by a lower substrate of cocoa plants, large trees tended to be scattered. Trees used for nesting were relatively tall and mature, with the lowest one measuring around 20 meters. Only two nests were in branch bifurcations, and both of these had significant canopy cover, conferring protection from the sun and rain, which are known to be vital for reproductive success (Philips, 1987). Most nests were found in coral trees, both *Erythrina fusca* and *E. poeppigiana*, with only one nest recorded on a strangler fig (*Ficus* sp.). This pattern suggests a strong preference for *Erythrina*, a genus characterized by large, soft trunks and highly abundant in São Tomés' shade plantations (de Lima et al., 2014). This tree species is a fast-growing tree that are also known to be prone to form hollows (Strauß et al., 2018).The observed preference for taller stands is likely linked to the fact that older and more mature trees are more cavity prone than younger and smaller trees as they have been exposed longer to external factors such as fungal infections that can lead to cavity formation (Fu et al., 2024). The nests and the first branching were located at considerable heights. High cavities in relative isolated trees confer more security against predation, as they are harder to access by humans or other land predators and a certain degree of crown isolation confers better protection from arboreal threats (Cockle et al., 2011). Since there are less arboreal predators, nesting in large isolated trees reduces predation rates and increases breeding success (Malan & Hagens, 2009). Although we observed dead trees with available cavities, and having collected anecdotical reports of WTTB nesting in dead trees, all nests we found were in large living trees. This could partially be linked to living stands offer more structural stability and security when faced with adverse climatic events such as tropical storms.

Tree nest site selection at landscape level

Of all the environmental variables, distance to the coast was clearly the best to explain the occurrence of tree nests at landscape level. This is most likely due to higher concentrations of people and the relative absence of large trees with cavity potential near the coast comparative to more remote tree heavy inland areas. The higher number of tree nests identified in the more accessible northern and northeastern parts of the island may have influenced this result. These areas are characterized by greater urbanization and human settlements close to the shoreline, as well as by the absence of coastal cliffs with nesting potential. Much of the surrounding land, up to 800 meters a.s.l., has been transformed for cultivation, consisting mainly of cocoa and coffee shade plantations (Jones & Tye, 2006). These shade plantations, which include a high abundance of coral trees to shading the man crops (de Lima et al., 2014), are located further inland, likely attracting WTTB away from the coast in search of suitable trees. This interpretation is supported by a nest found in a large remote southern coastal Kapok tree (*Ceiba pentandra*), showing that distance becomes irrelevant when absence of disturbance and suitable large trees are available.

Threats

The most severe and immediate threat to all breeding types of nests was the loss of prey species due to overfishing, and the risks of death by bycatch, marine debris and ghost fishing. Large- and small-scale fisheries have been proven to contribute to species decline (Dias et al., 2019). Overfishing is a top threat in marine ecosystems, leading to population declines through starvation, heavily impacting seabirds (Grémillet et al., 2018). São Tomé, in addition to having waters with low productivity, has intensive fishing to support the local market and a fishing agreement with the European Community, leading to the depletion of its fish stocks (Carneiro, 2012). The threat of overfishing is associated with mortality of seabirds due to bycatch, with more than 60% of the species affected also proven to be affected by bycatch (Dias et al., 2019). Industrial fishing employing longline and trawl fishing pose a severe threat to seabirds when foraging at sea (Dias et al., 2019). In addition to industrial fishing, small scale fishing also has a proven impact on seabird populations (Lewison et al., 2004). In São Tomé, fishermen reported that WTTB often swallow the bait and hook of their hand lines, sometimes swooping in and catching the bait mid-flight when the line is cast. Almost half the fishermen that we talked to reported this event and stated they would eat, offer or sell the bird. Marine debris including plastics and ghost fishing is a relatively recent whose effects on seabird are not yet fully understood (Dias et al., 2019). Our findings indicate this threat as high impact due to the risk of mortality linked to ingestion of marine plastic debris (Roman et al., 2019) and mortality of trapped individuals by entanglement (Croxall et al., 2012).

Threats with medium impact on all nest types included invasive species, egg and bird harvesting, and oil spill events. Invasive species such as rats are a major threat to seabird species globally (Holmes et al., 2019) and in São Tomé, three species are present, with *Rattus rattus* and *R. norvegicus* representing a threat to breeding avifauna (Melo et al., 2025). In addition, *Cercopithecus mona* was recently documented as a potential key nest predator in Príncipe Island (Guedes et al., 2025). Hunting and egg harvesting also pose significant threats to seabird populations, especially coastal ones (Dias et al., 2019). Despite this global trend, a previous study in São Tomé hinted that the inaccessibility of nesting areas might mitigate this risk (Jones & Tye 2006). Findings from Príncipe suggest otherwise, evidencing harvesting as a major contributor to population decline (Bollen et al., 2018; Rocha, 2022). Although consumption varied across the island, our results also suggest that human consumption is still highly prevalent. Oil spills were a notable global threat to seabirds in the 1970s and 1980s (Dias et al.,2019) that have since significantly decreased (Roser, 2018). Despite this, the threat of mineral resource exploration in the oceans of São Tomé is likely to increase since large offshore petroleum deposits were discovered in the 1990s (de Lima et al., 2022). Additionally, as hundreds of oil tankers sail close to São Tomé (ITOPF, 2003), the risk of spills or leaks is constant.

Threats with low impact included problematic native species. Native species can become problematic to breeding seabirds when predation pressures are high, namely when ecological changes promote population increases. We observed high numbers of *Milvus migrans parasitus* flying around areas with high densities of WTTB nests and, in a couple of instances, mock charging at adults entering or exiting cavities. *Tyto alba thomensis* was also recorded as a regular presence at Sete Pedras (Ricardo de Lima pers. comm.). Additionally, large land crabs are proven WTTB egg and chick predators (Phillips, 1987; Schaffner,1991). In Príncipe, the crab *Johngarthia weileri* was observed predating chicks (Rocha 2022), and in São Tomé it was present in all visited islets, except for Ilhéu Santana, which was dominated by the crab *Cardisoma armatum.* Ilhéu das Cabras did not host any WTTB nests and was had the largest concentration of large land crabs of all islets. This overabundance of crabs might have made the islet unsuitable for WTTB nesting, since it used to be abundant at this location (Bocage, 1889; Frade, 1959; Naurois, 1973).

Final remarks

This is the first study characterizing nesting of WTTB in São Tomé Island, laying a basis for future studies and conservation plans. Future studies should encompass other periods of the year, particularly the large dry season, to gain a more accurate understanding of population size and phenology. Additional visits to the islets, namely Cabras, Gabado, and Quixibá, are recommended to assess the current breeding status at these sites. Furthermore, surveys targeting inland cliffs would clarify if breeding occurs in these areas. Surveying native and secondary forests is demanding but would be useful to evaluate their relevance for nesting. In-depth studies addressing potential threats are also necessary, particularly to quantify the impacts of exotic and problematic native species, as well as the effects harvesting.

The vulnerability of islet nests calls for urgent conservation measures, namely by offering legal protection, since both Sete Pedras and Ilhéu de Santana remain outside the national network of protected areas (de Lima et al. 2022). Regulating human disturbance, controlling invasive species, and mitigating pollution is also imperative for WTTB conservation. Because tree nests rely on cavities in large trees, the preservation of mature trees is also important. We recommend full legal protection for the islets where nests occur, in specific Sete Pedras, that hosts not only WTTB, but also other breeding seabirds (Jones & Tye 2006). We also appeal to better coastal planning in areas with WTTB nests, namely by leaving a buffer between constructions and breeding sites. Awareness campaigns, especially with young boys, might also be relevant to help reduce direct pressure and promote the WTTB as a flagship species for the conservation of marine ecosystems and fisheries.

Supplementary material 2

Section A - Exploratory analysis

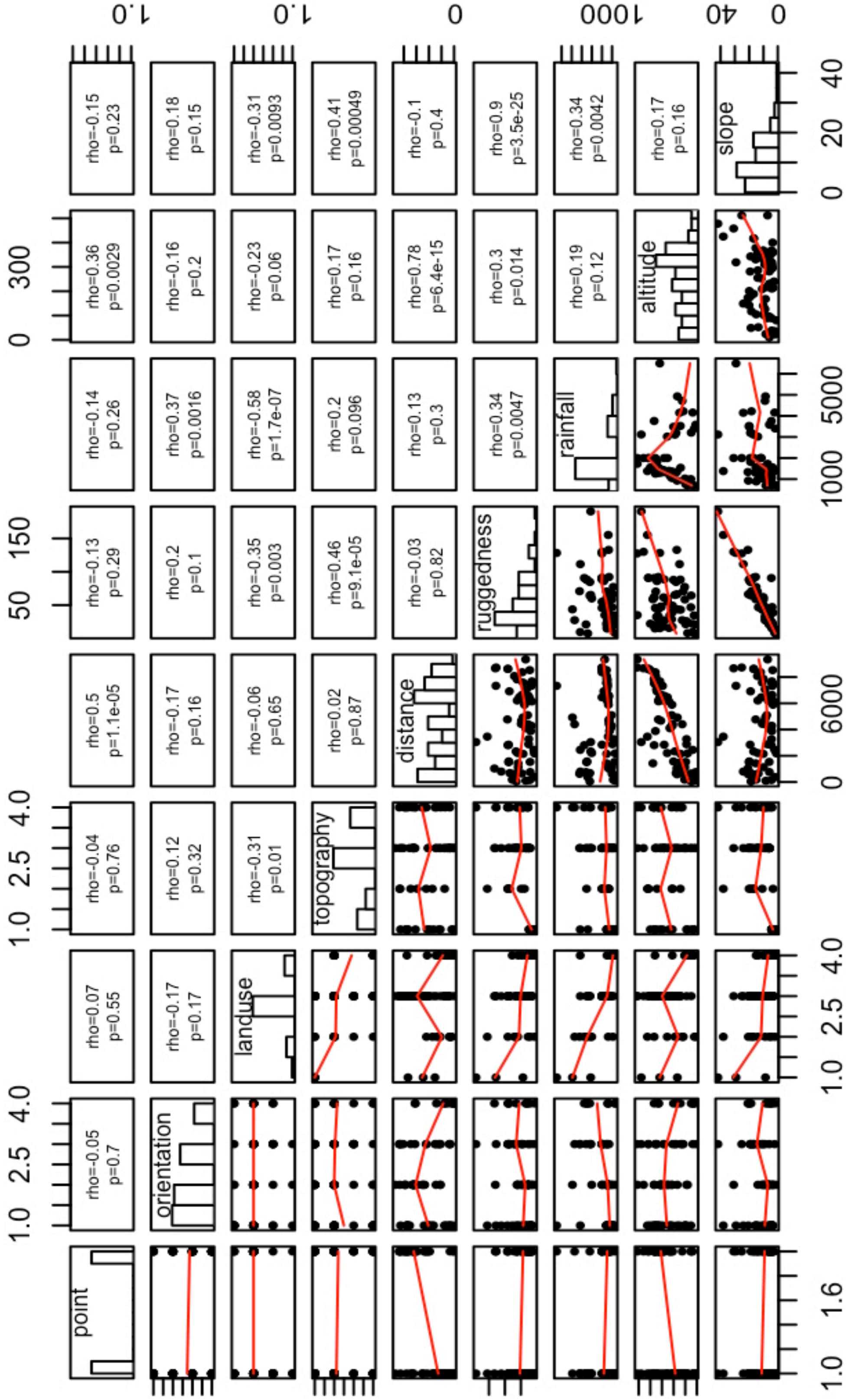


Figure 2A 22 - Correlogram showing Spearsman correlation coefficients among environmental variables and the response variable. Altitude and ruggedness were highly correlated (r > 0.7) with other predictors and were therefore excluded from further analyses

Section B - Threat classification scheme

Table B 1 - Threats to islet nesting pairs during the breeding . Summary of threats following the IUCN Threat Classification Scheme. These threats are evaluated based on their timing (past, ongoing, or future), scope (proportion of the population affected), severity (intensity of impact), and associated stress (e.g., habitat loss, reduced breeding success).

Threats			Timing	Stresses			Scope	Severity
3. Energy production & mining	3.1. Oil & gas drilling - offshore drilling		Only in the future	1. Ecosystem stresses	1.2. Ecosystem degradation		Unknown	Unknown
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.1. Intentional Use: subsistence/small scale – Egg harvesting, hunting for consumption	Ongoing	2. Species Stresses	2.1. Species mortality 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.4. Unintentional effects: large scale – Loss of prey species due to overfishing, bycatch	Ongoing	2. Species Stresses	2.1. Species mortality 2.3. Indirect Species Effects	2.3.8 Othe r- Impact on food source	Whole (>90%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.5. Persecution/control– Species perceived as competition	Ongoing	2. Species Stresses	2.1. Species mortality		Minority (<50%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
6. Human intrusions & disturbance	6.1. Recreational activities – recreational fishing		Ongoing	2. Species Stresses	2.3. Indirect Species Effects	2.3.8 Other – Impact on food source	Majority (50-90%)	Causing or likely to cause relatively slow but significant declines (<20% over 10 years or three generations; whichever is the longer)
8. Invasive & other problematic species, genes & diseases	8.1. Problematic invasive species	8.1.2. Named species – *Rattus rattus, Rattus norvegicus*	Ongoing	2. Species Stresses	2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
8. Invasive & other problematic species, genes & diseases	8.2. Problematic native species/diseases	8.2.2. Named species - *Johngarthia weileri, Cardisoma armatum, Milvus migrans parasitus, Tyto alba thomensis*	Ongoing	2. Species Stresses	2.2 Species Disturbance 2.3 Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause relatively slow but significant declines (<20% over 10 years or three generations; whichever is the longer)
9. Pollution	9.2. Industrial & military effluents	9.2.1. Oil spills – leakage from fuel tanks, boat sinking	Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.1. Species mortality 2.3. Indirect Species Effects	2.3.8 Other – Impact on food source	Whole (>90%)	Unknown
9. Pollution	9.4. Garbage & solid waste– Marine debris and ghost fishing gear		Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.1. Species mortality 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success 2.3.8 Other – Impact on food source	Whole (>90%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
11. Climate change & severe weather	11.4. Storms & flooding – Tropical storms		Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Majority (50-90%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)

Table B 2 - Threats to coastal cliff nesting pairs during the breeding . Summary of threats following the IUCN Threat Classification Scheme. These threats are evaluated based on their timing (past, ongoing, or future), scope (proportion of the population affected), severity (intensity of impact), and associated stress (e.g., habitat loss, reduced breeding success).

Threats			Timing	Stresses			Scope	Severity
1. Residential & commercial development	1.3. Tourism & recreation areas– coastal tourist resorts		Ongoing	1. Ecosystem stresses	1.2. Ecosystem degradation		Minority (<50%)	Causing or likely to cause relatively slow but significant declines (<20% over 10 years or three generations; whichever is the longer)
3. Energy production & mining	3.1. Oil & gas drilling - offshore drilling		Only in the future	1. Ecosystem stresses	1.2. Ecosystem degradation		Unknown	Unknown
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.1. Intentional Use: subsistence/small scale- Egg harvesting, hunting for consumption	Ongoing	2. Species Stresses	2.1. Species mortality 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.4. Unintentional effects: large scale – Loss of prey species due to overfishing, bycatch	Ongoing	2. Species Stresses	2.1. Species mortality 2.3. Indirect Species Effects	2.3.8 Other – Impact on food source	Whole (>90%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.5. Persecution/control– Species perceived as competition	Ongoing	2. Species Stresses	2.1. Species mortality		Minority (<50%)	No declines
6. Human intrusions & disturbance	6.1. Recreational activities – recreational fishing		Ongoing	2. Species Stresses	2.3. Indirect Species Effects	2.3.8 Other – Impact on food source	Minority (<50%)	unknown
8. Invasive & other problematic species, genes & diseases	8.1. Problematic invasive species	8.1.2. Named species – *Rattus rattus, Rattus norvegicus, Cercopithecus mona, Civettictis civetta, Mustela nivalis, Felis catus*	Ongoing	2. Species Stresses	2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
8. Invasive & other problematic species, genes & diseases	8.2. Problematic native species	8.2.2. Named species - *Johngarthia weileri, Cardisoma armatum, Milvus migrans parasitus, Tyto alba thomensis*	Ongoing	2. Species Stresses	2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause relatively slow but significant declines (<20% over 10 years or three generations; whichever is the longer)
9. Pollution	9.2. Industrial & military effluents	9.2.1. Oil spills – leakage from fuel tanks, boat sinking	Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.1. Species mortality 2.3. Indirect Species Effects	2.3.8 Other- Impact on food source	Whole (>90%)	Unknown
9. Pollution	9.4. Garbage & solid waste– Marine debris and ghost fishing gear		Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.1. Species mortality 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success 2.3.8 Other – Impact on food source	Whole (>90%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
11. Climate change & severe weather	11.4. Storms & flooding- Tropical storms		Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)

Table B 3 - Threats to tree nesting pairs during the breeding**.** Summary of threats following the IUCN Threat Classification Scheme. These threats are evaluated based on their timing (past, ongoing, or future), scope (proportion of the population affected), severity (intensity of impact), and associated stress (e.g., habitat loss, reduced breeding success).

Threats			Timing	Stresses			Scope	Severity
1. Residential & commercial development	1.1. Housing & urban areas-Villages		Ongoing	1. Ecosystem stresses	1.2. Ecosystem degradation		Minority (<50%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
2. Agriculture & aquaculture	2.1. Annual & perennial non-timber crops	2.1.2. Small-holder farming - Horticulture, small scale agroforestry systems	Ongoing	1. Ecosystem stresses	1.2. Ecosystem degradation		Minority (<50%)	Causing or likely to cause relatively slow but significant declines (<20% over 10 years or three generations; whichever is the longer)
2. Agriculture & aquaculture	2.1. Annual & perennial non-timber crops	2.1.3 Agro-industry farming - Oil palm plantation, cocoa plantation, coffee plantation	Ongoing	1. Ecosystem stresses	1.2. Ecosystem degradation		Minority (<50%)	Causing or likely to cause relatively slow but significant declines (<20% over 10 years or three generations; whichever is the longer)
3. Energy production mining	3.1. Oil & gas drilling - offshore drilling		Only in the future	1. Ecosystem stresses	1.2. Ecosystem degradation		Unknown	Unknown
4. Transportation & service corridors	4.1. Roads & railroads - Primitive roads, logging roads, secondary roads		Ongoing	1. Ecosystem stresses	1.2. Ecosystem degradation		Minority (<50%)	Causing or likely to cause relatively slow but significant declines (<20% over 10 years or three generations; whichever is the longer)
5. Biological resource use	5.3. Logging & wood harvesting	5.3.3. Unintentional effects: subsistence/small scale – Falling of trees with cavities	Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.2. Species Disturbance		Minority (<50%)	Causing or likely to cause relatively slow but significant declines (<20% over 10 years or three generations; whichever is the longer)
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.1. Intentional Use: subsistence/small scale – Egg harvesting, hunting for consumption	Ongoing	2. Species Stresses	2.1. Species mortality 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause rapid declines (20–30% over 10 years or three generations; whichever is the longer)
5. Biological resource use	5.4. Fishing & Harvesting Aquatic Resources	5.4.4. Unintentional effects: large scale – Loss of prey species due to overfishing, bycatch	Ongoing	2. Species Stresses	2.1. Species mortality 2.3. Indirect Species Effects	2.3.8 Other – Impact on food source	Whole (>90%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
8. Invasive & other problematic species, genes & diseases	8.1. Problematic invasive species	8.1.2. Named species – *Cercopithecus mona, Rattus rattus, Rattus norvegicus, , Mustela nivalis, Felis catus*	Ongoing	2. Species Stresses	2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause rapid declines (20–30% over 10 years or three generations; whichever is the longer)
8. Invasive & other problematic species, genes & diseases	8.2. Problematic native species	8.2.2. Named species - *Milvus migrans parasitus, Tyto alba thomensis*	Ongoing	2. Species Stresses	2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Unknown
9. Pollution	9.2. Industrial & military effluents	9.2.1. Oil spills – leakage from fuel tanks, boat sinking	Only in the future	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.1. Species mortality 2.3. Indirect Species Effects	2.3.8 Other – Impact on food source	Whole (>90%)	Unknown
9. Pollution	9.4. Garbage & solid waste– Marine debris and ghost fishing gear		Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.1. Species mortality 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success 2.3.8 Other – Impact on food source	Whole (>90%)	Causing or likely to cause very rapid declines (>30% over 10 years or three generations; whichever is the longer)
11. Climate change & severe weather	11.4. Storms & flooding- Tropical storms		Ongoing	1. Ecosystem stresses 2. Species Stresses	1.2. Ecosystem degradation 2.2. Species Disturbance 2.3. Indirect Species Effects	2.3.7. Reduced Reproductive Success	Minority (<50%)	Causing or likely to cause negligible declines

Table B 4 - Threats impact scores following the IUCN Threat Impact Scoring System (version 1.0). Impact colour coding: Red – High impact; Orange – medium impact; Yellow – Low impact; Blue – Negligible or No impact

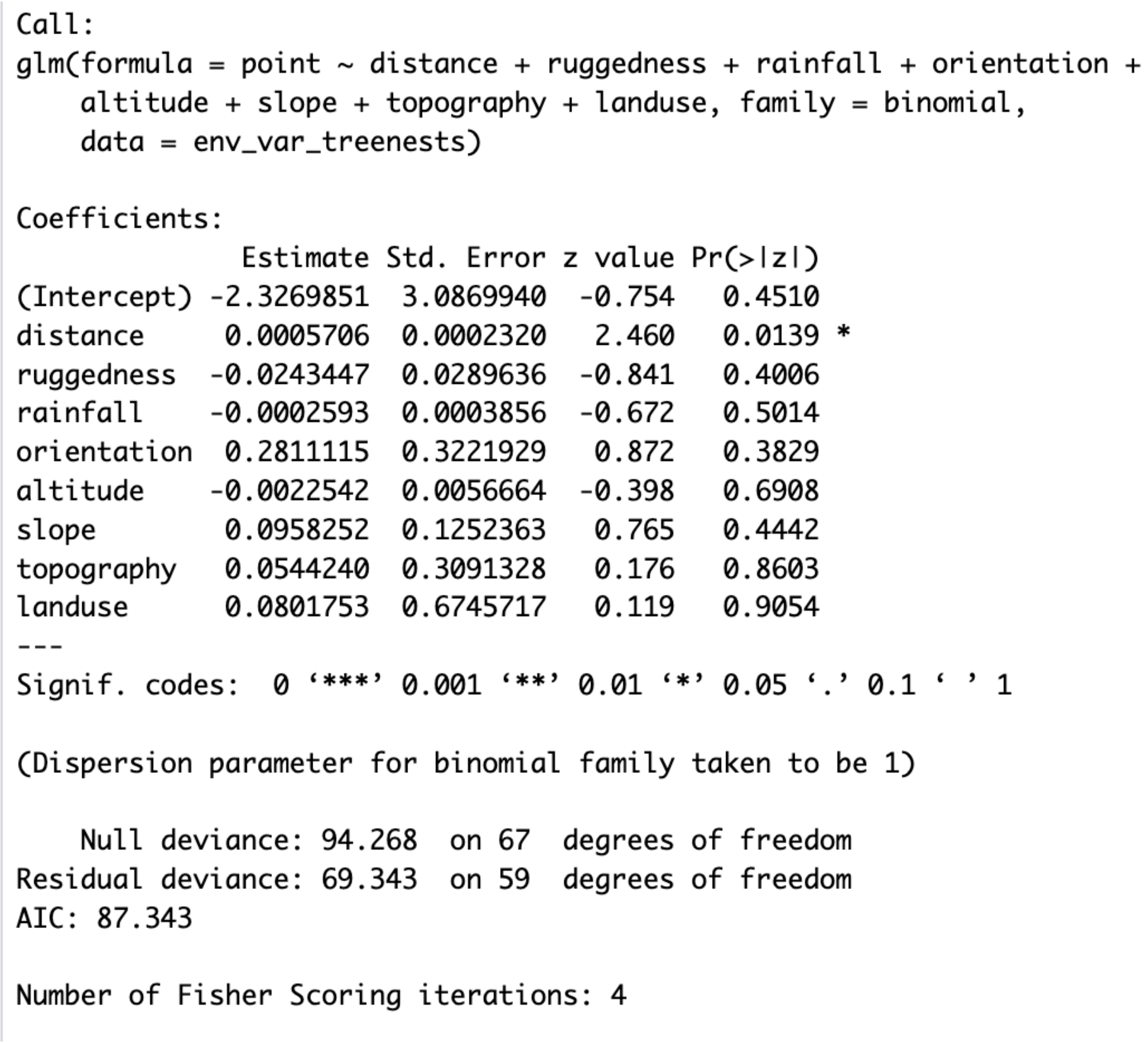
TREE impact scores				
Threat	**Timing**	**Scope**	**Severity**	**Score**
1.1	3	1	3	7
2.1.2	3	1	1	5
2.1.2	3	1	1	5
3.1	1	0	0	1
4.1	3	1	1	5
5.3.3	3	1	1	5
5.4.1	3	1	2	6
5.4.4	3	3	3	9
8.1.2	3	1	2	6
8.2.2	3	1	0	4
9.2.1	3	3	0	6
9.4	3	3	3	9
11.4	3	1	0	4
CLIFF impact scores				
1.3	3	1	1	5
3.1	1	0	0	1
5.4.1	3	1	3	7
5.4.4	3	3	3	9
5.4.5	3	1	0	4
6.1	3	1	0	4
8.1.2	3	1	3	7
8.2.2	3	1	1	5
9.2.1	3	3	0	6
9.4	3	3	3	9
11.4	3	1	3	7
ISLET impact scores				
3.1	1	0	0	1
5.4.1	3	1	3	7
5.4.4	3	3	3	9
5.4.5	3	1	3	7
6.1	3	2	1	6
8.1.2	3	1	3	7
8.2.2	3	1	1	5
9.2.1	3	3	0	6
9.4	3	3	3	9
11.4	3	2	3	8

Section C - Rscripts

```
# 1. Convert categorical into factors
env_var_treenests$point <- as.factor(env_var_treenests$point)
env_var_treenests$orientation <- as.factor(env_var_treenests$orientation)
env_var_treenests$landuse <- as.factor(env_var_treenests$landuse)
env_var_treenests$topography <- as.factor(env_var_treenests$topography)

# 2. Functions for panel
panel.cor <- function(x, y, digits=2, prefix="", cex.cor=0.6, ...) {
  # Se ambas categóricas, não calcula correlação
  if (is.factor(x) & is.factor(y)) {
    txt <- ""
  } else if (is.factor(x) | is.factor(y)) {
    # Uma categórica e uma contínua: Spearman com rank
    xnum <- ifelse(is.factor(x), as.numeric(x), x)
    ynum <- ifelse(is.factor(y), as.numeric(y), y)
    test <- cor.test(xnum, ynum, method="spearman")
    txt <- paste0("rho=", round(test$estimate,2), "\n", "p=", signif(test$p.value,2))
  } else {
    # Ambas contínuas: Spearman
    test <- cor.test(x, y, method="spearman")
    txt <- paste0("rho=", round(test$estimate,2), "\n", "p=", signif(test$p.value,2))
  }
  usr <- par("usr"); on.exit(par(usr))
  par(usr = c(0,1,0,1))
  text(0.5, 0.5, txt, cex=cex.cor)
}

panel.smooth2 <- function(x, y, col="black", bg=NA, pch=16, cex=0.7,
col.smooth="red", ...) {
  # Jitter se categórica
  if (is.factor(x)) x <- as.numeric(x) + runif(length(x), -0.2, 0.2)
  if (is.factor(y)) y <- as.numeric(y) + runif(length(y), -0.2, 0.2)
  points(x, y, pch=pch, col=col, bg=bg, cex=cex)
  ok <- is.finite(x) & is.finite(y)
  if (any(ok)) lines(lowess(x[ok], y[ok], f=2/3), col=col.smooth, lwd=1)
}

panel.hist <- function(x, ...) {
  usr <- par("usr"); on.exit(par(usr))
  par(usr = c(usr[1:2], 0, 1.5))
  if (is.factor(x)) {
    counts <- table(x)
    y <- counts / max(counts)
    rect(1:length(counts)-0.4, 0, 1:length(counts)+0.4, y, col="white", ...)
    axis(1, at=1:length(counts), labels=names(counts), cex.axis=0.7)
  } else {
```

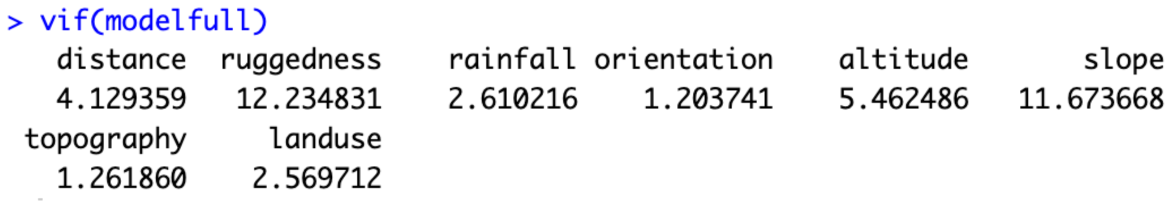
```
    h <- hist(x, plot=FALSE)
    y <- h$counts / max(h$counts)
    rect(h$breaks[-length(h$breaks)], 0, h$breaks[-1], y, col="white", ...)
  }
}

# 3. Select variables (numerical + categorical)
vars <- c("point", "orientation", "landuse", "topography",
          "distance", "ruggedness", "rainfall", "altitude", "slope")

# 4. Criate scatterplot matrix
pairs(env_var_treenests[, vars],
      lower.panel = panel.smooth2,
      upper.panel = panel.cor,
      diag.panel = panel.hist,
      gap = 0.5)


env_var_treenests$orientation <- as.numeric(env_var_treenests$orientation)
env_var_treenests$landuse     <- as.numeric(env_var_treenests$landuse)
env_var_treenests$topography  <- as.numeric(env_var_treenests$topography)
```

```
> #### Model all variables######
> modelfull <- glm(point ~ distance + ruggedness + rainfall + orientation +
+                  altitude + slope + topography + landuse,
+                data = env_var_treenests, family = binomial)
> summary(modelfull)
```



```
Call:
glm(formula = point ~ distance + ruggedness + rainfall + orientation +
    altitude + slope + topography + landuse, family = binomial,
    data = env_var_treenests)

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept) -2.3269851  3.0869940  -0.754   0.4510
distance     0.0005706  0.0002320   2.460   0.0139 *
ruggedness  -0.0243447  0.0289636  -0.841   0.4006
rainfall    -0.0002593  0.0003856  -0.672   0.5014
orientation  0.2811115  0.3221929   0.872   0.3829
altitude    -0.0022542  0.0056664  -0.398   0.6908
slope        0.0958252  0.1252363   0.765   0.4442
topography   0.0544240  0.3091328   0.176   0.8603
landuse      0.0801753  0.6745717   0.119   0.9054
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 94.268  on 67  degrees of freedom
Residual deviance: 69.343  on 59  degrees of freedom
AIC: 87.343

Number of Fisher Scoring iterations: 4
```

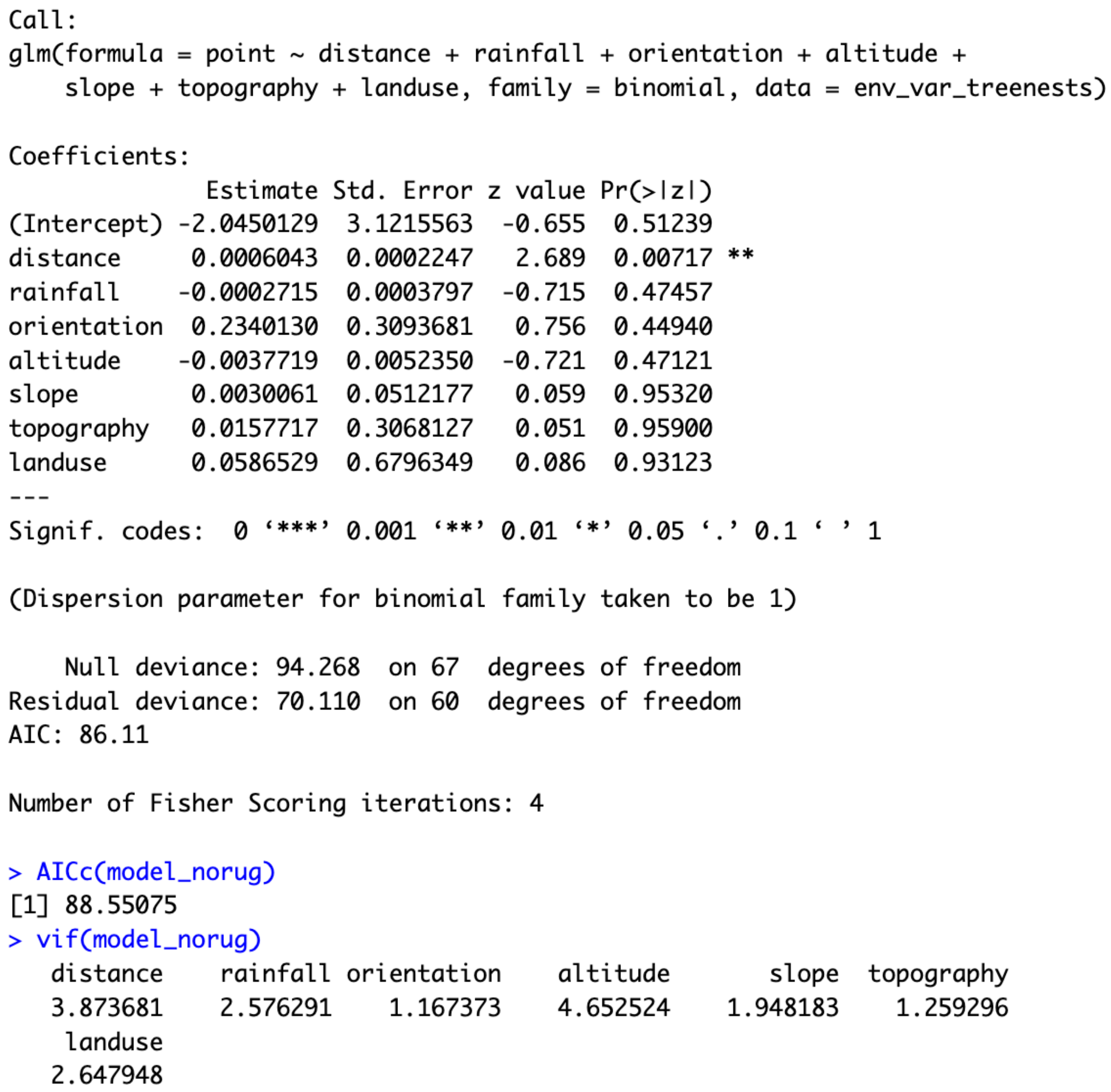
```
> library(MuMIn)
> AICc(modelfull)
[1] 90.44668

> library(car)
> # VIF for multicollinearity
> vif(modelfull)
```



```
> vif(modelfull)
   distance  ruggedness    rainfall orientation    altitude       slope 
   4.129359   12.234831    2.610216    1.203741    5.462486   11.673668 
 topography     landuse 
   1.261860    2.569712 
```

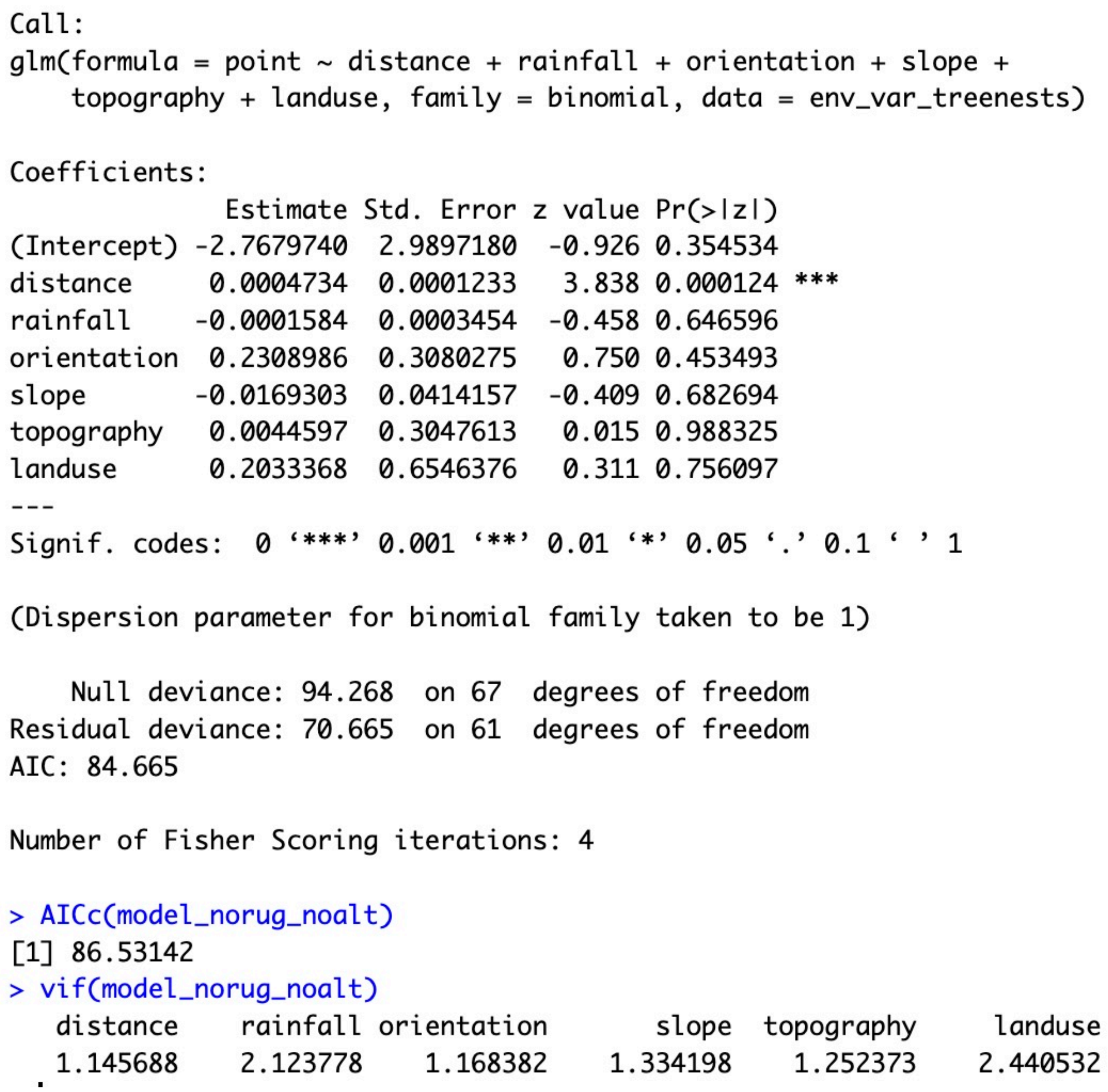
```
> # remove RUGGEDNESS
> model_norug <- glm(point ~ distance + rainfall + orientation +
```

```
+                 altitude + slope + topography + landuse,
+               data = env_var_treenests, family = binomial)
> summary(model_norug)
```



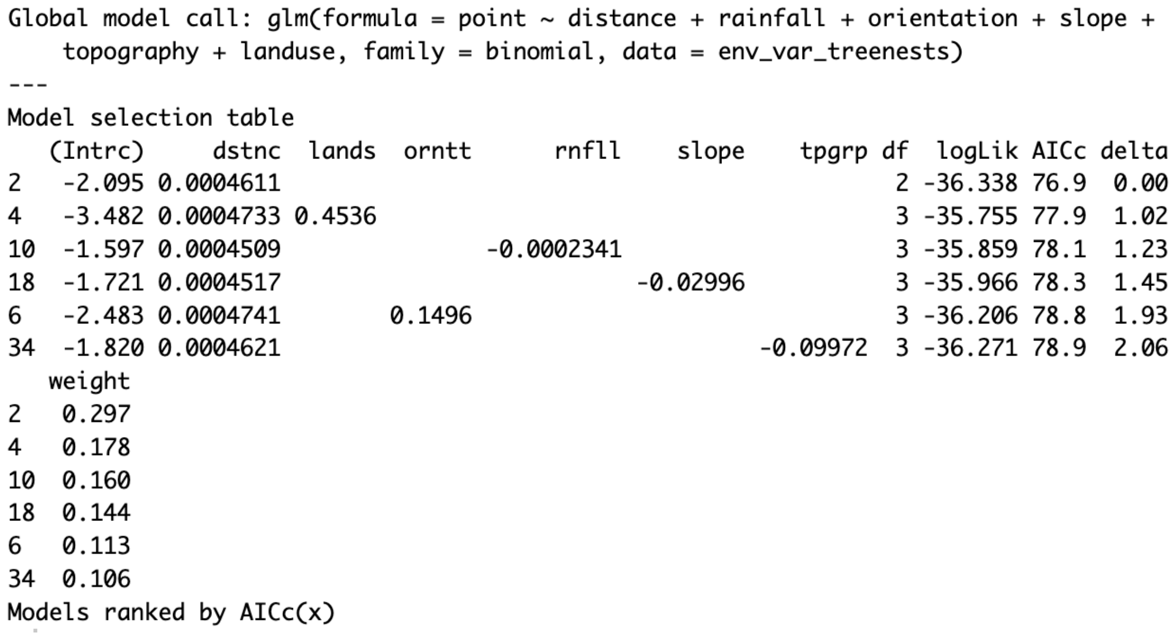
```
Call:
glm(formula = point ~ distance + rainfall + orientation + altitude + 
    slope + topography + landuse, family = binomial, data = env_var_treenests)

Coefficients:
              Estimate Std. Error z value Pr(>|z|)   
(Intercept) -2.0450129  3.1215563  -0.655  0.51239   
distance     0.0006043  0.0002247   2.689  0.00717 **
rainfall    -0.0002715  0.0003797  -0.715  0.47457   
orientation  0.2340130  0.3093681   0.756  0.44940   
altitude    -0.0037719  0.0052350  -0.721  0.47121   
slope        0.0030061  0.0512177   0.059  0.95320   
topography   0.0157717  0.3068127   0.051  0.95900   
landuse      0.0586529  0.6796349   0.086  0.93123   
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 94.268  on 67  degrees of freedom
Residual deviance: 70.110  on 60  degrees of freedom
AIC: 86.11

Number of Fisher Scoring iterations: 4

> AICc(model_norug)
[1] 88.55075
> vif(model_norug)
   distance    rainfall orientation    altitude       slope  topography 
   3.873681    2.576291    1.167373    4.652524    1.948183    1.259296 
    landuse 
   2.647948 
```

```
#remove RUGGEDNESS and ALTITUDE
> model_norug_noalt <- glm(point ~ distance + rainfall + orientation +
+                   slope + topography + landuse,
+                    data = env_var_treenests, family = binomial)
> summary(model_norug_noalt)
```



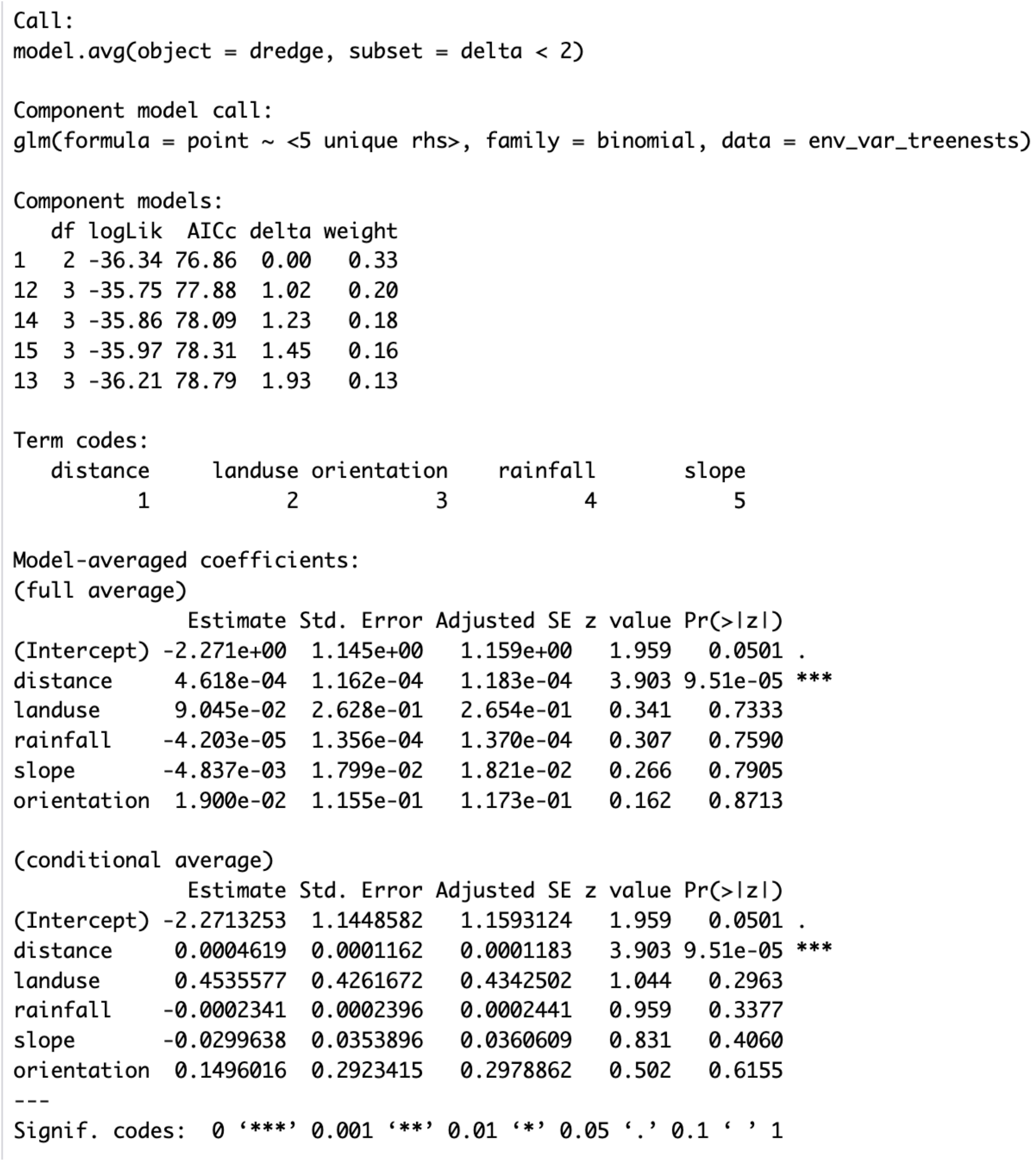
```
Call:
glm(formula = point ~ distance + rainfall + orientation + slope +
    topography + landuse, family = binomial, data = env_var_treenests)

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept) -2.7679740  2.9897180  -0.926 0.354534
distance     0.0004734  0.0001233   3.838 0.000124 ***
rainfall    -0.0001584  0.0003454  -0.458 0.646596
orientation  0.2308986  0.3080275   0.750 0.453493
slope       -0.0169303  0.0414157  -0.409 0.682694
topography   0.0044597  0.3047613   0.015 0.988325
landuse      0.2033368  0.6546376   0.311 0.756097
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 94.268  on 67  degrees of freedom
Residual deviance: 70.665  on 61  degrees of freedom
AIC: 84.665

Number of Fisher Scoring iterations: 4

> AICc(model_norug_noalt)
[1] 86.53142
> vif(model_norug_noalt)
   distance    rainfall orientation       slope  topography     landuse 
   1.145688    2.123778    1.168382    1.334198    1.252373    2.440532 
```

```
#DREDGE
options(na.action = "na.fail")
dredge <- dredge(model_norug_noalt, rank = "AICc")

head(dredge)
```



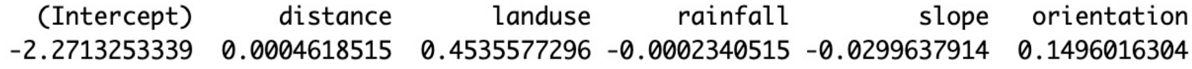
```
Global model call: glm(formula = point ~ distance + rainfall + orientation + slope + 
    topography + landuse, family = binomial, data = env_var_treenests)
---
Model selection table 
   (Intrc)     dstnc  lands  orntt      rnfll    slope    tpgrp df  logLik AICc delta
2   -2.095 0.0004611                                              2 -36.338 76.9  0.00
4   -3.482 0.0004733 0.4536                                       3 -35.755 77.9  1.02
10  -1.597 0.0004509               -0.0002341                     3 -35.859 78.1  1.23
18  -1.721 0.0004517                          -0.02996            3 -35.966 78.3  1.45
6   -2.483 0.0004741        0.1496                                3 -36.206 78.8  1.93
34  -1.820 0.0004621                                   -0.09972  3 -36.271 78.9  2.06
   weight
2   0.297
4   0.178
10  0.160
18  0.144
6   0.113
34  0.106
Models ranked by AICc(x) 
```

```
> # Model averaging of best modelos
> avg_model <- model.avg(dredge, subset = delta < 2)
> summary(avg_model)
```



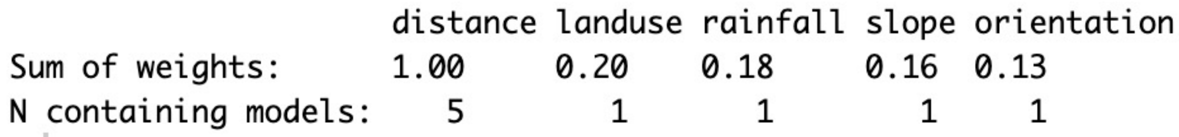
```
Call:
model.avg(object = dredge, subset = delta < 2)

Component model call:
glm(formula = point ~ <5 unique rhs>, family = binomial, data = env_var_treenests)

Component models:
   df logLik  AICc delta weight
1   2 -36.34 76.86  0.00   0.33
12  3 -35.75 77.88  1.02   0.20
14  3 -35.86 78.09  1.23   0.18
15  3 -35.97 78.31  1.45   0.16
13  3 -36.21 78.79  1.93   0.13

Term codes:
   distance     landuse orientation    rainfall       slope
          1           2           3           4           5

Model-averaged coefficients:
(full average)
              Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept) -2.271e+00  1.145e+00   1.159e+00   1.959   0.0501 .
distance     4.618e-04  1.162e-04   1.183e-04   3.903 9.51e-05 ***
landuse      9.045e-02  2.628e-01   2.654e-01   0.341   0.7333
rainfall    -4.203e-05  1.356e-04   1.370e-04   0.307   0.7590
slope       -4.837e-03  1.799e-02   1.821e-02   0.266   0.7905
orientation  1.900e-02  1.155e-01   1.173e-01   0.162   0.8713

(conditional average)
              Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept) -2.2713253  1.1448582   1.1593124   1.959   0.0501 .
distance     0.0004619  0.0001162   0.0001183   3.903 9.51e-05 ***
landuse      0.4535577  0.4261672   0.4342502   1.044   0.2963
rainfall    -0.0002341  0.0002396   0.0002441   0.959   0.3377
slope       -0.0299638  0.0353896   0.0360609   0.831   0.4060
orientation  0.1496016  0.2923415   0.2978862   0.502   0.6155
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
> coef(avg_model)
```



```
  (Intercept)      distance       landuse      rainfall         slope   orientation 
-2.2713253339  0.0004618515  0.4535577296 -0.0002340515 -0.0299637914  0.1496016304 
```

```
> sw(avg_model)
```



```
                     distance landuse rainfall slope orientation
Sum of weights:      1.00     0.20    0.18     0.16  0.13       
N containing models:    5        1       1        1     1       
```

```
> # Pseudo-R² (McFadden)
> pseudoR2 <- 1 - (current_model$deviance / current_model$null.deviance)
```

```
> pseudoR2
[1] 0.2562688
```

Section D – Photographic data

Figure D1 – Nest cavity occupied by a WTTB classified as Stable located in Ilhéu Santana

Figure D1 – Nest cavity occupied by a WTTB classified as Stable located in Ilhéu Santana

Figure D2 – Nest cavity occupied by a WTTB classified as Stable located in Sete Pedras located 4 meters above water hight

Figure D3 – Nest cavity occupied by a WTTB classified as Eroding located in Sete Pedras

Figure D3 – Nest cavity occupied by a WTTB classified as Eroding located in Sete Pedras

Figure D4 – Nest cavity occupied by a WTTB classified as Eroding located in Sete Pedras

Figure D4 – Nest cavity occupied by a WTTB classified as Eroding located in Sete Pedras

Figure D5 – Nest cavity occupied by a WTTB classified as Eroding located in Sete Pedras

Figure D5 – Nest cavity occupied by a WTTB classified as Eroding located in Sete Pedras

Figure D6 – Exposed nest under rock ledge occupied by a WTTB located in Ilhéu Santana

Figure D6 – Exposed nest under rock ledge occupied by a WTTB located in Ilhéu Santana

Figure D7 – Nest occupied by a WTTB located in rock cavity of block-and-ash flow origin located in Buraco Pablo

Figure D8 – Lahar deposits of Santa Catarina cliffs located in Santa Catarina tunnel

Figure D8 – Lahar deposits of Santa Catarina cliffs located in Santa Catarina tunnel

Figure D9 – Nest cavity occupied by a WTTB classified as Stable located in Santa Catarina tunnel

Figure D9 – Nest cavity occupied by a WTTB classified as Stable located in Santa Catarina tunnel

Figure D10 – Nest cavity occupied by a WTTB classified as Stable located in BP beach

Figure D10 – Nest cavity occupied by a WTTB classified as Stable located in BP beach

Figure D11 – Nest cavity occupied by a WTTB classified as Stable located in BP beach

Figure D11 – Nest cavity occupied by a WTTB classified as Stable located in BP beach

Figure D12 – Nest cavity occupied by a WTTB classified as Stable located in Ilhéu das Rolas

Figure D12 – Nest cavity occupied by a WTTB classified as Stable located in Ilhéu das Rolas

Figure D13 – Nest cavity occupied by a WTTB classified as Stable located in Ilhéu das Rolas

Figure D13 – Nest cavity occupied by a WTTB classified as Stable located in Ilhéu das Rolas

Figure D14 – Nest cavity occupied by a WTTB classified as Eroding located in Buraco Pablo

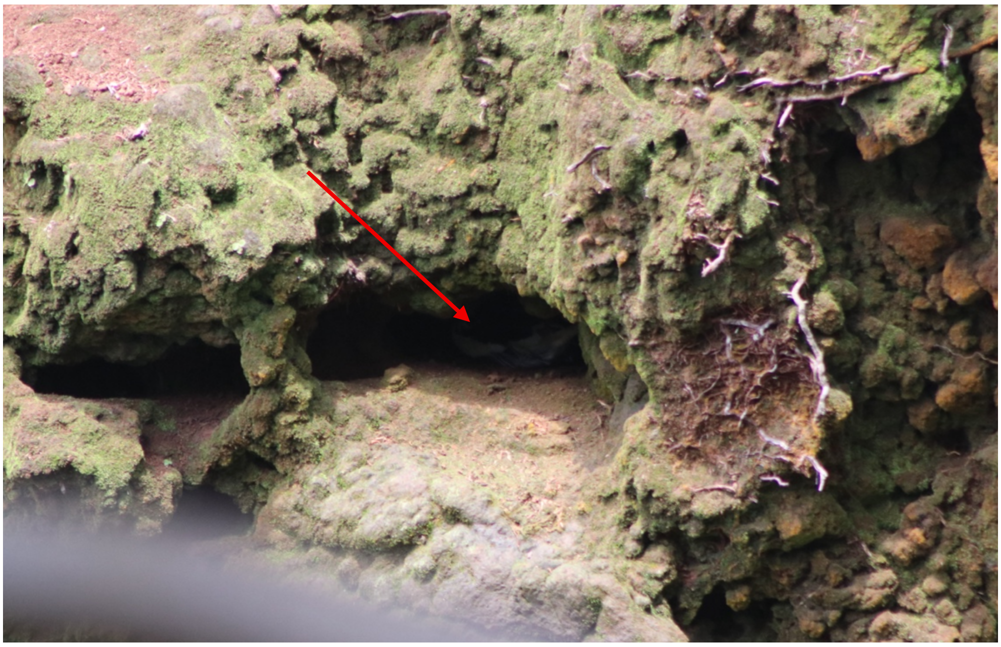


Figure D15 – Nest cavity occupied by a WTTB classified as Eroding located in Buraco Pablo

Figure D16 – Nest cavities occupied by a WTTB located in Buraco Pablo with different distance classes

Figure D17 – Nest cavity occupied by a WTTB with moderate vegetation cover located in BP beach. Same nest as Figure D10

Figure D18 – Nest cavity occupied by a WTTB with moderate vegetation cover located in Homem de Capa

Figure D19 – Nest in tree bifurcation occupied by a WTTB with dense vegetation cover located in Potô

Figure D20 – Nest in tree cavity occupied by a WTTB located in Monte Macaco

Figure D20 – Nest in tree cavity occupied by a WTTB located in Monte Macaco

Figure D21 – Nest in tree cavity occupied by a WTTB located in Santa Fé

Figure D21 – Nest in tree cavity occupied by a WTTB located in Santa Fé

Figure D22 – Nest in tree cavity occupied by a WTTB with no epiphyte cover located in Potô

Figure D22 – Nest in tree cavity occupied by a WTTB with no epiphyte cover located in Potô

Figure D23 – Top view of Buraco Pablo during low tide

Figure D23 – Top view of Buraco Pablo during low tide

Figure D24 – View of the aftermath of a mud slide caused by heavy rains and strong winds in Santa Fé, felling multiple tree

Figure D25 – One of multiple logged trees observed in Santa Fé This area is characterized by cocoa shade plantation rich in large trees bordered by mature secondary forest.

Final Considerations

The WTTB is a widespread pantropical species that has been relatively well studied, especially when compared to other seabird species. Populations are declining in parts of its range due to habitat loss, introduced predators, overfishing reducing prey availability, bycatch, and increasing frequency of severe storms linked to climate change (Lee & Walsh-McGehee, 2000; BirdLife International, 2020). The subspecies that occurs in the tropical Atlantic, *P. l. ascensionis*, has been studied in the Brazilian archipelagos of Fernando de Noronha and Abrolhos (Leal et al., 2016), on the British Overseas Territory of Saint Helena, Ascension and Tristan da Cunha (Stonehouse, 1962), and even on Príncipe Island (Rocha 2022). However, no study has ever focused on this species on São Tomé Island, despite thought to have a significant breeding population and being the only place where this subspecies is known to also breed on trees. Most of what is known about the WTTB on the island comes from an assessment of the status of seabirds conducted almost three decades ago (Monteiro et al., 1997), and from sporadic records (e.g., Jones & Tye, 2006).

Our results confirm that the species is widely distributed across São Tomé Island and surrounding islets. In alignment with previous studies, we registered WTTB occupying three distinct nesting habitats: rocky islets, coastal cliffs and trees (Jones & Tye, 2006). The islets of Sete Pedras and Rolas, and the cliffs of Santa Catarina Tunnel and Homem de Capa registered the highest concentrations of WTTB nests. The breeding population for the whole study area was estimated at 4,715 pairs (2,358 to 9,430), roughly 90% of which referring to tree nesting birds. These results suggest that São Tomé holds a globally significant population, potentially representing 0.6% to 2.4% of the global number of breeding pairs and the largest number of breeding pairs for *P. l. ascensionis* (Lee & Walsh-McGehee, 2020). Population estimates for Ascension Island range from 1,050 pairs (Stonehouse, 1962) to 2,200 pairs (Ashmole et al., 1994). In Príncipe, the breeding population has been estimated at 50 to 100 pairs (Bollen et al., 2018), while in Fernando de Noronha it ranges between 50 and 150 pairs (Leal et al., 2016). When compared with our results, São Tomé holds more than half of the number of breeding pairs for this subspecies, its importance for the conservation of this species. Data obtained from questionnaires suggest that the species breeds year-round on the island (Monteiro et al., 1997) but that it is more abundant during the dry seasons. Considering this and that our data were collected only during a short portion of the year, the actual population size is likely to be much greater.

Nest-site characterization revealed strong ecological differences between nesting habitats. This highlights the ecological plasticity of the species when it comes to nesting habitat, as it has been described elsewhere (Nelson, 2005). However, all nests tended to be found in cavities with limited vegetation cover, and almost all tree nests were found on large coral trees in mature cocoa shade plantations. At the landscape level, tree nests also tended to be found away from the coast, which might be linked to most of these being identified in the most accessible portion of the island, where most of the coast lacks suitable cliffs or trees, but also where anthropogenic pressures are felt the most. Overfishing, bycatch, invasive species, native predators, nest harvesting and hunting affect all nest types, but islet nests seem to be the most threatened, namely because they are additionally threatened by marine debris and tropical storms. Cliff and tree nests are the most impacted by habitat loss. The threats we identified in São Tomé mostly coincide with those affecting seabirds globally (Lee & Walsh-McGehee, 2000; Dias et al., 2019).

Our findings show that São Tomé is a stronghold for the breeding population of WTTB globally, and especially in the tropical Atlantic, highlighting the need for further studies and conservation action. Sustained monitoring, particularly during the dry seasons, will be crucial to track long-term trends and guide adaptive management (Johnson & Krohn, 2001). This should include not only changes in the WTTB breeding population, but also in their distribution (e.g., searching for nests in new areas), seasonality (namely to clarify potential breeding peaks), breeding success, habitat use (extended to feeding areas), movement and feeding ecology, and threats. Priority conservation measures should include protecting key breeding sites, such as Sete Pedras, and Santana, as well as protecting large trees in shade plantations. Environmental education focusing on the ecological importance of the WTTB and other seabirds is also crucial to inform Santomeans and help them taking informed decisions about their natural heritage towards a more sustainable use of resources. Protecting the WTTB on this island is relevant for the species but it can also be used a flagship for marine conservation, and specifically for the conservation of fish stocks, which are fundamental to ensure food safety and the quality of life of human populations in São Tomé.

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Annex I

EVIDENCE OF RED-BILLED TROPICBIRD *PHAETHON AETHEREUS* BREEDING IN THE GULF OF GUINEA

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ABSTRACT

Marino, G., Oquiongo, G., Hahn, I. L., Pereira, P., Pereira, J., & de Lima, R. F. (2025). Evidence of Red-billed Tropicbird *Phaethon aethereus* breeding in the Gulf of Guinea. *Marine Ornithology*, *53*(2), 409–413. http://doi.org/

Red-billed Tropicbird *Phaethon aethereus* has been considered vagrant in the Gulf of Guinea, although with suggestions of sporadic breeding at Tinhosas Islets, south of Príncipe Island. Here, we report repeated visits of birds to potential nesting sites, aggressive territorial behavior, and pair interactions on the coastal cliffs in the southern portion of São Tomé Island and nearby islets of Rolas and Sete Pedras. These observations strongly suggest that the species breeds at these locations, which would expand the known breeding range in the eastern Atlantic. Future work is needed to clarify the status of the species in the region.

RESUMO (ABSTRACT IN PORTUGUESE)

O Rabijunco *Phaethon aethereus* tem sido considerado vagrante no Golfo da Guiné, embora já tenha sido sugerido que se pode reproduzir ocasionalmente nos ilhéus das Tinhosas, a sul da ilha do Príncipe. Aqui, reportamos visitas repetidas de aves a potenciais locais de nidificação, comportamento territorial agressivo e interações de casais nas arribas costeiras no sul da ilha de São Tomé e ilhéus adjacentes das Rolas e Sete Pedras. Estas observações sugerem fortemente que a espécie se reproduz nestes locais, o que expandiria a área conhecida de reprodução no Atlântico Oriental. Trabalhos futuros devem clarificar o estatuto da espécie na região.

Key words: distribution, expansion, eastern South Atlantic, São Tomé and Príncipe, seabird nesting

INTRODUCTION

The Red-billed Tropicbird *Phaethon aethereus* is a pelagic species distributed across tropical and subtropical waters. Usually, it is only found near land on the islands where it breeds. Three subspecies are currently recognized (Orta et al., 2020): *P. a. aethereus* breeds in tropical islands in the South Atlantic, namely on the Brazilian archipelagos of Fernando de Noronha and Abrolhos and on Ascension and St. Helena Islands in the British Overseas Territory of Saint Helena, Ascension and Tristan da Cunha (Beard et al., 2023; Mancini et al., 2016; Stonehouse, 1962); *P. a. mesonauta* breeds in the eastern Pacific (from Chile and the Galápagos Islands north to Mexico), Caribbean Sea, and eastern North Atlantic (Cape Verde, Canary Islands, and Madeleine Islands in Senegal: Diop et al., 2019; Santos et al., 2017); *P. a. indicus* is restricted to the northwestern Indian Ocean, around the Arabian Peninsula, and is sometimes treated as a separate species, Arabian Tropicbird *P. indicus* (Howell & Zufelt, 2019).

The species' breeding becomes more seasonal at higher latitudes, and breeding density is associated with oceanographic events linked to food availability (Beard et al., 2023). Breeding colonies of *P. a. mesonauta* in the Gulf of California concentrate reproductive efforts around winter upwelling events (Castillo-Guerrero et al., 2011). At lower latitudes, breeding tends to become protracted, as is the case for the nominal subspecies at St. Helena and Ascension Islands, where egg laying peaks around September (Beard et al., 2023; Stonehouse, 1962). Nevertheless, individual breeding phenology is also variable, for instance between years, and it can depend on factors such as time since the last breeding attempt (Beard et al., 2023).

Although the Red-billed Tropicbird has long been mapped as occurring in the Gulf of Guinea (Brown et al., 1982), the first specific report we could find for the region dates to an undocumented sighting in September 1987 in Kribi, Cameroon (Holyoak, 1987). Subsequent observations have been limited to the small island nation of São Tomé and Príncipe, where it was first registered in March 1992 near Sete Pedras, a cluster of rocky islets *ca.* 5 km southeast of São Tomé Island (Jones & Tye, 2006). In July 1996, it was spotted near Tinhosa Pequena, one of three small, unvegetated islets that make up the Tinhosas, some 20 km south of Príncipe Island (Christy & Clarke, 1998; Roberson, 1996). The first physical evidence of its presence, however, dates only from January 2017, when two individuals were photographed near Tinhosinha, another one of the Tinhosas Islets (Bollen et al., 2018). In November 2019, one of two reported birds was photographed near Sete Pedras (Sineux, 2019; Sineux, 2022). Again on Tinhosinha, three adults were photographed flying together over the sea on 28 February 2020 (Paulo Catry, personal communication, May 26, 2025), and a single bird was seen entering a cavity on 10 February 2021 (Nina da Rocha, personal communication, February 23, 2021). On Tinhosa Pequena, there is also anecdotical evidence of nests in previous years (Nina da Rocha, personal communication, February 23, 2021), suggesting that the species might be breeding sporadically in the region (de Lima & Melo, 2021).

OBSERVATIONS

In February 2025, GM observed Red-billed Tropicbirds in waters south of São Tomé Island on multiple occasions (Table 1, Fig. 1). They were readily identified by the red bill, by the distinctive pattern of black feather markings (Fig. 2), and by being visibly larger than the locally abundant White-tailed Tropicbird *P. lepturus*. The first sighting took place on 05 February at Homem da Capa, a coastal cliff next to Porto Alegre, on the main island. Subsequent inquiries of people living in the vicinities confirmed that most were unfamiliar with the Red-billed Tropicbird, even though a few people reported regular sightings at specific coastal locations. Taking these accounts into consideration, areas with suitable tropicbird nesting habitat were targeted for further searches. On 07 February, an individual was observed at the same location as the previous sighting, interacting with White-tailed Tropicbirds and seemingly searching for a cavity on the rocky cliffs. On 10 February, a pair was seen entering a rocky cavity after a 10-min period of conjoint aerial display at Sete Pedras, where there are breeding populations of several other seabird species, including White-tailed Tropicbird (Jones & Tye, 2006; Monteiro et al., 1997). On 12 February, a single bird approached from the sea, vocalized, chased a few White-tailed Tropicbirds, and entered a cavity at Ilhéu das Rolas. At *ca.* 2 km^2, this is the largest islet next to São Tomé, *ca.* 2.5 km south of the main island. The islet has a prominent oceanic cliff on its southwestern face, known to support a nesting population of White-tailed Tropicbirds (Jones & Tye, 2006; Monteiro et al., 1997).

Our observations indicate that the birds occurring in the Gulf of Guinea do not belong to the Indian Ocean subspecies (Fig. 2), which would have a shorter eye mask, shorter tail streamers, stronger black upperwing markings, and black cutting edges to the bill (Howell & Zufelt, 2019). The distribution of the remaining subspecies might suggest that the Gulf of Guinea birds belong to the nominal subspecies, which breeds in the South Atlantic. However, *P. a. mesonauta* cannot be disregarded, given that it has expanded its distribution into the eastern and western North Atlantic over the past few decades (Furness & Monteiro, 1995; Gil-Velasco et al., 2022; Kennerley et al., 2025). Since most records of the species in São Tomé and Príncipe have been sporadic and the breeding seasonality of the species is flexible, there is not much we can infer about the seasonality or origin of these birds.

The repeated visits to potential nesting sites, the aggressive territorial behavior, and the pair interactions provide compelling evidence that the Red-billed Tropicbird is breeding in the oceanic islands of the Gulf of Guinea, even though our observations do not offer a definitive proof. It also remains unclear if these occurrences refer to sporadic breeding. An increased number of records might result from more people recording birds on the islands (de Lima & Melo, 2021), but the species might also have increased its presence in São Tomé and Príncipe to becoming a regular, even though scarce, breeding species.

TABLE 1
Observations of Red-billed Tropicbird *Phaethon aethereus* in São Tomé, São Tomé and Príncipe, made by Gustavo Marino in February 2025

Date, time	Location[a]	Observations
05, 14h00	Homem da Capa (A)	One briefly flying in the distance.
07, 12h10	Homem da Capa	One flying, vocalizing, and actively displacing a pair of White-tailed Tropicbirds *Phaethon lepturus* from a cavity.
07, 12h40	Homem da Capa	The same individual as above trying twice to land in that same cavity while it was still occupied by a White-tailed Tropicbird.
07, 13h00	Homem da Capa	The same individual trying to enter another cavity, less than 5 m away from the one occupied by the pair of White-tailed Tropicbirds.
10, 09h45	Sete Pedras (C)	Two individuals approaching from the sea, vocalizing in coordinated circular flight for a couple of minutes. After *ca.* 10 minutes of aerial display, both birds entered the same rocky cavity.
12, 06h34	Ilhéu das Rolas (B)	One individual approaching from the sea in circular flight whilst vocalizing. It chased several White-tailed Tropicbirds, but at one point, it also flew with a group of four White-tailed Tropicbirds, exhibiting no aggressive behaviour.
12, 06h56	Ilhéu das Rolas	One individual entering a cavity.

[a] Capital letters in brackets refer to the locations shown in Fig. 1.

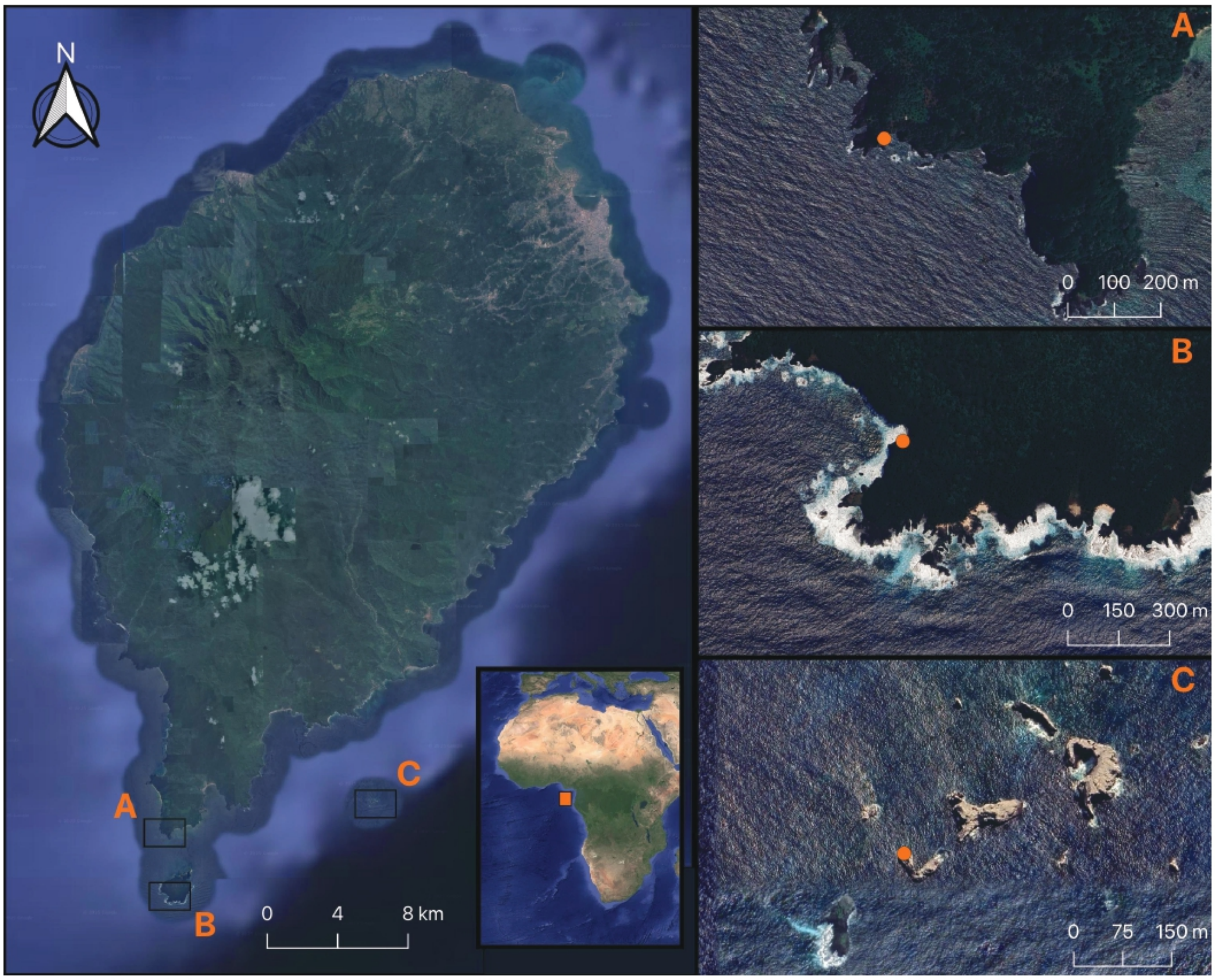

Fig. 1. Map of São Tomé Island, São Tomé and Príncipe, highlighting (A) Homem da Capa cliff, (B) Ilhéu das Rolas, and (C) Sete Pedras. The orange dots show the approximate locations where Red-billed Tropicbird *Phaethon aethereus* was spotted entering cavities during fieldwork in February 2025. (Background aerial photos from Google Maps: São Tomé Island—Google Maps, Map data ©2025, Map data ©2025; African continent—Google Maps, Imagery ©2025 NASA, Map data ©2025 Google; panels A, B, and C—Google Maps, Imagery ©2025 Airbus, CNES / Airbus, Maxar Technologies, Map data ©2025)

Future work should monitor the occurrence of the species in São Tomé and Príncipe to clarify its status in the region. These efforts should focus on the locations where the presence of the species has been confirmed, namely in the Tinhosas Islets and on the coastal cliffs and islets to the south of São Tomé Island. We appeal for care while identifying tropicbirds in the Gulf of Guinea, as it is likely that the species is underreported by confusion with the locally abundant White-tailed Tropicbird. It would also be important to monitor distribution by visiting other islets and coastal cliffs in the region and to record potential population changes and seasonality. There is some information on the distribution and population size of the White-tailed Tropicbird in the country (Monteiro et al., 1997; Rocha, 2022), and breeding is currently being studied in São Tomé (Marino, 2025). Since antagonistic interactions between the two species have been reported (Stonehouse, 1962), it would be relevant to monitor how the potential expansion of the Red-billed Tropicbird might affect the smaller species.

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Fig. 2. Red-billed Tropicbirds *Phaethon aethereus* at São Tomé Island, São Tomé and Príncipe, in February 2025: A) Flying at Homem da Capa; B) the same individual vocalizing while chasing a pair of White-tailed Tropicbirds *P. lepturus* that had occupied a nest cavity; C) chasing multiple White-tailed Tropicbirds at Ilhéu das Rolas; D) the same individual entering a nest cavity; E) two individuals vocalizing while in coordinated circular flight over Sete Pedras; F) the second of two individuals, also seen in photo (E), entering the same cavity. Photo credit: Gustavo Marino

AUTHOR CONTRIBUTIONS

Conceptualization: GM, RFL. Data curation: GM, RFL. Funding acquisition: JP, RFL. Investigation: GM, GO, ILH. Supervision: PP, RFL. Visualization: GM, RFL. Writing—original draft: GM, RFL. Writing—review & editing: GM, ILH, PP, JP, RFL.

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