

A review of the status and biology of an enigmatic pelagic species, the Red-tailed Tropicbird *Phaethon rubricauda*

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The Red-tailed Tropicbird *Phaethon rubricauda* occurs throughout the tropical regions of the Pacific and Indian Oceans. The species' breeding biology is quite well documented, but its population status, at-sea behaviour and ecology are poorly understood. This review summarises information on its status, morphology, behaviour and ecology and identifies aspects of its biology requiring further research that could facilitate its conservation management. The species' global population comprised an estimated 17-21,000 pairs in 2014, most of which bred on remote oceanic islands and atolls. Red-tailed Tropicbirds have short, narrow femurs and a long, straight pygostyle, making them highly efficient at oceanic foraging but cumbersome in their terrestrial locomotion. Courtship involves aerial displays in which the tail streamers possessed by both sexes play a prominent role. Clutch size is one and brood care is biparental, the parents employing a bimodal provisioning strategy involving long and short foraging trips. Breeding occurs on both bare and well vegetated substrates, vegetation cover being a key factor in nest site selection and breeding success in vegetated sites. The diet comprises mainly relatively large epipelagic fish and squid that are caught by solitary plunge-diving. The main threats to the species' survival are nest predation, sea level rises due to climate change, competition for food with commercial fisheries and extreme weather events. The main deficiencies in our knowledge of Red-tailed Tropicbird biology are the at-sea behaviour of the species and its genetic structure.

Keywords: Red-tailed Tropicbird, climate change, population status, behaviour, ecology, conservation, breeding biology

INTRODUCTION

The Red-tailed Tropicbird (RTT) *Phaethon rubricauda* is a pelagic seabird found throughout the tropical regions of the Indian and Pacific Oceans, where it is described as being widespread but uncommon (Vanderwerf and Young 2014; Schreiber and Schreiber 2020). Observations on RTTs mostly originate from the oceanic islands where they breed, as every other aspect of their lives is conducted on the open ocean (Howell and Bartholomew 1969; Schreiber and Burger 2001).

The RTT is one of only three extant representatives in the family Phaethontidae, the other species being the White-tailed Tropicbird *P. lepturus* and the Red-billed Tropicbird *P. aethereus*. Interspecific mingling among tropicbird species has been recorded where their known ranges overlap in the Pacific and Indian Oceans, but *P. rubricauda* is the only species whose range does not extend to the Atlantic Ocean (Vanderwerf and Young 2007). The RTT is regarded as the most oceanic of the tropicbird species, ranging farther from its terrestrial breeding grounds than either of the other two species (Sommerfeld and Hennicke 2010). It is also the largest of the tropicbird species, with body mass generally ranging between 600-900g (Schreiber 1996; Schreiber 1996; Le Corre *et al.* 2003a).

This review identifies and interprets significant findings in the scientific literature regarding the RTT's behaviour, ecology, morphology and population status. The aim is to assemble and synthesise available information on RTT biology, identify aspects where data are lacking and provide information that

can assist conservation management of the species. Reports of recent substantial reproductive losses highlight the necessity of proactive conservation of this species.

METHODS

This review synthesises most of the information available in peer-reviewed publications that focus on the biology, physiology and conservation of the RTT. Research on the species was accessed through an institutional library data base (University of the Sunshine Coast), Google Scholar, Web of Science and Scopus. Other sources were also identified from the reference lists in peer-reviewed publications accessed from these sources. We used the search terms "*Phaethon rubricauda*" and "Red-tailed Tropicbird," targeting the title and/or abstract of publications. A summary of our literature search by year of publication is presented in Figure 1; it comprised 88 publications since 1965 that focus on this species. Additional peer-reviewed information regarding general seabird conservation and population ecology was also accessed to support and contextualise RTT research findings within the broader framework of seabird ecology.

RESULTS

Distribution

Red-tailed Tropicbirds are distributed throughout the tropical regions of the Pacific and Indian Oceans (Spear and Ainley 2005). Much of the life of a RTT is spent at sea, where all daily activities including feeding and roosting occur (Schreiber

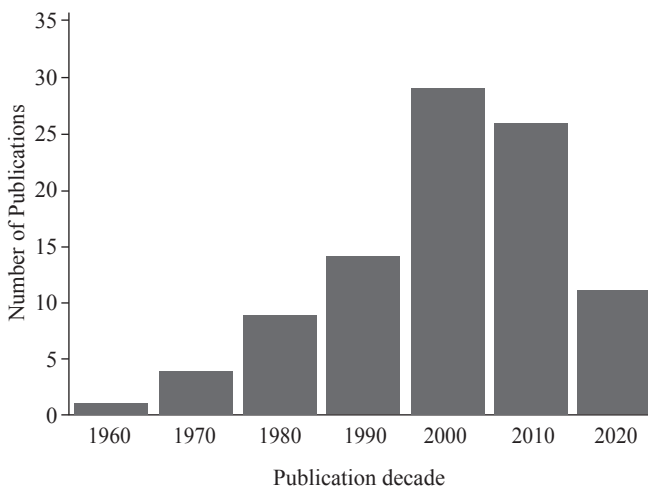


Figure 1. Number of peer-reviewed publications sourced from scholarly internet repositories including “Red-tailed tropicbird*” or “Phaethon rubricauda” in the title or abstract published since 1960. A list of the 88 publications is available from the corresponding author on request.

and Burger 2001). The only exception to this is breeding, which takes place on land, typically on oceanic islands and atolls (Spear and Ainley 2005).

The RTT occurs primarily in tropical and subtropical waters where sea surface temperatures exceed 22°C (Schreiber and Burger 2001; Dunlop *et al.* 2001; Spear and Ainley 2005). The at-sea ecology and distribution of *P. rubricauda* across its range are not thoroughly understood, as its widespread distribution does not readily facilitate comprehensive surveillance (Le Corre *et al.* 2003a). The Pacific distribution of *P. rubricauda* off the coast of the Americas was surveyed from 1980 to 1995 by Spear and Ainley (2005) and revealed seasonal variation in at-sea distribution and abundance. This variation was related to breeding seasonality, with distribution not surprisingly becoming more concentrated within the vicinity of breeding grounds as birds arrived to breed, followed by spikes in abundance approximately 3,000 km from breeding colonies as fledglings headed out to sea during autumn (Spear and Ainley 2005).

Dispersal and distribution data have been garnered in various banding programs, including those overseen by the Australian Bird and Bat Banding Schemes (ABBBS). Many recoveries of banded individuals have been recorded at natal colonies (Dobbs 2005), but band recoveries away from the breeding colony at which individuals were originally banded are scarce. Those that do exist have revealed that *P. rubricauda* is capable of dispersing over thousands of kilometres (Le Corre *et al.* 2003b). As banding data and most observational dispersal data come from breeding colonies on land rather than oceanic locations, behaviour and dispersal at sea are poorly documented. However, new technologies are making the study of individual movements and dispersal patterns more feasible, and although these have thus far only produced short-distance dispersal data their potential for providing longer-distance data and allowing longer-term tracking is considered substantial (Sommerfeld and Hennicke 2010).

Morphology and physiology

The RTT is a predominantly white seabird with black eye markings and eponymous, long, red tail streamers (Fig. 2; Schreiber and Burger 2001). Its energetic, flapping flight is sustained by well-developed pectoral muscles (Schreiber and Burger 2001). The species is sexually monochromatic during both the adult and juvenile life stages; males and females are also of a similar size, as is the case in many socially monogamous bird species (Jones and Hunter 1993; Veit and Jones 2003). The mass-specific basal metabolic rate of *P. rubricauda* (0.484 kJ/g/day) is rather high compared with those of many other seabirds of similar mass, data from which would generate a predicted rate of 0.378 kJ/g/day for this species (Pettit *et al.* 1985). A study of the energetic demands of breeding *P. rubricauda* suggests that male and female parents invest equally in energy expenditure during both incubation and chick-rearing and no significant changes in the body condition of either sex occur during the breeding period (Dehnhard and Hennicke 2013).

The RTT’s name is inspired by the two red tail streamers that adults display when they reach sexual maturity: development and use of these streamers has been studied on Tern Island, Hawaii (Veit and Jones 2003; Veit and Jones 2004). The streamers are grown and moulted alternately in a continuous process; for this reason, it is typical for a RTT to have one fully-grown streamer and one developing, partial streamer. However, coordinated streamer growth has been observed between members of a breeding pair, and the possession of two fully-grown streamers by both members is typical during courtship. A consensus on streamer function has not been reached, but no aerodynamic benefits or correlation with an individual’s breeding fitness (e.g. fledging success) have been found. The streamers are prominently displayed during aerial courtship and have been described as an ornamental trait used as a means of communication between breeding individuals (see *Courtship and mating* below).

Red-tailed tropicbirds cannot easily navigate terrestrial habitats (Hennicke and Flachsbarth 2009) due to their hind limb morphology. The structure of their legs is not efficient for walking: femoral length and width are relatively short and femoral strength consequently relatively weak, so their terrestrial locomotion is essentially a clumsy shuffle (Morrell and Aquilani 2000; Schreiber and Burger 2001; Habib and Ruff 2008). The pygostyle of tropicbirds is long and straight, which is an adaptation that has evolved in plunge-diving bird species that counteracts the bending and torsional forces of water (Felice and O’Connor 2014). Together, these skeletal features support the view that the hind limb morphology of tropicbirds enhances manoeuvrability at sea, whilst impairing locomotion on land, a syndrome that has been termed ‘hyperaerial’ by some researchers (Habib and Ruff 2008).

Diet

The foraging niche of *P. rubricauda* is that of a solitary plunge-diver that avoids intra- and inter-specific flocks (Dunlop *et al.* 1988). Schreiber and Burger (2001) assert that the species roosts on the sea surface, drifting with currents. This is corroborated by a study that reported RTTs spending 80.8% of their time on the sea surface, particularly throughout the night (Sommerfeld and Hennicke 2010).



Figure 2. Female Red-tailed Tropicbird transferring newly laid egg to be incubated underneath the body.

Photo by Kathy Townsend



Figure 3. A Red-tailed Tropicbird at nest site with a newly hatched chick and egg-shell under the wing.

Photo by Kathy Townsend

The diet of the RTT consists of epipelagic species, primarily small flying fish and squids (Schreiber and Schreiber 2020), and varies both seasonally and regionally (Harrison *et al.* 1983; Sommerfeld and Hennicke 2010). Individuals that nest on the Hawaiian Islands in the central Pacific Ocean have a distinct diet that seasonally incorporates Mahi-mahi *Coryphaena hippurus* and the early developmental stages of the Common Mola *Mola mola* that are vulnerable to seabird predation (Harrison *et al.* 1983). Despite their relatively small body mass, RTTs consume comparatively large prey (Le Corre *et al.* 2003a). Thus the mean mass of consumed Mahi-mahi is 120 g, or 16% of the average adult RTT body mass (Le Corre *et al.* 2003a). The catching and handling of this prey item is facilitated by having a strong, serrated bill (average length 6.1 cm, with a mandible hinge capable of facilitating wide gaping and high-pressure gripping) combined with the power of the bird's flight (Harrison *et al.* 1983; Schreiber and Burger 2001; Le Corre *et al.* 2003a). The length of flying fish prey ranges from 130-160 mm and that of squid prey from 70-90 mm (Harrison *et al.* 1983). Dietary variation is probably linked with breeding cycles and the movement and abundance of prey species (Le Corre *et al.* 2003a; Sommerfeld and Hennicke 2010). Red-tailed Tropicbird chicks receive the same diet as their parents in a regurgitated form (Schreiber and Burger 2001; Le Corre *et al.* 2003a). Further investigation into the variation in diets regionally would help to quantify any threats to key prey abundance caused by anthropogenic fishing practices or ocean warming.

Breeding behaviour and ecology

Courtship and mating

Pair bonds are established between RTT adults during complex aerial courtship displays in which the birds 'loop' through the air, at times appearing to fly backwards (Veit and Jones 2003; Sommerfeld *et al.* 2015). Red-tailed Tropicbirds engage in these displays near the breeding grounds, suggesting that the breeding sites are landmarks that facilitate the reunion of pair members (Vanderwerf and Young 2014; Sommerfeld *et al.* 2015). Even established pairs will perform such courtship flights annually at the commencement of their breeding period (Vanderwerf and Young 2014). Established pair bonds appear to

strengthen over time and are not easily disrupted even if breeding failure occurs, divorce being a more common occurrence between younger birds with newly-formed bonds (Sommerfeld *et al.* 2015). When breeding failure occurs, a replacement egg may be laid, but this is less likely towards the end the breeding season (Sommerfeld *et al.* 2015).

The RTT is one of the few seabirds having ornamental tail plumage that is used in courtship, but this plumage is a sexually monomorphic trait. The two tail streamers are readily visible during courtship displays. This prominence, individual variation in streamer length, the potential cost (for flight aerodynamics) of possessing streamers and their bright colouration are consistent with a role in mate selection, a contention further supported by the observation of assortative mating according to tail length in one population (Boland *et al.* 2004) and by streamer symmetry in another (Veit and Jones 2003).

Nesting

The RTT nests on remote islands and tropical atolls, and breeding habitat varies in complexity across the species' range. The birds form colonies, with aggressive interactions being recorded between nesting pairs, behaviour that has been theorised to determine nest site area and effect nest spacing, thus lowering female stress levels during laying (Jovani and Grimm 2008). A single egg is typically laid in a scrape on the ground sheltered by vegetation or rocks (Fleet 1972) (Figs. 2 and 3). Key features of nest sites are the degree and type of overhead cover and the substrate on which the egg is laid. On Rapa Nui (Easter Island), *P. rubricauda* nests in naturally occurring scrapes on rocky ground and vegetative cover is provided by abundant Molasses Grass *Melinis minutiflora* (Flores *et al.* 2017). On the coral atoll of Midway Island, nest sites have been described as scrapes in the sand, with cover provided by *Scaevola* spp. bushes and buildings (Howell and Bartholomew 1969). On Rose Atoll, all *P. rubricauda* nests have been found under Beach Heliotrope *Messerschmidia argentea* bushes or *Pisonia* *Pisonia grandis* trees, whilst nests on Christmas Island (in the Indian Ocean) were associated with *Pandanus* *Pandanus christmatensis*, Salt Bush *Pemphis acidula*, Octopus Bush *Argusia argentia* and Beach Naupaka *Scaevola sericea* (Morrell and Aquilani 2000;

Hennicke and Flachsbarth 2009). Proximity to vegetation and shade availability appear to be important predictors of nest site selection and nesting success in the RTT (Prys-Jones and Peet 1980; Morrell and Aquilani 2000). Vegetation provides shade and cover, and plant stem density is thus an important predictor of nest site occurrence in vegetated breeding sites (Clark *et al.* 1983).

However, RTTs sometimes nest in relatively stark and bare environments, as observed in the colony on Sugarloaf Rock off the west coast of Australia. Here, a small colony nests on a slope where both rock ledges and flat terrain are available and Pigface *Carpobrotus aequilaterus* forbs and *Salsola kale* shrubs grow (Tarburton 1977). At this location, nests were *either protected or exposed*, although most were in relatively sheltered areas (Tarburton 1977). Shelter is a paramount concern for RTT, as both adults and chicks are susceptible to heat stress while on land (Morrell and Aquilani 2000). Region-specific associations of nests with particular vegetation characteristics (e.g. number of stems at ground level, amount of protection on the side facing the prevailing winds) are dictated by availability and the quality of shelter that such variables provide (Clark *et al.* 1990). Nest-site selection can also be affected by the presence of predators and can confine breeding colonies to less accessible locations, such as the steep cliffs of Lord Howe Island.

Parental care

Offspring care is performed by both parents, and a detailed study on Christmas Island using GPS tracking showed that during incubation and chick-rearing the RTT adopts a bimodal foraging pattern in which bonded parents alternate between long and short foraging trips (Sommerfeld and Hennicke 2010). One parent typically made an extended trip to richer foraging waters, while the remaining parent undertook shorter, more frequent trips to less prolific foraging waters closer to the breeding ground. Longer foraging trips lasted up to 57 hours and shorter trips took an average of three hours. The parent that remained at the nest site made one or two of these shorter trips daily, leaving the chick unattended. When the other parent returned from its long foraging trip, a changeover took place and the roles were reversed. Using this bimodal foraging strategy, parent RTTs maintained body condition throughout the breeding period when they were ‘tethered’ to the land (Sommerfeld and Hennicke 2010).

Heat stress is a particular hazard for unattended chicks, with a high risk of mortality occurring during the hottest hours of the day (Clark *et al.* 1990). The quality of cover (both overhead and laterally) and the thermal load from the substrate are thus likely to greatly influence nest site selection and breeding success (Clark *et al.* 1990). Suitable nest site shade removes the necessity of continuous brooding, allowing the chick to be left alone in relative safety while the nest-attending parent undertakes its short foraging trips during the day (Clark *et al.* 1990). This is one of the main reasons why an abundance of suitable vegetation and other shade-providing obstacles have been highlighted as influencing nest site selection (see *Nesting* above).

Breeding seasons are region-specific, but RTTs primarily breed in the warmer spring and summer months, and it is hypothesised not surprisingly that breeding cycles are determined by food availability (Le Corre 2001; Schreiber and



Figure 4. Red-tailed Tropicbird chick at approximately four weeks old, seen with parent at nest site.

Photo by Kathy Townsend

Burger 2001). In some instances, a breeding ground will be used year-round, as on Christmas Island and Ashmore Reef (Spear and Ainley 2005; Clarke *et al.* 2011). Breeding RTTs show strong nest site fidelity, typically returning to the same nest site for as long as it remains viable (Clark *et al.* 1990), although breeding failures appear to prompt some nest-site switching in subsequent seasons (Sommerfeld *et al.* 2015).

Red-tailed Tropicbirds incubate their one egg for an estimated 41-50 days (Fleet 1972; Vanderwerf and Young 2014; Schreiber and Schreiber 2020). Hatchlings are brooded for approximately one week, being sheltered beneath the body of the parent for the first three to four days, and later beneath a wing (Howell and Bartholomew 1969; Fleet 1972) (Fig. 4). Adults gradually spend less time at the nest site as chicks age, spending more time at sea and returning only to feed their chick (Fleet 1972). The distinctive plumage of the nestling is illustrated in Figures 5 and 6.

Observations have been recorded of extended parental care lasting for up to 30 days post-fledging when juveniles were still close to the breeding grounds (Fleet 1974; Ainley *et al.* 1986). However, we have a poor understanding of the at-sea movements of both adults and juveniles, and so the extent and nature of any such parental assistance to young when they are further away from the breeding grounds is unknown. How the young learn to forage has not been documented; however, adults and juveniles have been observed interacting at sea, which may indicate that some offshore post-fledging parent-chick relationship occurs, but more evidence is required to test this suggestion (Ainley *et al.* 1986). Breeding age is reached after three years and the annual survival rate of adults has been estimated as 90%, producing a generation time of 13 years (Doherty *et al.* 2004; Sommerfeld *et al.* 2015). The lifespan of the RTT is unknown, but breeding individuals over 20 years of age have been recorded (Sommerfeld *et al.* 2015; personal observations).

Population status

The global population of RTT is not considered to be threatened and the species is listed as being of Least Concern (Birdlife International 2017). The International Union for Conservation of Nature gives a global population estimate of



Figure 5. a) Red-tailed Tropicbird chick aged approximately eight weeks, showing loss of downy feathers and development of sub-adult markings. Chick is left alone at nest site for extended periods at this stage. b) Relative size of chick in relation to size of adult.

Photos by Zerra Egerton

>32,000 individuals; however, this figure is probably outdated as it is based on data from 1992 (Del Hoyo *et al.* 1992; Birdlife International 2017). Spear and Ainley (2005) cite the results of surveys conducted under the Pacific Ocean Biological Survey Program between 1980-1995, which recorded a minimum of 31,000 individuals nesting on islands in the eastern and central Pacific Ocean. A more recent global population estimate of 17,000-21,000 pairs is given by Vanderwerf and Young (2014), who also state that most of these pairs (~9,000-12,000) utilise breeding grounds on the north-western Hawaiian Islands. The largest colonies in this region are found on the Kure, Laysan and Midway Atolls (Table 1; Vanderwerf and Young 2014). Thus there is variability among global and regional population estimates stemming from multiple sources which is probably due to the widespread oceanic distribution of RTTs, their enigmatic at-sea distribution and the remoteness of their breeding grounds (Vanderwerf and Young 2014).

Assessments of global seabird population trends show a community level decline of 70% over the last 60 years due to a wide variety of factors, primarily competition with fisheries for food resources, changes in prey distribution and accessibility and the introduction of predator species at breeding grounds (see also *Threats* below; Grémillet *et al.* 2018)). Red-tailed Tropicbirds are vulnerable to some of these pressures, and thus a paucity of population surveys is cause for concern (Dias *et al.* 2019). The Australian breeding population of the species has been listed as Near Threatened after significant losses were caused by introduced predator species on Christmas Island, particularly rats and cats (Garnett *et al.* 2010; Luna *et al.* 2018). Population decline has also been observed on Raine Island off the Queensland coast, although the cause of this decline is unknown (Garnett *et al.* 2010). Whilst new colonies and increasing numbers have been identified on some islands over the past 50-100 years, RTT numbers are variable and the population growth patterns are difficult to disentangle from dispersal, an issue which genetic information could help to resolve (Jones 2001; Priddel *et al.* 2010; Buden 2012; Raine *et al.* 2017; Donegan *et al.* 2018). This situation highlights the necessity for regional management of breeding populations and a comprehensive synthesis of global RTT population data.



Figure 6. Red-tailed Tropicbird chick at approximately 12 weeks old, nearing fledging with sub-adult feathers fully developed. As chicks approach fledging, they sometimes leave their nest site and explore their surroundings.

Photo by Zerra Egerton

Threats to survival

Populations of RTT have been significantly impacted in several locations by high levels of predation. Red-tailed Tropicbirds nest on the ground where hatchlings are particularly vulnerable to predation. This is possibly a reason for their avoidance of predator-abundant mainland sites and their attraction to predator-free remote islands as breeding grounds (Tarburton 1977). On islands where predators have been introduced and the situation has been monitored, significant losses have been recorded. For example, on Kure Atoll introduced Polynesian rats *Rattus exulans* caused 89% of total hatchling losses in 1964 and 100% the following year (Luna *et al.* 2018). On Rapa Nui, RTT hatchlings are also threatened by depredation by introduced species (Flores *et al.* 2017); here the most voracious predator of chicks is the raptor the Chimango Caracara *Milvago chimango*, an introduced species which feeds on both eggs and hatchlings at unattended nest sites (Flores *et al.* 2017). On this island, the introduced Polynesian rat and the Brown rat *R. norvegicus* have not been observed preying upon

Table 1

Red-tailed Tropicbird breeding ground locations and estimated colony sizes as described in published literature.

Region	Location	Estimated breeding colony size	Source
East Indian Ocean	Ashmore Reef	17-24 pairs	(Clarke 2010; Clarke et al. 2011)
East Indian Ocean	Christmas Island	~1400-2000 pairs	(Sommerfeld et al. 2015)
East Indian Ocean	North Keeling	Unknown	(Dunlop et al. 2001)
East Indian Ocean	Rowley Shoals	Unknown	(Dunlop et al. 2001)
East Indian Ocean	Sugarloaf Rock	~10 pairs	(Anon 2009)
West Indian Ocean	Europa Island	~1027 pairs	(Saunier et al. 2022)
West Indian Ocean	Nosy Ve	~100 pairs	(Saunier et al. 2022)
West Indian Ocean	Aldabra Atoll	~1879 pairs	(Diamond 1975)
West Indian Ocean	Mauritius Channel Islands	~250 pairs	(Le Corre and Jaquemet 2005)
North Pacific Ocean	Kure Atoll	~2,000 birds	Harrison et al. 1983
North Pacific Ocean	Laysan Atoll	~4,000 birds	Harrison et al. 1983
North Pacific Ocean	Lisianski Island	~4,500 birds	Harrison et al. 1983
North Pacific Ocean	Midway Atoll	~3,000 birds	Harrison et al. 1983
North Pacific Ocean	Necker Island	~200 birds	Harrison et al. 1983
North Pacific Ocean	Nihoa Island	~500 birds	Harrison et al. 1983
North Pacific Ocean	O'ahu Island	Unknown	Vanderwerf and Young 2014
North Pacific Ocean	Pearl and Hermes Reef	~200 birds	Harrison et al. 1983
North Pacific Ocean	Tern Island	~590 birds	Seavy and Reynolds 2007
South-east Pacific Ocean	Desventuradas Island	Unknown	Luna et al. 2018
South-east Pacific Ocean	Rapa Nui (Easter Island)	Unknown	Varela et al. 2018
South-east Pacific Ocean	Salas y Gomez Island	Unknown	Varela et al. 2018
South-west Pacific Ocean	Bedwell Island	Unknown	Lapwood 2004
South-west Pacific Ocean	North-east Herald Cay	~205 pairs	Marchant and Higgins 1990
South-west Pacific Ocean	South-west Herald Cay	~5 pairs	Marchant and Higgins 1990
South-west Pacific Ocean	Kermadec Island Group	Unknown	Ismar et al. 2011
South-west Pacific Ocean	Lady Elliot Island	~5 pairs	Marchant and Higgins 1990
South-west Pacific Ocean	Lord Howe Island	~400 birds	Lapwood 2004
South-west Pacific Ocean	Norfolk Island	~400 birds	Lapwood 2004
South-west Pacific Ocean	Raine Island	~58 pairs	Dobbs 2004
South-west Pacific Ocean	Rose Atoll	Unknown	Morrell and Aquilani 2000

eggs, but predation of young, unattended hatchlings has been recorded (Luna *et al.* 2018). Early-stage chicks on Rapa Nui are also vulnerable to the invasive Argentine Ant *Linepithema humile* (Varela *et al.* 2018). This ant is present at nest sites and the death of a 2-day old chick from predation by the ants has been recorded (Varela *et al.* 2018). Recent breeding success rates on Rapa Nui are low, with reports showing just a 37% success rate in 2014 and an even lower 26% in 2015 (Flores *et al.* 2017).

The largest Australian breeding colony is on Christmas Island, where RTT have suffered breeding failures due to intense predation on chicks by feral cats *Felis catus*. The size of the colony has been estimated to be 1,400- 2,000 breeding pairs (Stokes and Baker 2015). However, population estimates for this location originate from research projects undertaken in the late 1980s and, given the severity of recent nest failures, these

figures require further supplementation to ascertain the stability of the Christmas Island breeding colony. We know that in 2006 feral cat predation eliminated 97.6% of RTT chicks at this location (Stokes and Baker 2015). Feral cat eradication schemes have been conducted on Christmas Island to conserve seabird breeding populations, and whilst consequent RTT recovery has yet to be documented in the literature, recent analysis suggests that there will be increases in RTT reproductive success provided that increased rat predation is not observed as a result of cat eradication (Plein *et al.* 2022).

Predator control efforts on O'ahu resulted in a positive effect on RTT reproduction rates (Vanderwerf and Young 2014). Between 2006 and 2013, the introduced mongoose *Herpestes auropunctatus*, feral cats and rats *Rattus* spp. were trapped and removed, which apparently increased nesting success. Throughout these years, however, 18% of nest failures were

still attributable to predation (Vanderwerf and Young 2014). Continued monitoring of breeding populations on O'ahu shows encouraging results, with an annual population growth rate of 11% estimated as recently as 2021 (Vanderwerf 2021; Saunier *et al.* 2022).

As well as the effects of predation, there is also the predicted negative impact of climate change on RTT populations due to rising sea levels. There have been global sea-level rise predictions of 1-2 m by the year 2100, which will result in substantial losses of nesting habitat for a broad range of seabird species, including *P. rubricauda* (Reynolds *et al.* 2013). Recorded declines in *P. rubricauda* presence attributed to the loss of viable nesting habitat on Tern Island have been directly linked to rising sea levels (Hatfield *et al.* 2012). The threat of rising sea levels has also been identified on Midway, Laysan and Kure Atolls, which are important breeding grounds for the RTT (Table 1; Vanderwerf and Young 2014).

Extreme weather events, such as tropical cyclones, can also greatly reduce RTT nesting success. The response of RTTs to Cyclone Rosie was documented by Hennicke and Flachsbarth (2009). The cyclone impacted the Christmas Island colony and caused significant losses of nest sites, active nests and eggs (Hennicke and Flachsbarth 2009). However, adult mortality was not observed, as adults can move out of the path of the storm (Hennicke and Flachsbarth 2009). Adult RTTs typically do not delay breeding in response to extreme weather, but most nests fail in the aftermath of the event (Hennicke and Flachsbarth 2009). Climate change models predict the continued rise of sea levels and increasing storm magnitudes as global average temperature rises; this could heavily impact RTT nesting sites and influence population trends in the near future (Hansen *et al.* 2016; Dias *et al.* 2019). Studies that explore practical solutions to mitigate these predicted climate change impacts are urgently needed.

DISCUSSION

This review highlights areas in which information on the biology of RTTs is lacking. Most importantly, there are elements of RTT at-sea distribution that require further research which could greatly enhance future conservation strategies. Analysis of global threats to seabirds emphasises their vulnerability to (a) fisheries that target surface-dwelling fish species (Le Corre and Jaquemet 2005; Danckwerts *et al.* 2014), (b) invasive species (Kropidowski 2014; Varela *et al.* 2018; Luna *et al.* 2018; Saunier *et al.* 2022) and (c) climate change (Dias *et al.* 2019). Two of these major threats are already known to affect RTT populations, but recent research has identified potential Marine Protected Areas that could benefit their at-sea distribution (Le Corre *et al.* 2012). The need for research on RTTs' oceanic distribution, as well as their genetic health (Varela *et al.* 2021), is highlighted here in the context of these ever-growing threats in order to allow more accurate prediction of the future status of the species.

Little literature describing genetic variation among RTT populations was uncovered during this review. Currently four subspecies of RTT are recognized (Clements *et al.* 2021). However, recent mitochondrial DNA analysis suggests a much higher level of genetic connectivity among breeding colonies than might be hypothesized from our understanding of levels of

nest-site fidelity (Varela *et al.* 2021). Given that nest-site fidelity and philopatry appear to be strong, there is the expectation that breeding colonies should be highly genetically distinct, but this does not appear to be the case. This also raises the question of which individuals disperse from their natal sites and how they find established colonies. Moreover, the establishment of new colonies is not uncommon (Priddel *et al.* 2010; Buden 2012; Raine *et al.* 2017; Donegan *et al.* 2018). Further genomic research, together with the parallel collection of data on sex, age and the status of populations, would be valuable in allowing us to better understand which individuals disperse, at what ages, and from which sites. Studies of the closely related White-tailed tropicbird have already used genetic information to establish conservation management priorities (e.g. determining effective population sizes), and could also inform future approaches in RTT research and conservation (Wang *et al.* 2016; Nunes *et al.* 2017; Humeau *et al.* 2020).

Breeding colonies are susceptible to physical environmental disturbances and increasing predation, so breeding grounds must be monitored and protected in order to sustain the species. The RTT has specific resource requirements in terms of food and nest site availability that must be met for population growth and sustainability. Very limited up-to-date information is available on breeding colonies in Australian waters and elsewhere, and this is particularly concerning because the Australian RTT breeding population is Near Threatened (Garnett *et al.* 2011) and other populations may also be nearing the threatened threshold.

The fundamental resource requirements of the RTT are outlined in this review, but we also detail regional variability in these requirements. To best protect this species from further reproductive losses, the bodies governing breeding ground islands need to focus on facilitating research that will identify the *regionally-specific* terrestrial and marine resources upon which RTTs rely.

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