BREEDING ECOLOGY OF
RED - TAILED TROPICBIRDS (*PHAETHON RUBRICAUDA*)
ON NUKUTEPIPI, FRENCH POLYNESIA

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science in Zoology at Massey University, Palmerston North.

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2025

Abstract

This thesis investigated the breeding ecology of red-tailed tropicbirds (*Phaethon rubricauda*) on the atoll Nukutepipi, French Polynesia, focusing on parental behaviours during the incubation and chick-rearing periods, and chick growth rates. From 1 March to 25 May 2024, the study monitored 55 eggs, 13 of which failed to hatch, resulting in a hatching success rate of 76.4%. Additionally, 24 hatched chicks present at the study's outset were included. Parental behaviours during incubation were characterised by alternating shifts of incubation and foraging trips, which lasted an average of 10.4 days. Occasional desynchronisation between parents sometimes left eggs unattended, making them vulnerable to predation by strawberry hermit crabs (*Coenobita perlatus*). During the chick-rearing period, parental attendance decreased as chicks matured, dropping from 60% in the first 10 days to just 1% by day 80, with a slight increase approaching fledging. A bimodal foraging strategy was observed: long foraging trips for self-feeding (11.3 days) and short trips for chick provisioning (1.1 days). Meal sizes increased with chick age, starting at 18 g for younger chicks and reaching 86 g for older ones. The diet included fish from eight families, with Carangidae, Exocoetidae, and Balistidae being the most common. Chick growth varied significantly, with fledglings exhibiting adult-like head and tarsus-to-middle-toe lengths but shorter culmen, wing, and tail lengths. Body mass increased rapidly early in development, reaching an asymptotic mass of approximately 700 g before declining near fledging. Fasting periods, averaging 2.9 days, consisted of two phases. Of the 65 chicks monitored, only five fledged and 26 died, yielding a fledging success rate estimated to be between 7.7% and 60%. Starvation was the leading cause of chick mortality, accounting for 65.4% of deaths. This study provides valuable insights into the breeding ecology of red-tailed tropicbirds in the previously unstudied Nukutepipi colony.

Résumé

Cette thèse a exploré l'écologie de reproduction des phaétons a brins rouges (*Phaethon rubricauda*) à Nukutepipi, un atoll situé en Polynésie Française. Elle se concentre sur les comportements parentaux durant l'incubation et l'élevage du poussin, ainsi que sur la croissance des juvéniles. L'échantillonnage a identifié 55 œufs, dont 76,4% d'éclosion, et 24 poussins déjà éclos. Les comportements parentaux pendant le couvage se caractérisaient par des relais alternés entre des périodes d'incubation et des vols pour s'alimenter. Une désynchronisation entre les parents laissait parfois les œufs sans surveillance, les exposant à des prédateurs, comme les bernards-l'hermite. Pendant la période d'élevage des poussins, les parents adoptaient une stratégie d'approvisionnement bimodale : un partait en quête de nourriture pour s'alimenter (11,3 jours), tandis que l'autre s'absentait pour une courte durée pour nourrir leur poussin (1,1 jour). La quantité des repas corrélait avec l'âge des poussins, passant de 18g pour les petits à 86g pour les plus grands. Le développement physique des poussins variait considérablement. À l'envol, les jeunes présentaient des longueurs de tête et de tarses similaires aux adultes. En revanche, les becs, ailes et queues étaient plus courts. La masse des juvéniles augmentait rapidement au début de leur développement, atteignant un pic asymptotique d'environ 700g avant de diminuer à l'approche de l'envol. Et enfin, l'étude s'est également focalisée sur les périodes de jeun chez les juvéniles, qui duraient en moyenne 2,9 jours. Parmi les 65 poussins suivis, cinq ont pris leur envol et 26 sont morts, ce qui donne un taux de succès à l'envol estimé entre 7,7% et 60%. Les causes de mortalité juvénile sont multiples, dont la principale serait la famine (65,4%). Cette étude permet de comprendre les comportements parentaux et l'évolution des phaétons à brins rouges dans un environnement encore non étudié, Nukutepipi.

Acknowledgements

I would like to begin by expressing my deepest gratitude to my main supervisor, Professor Murray Potter, for his unwavering guidance, expertise, and encouragement throughout this journey, as well as for his insightful comments on the manuscript. His mentorship has been a cornerstone of my academic growth. Special thanks to Associate Professor Phil Battley for his support, invaluable advice on statistical analyses in R, and constructive feedback on the manuscript.

I am also profoundly thankful to Xavier Bessou for facilitating access to Nukutepipi and for serving as an indispensable liaison. My sincerest thanks go to Guy Laliberté for his generosity in granting me the privilege of conducting my research on his private island – an opportunity that would not have been possible without their support.

I am deeply grateful to Joël Haereraaroa for his invaluable support in the field and for allowing Tuterai and Heiry to work with me as field assistants. I extend special thanks to Tuterai and Heiry for their exceptional assistance in handling red-tailed tropicbird adults and juveniles with care and expertise. Their help was essential for managing the challenging aspects of data collection and ensuring the welfare of the birds during the study. I wish to thank Rémi for his contributions to data analysis in Excel, which facilitated the analysis of complex data.

Finally, I am also grateful for the love and emotional support of my family: my mother and father, Brigitte and David Loussan; my partner, Hunter Tito; and my cousin, Jason Vandal. This thesis represents a collaborative effort, and I am deeply appreciative of everyone who played a role in making it possible.

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1. General Introduction

The red-tailed tropicbird (*Phaethon rubricauda*) belongs to the family Phaethontidae. It is sexually monomorphic, meaning that males and females cannot be visually distinguished (Veit & Jones, 2003). The adult red-tailed tropicbird is a medium-sized seabird, weighing between 600 and 800 g (Fleet, 1974). It has a unique distinctive appearance, characterised by two long red tail streamers and red serrated bill, which contrast with its predominantly white plumage. Additionally, it has a black patch located in front of the eye that extends in a linear shape past the eye (Fleet, 1974).

The breeding season of red-tailed tropicbirds, which typically occurs during austral summer, is believed to be driven by prey availability (Le Corre, 2001). Red-tailed tropicbirds forage solitarily and exhibit remarkable diving capabilities, using a plunge-diving technique that combines momentum, wing movement, and foot propulsion to reach depths of up to 25.6 m (Le Corre *et al.*, 2003; Sommerfeld & Hennicke, 2010). Their diet is highly varied and includes a broad range of surface-dwelling fish and cephalopod species. Although prey composition varies seasonally and regionally, flying fish, mahi mahi (dolphin fish; *Coryphaena hippurus*), and squid are consistently the most common components of their diet (Fleet, 1974; Diamond, 1975; Le Corre *et al.*, 2003; Sommerfeld & Hennicke, 2010). Le Corre and his colleagues (2003), who studied the feeding ecology of this seabird species on Europa Island, documented a diet consisting of 13 fish families and three cephalopod families in their diet, with prey items averaging 49.4 g in mass and ranging from 2.8 to 197 g. Red-tailed tropicbirds are capable of carrying prey weighing up to 26% of their body mass (Le Corre *et al.*, 2003).

Red-tailed tropicbirds are pelagic seabirds that spend most of their lives foraging and resting in open ocean waters (Egerton *et al.*, 2022). As shown in Figure 1-1, this species has a broad at-sea distribution, occurring primarily in the tropical and subtropical regions of the Pacific Ocean, but also in the Indian and Atlantic Oceans. This range is similar to that of its congeners, the white-tailed tropicbird (*P. aethereus*) and red-billed tropicbird (*P. lepturus*) (Fleet, 1974; Le Corre *et al.*, 2003; Spear & Ainley, 2005; Bond *et al.*, 2015; Flores *et al.*, 2017).

During the breeding season, however, its range becomes restricted to the Pacific and Indian Oceans, where they come ashore to breed on remote islands or atolls with minimal disturbances (Spear & Ainley, 2005). Due to their vast, open-ocean range, the ecology and behaviour of red-tailed tropicbirds during the non-breeding season have been studied less extensively, making them less well understood compared to their breeding season ecology (Le Corre *et al.*, 2003).

A comprehensive summary of breeding ecology observations from various breeding sites worldwide is compiled in Appendix A, providing valuable insights into variations and commonalities across their range.

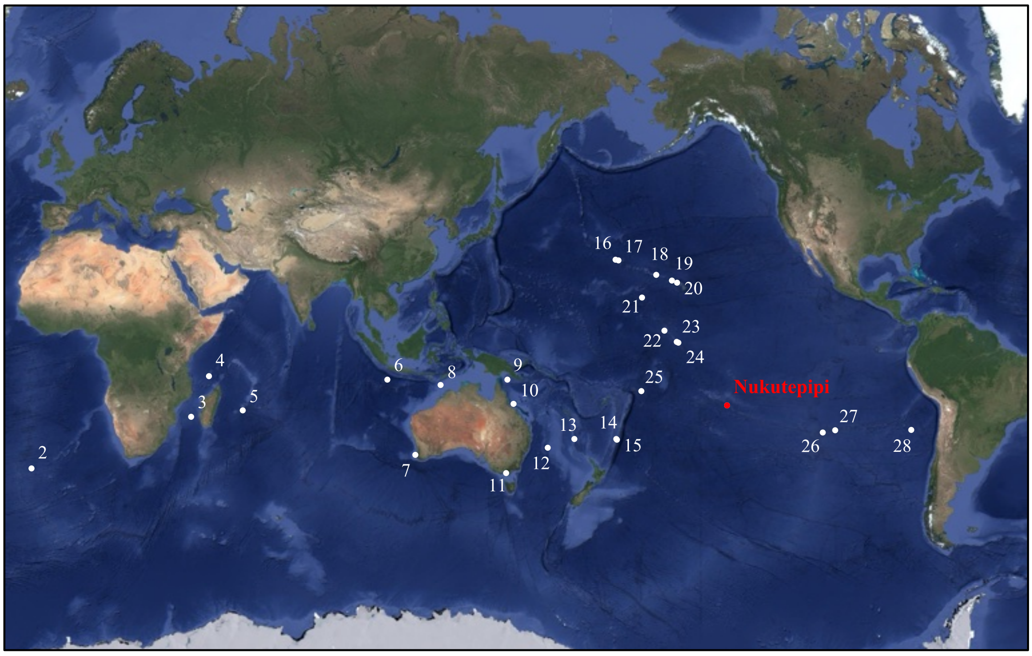

Figure 1-1. Sites with published observations of red-tailed tropicbirds (refer to Table 1-1 for site names).

Table 1-1. Literature review of the distribution of red-tailed tropicbirds.

Site number	Site name	Latitude	Longitude	No. of publications	Reference key*
1	Nukutepipi	-18.7747	-141.2246	0	
2	Inaccessible Is.	-37.2515	-12.7765	1	2
3	Europa Is.	-22.3500	40.3667	4	24, 25, 26, 37
4	Aldabra Atoll	-9.3000	46.3000	4	8, 12, 35, 49
5	Mauritius	-20.3484	57.5521	1	18
6	Christmas Is.	-10.4475	105.6904	9	6, 7, 10, 11, 19, 34, 46, 47, 51
7	Sugarloaf Rock	-33.5593	115.0051	2	48, 49
8	Ashmore Reef	-12.1961	123.4125	1	33
9	Raine Is.	-10.4433	145.6517	2	1, 36
10	Great Barrier Reef Is.	-18.2871	147.6992	1	36
11	Phillip Is.	-38.4833	145.2333	1	52
12	Lord Howe Is.	-31.5580	159.0833	1	32
13	Norfolk Is.	-29.0300	167.9500	1	49
14	Kermadec Is.	-29.0333	-178.1000	1	22
15	North Meyer Is.	-29.2458	-177.8775	2	22, 52
16	Kure Atoll	28.3986	-178.3307	3	14, 15, 49
17	Midway Is.	28.2000	-177.3660	5	20, 21, 27, 44, 45
18	Tern Is.	23.8533	-164.7900	5	5, 43, 55, 56, 57
19	Kauai	22.0964	-159.5734	2	13, 52
20	0'ahu	21.4389	-157.8583	3	50, 51, 52
21	Johnston Is.	16.7364	-169.5306	7	9, 17, 38, 39, 40, 41, 42
22	Palmyra Atoll	5.8832	-162.0664	1	58
23	Kiribati	1.8721	-157.4278	4	3, 4, 38, 39, 43
24	Caroline Is.	2.1430	-157.9684	1	23
25	Rose Atoll	-14.1953	-169.7467	1	31
26	Easter Is.	-27.1225	-109.3497	4	16, 28, 29, 54
27	Salas & Gomez Is.	-26.4500	-105.2200	1	53
28	Desventuras Is.	-26.3436	-79.8911	1	30

*References cited here are presented in Appendix B

Red-tailed tropicbirds typically nest in cliff cavities or on the ground under shrubs or trees such as molasses grass (*Melinis minutiflora*), beach naupaka (*Scaevola taccada*), pisonia (*Pisonia grandis*), salt bush (*Pemphis acidula*), and pandanus (*Pandanus christmatensis*) (Fleet, 1974; Prys-Jones & Peet, 1980; Clark *et al.*, 1983; Morrell & Aquilani, 2000; Hennicke & Flachsbarth, 2009; Flores *et al.*, 2017). Their nest sites must provide sufficient shade to prevent egg addling (i.e., the cessation of embryo development) and to protect chicks from heat stress, as these seabirds lack the ability to thermoregulate through gular fluttering, a heat-dissipating mechanism present in many other bird species. Additionally, due to their poor walking ability caused by reduced and posteriorly located hind limbs, they require nest sites that are relatively free of obstructive stems (Prys-Jones & Peet, 1980; Clark *et al.*, 1983; Morrell & Aquilani, 2000). Finding a nest site that meets both shade and accessibility requirements can be challenging in their natural environment. Morrell and Aquilani (2000) observed that on Rose Atoll, red-tailed tropicbirds prioritised shade over stem-free areas, nesting further beneath vegetation. In contrast, Clark and his colleagues (1990) reported an opposite trend on Kiribati (Christmas Island, central Pacific Ocean), where red-tailed tropicbirds nested closer to shrub edges.

The clutch size of red-tailed tropicbirds consists of a single egg, which requires between 40 and 50 days to hatch (Fleet, 1974; Sommerfeld *et al.*, 2015). Due to the scarcity and uneven distribution of prey in tropical regions, red-tailed tropicbird parents must balance reaching productive foraging areas and returning to the nest to incubate (Sommerfeld & Hennicke, 2010). As a result, incubation duties are equally shared between males and females, with one partner incubating the egg while the other forages at sea. The duration of incubation shifts varies among colonies. For example, on Aldabra, Europa, and Christmas Island, parents incubate the egg for 4 to 6 days per shift, whereas on Kure Atoll, shifts can last up to 8 days (Fleet, 1974; Diamond, 1975; Le Corre *et al.*, 2003; Sommerfeld & Hennicke, 2010).

Newly hatched chicks are covered in white or grey down feathers (Fleet, 1974). They are brooded under a parent's body or wing for up to 10 days on Johnston Atoll and up to 25 days on Kure Atoll (Fleet, 1974; Amerson & Shelton, 1976). After this brooding period, parental attendance at the nest gradually decreases, with parents returning primarily to feed the chick. As in the incubation period, high synchronisation between parents is essential during the chick-rearing period to ensure the survival of both the chick and the parents themselves. Although the foraging behaviour of red-tailed tropicbirds has not been studied extensively, researchers have identified two distinct strategies.

On Europa Island, red-tailed tropicbirds adopted a unimodal foraging strategy, with foraging trips lasting about 34 hours (Le Corre *et al.*, 2003). In contrast, on Christmas Island, they employed a bimodal foraging strategy (Sommerfeld & Hennicke, 2010). Due to the low and unpredictable food availability around Christmas Island, parents alternated between short (ST) and long (LT) foraging trips. During a series of STs – each lasting approximately 3 hours – one parent foraged in nearby waters, which, although low in prey, allowed frequent provisioning for the chick. Meanwhile, the other parent embarked on an LT of 57 hours to distant, more productive feeding areas to replenish its own body reserves. Upon the LT-parent's return, roles were reversed. This allowed the ST-parent to undertake an LT and recover from the mass loss incurred during STs. This bimodal foraging strategy enabled red-tailed tropicbird parents to maintain their body condition while ensuring the chick received a consistent supply of food (Sommerfeld & Hennicke, 2010). This strategy has also been observed in other seabird species, including white-tailed tropicbirds (Campos *et al.*, 2018), red-billed tropicbirds (Beard *et al.*, 2023), little shearwaters (*Puffinus assimilis haurakiensis*) (Booth *et al.*, 2000), Cory's shearwaters (*Calonectris diomedea*) (Granadeiro *et al.*, 1998), and wandering albatrosses (*Diomedea exulans*) (Weimerskirch *et al.*, 1993).

Regardless of their foraging strategy, red-tailed tropicbird parents must coordinate effectively to ensure their chick's survival by providing food frequently and in sufficient amounts. Meal sizes generally increase as chicks grow, as smaller chicks have a limited capacity for swallowing and digestion compared to larger ones (Schaffner, 1990; Schreiber, 1996; Ramos & Pacheco, 2003). Consequently, seabird parents forage for an optimal meal size rather than maximising carrying capacity. On Kure Atoll, Fleet (1974) reported that red-tailed tropicbird parents delivered meals averaging 66 g. Additionally, white-tailed tropicbird parents have been observed to carry only 40% of the maximum transportable payload (Ramos & Pacheco, 2003).

In tropical areas, where prey is scarce and unevenly distributed, growth rates of pelagic seabird juveniles tend to be relatively slow (Ramos & Pacheco, 2003). While the growth patterns of many pelagic seabirds are well-documented, red-tailed tropicbird chick growth remains poorly studied.

Red-tailed tropicbird chicks fledge after 80 to 90 days. Upon fledging, they have an immature plumage characterised by white and black feathers (Fleet, 1974; Diamond, 1975; Amerson & Shelton, 1976; Vanderwerf & Young, 2014). At fledging, the culmen and wings are still shorter than those of adults, whereas their tibiotarsi and feet reach adult size by day 35. Tail feathers stop growing at 75 days but remain shorter than adult tails, as juveniles lack the species' distinctive long red tail streamers (Fleet, 1974).

Weight gain during development follows a consistent pattern. Chicks experience rapid mass gain during the first 40 days, followed by gradual increases until they reach a "pre-fledging asymptotic mass" that is 10–20% greater than adult mass (Diamond, 1975; Schreiber, 1996). In the final 6–12 days before fledging, parents stop feeding the chick, leading to a drop in mass that reduces wing loading and ultimately facilitates first flight (Schreiber, 1996). Although specific data on mass gain and loss rates for red-tailed tropicbirds are unavailable, studies on white-tailed tropicbirds provide valuable insights. White-tailed tropicbird chicks gain mass at a mean rate of 7.8 g/day for the first 35 days, slowing to 3.7 g/day from days 36–60, then losing 1.5 g/day from days 61–80 in preparation for flight (Ramos & Pacheco, 2003). This pattern of excess weight gain followed by pre-fledging mass loss is typical in tropicbirds (Schaffner, 1990) and other pelagic seabirds such as Leach's storm-petrels (*Hydrobates leucorhous*) and northern fulmars (*Fulmarus glacialis*) (Ricklefs & Schew, 1994; Philips & Hamer, 1999).

Throughout their development, red-tailed tropicbird juveniles spend the majority of their time alone at the nest, as their parents forage at sea and return only to feed their chick (Fleet, 1972). However, these youngsters may go unfed for extended periods due to the limited and uneven distribution of prey in their marine environment, often resulting in prolonged parental foraging trips, which can disrupt parental coordination in provisioning their chick (Sommerfeld & Hennicke, 2010).

In general, birds undergo three distinct phases during fasting periods. Phase I begins immediately after a feeding event and can last from hours to days, depending on the species. This phase is characterised by a rapid decline in body mass due to the excretion of urine and faeces, as well as the breaking down of carbohydrates – primarily glycogen – to meet immediate energy demands (Jenni-Eiermann & Jenni, 2012). Once glycogen reserves are exhausted, birds transition to Phase II, known as the "long phase of economy" (Cherel *et al.*, 1987). During this phase, the rate of mass loss is significantly lower than in Phase I, as lipids become the primary energy source. The duration of Phase II depends on an individual bird's initial fat reserves and overall body condition (Jenni-Eiermann & Jenni, 2012). When fat stores are depleted, birds enter the critical and final stage of fasting, Phase III. In this phase, birds lose body mass at a rapid rate as the body begins breaking down muscle protein to sustain energy requirements. This muscle catabolism leads to severe physiological stress, significantly weakening the bird's overall condition and ultimately leading to death if food intake is not resumed (Cherel *et al.*, 1987; Jenni-Eiermann & Jenni, 2012).

The duration of these fasting periods varies widely among seabird species. For instance, Fleet (1974) observed that red-tailed tropicbird juveniles on Kure Atoll were rarely unfed for more than 3.5 days – a pattern common among most procellariiform chicks. In contrast, fasting periods can reach extreme durations such as 13 nights in short-tailed shearwaters (*Puffinus* *tenuirostris*) or even five months in king penguin chicks (*Aptenodytes patagonica*) (Cherel *et al.*, 1987; Hamer *et al.*, 1997). While fasting durations of many seabird species have been studied, those of red-tailed tropicbird chicks remain poorly quantified.

As previously mentioned, well-coordinated foraging behaviour in seabird parents plays a crucial role in enhancing the survival of their egg or chick. However, due to various environmental factors, survival outcomes can vary among colonies. For example, Richardson and colleagues (2023) reported that most nest failures among red-tailed tropicbirds on Raine Island occurred during the incubation period rather than the chick-rearing period. This resulted in a hatching success rate of 39.3%, significantly lower than the fledging success rate of 77.8%. A similar trend was recorded on Johnston Island, where the hatching success rate reached 71.9%, while fledging success rate was even higher at 98% (Amerson & Shelton, 1976). In contrast, other colonies of red-tailed tropicbirds showed the opposite pattern. On Christmas Island, hatching success was 60.5%, compared to a lower fledging success rate of 54.7%. Similarly, on O'ahu, hatching success and fledging success rates were 79.2% and 77%, respectively (Vanderwerf & Young, 2014; Sommerfeld *et al.*, 2015).

Despite being classified as "Least Concern" by the IUCN (Egerton *et al.*, 2022), red-tailed tropicbirds face various challenges that contribute to nest failures during both the incubation and chick-rearing periods. A significant risk is the lack of synchrony between parent birds in their foraging and nesting duties, which may arise from difficulties in finding prey, thereby prolonging foraging trips (Sommerfeld & Hennicke, 2010). When parents are not well coordinated, the nest may be left unattended for extended periods, leaving their egg or young chick exposed to predators. Among these predators, rats (*Rattus* spp.) are particularly prevalent, posing a serious threat to seabird nests by preying upon eggs and small chicks (Fleet, 1972; Vanderwerf & Young, 2014; Sommerfeld *et al.*, 2015; Flores *et al.*, 2017; Luna *et al.*, 2018).

On Kure Atoll, Fleet (1972) observed that rat predation accounted for more than half of all red-tailed tropicbird egg losses and was responsible for the loss of all chicks. Other predators include feral cats (*Felis catus*) (Vanderwerf & Young, 2014; Sommerfeld *et al.*, 2015), feral pigs (*Sus scrofa*) (Clark *et al.*, 1983), mongooses (*Herpestes auropunctatus*) (Vanderwerf & Young, 2014), chimango caracaras (*Milvago chimango*) (Flores *et al.*, 2017; Luna *et al.*, 2018), buff-banded rail (*Hypotaenidia philippensis*) (Richardson *et al.*, 2023), and bristle-thighed curlews (*Numenius tahitiensis*) (Schreiber, 2003). Additionally, as mentioned earlier, asynchronous parental care can lead to extended periods without food for chicks, sometimes resulting in starvation and death (Sommerfeld *et al.*, 2015; Vanderwerf, 2021).

In addition to the introduction of invasive species, nest failures can be attributed to other human activities such as vegetation trimming which leaves nests exposed to the sun (Amerson & Shelton, 1976; Schreiber, 2003), the exploitation of birds for ornamental purposes or food (Flores *et al.*, 2017), and industrial fisheries that compete with seabird species for food resources (Bertrand *et al.*, 2012; Danckwerts *et al.*, 2014; Egerton *et al.*, 2022). Climate change further exacerbates these challenges by altering ocean temperatures and currents, impacting prey availability, and rising sea levels that reduce suitable nesting habitat for red-tailed tropicbirds (Hatfield *et al.*, 2011; Hazen *et al.*, 2012; Vanderwerf & Young, 2014).

Additionally, climate change increases the frequency and intensity of El Niño-Southern Oscillation (ENSO) events – a natural climate pattern driven by ocean-atmosphere interactions – posing further challenges. ENSO is characterised by warmer sea temperatures and disrupted weather patterns during El Niño, while La Niña brings cooler waters and stronger trade winds (England, 2000; Wang & Fiedler, 2006). These fluctuations alter ocean currents, weakening or reversing upwelling systems during El Niño and strengthening them during La Niña, which in turn affects nutrient distribution and marine productivity (England, 2000; Wang & Fiedler, 2006). As a result, prey availability becomes more unpredictable for seabirds, leading to reduced foraging success, lower breeding rates, and even starvation-induced mortality (England, 2000; Jaksic, 2004; Wang & Fiedler, 2006). Moreover, heavy rainfall and storms associated with strong El Niño events can cause flooding, which directly threatens ground-nesting seabirds like red-tailed tropicbirds by submerging nests and further limiting available nesting sites (England, 2000; Jaksic, 2004). One of the most severe ENSO events, which occurred in 1982–1983, resulted in the death of an estimated 75–90% of the 10–12 million seabirds breeding on Kiribati (Schreiber & Schreiber, 1989).

The study conducted on Nukutepipi took place from 1 March to 25 May 2024. According to The International Research Institute for Climate and Society, Columbia University Climate School (2024), the central-eastern Pacific experienced a moderate to strong El Niño event beginning in mid-February 2024, which began to weaken in mid-March but persisted through April and May. Moderate to strong El Niño events have previously been associated with slower chick growth in red-tailed tropicbirds on Kiribati, likely due to reduced food supply by parents, although high fledging success rates were still observed (Schreiber, 1996).

This thesis explores the breeding ecology of red-tailed tropicbirds on Nukutepipi, a predator-free island located in the Pacific Ocean. The absence of mammalian predators offers a unique opportunity to examine alternative environmental factors that contribute to nest failures. The study focuses on three main topics: (1) parental behaviours during incubation, (2) parental behaviours during the chick-rearing period, and (3) chick growth rates. Each chapter consists of an introduction, methods and materials, and a results section, followed by a general discussion of the findings. The research is structured around several hypotheses designed to explore the factors influencing breeding success and chick development in red-tailed tropicbirds on Nukutepipi. Data analyses were conducted using Microsoft Excel and R (version 2023.06.0+421).

First, it was hypothesised that parents alternate between incubation shifts and foraging trips during the incubation period. To test this, nest visits were conducted two to three times daily to document which parent was present at the nest. Since males and females are visually indistinguishable, individual parents were identified using coloured markers.

Second, parental behaviours during the chick-rearing period were analysed. It was hypothesised that parental attendance decreases as chicks grow older. Additionally, parents were expected to exhibit a unimodal foraging strategy, given Nukutepipi's remote location in the central Pacific Ocean, far from major landmasses and presumably less affected by industrial fisheries. To test these hypotheses, nest visits were conducted two to three times daily to document parental presence or absence. The data were then analysed to determine the duration of their foraging trips. Furthermore, it was hypothesised that meal sizes delivered to chicks positively correlate with chick age. Chicks were weighed two to three times daily, and meal sizes were estimated by calculating the mass increments between consecutive weighings.

Finally, chick development was investigated. It was hypothesised that fledglings leave the nest with body mass and morphometrics similar to adults. Additionally, chicks were expected to undergo fasting periods consisting of three distinct phases. To evaluate these hypotheses, chicks were weighed two to three times daily, and their morphometrics (head, culmen, tarsus-to-middle-toe, wing, and tail lengths) were measured weekly.

2. Study Site & Ethical and Regulatory Considerations

2.1 Study site

The study was conducted on Nukutepipi (20°70'S, 143°05'W), a tropical atoll in French Polynesia. It is approximately 750 km east-south-east of Tahiti, where the capital city Papeete is situated. Nukutepipi's closest neighbouring island is Anuanuranga, located 22 km away and uninhabited. Nukutepipi is a 2.7 km long trapezoid-shaped atoll, compromising two motu (islands), with a total area of 5.6 km^2. Inhabited by less than 50 people, Nukutepipi is privately owned. Human activity is limited and restricted to the larger motu.

Nukutepipi was discovered by Pedro Fernández de Quirós in 1606, but it remained uninhabited for many years. The atoll saw its first settlement in 1908, after which it underwent several ownership changes. Early owners cleared vegetation to establish a coconut plantation for copra production, and the lagoon was used to harvest mother-of-pearl oysters. These exploitations ended in 1991, though ownership continued to change until 2019, when the island was acquired by Guy Laliberté. Laliberté transformed Nukutepipi into a luxury eco-retreat with a focus on preserving its natural flora and fauna. Despite its varied ownership history, fishing in the lagoon has always been prohibited, and this restriction remains in place under Laliberté's ownership. Currently, human infrastructure occupies about 25% of the larger motu, and approximately 85% of the vegetation consists of native species. The dominant plant species include pisonia or pu'atea (*Pisonia grandis*), pandanus or fara (*Pandanus tectorius*), tree heliotrope or tāhinu (*Heliotropium foertherianum*), bantigue or miki miki (*Pemphis acidula*), and coastal she-oak or 'aito (*Casuarina equisetifolia*). Their distribution across the motu is illustrated in Figure 2-1.

Figure 2-1. Distribution of dominant vegetation under which most red-tailed tropicbirds nested on Nukutepipi.

Nukutepipi was until recently populated by Pacific rats (*Rattus exulans*), likely introduced by the island's first settlers. To support his vision of achieving self-sufficiency while protecting the island's native fauna, Laliberté initiated an eradication program. This was implemented in May 2023, and by May 2024, Nukutepipi was officially declared predator-free. No rodents were seen or heard during the fieldwork period. Nukutepipi's native avian fauna is dominated by red-tailed tropicbirds. They coexist with numerous other bird species, including great frigatebirds (*Fregata minor*), red-footed boobies (*Sula sula*), brown noddies (*Anous stolidus*), white terns (*Gygis alba*), and sooty terns (*Onychoprion fuscatus*). Migratory birds such as the Pacific long-tailed cuckoos (*Urodynamis taitensis*), Murphy's petrels (*Pterodroma *ultima*), bristle-thighed curlews (*Numenius tahitiensis*), and Pacific reef-egret (*Egretta sacra*) were also seen on Nukutepipi.

2.2 Ethical and regulatory considerations

The project was conducted in accordance with French Polynesia's Department of Environment (*Direction de l'Environnement*) Act LP. 2220-1 regulations. As the red-tailed tropicbird is an avian species declared to be of "Least concern", no authorisation was required to handle the birds. However, to enable future determination of the sex of the subjects via DNA analysis from collected feathers, regulations of the French Environmental Code (*Code de l'Environnement*) and, more specifically, the Access and Benefit-Sharing (*Accès et Partage des Avantages* or *APA*) Acts from LP 125-4 to LP 125-18, were respected. In addition, as all laboratory work needed to take place at Massey University, Palmerston North, New Zealand, both parasites and feathers had to be preserved in 70% ethanol for aerial transportation.

3. Parental Behaviours During Incubation Period

3.1 Introduction

Red-tailed tropicbirds typically breed during the austral summer, when prey availability tends to be higher (Le Corre, 2001). They select nest sites with specific characteristics to maximise the survival chances of their offspring. Due to their unusual anatomy – reduced, posteriorly located hind limbs that impair their walking ability – their nests must be located at ground level with minimal obstructions. Furthermore, suitable nest sites must provide adequate shade to protect chicks from heat stress, as this pelagic seabird species lacks the ability to thermoregulate via gular flutter (Prys-Jones & Peet, 1980; Clark *et al.*, 1983; Morrell & Aquilani, 2000). In their natural environment, finding nest sites that fulfil these requirements can be challenging. Studies have observed that red-tailed tropicbirds typically nest in sheltered locations such as cliff cavities or under vegetation like molasses grass, beach naupaka, pisonia, salt bush, and pandanus (e.g., Fleet, 1974; Prys-Jones & Peet, 1980; Clark *et al.*, 1983; Morrell & Aquilani, 2000; Hennicke & Flachsbarth, 2009; Flores *et al.*, 2017).

Red-tailed tropicbirds lay one egg which takes approximately 40–50 days to hatch (Fleet, 1974; Sommerfeld *et al.*, 2015). In tropical regions, where prey is often scarce and unevenly distributed, successful hatching requires strategic coordination between parents (Sommerfeld & Hennicke, 2010). To achieve this, breeding pairs alternate between incubation duties and foraging trips: while one parent incubates the egg, the other forages at sea. On Aldabra, Europa, and Christmas Islands, red-tailed tropicbird parents have been observed taking incubation shifts lasting 4 to 6 days (Diamond, 1975; Le Corre *et al.*, 2003; Sommerfeld & Hennicke, 2010). However, on Kure Atoll, shifts tend to be longer, extending up to 8 days (Fleet, 1974). The duration of incubation shifts – and consequently foraging trips – is primarily influenced by prey availability. When prey is limited and/or unevenly distributed, seabirds are forced to spend more time at sea, travelling longer distances to increase their chances of finding sufficient food. In other words, the scarcer the prey, the longer the foraging trips (Sommerfeld & Hennicke, 2010).

This study investigated parental behaviours under the hypothesis that parents alternate between incubation and foraging shifts. To test this, nests were visited two to three times daily to record shift durations. Because red-tailed tropicbirds are monomorphic, coloured markers were applied to their heads to distinguish individuals.

3.2 Methods and materials

3.2.1 Field work

Research was undertaken from 1 March to 25 May 2024, with a one-week break from 18–25 April. As the breeding season of red-tailed tropicbird colonies on Nukutepipi peaked midway through the study, 60 active nests, each containing either an egg or a chick, were monitored during the first month. Because chicks required more time to fledge than the duration of the study, priority was given to nests that already had a chick. Once the breeding season reached its peak, 20 more nests were added to the study, bringing the total to 80 nests. All nests were sampled on the larger motu, and their coordinates (latitude, longitude) were recorded and plotted on a map of Nukutepipi using QGIS to provide a spatial overview of their locations.

Apart from the addition of pink plastic tags for nest identification, the environments surrounding all red-tailed tropicbird nests remained unchanged. However, during the study, local staff trimmed the vegetation around three nests, exposing them to direct sunlight. To mitigate the loss of natural shade, wooden boxes were introduced to provide shelter and reduce heat stress on birds.

Red-tailed tropicbird parents were marked, measured, and weighed when first encountered. Since they are monomorphic, each individual in a pair was marked with either three vertical blue or red lines on the top of their head. Markings were reapplied as needed when adults returned to their nest. Streamers found on the ground were collected and labelled with the number of the nest to which they belonged, and, if possible, the colour of the individual (blue or red) was noted. In addition, three chest feathers of each adult were plucked for later sex determination via DNA analysis. These feathers were preserved in separate labelled zip-lock plastic bags containing 70% ethanol. Although the feathers were imported to New Zealand, sex determination of adults was not possible due to the limited timeframe available for the study. In addition, invertebrates parasitising the birds were documented, with a few samples were collected and preserved in 70% ethanol, each in an individual zip-lock plastic bag. Despite the parasites being brought into New Zealand, the identification of parasite species was not feasible due to the short duration of the study.

Visiting all nests required a considerable amount of time, so 24 nests were visited three times a day (i.e., morning, early afternoon, and late afternoon), while the remaining 56 nests were checked twice daily (i.e., morning and early afternoon). The set of parameters recorded at each nest included the date, time, nest number, bird identification (blue or red), number of streamers, and bird status, which included incubating, brooding a chick, resting next to a chick, and feeding. Nest visits were conducted 6 days a week.

3.2.2 Statistical analyses

The locations of the nests and their survival outcomes (as of late May 2024) were mapped on Nukutepipi using QGIS. The hatching success rate was then calculated. Additionally, factors contributing to egg losses were identified through field observations and expressed as percentages of the total egg losses.

To evaluate the breeding seasonality of red-tailed tropicbirds on the island, egg-laying and egg-hatching dates were visualised using a histogram. Since the age of most chicks was unknown, their hatching dates were predicted as outlined in Section 5.2.2. Egg-laying dates were then estimated by subtracting 40 days from the predicted hatching dates, based on observations from other red-tailed tropicbird colonies indicating that eggs typically require approximately 40 days to hatch. These data were then represented in a histogram to determine the breeding season of red-tailed tropicbirds on Nukutepipi. To assess whether the distributions of egg-laying and egg-hatching deviated from normality, the Shapiro-Wilk test was performed using the `shapiro.test` function in base R.

Daily nest attendance data were recorded in Excel. A scatterplot was generated to illustrate the presence of each parent within each pair at the nest during both the incubation and chick-rearing periods, relative to their chick's hatch date. Since nests that failed during the incubation period did not have a hatch date, the data were adjusted so that their hatch date corresponded to the date when eggs were observed to have broken or gone missing.

Since nests could not be monitored continuously, all subsequent calculations were based on the time and date (DateTime) of visits. The duration of parental incubation shifts was estimated using Excel by calculating the time difference between Visit 1 (when an individual was last observed incubating) and Visit 2 (when the individual was first observed incubating). Uncertainties regarding incubation shift durations, such as those occurring during the study break or weekends, were excluded from the data analysis. The remaining values were plotted against hatch dates in a scatterplot using the `ggplot2` package in R. Trends in incubation shift duration within nests were visualised using `geom_smooth` with a linear method (`lm`).

3.3 Results

The map of Nukutepipi, shown in Figure 3-1, displays the locations of the red-tailed tropicbird nests included in this study, along with their respective survival outcomes as of May 2024. Since most nests were selected at the start of the breeding season, their distribution appeared to be uneven across the main motu of Nukutepipi (Figure 3-1). However, as the breeding season progressed, more nests (unstudied) were spotted on the eastern and southern parts of the island, leading to a more even distribution throughout Nukutepipi. The far northern section seemed less suitable for nesting due to reduced vegetation and, consequently, less shade. Out of curiosity, the smaller motu was visited, but no red-tailed tropicbird nests were found. This was unexpected, as this motu had remained largely unchanged and unaffected by human activity.

A total of 80 nests were monitored, with 55 containing an egg. Of these, 13 failed to hatch, yielding a hatching success rate of 76.4% (Table 3-1). The primary factors contributing to egg mortality were broken eggs found in the nest and the absence of parental attendance, which made the eggs vulnerable to predation by strawberry hermit crabs (*Coenobita perlatus*) (Table 3-2). Other causes included trimming of bushes or trees by local staff, which led to nests being more exposed to the sun, and inadequate nest sites.

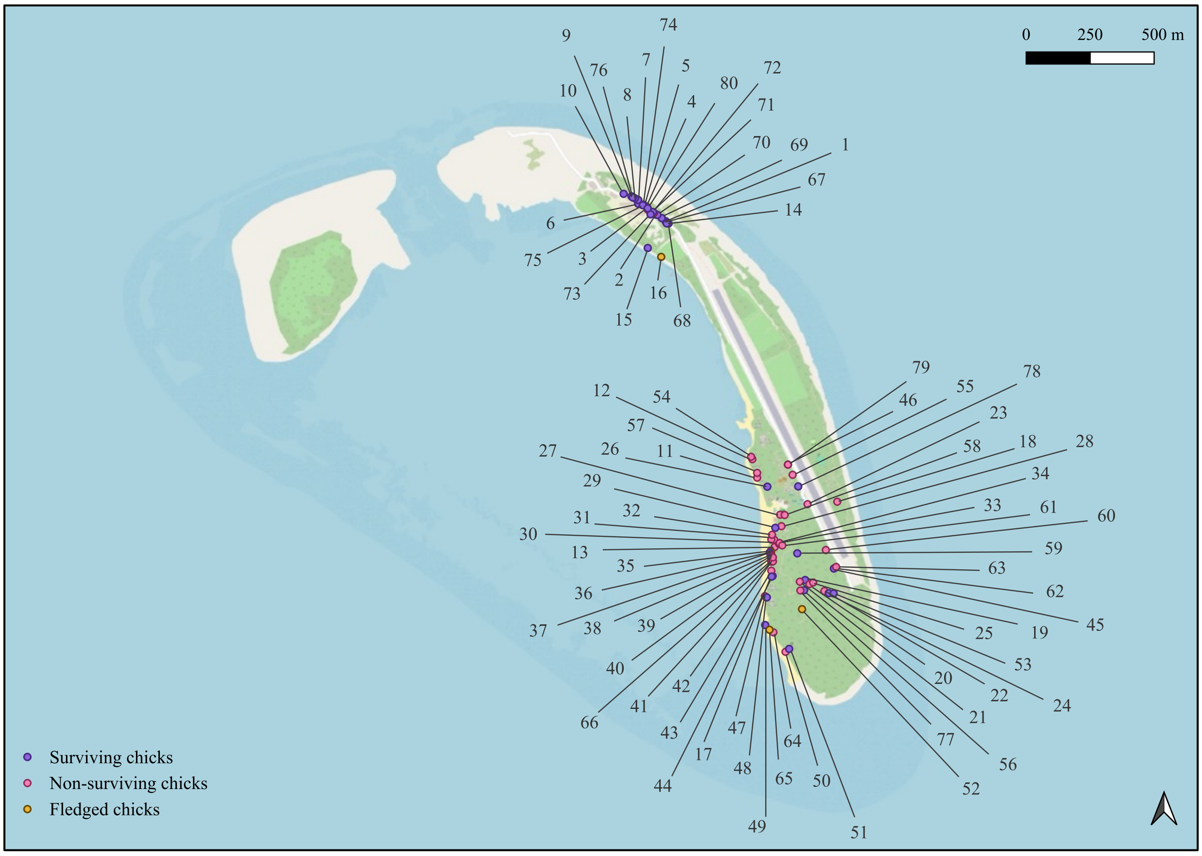

Figure 3-1. Distribution of nest sites on Nukutepipi and their survival outcomes (as of late May 2024).

Table 3-1. Summary of egg survival.

Eggs	***n***	**%**
Eggs lost	13	23.6
Eggs hatched	42	76.4
Total	55	100.0
Hatching success rate		76.4

Table 3-2. Factors contributing to egg losses.

Cause of failure	***n***	**%**
Egg broken in nest	4	30.8
Parent absent leading to egg predation	4	30.8
Unknown cause	2	15.4
Trimming bushes/trees	2	15.4
Inadequate nest site	1	7.7
Total	13	100.0

Figure 3-2 illustrates the seasonality of red-tailed tropicbirds on Nukutepipi. The egg-laying period began in early November, peaked in late February, and ended in early April, while egg hatching commenced in early December, reached its peak in early April, and concluded in late May. The Shapiro-Wilk test indicated that both egg-laying (W=0.967, P=0.08) and egg-hatching (W=0.970, P=0.11) followed a normal distribution.

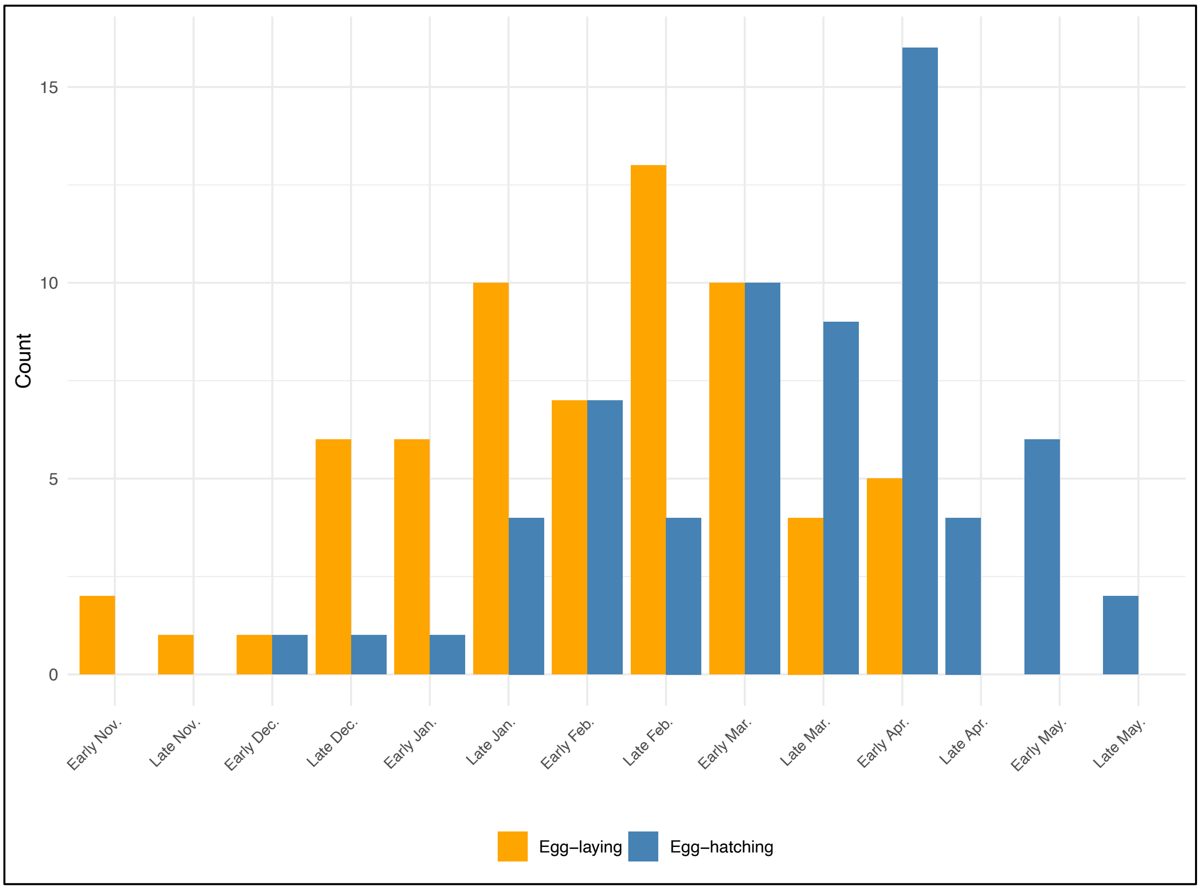

Figure 3-2. Seasonality of red-tailed tropicbirds on Nukutepipi from November 2023 until May 2024.

The attendance of red-tailed tropicbird parents on Nukutepipi at their nests is illustrated in Figure 3-3, where each data point represents a single visit. In general, parental duties appeared to be evenly shared between members of pairs during egg incubation. On average, one parent stayed at the nest for 250.4 hours (10.4 days), with durations ranging from 148.3–360.9 hours (6.2–15.0 days). After completing its incubation shift, the roles were reversed: the departing parent was no longer observed at the nest, while its partner returned to resume incubation.

Among nests that failed during incubation, some eggs were left unattended for periods of up to two weeks. A few eggs that successfully hatched (i.e., nests 45, 57, and 68) were also left unincubated, but for shorter periods of only 1 to 2 days.

On a side note, parents were observed at the nest much more frequently before their egg hatched than afterward. A similar alternating pattern was noted during the chick-rearing period, with one parent observed at the nest for several consecutive days before the other parent took over. As chicks grew older, parental attendance became increasingly rare.

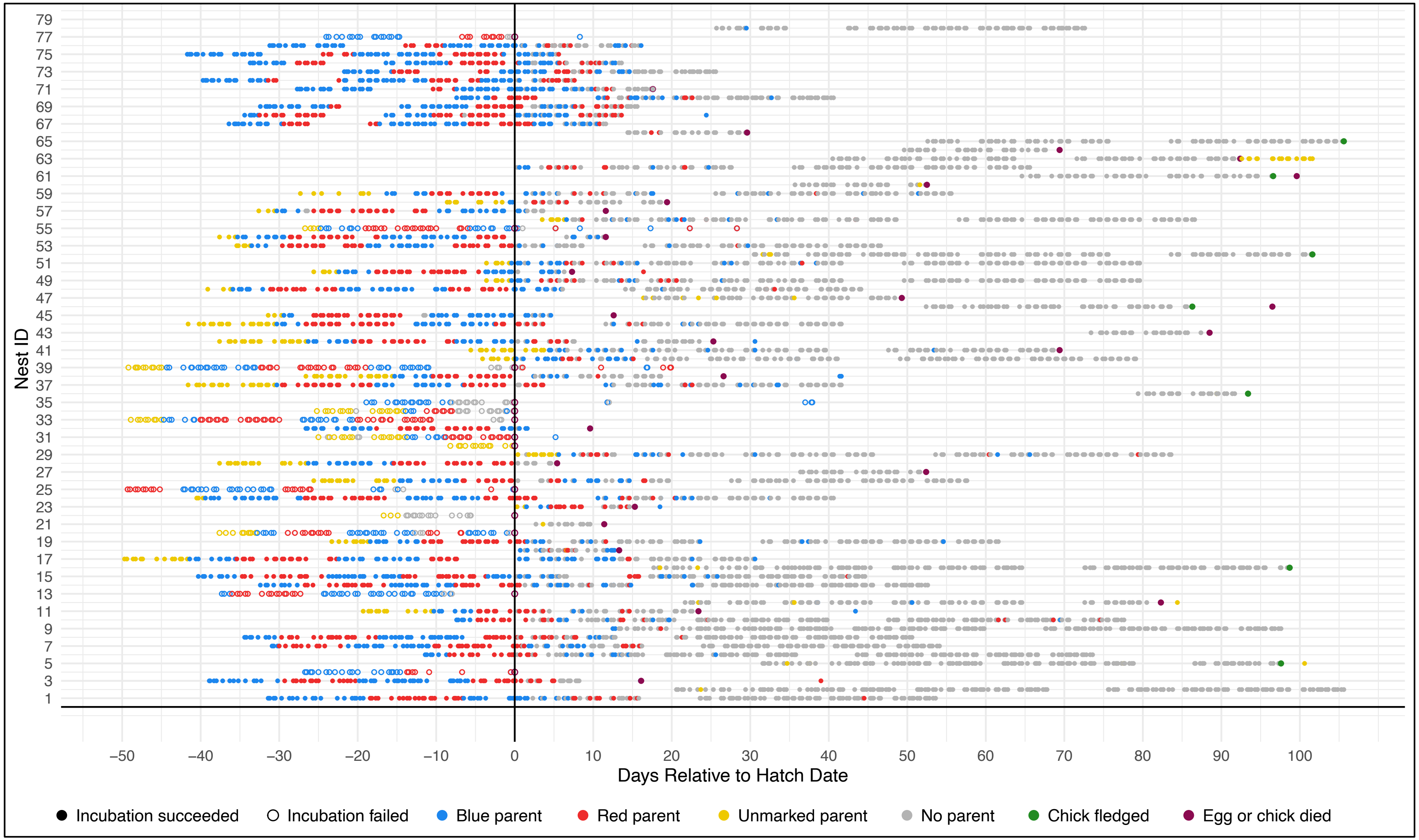

Figure 3-3. Presence of red-tailed tropicbird parents on Nukutepipi at the nest throughout the incubation period and chick development. Yellow data points indicate adults that were observed before the marking of individuals began.

Figure 3-4 indicates the duration of incubation shifts of individual red-tailed tropicbirds relative to the hatch date of their egg. In five of the seven nests, the durations of incubation shifts decreased as egg-hatching date approached. When considering the data at the population level, the durations of incubation shifts varied significantly, ranging from approximately 6 to 15 days, regardless of the incubation stage.

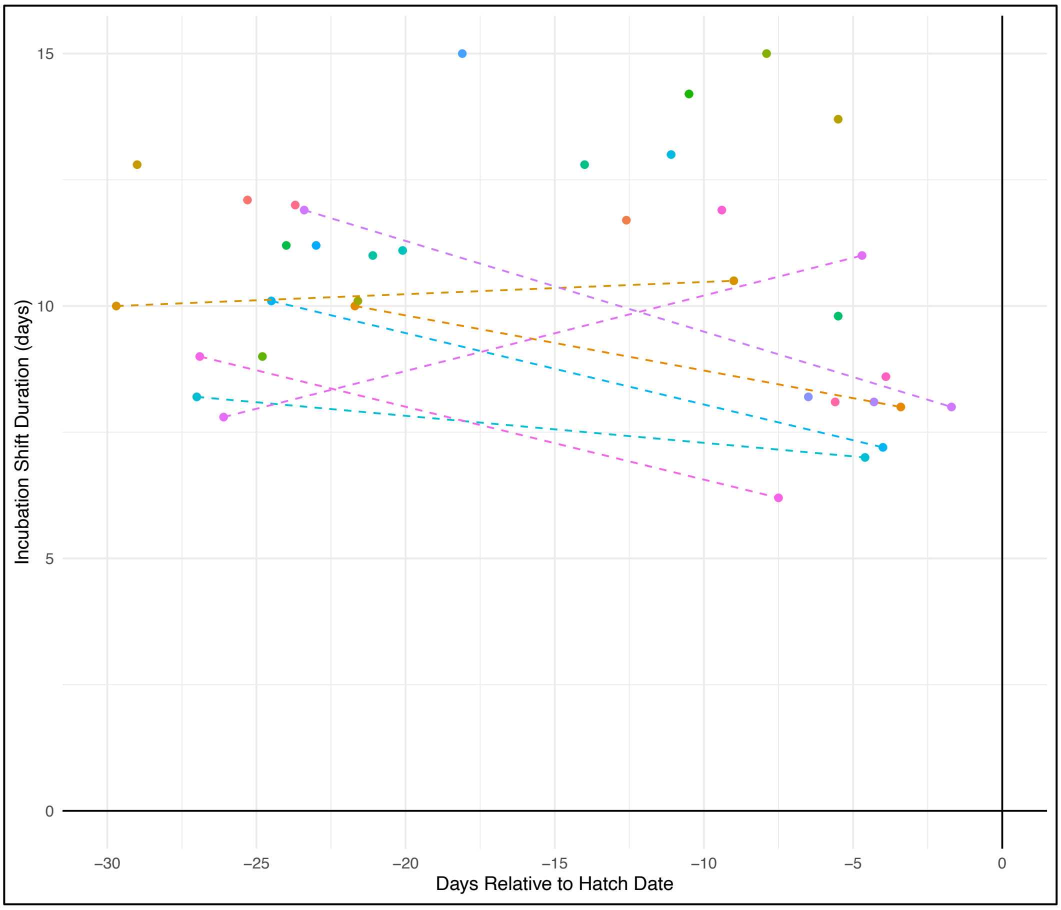

Figure 3-4. The duration of incubation shifts of red-tailed tropicbird parents on Nukutepipi in relation to the hatch date of their egg. Data points represent accurately observed incubation shift durations; changes in shifts that occurred on non-observation days are not included. Dashed lines connect observations from the same nest.

4. Parental Behaviours During Chick-Rearing

4.1 Introduction

Red-tailed tropicbird parents play a crucial role in early chick development by exhibiting brooding behaviours that provide warmth and protection against unfavourable weather conditions and predators. Typically, they shelter their young under either their body or wing. Observations on the duration of the brooding period vary significantly: on Johnston Atoll, hatchlings are brooded for up to 10 days, while on Kure Atoll, this period can extend to as long as 25 days (Fleet, 1974; Amerson & Shelton, 1976).

As chicks grow older, parental attendance becomes less consistent, with parents returning primarily to feed their offspring (Fleet, 1974). Similar to the incubation period, successful chick-rearing requires parents to coordinate their foraging trips to ensure the survival of both their chick and themselves. Red-tailed tropicbird parents exhibit two distinct foraging strategies – unimodal and bimodal – based on prey availability.

The unimodal foraging strategy, documented by Le Corre *et al.* (2003) on Europa Island, involves alternating foraging trips of approximately 34 hours. During these trips, one parent forages to feed the chick, while the other feeds itself. In contrast, the bimodal foraging strategy, observed by Sommerfeld and Hennicke (2010) on Christmas Island, is thought to be adopted in regions where food resources are scarce. This strategy involves alternating between short trips (ST) and long trips (LT). A series of STs, with each lasting approximately 3 hours, allows a parent to forage in nearby waters and frequently feed the chick, though prey availability is relatively low. Meanwhile, the other parent undertakes an LT, lasting around 57 hours, to forage in distant waters rich in food resources and replenish its body reserves. After completing an LT, this parent switches to STs, while the other begins an LT to recover mass lost during its STs. This bimodal foraging strategy is not unique to red-tailed tropicbirds. It has been observed in various seabird species, including white-tailed tropicbirds (Campos *et al.*, 2018), red-billed tropicbirds (Beard *et al.*, 2023), little shearwaters (Booth *et al.*, 2000), Cory's shearwaters (Granadeiro *et al.*, 1998), and wandering albatrosses (Weimerskirch *et al.*, 1993), highlighting the efficiency of the strategy in managing resource constraints while maintaining reproductive success.

An effective foraging strategy is critical for ensuring frequent food provisioning to developing chicks, a factor essential for their survival and growth. Studies suggest that feeding frequency, rather than meal size, plays a more pivotal role in influencing chick survival (Ricklefs *et al.*, 1985; Schaffner, 1990; Ramos & Pacheco, 2003). However, the feeding frequency of red-tailed tropicbirds remains poorly studied.

Similarly, research on meal sizes in red-tailed tropicbirds is limited. Fleet (1974), in a study on Kure Atoll, reported that red-tailed tropicbird parents delivered meals averaging 66 g on average. Ramos and Pacheco (2003) suggested that white-tailed tropicbirds may not forage at their full capacity. Instead, they appear to target an "optimal payload size" based on the capacity of chicks to digest and swallow food efficiently. This payload size is estimated to be approximately 40% of the adults' maximum carrying capacity (Ramos & Pacheco, 2003). Le Corre and colleagues (2003) further proposed that a profitable prey item meeting the optimal payload size for provisioning a mature red-tailed tropicbird chick would be a single mahi mahi weighing 120 g. However, due to the uneven distribution and unpredictability of prey in marine ecosystems, red-tailed tropicbirds have been observed to catch a wide variety of prey, with flying fish and squids being the most prevalent (Fleet, 1974; Diamond, 1975; Le Corre *et al.*, 2003; Sommerfeld & Hennicke, 2010).

The study explored the parental behaviours of red-tailed tropicbirds on Nukutepipi during the chick-rearing period. Seabird parents were hypothesised to progressively decrease their presence at the nest as chicks develop. Additionally, it was hypothesised that parents adopt a unimodal foraging strategy, as the island's remoteness may suggest lower impacts from industrial fisheries. To test these hypotheses, parental attendance was recorded two to three times daily, enabling an assessment of foraging trip durations. Furthermore, it was hypothesised that meal sizes provided to chicks increase with age. Meal sizes were estimated by weighing chicks two to three times a day and calculating the mass difference between consecutive weighings.

4.2 Methods and materials

4.2.1 Field work

Hatch dates and times were recorded when hatching was observed. For eggs that were not witnessed hatching, the time was estimated as either 00:00 or 12:00, depending the first observed presence of the chick. During each daily nest visit, the status of parents (brooding a chick, resting beside a chick, feeding, or absent) was recorded. Additionally, chicks were weighed using an electronic digital scale. To minimise disturbance, chicks were not weighed if a parent was present at the nest. A positive weight difference between consecutive weighings indicated a feeding event having occurred between measurements. If regurgitation occurred due to handling, or if regurgitated prey or pellets were found at the nests, these were visually identified whenever possible and weighed using the scale. All individuals remained in their natural habitat and were manipulated with care.

4.2.2 Statistical analyses

The durations of brooding period – defined as the age at which chicks were last observed being brooded under the body or wing of a parent – were plotted in boxplots using R, comparing chicks that survived the brooding period with those that did not. A Welch's two-sample t-test, implemented in base R, was performed to determine whether the difference between the two groups was statistically significant. Chicks that were still being brooded at the end of the study were excluded from this analysis to avoid unreliable results, as these individuals may have experienced longer brooding periods that could not be documented due to the study's limited duration on Nukutepipi. The proportion of visits with at least one parent present at the nest, relative to the total number of visits across different chick age classes, was calculated and displayed in a histogram, with the total number of nests indicated by *n*.

The durations of foraging trips (STs and LTs) performed by red-tailed tropicbird parents on Nukutepipi were estimated using the same method applied to calculate the duration of incubation shifts. Foraging trips duration was determined from visit records in Excel by calculating the time difference between Visit 1 (when an individual returned from a foraging trip) and Visit 2 (when it was last observed before departing). The resulting data were visualised using boxplots, and a Welch's two-sample t-test was conducted in base R to assess differences between trip types.

The amount of food delivered to chicks was analysed in R by calculating mass differences between consecutive weighings. Positive mass increments, interpreted as feeding events, were grouped by age class and visualised using boxplots. A Tukey's HSD test was conducted to evaluate statistically significant differences between age groups. Additionally, the number of chicks with detected positive mass increments per age class was displayed.

4.3 Results

The durations of brooding period for red-tailed tropicbird chicks that survived the brooding period was significantly longer than for those that did not (Figure 4-1; Welch's two-sample t-test, P=0.0037). All surviving chicks had been brooded for at least 5 days, with parents typically ceasing brooding when their chick reached 2 weeks of age. However, some chicks were brooded for as long as 22.6 days. In contrast, the brooding durations for chicks that did not survive exhibited greater variability, ranging from 0 to 14 days. Notably, the brooding period for the non-surviving chicks was, on average, about half as long as that of the surviving chicks (~ 7 days). Interestingly, a few chicks that survived experienced a shorter brooding period, as brief as 5.4 days.

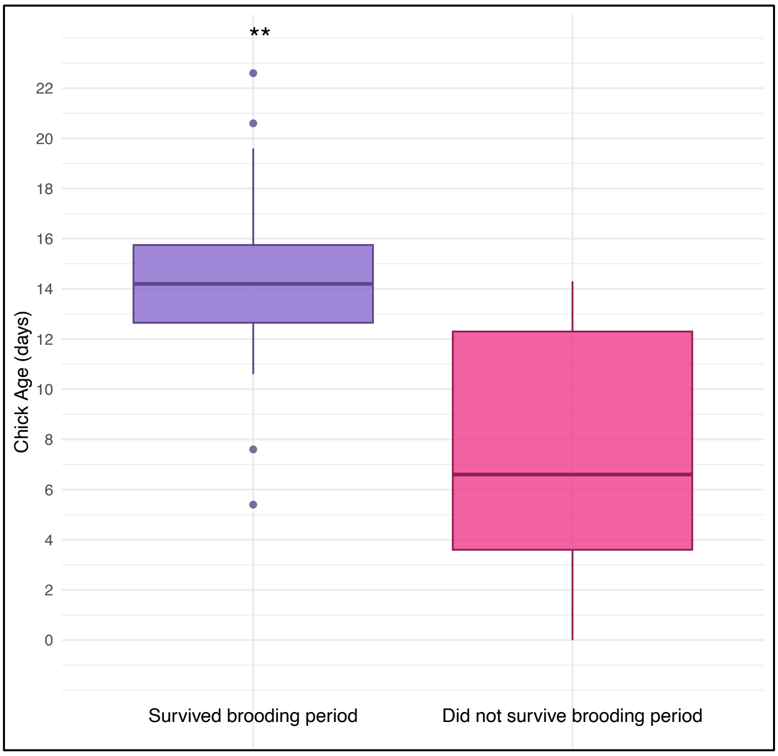

Figure 4-1. Chick age at which red-tailed tropicbird parents ceased brooding their chick on Nukutepipi. Boxplots display the median (bold line), interquartile range (boxes), whiskers extending to 1.5 times the interquartile range, and outliers (individual points). Asterisks (**) indicate a statistically significant difference between groups based on Welch's two-sample t-test.

Figure 4-2 shows the proportion of visits where at least one parent was present at the nest in relation to the total number of visits throughout chick development. Parental attendance reduced sharply as chicks aged. In fact, during the first 10 days, red-tailed tropicbird parents were present at the nest approximately 60% of the time. By the time the chicks reached 10–20 days old, parental attendance decreased by nearly half. When chicks were between 20 and 90 days of age, parents were rarely seen at the nest; the lowest parental attendance recorded was 1% when chicks were 70–80 days old. Interestingly, as the fledging period approached, there was a progressive increase in parental attendance. For chicks of 90–100 days old, parents were present 15% of the time. This increased to 19% during the last 10 days of the chick-rearing period.

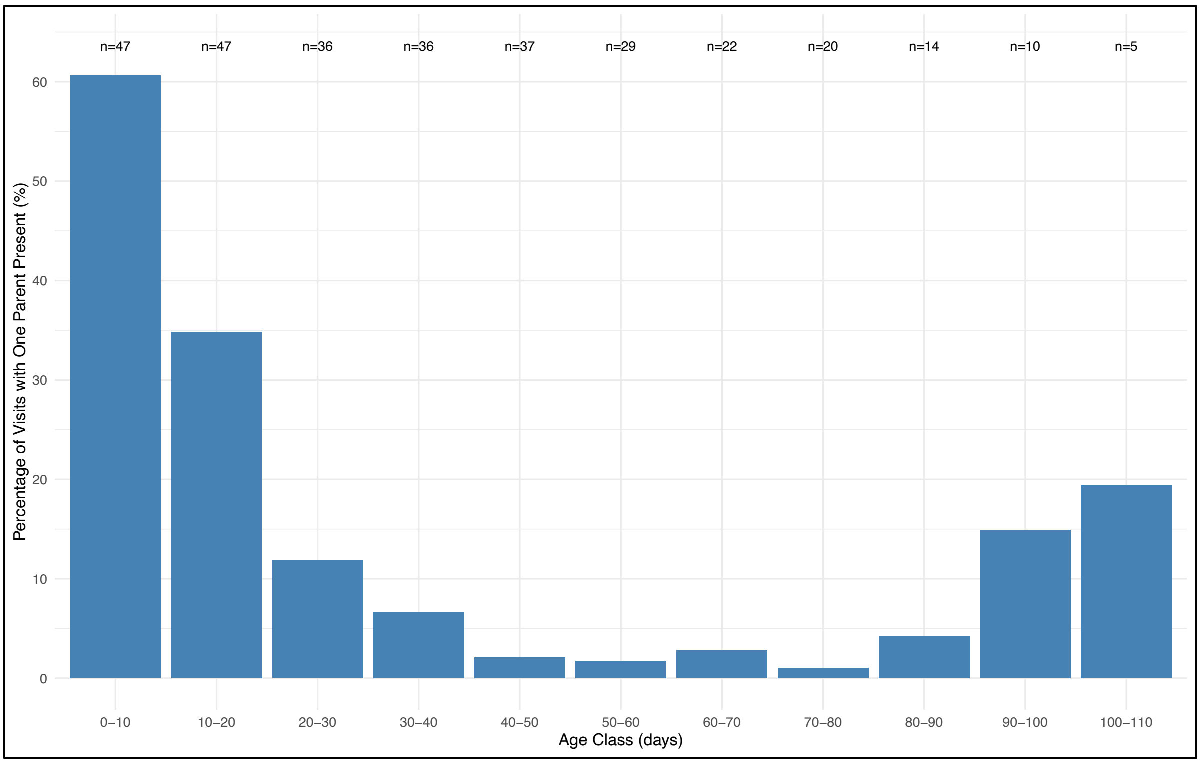

Figure 4-2. Percentage of visits with at least one red-tailed tropicbird parent present at the nest throughout chick development on Nukutepipi. Note that sample sizes decrease with chick age due to the timing of the study, which began early in the breeding season and ended before most chicks completed development.

On Nukutepipi, members of red-tailed tropicbird pairs exhibited a distinct pattern in trip duration, alternating between STs and LTs, which were significantly different (Figure 4-3; Welch's two-sample t-test, P<2.2e-16). On average, STs lasted 26.8 hours (1.1 days), with some trips as brief as six hours (0.25 days) and others extending up to 129.6 hours (5.4 days). In contrast, LTs were considerably longer, with an average duration of 271.4 hours (11.3 days). The shortest LT recorded was 119 hours (5 days) long, while the longest lasted for 450.8 hours (18.8 days).

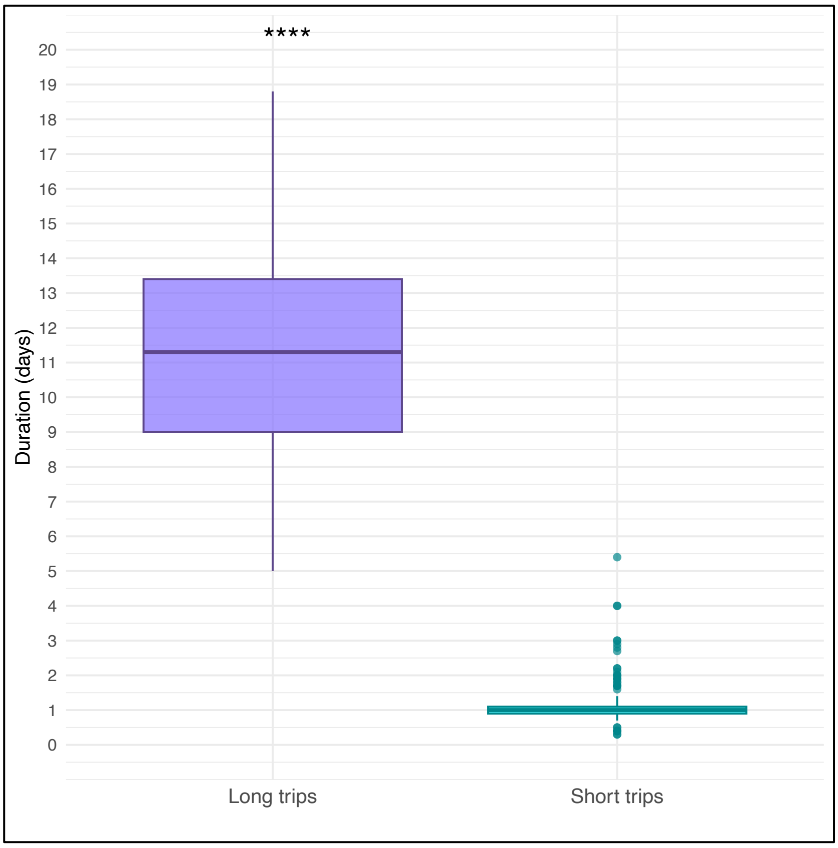

Figure 4-3. Approximate durations of long and short foraging trips undertaken by red-tailed tropicbird parents during chick-rearing on Nukutepipi. Boxplot and asterisks (****) conventions follow those described in Figure 4-1.

Boxplots of estimated meal sizes provisioned to chicks between consecutive weighings across different age classes are shown in Figure 4-4. Meals delivered to juveniles were statistically lighter during the first 10, 20, and 30 days of age, weighing 18, 38, and 68 g, respectively (Tukey's HSD test, P<0.001). Following these stages, meal sizes remained relatively consistent throughout the juveniles' remaining time at the nest, with an average mass of 86 g. The frequency of feed delivery could not be assessed as nests were not monitored continuously.

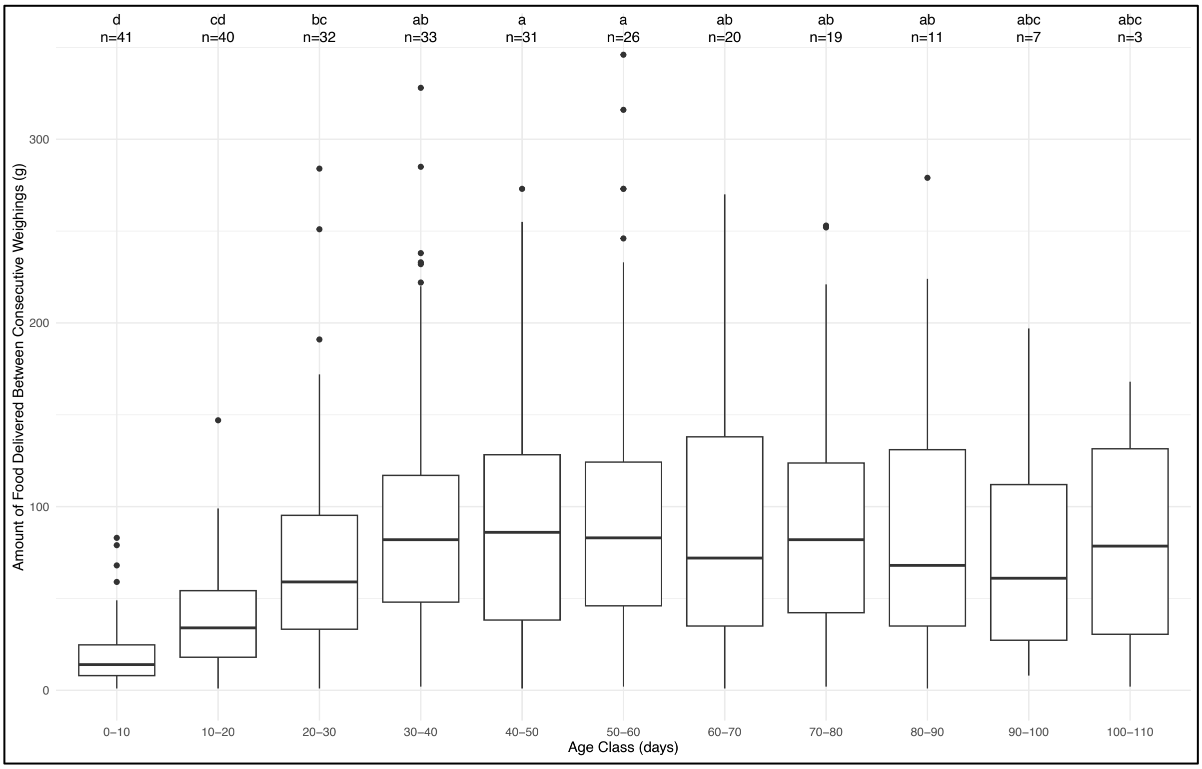

Figure 4-4. Boxplots of the amount of food delivered to chicks between consecutive weighings for different age classes. Boxplot conventions follow those described in Figure 4-1. Different letters above boxplots indicate statistically significant differences between age classes based on Tukey's HSD test (P<0.05). Age classes sharing the same letter are not significantly different. Note that sample sizes decrease with chick age due to the timing of the study, which began early in the breeding season and ended before most chicks completed development.

Table 4-2 presents the various types of prey collected from nests or regurgitated by seabirds during handling. A total of 25 prey items were recovered, with most identified to the family or species level. The most frequently occurring fish family was Carangidae, represented by four Atlantic horse mackerels (*Trachurus trachurus*) and three unidentified trevallies (*Caranx* spp.). Other notable items included three gray triggerfish (*Balistes capriscus*) and three flying fish (*Exocoetus volitans*). Additional fish species included hound needlefish (*Tylosurus crocodilus*), red mullet (*Mullus barbatus*), scrawled filefish (*Aluterus scriptus*), mahi mahi, and an unidentified surgeonfish from the family Acanthuridae. Cephalopods were also present in their diet, including both an octopus and a squid. Although octopus hooks were occasionally observed at the nests, no formal data on these were recorded.

Regurgitated fish had an average mass of 61.8 g, with masses varying between 49 to 69 g. In comparison, the average mass of prey items found at the nests was 43.5 g, with a broader range from 3 to 228 g.

Table 4-1. Reconstituted masses of regurgitated and found prey. Percentage represents the frequency of prey species occurrence and "–" means that mass was not recorded.

Prey	**Reconstituted masses of regurgitated prey (g)**	**Reconstituted masses of prey found (g)**	**Number**	
			n	**%**
Fish				
Acanthuridae				
Unidentified Acanthuridae	N/A	13	1	4.0
Balistidae				
Balistes capriscus	N/A	7, 10, 15	3	12.0
Belonidae				
Tylosurus crocodilus	N/A	4, 21	2	8.0
Canragidae				
Caranx spp.	68	6, 33	3	12.0
Trachurus trachurus	69	23, 80, 82	4	16.0
Coryphaenidae				
Coryphaena hippurus	–	N/A	1	4.0
Exocoetidae				
Exocoetus volitans	N/A	28, 41, 74	3	12.0
Monacantidae				
Aluterus scriptus	N/A	48	1	4.0
Mullidae				
Mullus barbatus	N/A	228	1	4.0
Unidentified fish	49, 61	67, –	4	16.0
Other				
Unidentified octopus	–	N/A	1	4.0
Unidentified squid	N/A	3	1	4.0
Total count			**25**	**100.0**
Average mass (g)	**61.8**	**43.5**		

5. Chick Growth Rate

5.1 Introduction

Red-tailed tropicbird juveniles typically take 80 to 90 days to fledge. Despite this extended development period, their culmen and wing measurements remain smaller than those of adults at fledging (Fleet, 1974). In contrast, their hindlimbs stop growing and reach adult size by day 35. Tail feather growth concludes by day 75; however, fledglings lack the long red tail streamers characteristic of adults, resulting in distinctly shorter tail feathers (Fleet, 1974). Unlike culmen, wing, hindlimb, and tail lengths, the body mass of red-tailed tropicbird juveniles fluctuates significantly during growth, largely due to the irregularity of feeding events, which depend on parental foraging success. During the first 40 days of life, chick mass increases rapidly. To reduce the risk of starvation, parents overfeed their chicks, leading to a pre-fledging asymptotic mass reported to be 10–20% greater than adult body mass. This is followed by a gradual decline in mass beginning approximately six to 12 days before fledging (Diamond, 1975; Schreiber, 1996). On average, fledglings leave the nest with a body mass 11–15% higher than that of adults (Fleet, 1974; Le Corre *et al.*, 2003).

While specific rates of mass change in red-tailed tropicbird chicks remain unquantified, studies on white-tailed tropicbird chicks by Ramos and Pacheco (2003) provide valuable insights. They observed that during the first 35 days post-hatch, chicks gained mass at a rate of 7.8 g/day. This rate decreased to 3.7 g/day by day 60 and turned negative by day 80, with juveniles losing approximately 1.5 g/day.

As previously mentioned, red-tailed tropicbird juveniles may experience irregular food delivery, resulting in fasting periods that typically last up to 3.5 days (Fleet, 1974). During these fasting periods, birds typically go through three distinct phases. Phase I, which occurs immediately after feeding, lasts from several hours to a few days and is characterised by a rapid reduction in body mass, primarily due to the excretion of urine and faeces and the metabolism of glycogen stores (Jenni-Eiermann & Jenni, 2012). Phase II, referred to as the "long phase of economy", follows. During this phase, body mass loss slows significantly, as birds primarily metabolise lipids for energy (Cherel *et al.*, 1987; Jenni-Eiermann & Jenni, 2012). Once fat reserves are depleted, Phase III begins. This critical phase involves the breakdown of muscle protein, resulting in accelerated mass loss, physiological stress, and a deterioration in overall body condition. If birds remain unfed, this stage ultimately proves fatal (Cherel *et al.*, 1987; Jenni-Eiermann & Jenni, 2012).

The study examined the growth and development of red-tailed tropicbird chicks on Nukutepipi. It was hypothesised that fledglings leave the nest with body mass and morphometric measurements comparable to those of adults. In addition, juveniles were hypothesised to experience fasting periods, which are expected to progress through three distinct phases, throughout their development at the nest. To test these hypotheses, chicks were weighed two to three times per day, and their head, culmen, tarsus-to-middle-toe, wing, and tail lengths were measured weekly.

5.2 Methods and materials

5.2.1 Field work

A series of morphometric measurements were made on red-tailed tropicbird chicks: head length (distance between the tip of the beak and the proximal end of the occipital bone), culmen length (base of the upper mandible to the tip of the bill), wing length (length of the manus, extending from the carpometacarpus to the tip of the first primary feather), tarsus-to-middle-toe length (length from the posterior end of the tarsal joint (heel) to the distal tip of the third digit), and tail length (distance between the pygostyle and the rectrices). All measurements are given in cm and were made using a ruler, except for culmen length, for which callipers were used. If a chick was too young and still covered by down feathers, those feathers were excluded from tail measurements. These measurements were taken weekly for all chicks.

In addition, chick mass was measured daily using an electronic digital scale. For 24 chicks, mass was recorded three times per day (morning, early afternoon, and late afternoon), while the remaining 56 chicks were weighed twice daily (morning and early afternoon). To minimise disturbance, chicks were not weighed when a parent was present at the nest, and if a feeding event was observed, chicks were weighed only after the parent had departed.

To compare the morphometrics of fledged chicks with those of adults, the same five morphometric measurements (head, culmen, wing, tarsus-to-middle-toe, and tail lengths) was collected for the parents, along with their mass. However, unlike the chicks, adults were measured and weighed only once, upon their first capture. All individuals were handled with care. A two-person team was required to measure large chicks and adults, with one person safely restraining the birds, while the other took the measurements. Small- to medium-sized chicks, however, could be handled by a single person.

As with adults, weekly assessments of invertebrate parasites on each juvenile were conducted. Parasite samples were collected for later identification, and three chest feathers were plucked from older chicks for DNA sexing. However, due to the limited duration of the study, neither parasite identification nor sexing analyses could be completed.

5.2.2 Statistical analyses

Due to the limited duration of the study on Nukutepipi, fledging success rate could only be determined within a broad range. Factors contributing to chick losses were identified through field observations and expressed as percentages of the total chick losses.

Chicks were categorised into three groups (surviving, non-surviving, and fledged) based on their survival outcomes as of late May 2024. Growth rate data of all chicks were updated daily in an Excel spreadsheet. Once data collection was complete, the ages of chicks with unknown hatch dates were estimated. To achieve this, scatterplots were generated in R for each measurement (i.e., head, culmen, wing, tarsus-to-middle-toe, and tail lengths) of chicks with known hatch dates. Chicks which did not survive were excluded from these plots, as they may have grown more slowly, which could skew age prediction. Since all measurements showed changes in growth rates during chick development, affecting the reliability of age predictions, separate linear regressions were fitted for measurements of each body part within specific age ranges where growth rate remained linear. The R^2 values of these models were calculated in base R using the `summary` function to evaluate their fit, and the equations were expressed as $y = slope * x + intercept$, where y represents body part length and x represents age. Using these equations, the ages of chicks with unknown hatch dates were estimated. Since different body measurements varied in their predictive accuracy depending on chick age, multiple age estimates were obtained for each individual. To determine a final predicted age, these estimates were averaged.

Once hatch dates had been estimated for chicks with unknown hatch dates, their measurements, along with those of the non-surviving ones, were added to the morphometric plots of surviving chicks with known hatch dates. Masses of all juveniles were then plotted. To assess the growth trend of the body parts and mass of each chick group, Generalised Additive

Models (GAMs) were applied to the data using the `mgcv` package in R. In addition, the morphometrics and masses of adults were added to these graphs in the form of boxplots to compare their measurements with those of juveniles. ANOVA and post-hoc Tukey's HSD tests were performed in base R to compare the masses across different chick groups.

The daily mass change of red-tailed tropicbird chicks on Nukutepipi was computed in R. The data were filtered to include only the first mass recorded for each chick on each day to ensure consistency in daily mass change calculations. Including all recorded masses would have introduced inconsistencies, as multiple measurements taken within a single day could result in artificial fluctuations caused by feeding events. The daily mass change was calculated as the ratio of the mass difference to age difference. Chicks were then grouped into different age classes (i.e., 0–10, 10–20 days, etc.) and the average of daily mass change for each class was calculated and visualised using a line graph. An additional line graph was also included to illustrate the average chick mass within each age class.

Since chicks on Nukutepipi experienced prolonged fasting periods after feeding events, their resulting mass declines were plotted against their age in R using `ggplot2`. The graph also included the final recorded mass of chicks before they either succumbed to starvation or fledged. Additionally, the durations of these fasting periods were visualised using boxplots, categorised into three groups: (1) chicks that fasted and were subsequently fed, (2) chicks that remained unfed and died, and (3) chicks that fledged successfully after fasting. A Tukey's HSD test was conducted using base R to evaluate statistically significant differences among these groups.

Fasting periods experienced by red-tailed tropicbird chicks on Nukutepipi consisted of two distinct phases. To determine the rates of mass loss during fasting periods, a segmented regression analysis was performed using the `segmented` package in R. A custom function was developed to process each fasting event for individual nests. The function first fitted a simple linear regression model (`lm`), with mass as the dependent variable and age as the independent variable. If at least five data points were available, a segmented regression model was then applied using the `segmented` function to identify the age at which the rate of mass loss changed. Phase-specific mass loss rates were computed using the `slope` function from the `segmented` package.

Mass losses during each phase of every fasting period were plotted on scatterplots against chick age. These values were then expressed as percentages of the chicks' initial mass recorded at the start of each fasting period and plotted against both age and initial mass. Additionally, the mass losses of chicks before dying or fledging experienced were included in the Phase II graphs.

To examine the daily mass loss rates, the slope coefficients from the segmented regression – representing the rate of mass loss during Phase I and Phase II – were plotted against different age classes using boxplots in `ggplot2`. Additionally, the average meal size, calculated as described in Section 4.2.2, was incorporated in this graph. A Welch's two-sample t-test, conducted using base R, was used to assess whether the difference between the two phases was statistically significant.

Finally, the durations of each phase were calculated in R and visualised as boxplots for each age class. Mass losses prior to chick mortality or fledging were also included in this representation. To assess statistical significance, a Welch's two-sample t-test was conducted in base R to compare the phase durations.

5.3 Results

Table 5-1 presents a summary of the survival of red-tailed tropicbird chicks on Nukutepipi. A total of 65 red-tailed tropicbird juveniles were monitored during the study. Of these, 26 did not survive, and only five successfully fledged. The fate of the remaining 34 chicks is unknown, as the study concluded before they fledged. Consequently, only a range for fledging success rate could be determined. With just five chicks successfully fledging, the minimum fledging success rate was 7.7%. Given that 40% of chicks did not survive, the maximum survival rate, or maximum fledging success rate, was 60%.

On Nukutepipi, red-tailed tropicbird chicks were affected by numerous factors. Starvation was the primary cause of chick losses, accounting for 65.4% of chick mortality (Table 5-2). Other mortality factors included intraspecific competition, chick predation by strawberry hermit crabs, inadequate nest sites, and parasites.

Table 5-1. Summary of chick survival.

Chicks	*n*	%
Non-surviving chicks	26	40.0
Surviving chicks (unknown if fledged)	34	52.3
Fledged chicks	5	7.7
Total	65	100.0
Min. fledging success rate		7.7
Min. mortality rate of chicks		40.0
Max. survival rate or fledging success rate		60.0
Estimated fledging success rate range		7.7 – 60.0

Table 5-2. Factors contributing to chick losses.

Cause of failure	*n*	%
Starvation	17	65.4
Unknown cause	3	11.5
Intraspecific competition	2	7.7
Chick predation	2	7.7
Inadequate nest site	1	3.8
Parasites	1	3.8
Total	26	100.0

Plots of body measurement growth with age, based on a sample of 40 chicks with known hatch dates, revealed two distinct growth patterns (Figure 5-1). Three measurements increased linearly before plateauing (Table 5-3): head length at 0.19 cm/day to ~day 30, culmen length at 0.09 cm/day to ~day 40, and tarsus-to-middle-toe length at 0.15 cm/day to ~day 30. The remaining two measurements exhibited little or no initial growth before transitioning to a linear increase. Wing length grew slowly until ~day 30, then increased linearly at 0.43 cm/day, while tail length showed no growth until 25 days, followed by linear growth of 0.23 cm/day from day 40 onwards.

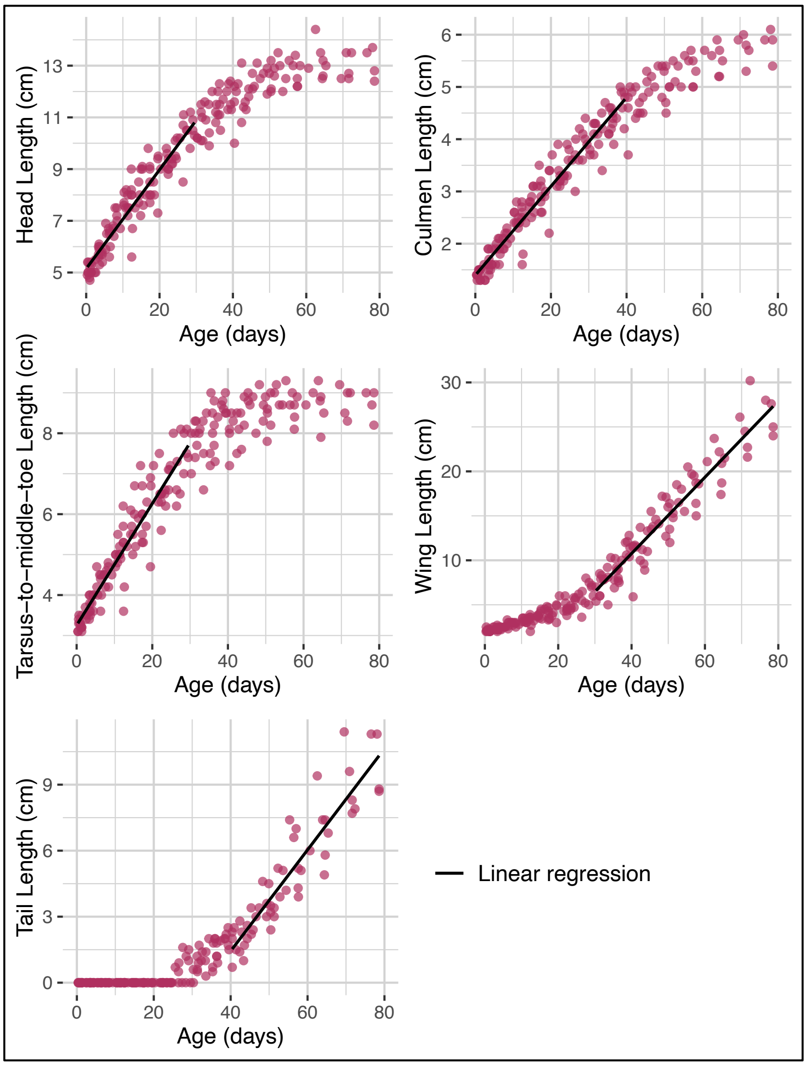

Figure 5-1. Measurements of head, culmen, tarsus-to-middle-toe, wing, and tail lengths of surviving red-tailed tropicbird chicks (as of late May 2024) with known hatch dates, throughout their development at the nest on Nukutepipi.

Table 5-3. Regressions of constant growth periods in morphometric measurements of red-tailed tropicbird chicks.

Measurements	Fitted model	Age range (days)	Equation	R^2
Head length	Linear	0 - 30	$y = 5.15 + 0.19x$	0.89
Culmen length	Linear	0 - 40	$y = 1.39 + 0.09x$	0.93
Tarsus-to-middle-toe length	Linear	0 - 30	$y = 3.25 + 0.15x$	0.88
Wing length	Linear	30 - 80	$y = -6.31 + 0.43x$	0.90
Tail length	Linear	40 - 80	$y = -7.73 + 0.23x$	0.84

Measurements of all juveniles (40 chicks with known hatch dates and 25 chicks with unknown hatch dates), as well as those of their parents are displayed in Figure 5-2, using scatterplots and boxplots, respectively. Of the 160 parents, measurements were successfully obtained from 113 individuals, while the remaining 47 adults were never encountered because their chick had matured enough to be left unattended at the nest.

Fledglings left the nest with an average head length of 14.0 cm, slightly exceeding the adult average of 13.8 cm. However, their culmen and wing lengths were not fully developed, averaging 6.1 cm and 30.7 cm, respectively, compared to adult averages of 6.6 cm and 35.2 cm. Interestingly, many juveniles had longer tarsus-to-middle-toe lengths than adults, with a maximum recorded length of 9.6 cm – 7.9% greater than the adult average of 8.7 cm. By the time fledglings left the nest, this length had shortened to an average of 8.9 cm, closely aligning with adult measurements. In terms of tail lengths, fledglings averaged 12.2 cm, surpassing the adult average of 11.1 cm. Overall, growth patterns across all body parts appeared consistent, regardless of the juveniles' survival outcomes.

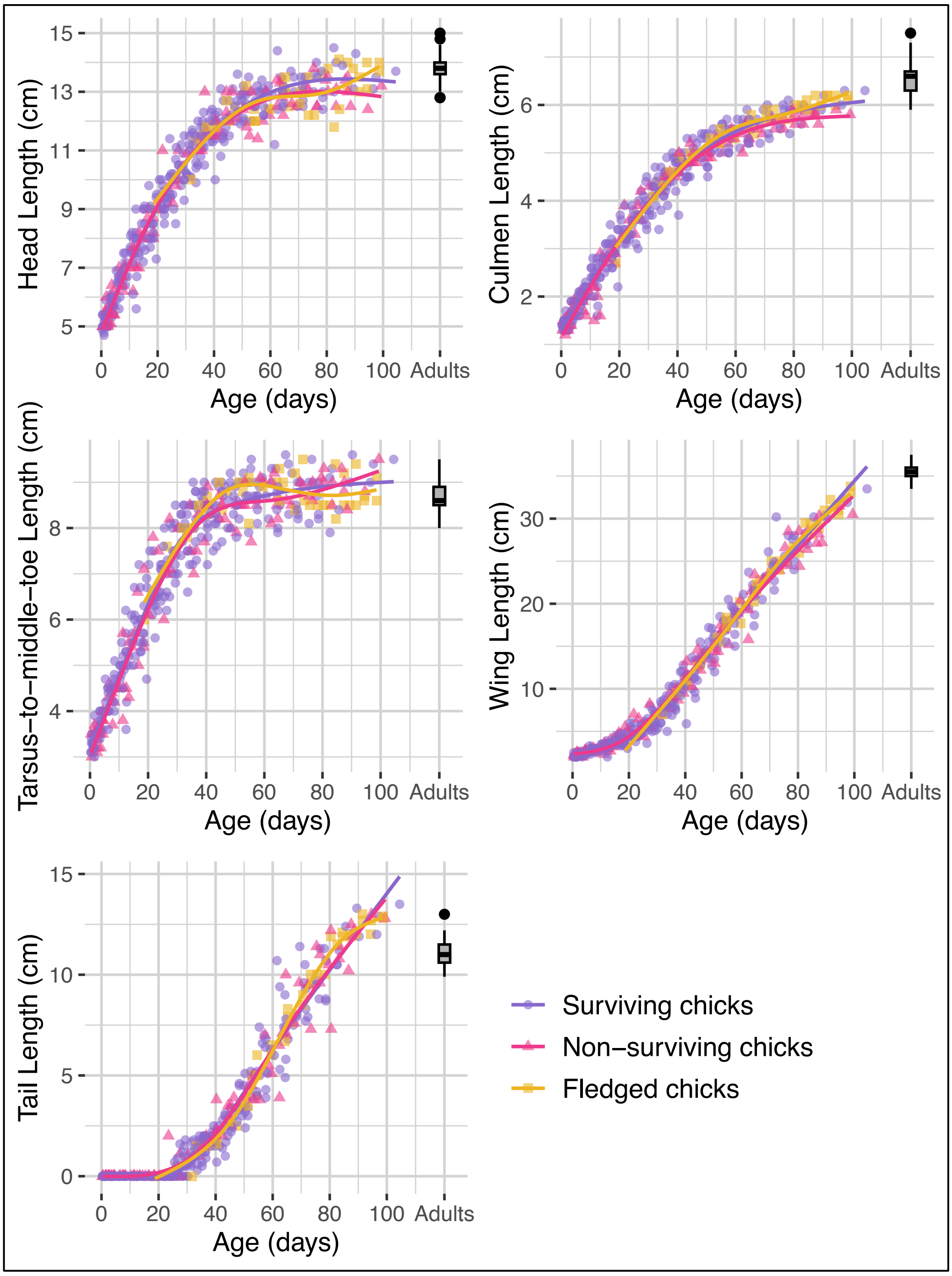

Figure 5-2. Measurements of head, culmen, tarsus-to-middle-toe, wing, and tail lengths of all juveniles throughout their development at the nest and those of their parents. Smooth curves represent growth trends of each chick group, modelled using Generalised Additive Models (GAMs). Boxplots display the median (bold line), interquartile range (boxes), whiskers extending to 1.5 times the interquartile range, and outliers (individual black points).

Figure 5-3 plots the mass changes of red-tailed tropicbird chicks throughout their development at the nest on Nukutepipi, with adult masses summarised in a boxplot. Chick masses generally increased over time, reaching an asymptote around 70–80 days before declining. Although a few juveniles reached the average adult mass of 757 g by day 40, the overall mass trends show a peak that does not exceed this value, with surviving and fledged chicks peaking at 688 g and 723 g, respectively. Twenty-four juveniles (15 surviving, 5 fledged, 4 non-surviving) surpassed the adult average by 10%, on average. The maximum recorded mass was 1,090 g – 44% above the average adult. Following this peak, juvenile mass gradually declined until fledging. Juveniles left the nest between 94 and 106 days of age, weighing an average of 611 g (range: 532–660 g), which was lighter than adults at departure.

The ANOVA test revealed a highly significant difference in mass between the chick groups (P<0.001). Post-hoc Tukey's HSD tests showed that the masses of non-surviving chicks were significantly different from those of both fledged (P<0.001) and surviving chicks (P<0.001). Additionally, fledged chicks had significantly higher masses than surviving individuals (P<0.001).

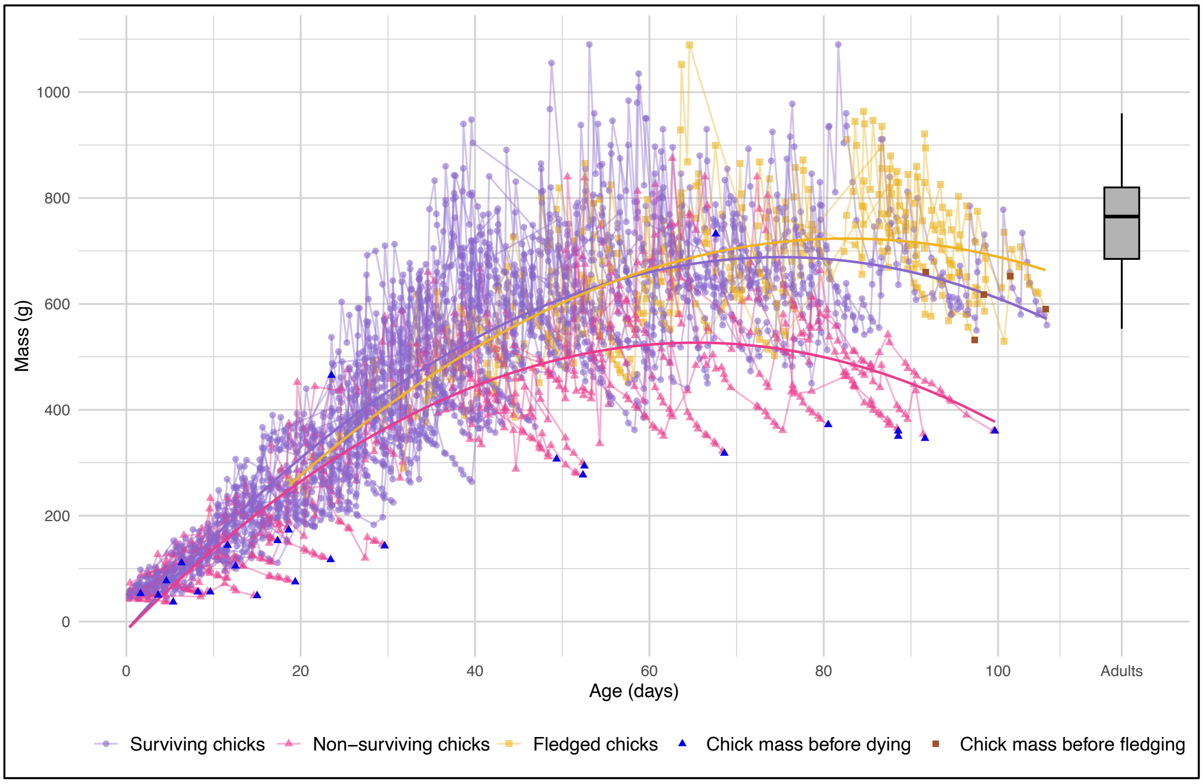

Figure 5-3. Masses of all red-tailed tropicbird juveniles throughout their development at the nest on Nukutepipi and those of adults. Smooth curves and boxplot follow the same conventions as in Figure 5-2.

Figure 5-4 presents the average daily mass change and average mass of all red-tailed tropicbird juveniles (surviving, non-surviving, and fledged chicks) across varying age classes. In general, chicks experienced rapid mass increases during the first 50 days, after which their growth plateaued. This pattern is reflected in the average daily mass change. Indeed, red-tailed tropicbird juveniles showed a positive daily mass change until 50 days of age, with mass gains ranging from 7.1 g/day to 9.7 g/day. From days 50–60, the average chick mass slope became less steep, reflected by a daily mass change of -8.1 g/day. Both the average mass and daily mass change of chicks rose again between days 60 and 70, with juveniles gaining an average of 3.8 g/day. As the mass plateaued from day 70 onward, the daily mass change turned negative, ranging from -4.4 g/day to -16.4 g/day. Interestingly, between 100 and 110 days, the average daily mass change increased to 10.9 g/day, though that value is derived from only three chicks.

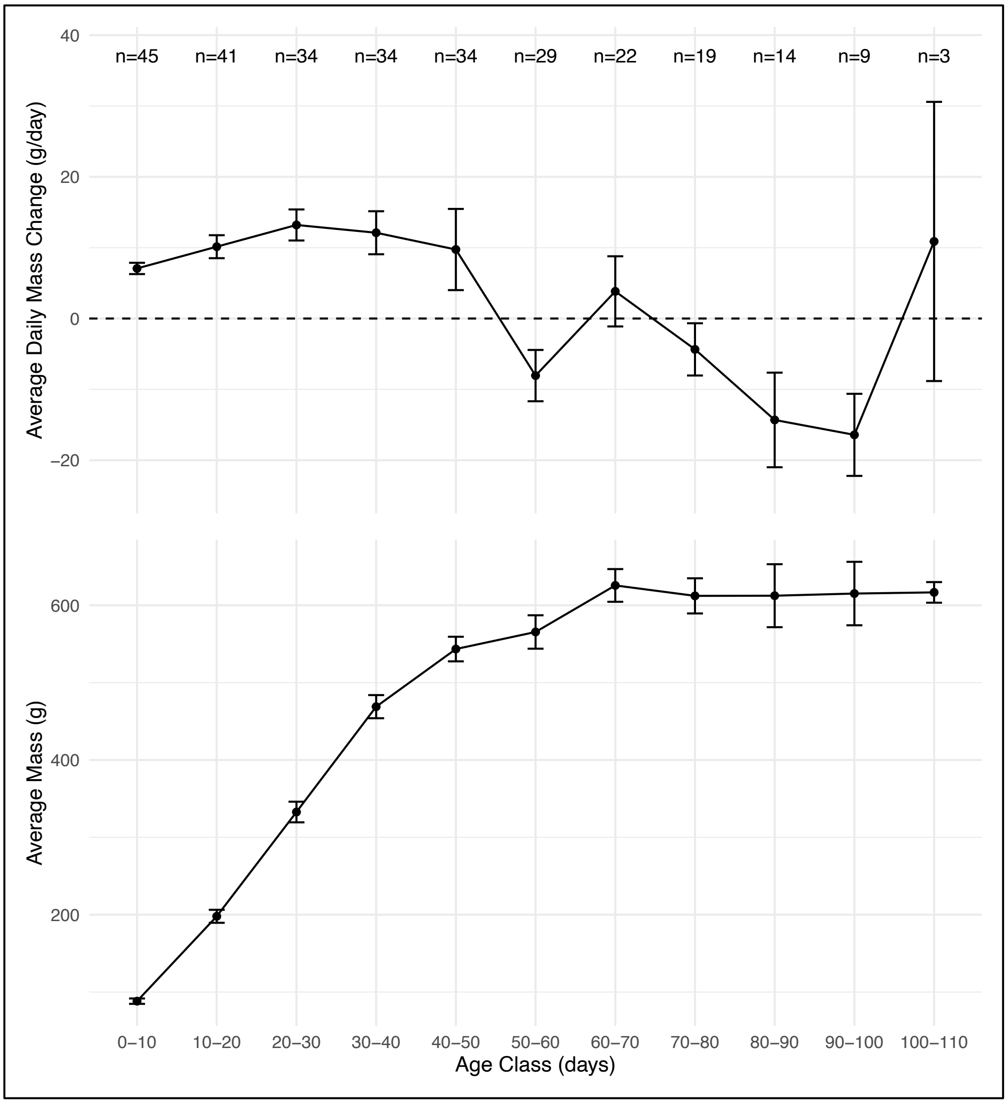

Figure 5-4. Average daily mass change and mass of red-tailed tropicbird chicks across age classes. Error bars represent standard errors, displayed as vertical lines with horizontal caps.

Red-tailed tropicbird juveniles growing on Nukutepipi experienced multiple periods of fasting, as reflected by the mass declines shown in Figure 5-5. Overall, mass losses did not appear to differ significantly across the various chick groups. Additionally, each fasting period followed a similar trend: chicks experienced rapid mass loss during the first two days after a feeding event, followed by a marked deceleration in the rate of mass loss over the subsequent days, suggesting that fasting periods endured by red-tailed tropicbird chicks comprised two distinct phases.

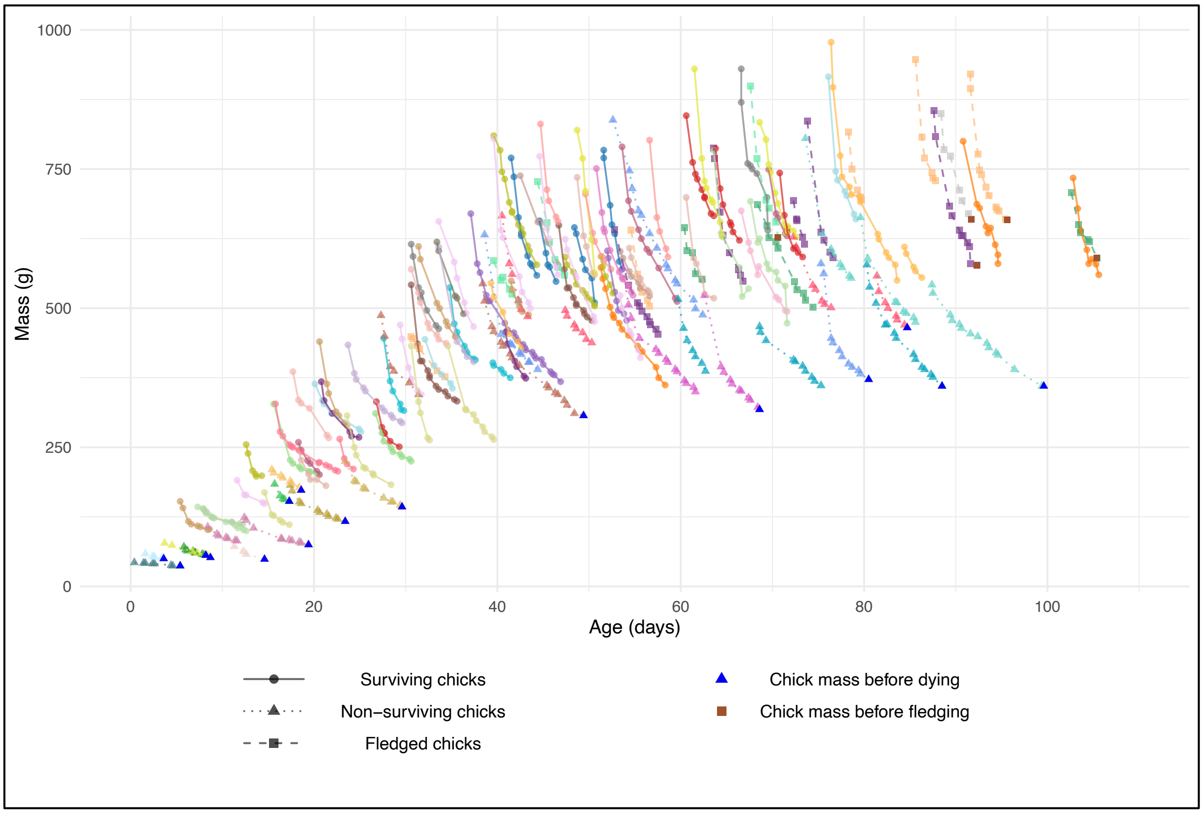

Figure 5-5. Mass losses of red-tailed tropicbird chicks throughout their development at the nest during fasting periods. Points are colour-coded to distinguish individual chicks; however, chick IDs are not displayed.

Figure 5-6 illustrates the duration of fasting periods experienced by juveniles after feeding events in relation to their survival outcomes at the end of these periods. Tukey's HSD test revealed statistically significant differences in the duration of fasting periods between chick groups. On average, juveniles that were refed after a fasting period went without food for approximately 3 days, while those that starved to death endured fasting periods of around 5 days. Some red-tailed tropicbird chicks survived fasting periods of up to 10 days. In contrast, the variability in fasting durations of non-surviving chicks was greater, with some fasting for as long as 12 days before succumbing to starvation. For the remaining group, which fledged successfully, fasting periods were less variable, averaging about 3 days before taking their first flight.

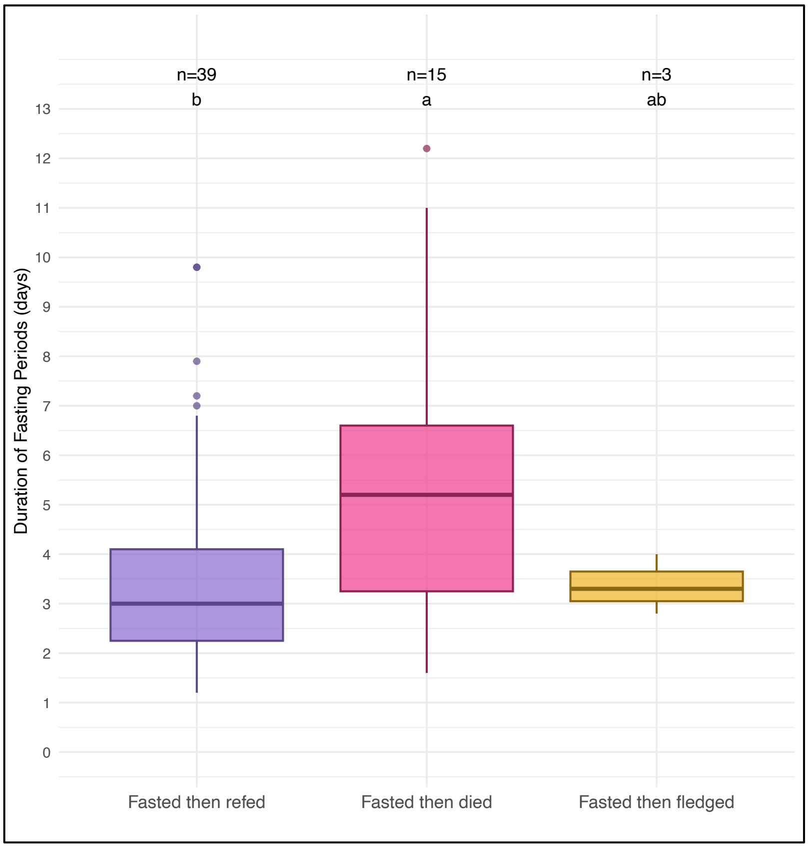

Figure 5-6. Duration of fasting periods experienced by red-tailed tropicbird chicks on Nukutepipi. Boxplots follow the same conventions as in Figure 5-2. Different letters above boxplots indicate statistically significant differences between chick groups based on Tukey's HSD test ($P<0.05$). Chick groups sharing the same letter are not significantly different.

Red-tailed tropicbird juveniles underwent fasting periods consisting of two distinct phases. Mass loss during these phases, in relation to age, is illustrated in Figure 5-7. Overall, mass loss increased with age in both Phase I and Phase II, with variability becoming more pronounced from 30 days onward. On average, chicks lost 77.3 g during Phase I and 50.1 g during Phase II, with maximum losses reaching 204 g and 186 g, respectively. Furthermore, the Phase II scatterplot highlights the substantial variation in mass losses among non-surviving chicks; some chicks exhibited losses comparable to older individuals before succumbing. In contrast, fledged juveniles experienced mass losses of 46 g, 59 g, and 113 g before leaving the nest.

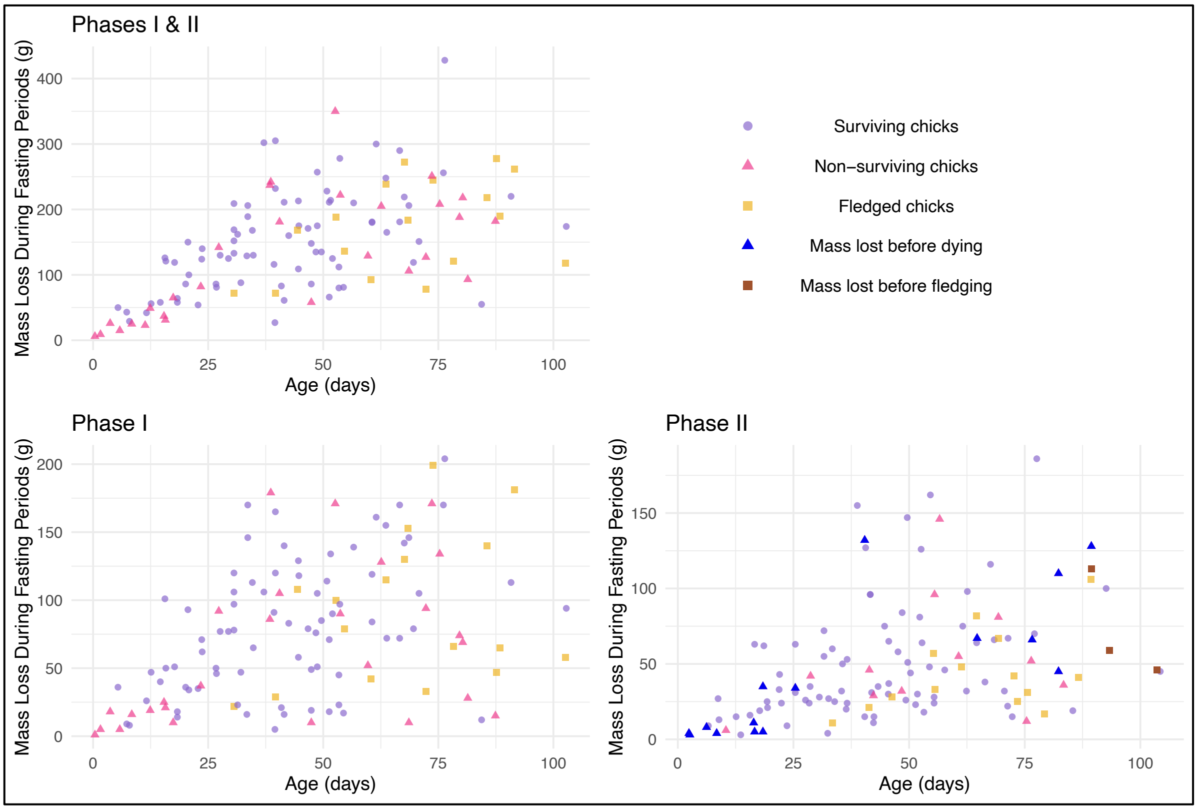

Figure 5-7. Mass losses of red-tailed tropicbird juveniles during fasting periods throughout their development at the nest.

Mass loss, expressed as a percentage of initial mass, is shown in relation to age (Figure 5-8) and initial mass (Figure 5-9). Overall, mass loss exhibited no relationship with age or initial mass. During fasting periods, chicks lost between 5% and 45% of their initial mass. When comparing the two phases, mass loss relative to initial mass was slightly higher in Phase I than in Phase II, averaging 13.5% and 10.7%, respectively. Survival outcomes did not appear to influence mass loss, as chicks that succumbed to starvation lost between 2.8% to 30.1% of their initial mass before dying, a range similar to that of surviving chicks. Those that fledged lost between 7.2% and 14.6% of their initial mass before leaving the nest.

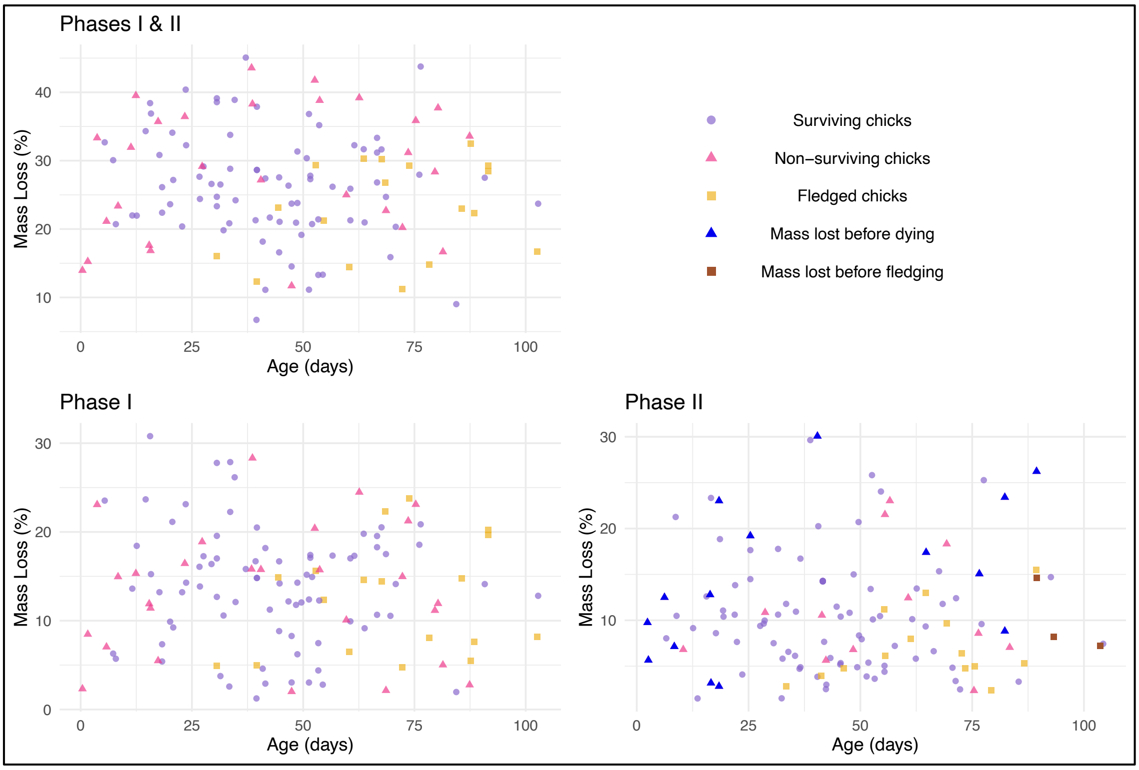

Figure 5-8. Mass loss of red-tailed tropicbird juveniles during fasting periods, expressed as a percentage of initial mass, in relation to age.

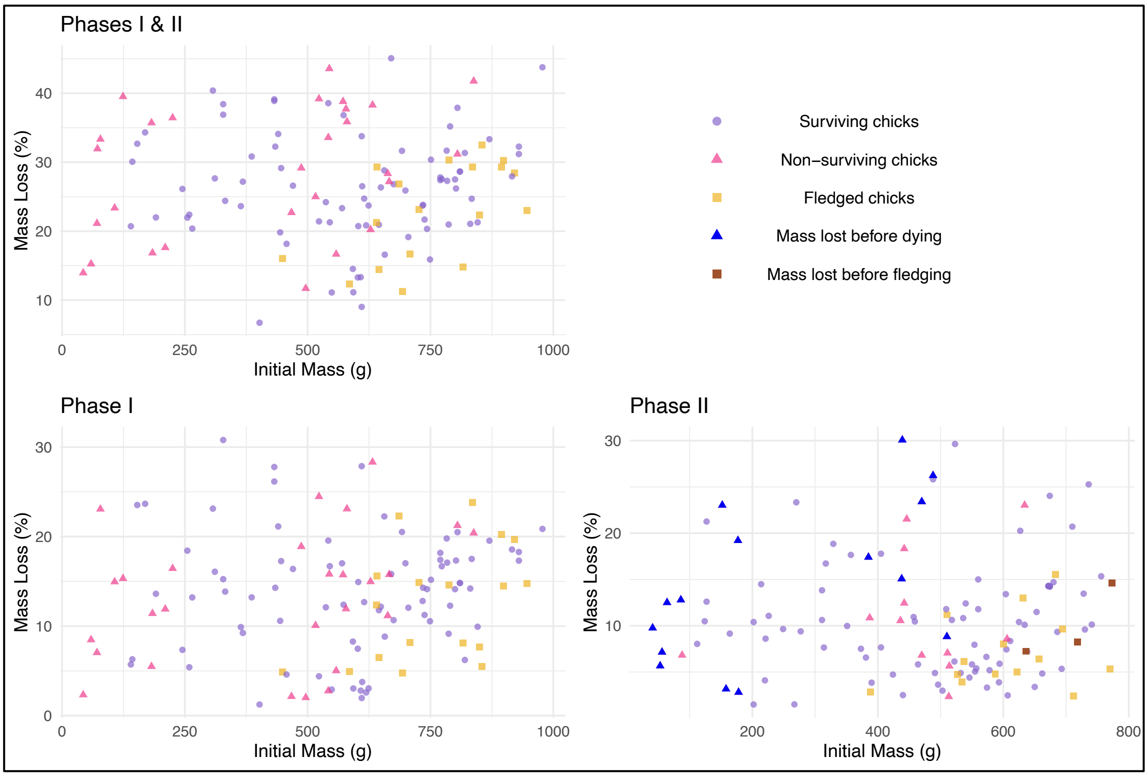

Figure 5-9. Mass loss of red-tailed tropicbird juveniles during fasting periods, expressed as a percentage of initial mass, in relation to their initial mass.

Figure 5-10 illustrates the daily mass loss experienced by juveniles during Phase I and Phase II of fasting across different age classes. It also plots the average mass of feed delivered to chicks in each age class. Overall, fasting phases showed a positive relationship with chick age. A Welch two-sample t-test revealed a significant difference in daily mass loss between Phase I and Phase II (P<0.001), with chicks losing significantly more mass per day during Phase I (92.3 g/day) compared to Phase II (27.3 g/day). Moreover, daily mass losses during Phase I exhibited greater variability than during Phase II. Notably, the trend in the average mass of meals delivered by parents closely aligned with the pattern of daily mass loss during Phase I.

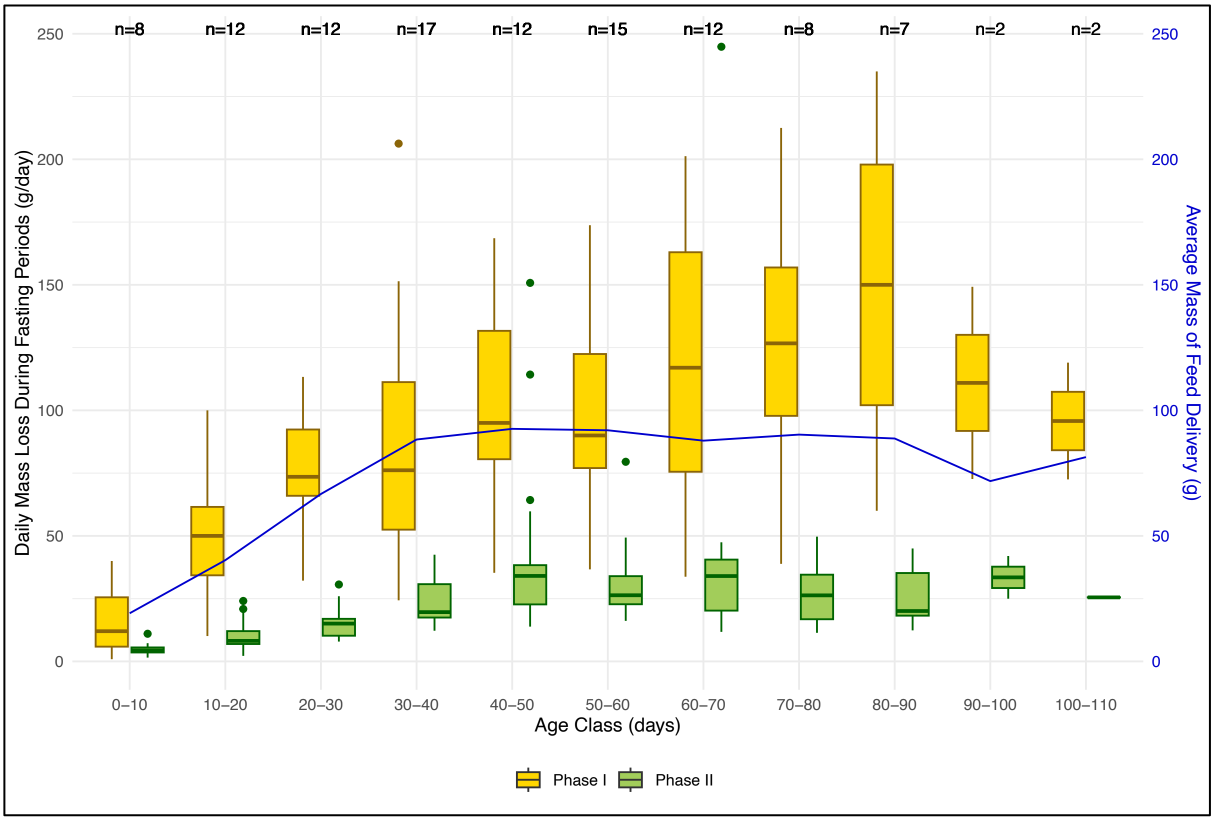

Figure 5-10. Daily mass loss of red-tailed tropicbird chicks during Phase I and II of fasting periods and the average mass of feed delivery, relative to various age classes. Boxplots follow the same conventions as in Figure 5-2 and represent mass losses during fasting periods. The blue line represents the average mass of feed delivery, with data extracted from Figure 4-4.

There was no clear relationship between the duration of fasting phases and chick age on Nukutepipi (Figure 5-11), though a Welch two-sample t-test indicated that Phase I was significantly shorter than Phase II (1.2 for Phase I versus 2.6 days for Phase II; P<0.001). Among surviving juveniles, the longest recorded duration of Phase II was 8.5 days, while those that succumbed to starvation endured up to 11.9 days. However, some chicks showed less resilience to fasting (Phase II), dying after only 0.2 days. In contrast, chicks that successfully fledged left the nest after experiencing Phase II for 2 to 3 days.

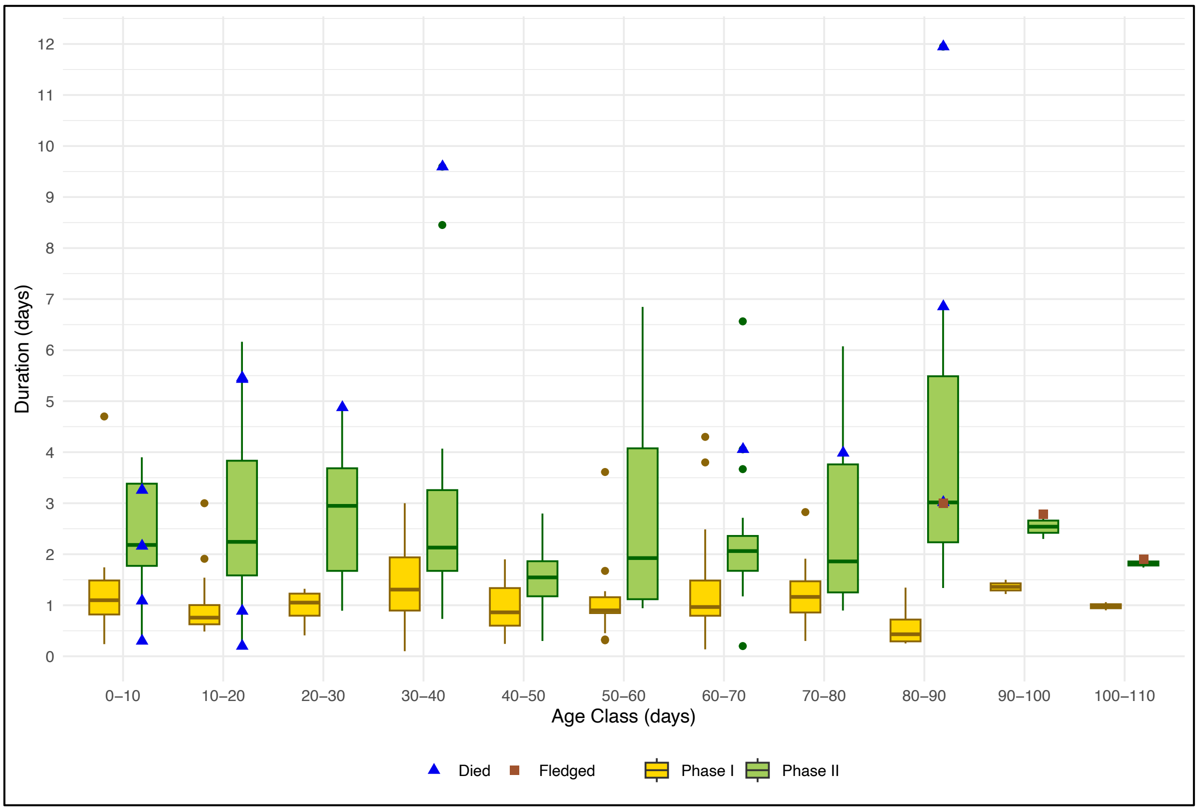

Figure 5-11. Duration of Phase I and Phase II of fasting periods across different chick age classes. Boxplots follow the same conventions as in Figure 5-2. Blue triangles and brown squares represent the final mass recorded before chicks died or fledged, respectively.

6. General Discussion

6.1 Seasonality of red-tailed tropicbirds on Nukutepipi

Studies suggest that the seasonality of red-tailed tropicbirds is triggered by longer photoperiods and maintained by the abundance of food resources (Schreiber & Ashmole, 1970; Fleet, 1974). For 25 chicks, hatching dates had to be estimated based on the morphometric measurements relative to the age of chicks with known hatch dates (n=40). These estimations enabled the calculation of laying dates. Since red-tailed tropicbird eggs take approximately 40 days to hatch (Sommerfeld *et al.*, 2015; Egerton *et al.*, 2022), 40 days were subtracted from the predicted hatching dates to estimate the laying dates. Based on these estimations, the breeding season of red-tailed tropicbirds on Nukutepipi roughly spanned from November to May (Figure 3-2). However, due to the limited duration of the study, it is possible that the breeding season extended into June. Peak egg-laying was observed in February, while peak egg-hatching occurring in March and April (Figure 3-2). These months correspond with the wet season or austral summer in French Polynesia, a period characterised by high precipitation. This timing aligns with observations by Prys-Jones and Peet (1980) on Aldabra Atoll, where red-tailed tropicbird numbers were observed to increase with rainfall. Similarly, other red-tailed tropicbird colonies such as those on Europa Island (Le Corre, 2001), Kure Atoll (Fleet, 1974), and Kiribati (Schreiber & Ashmole, 1970), have been documented to breed during this time of the year. While the study provides insights into seasonality on Nukutepipi, the observed breeding period may not fully capture the colony's complete breeding cycle.

Le Corre (2001) found a positive correlation on Europa Island between the breeding season of red-tailed tropicbirds, prey availability, and sea-surface temperatures. During the incubation period, the diet of red-tailed tropicbirds consists primarily of squid and flying fish.

As the austral summer progresses and sea temperatures rise to 27–28°C during the chick-rearing period, mahi mahi – a highly profitable food source (discussed further in Section 6.3.4) – becomes the most common prey (Le Corre, 2001). This suggests that red-tailed tropicbirds, likely including those on Nukutepipi, typically initiate breeding during spring or at the onset of the austral summer, a time when warming seas lead to a seasonal influx of mahi mahi (Le Corre, 2001; Le Corre *et al.*, 2003). Further studies on sea-surface temperatures and prey availability around Nukutepipi would provide critical insights to confirm whether similar patterns occur on this island.

6.2 Parental behaviours during incubation period

In this study, the duration of the incubation period could not be determined because nests that already contained an egg or a growing chick were selected, making the exact egg-laying dates unknown. One red-tailed tropicbird female was observed laying an egg, but the hatch date could not be recorded as the chick hatched during a break in the study. Many other studies (e.g., Fleet, 1974; Sommerfeld *et al.*, 2015; Egerton *et al.*, 2022) have reported that red-tailed tropicbird parents typically incubate their eggs for 40–50 days. In contrast, Diamond (1975) noted that individuals breeding on Aldabra Atoll incubate their egg for at least 51 days. They speculated that this extended incubation period may have been due to prolonged absences of the incubating parents. Furthermore, Diamond (1975) observed that red-billed tropicbird eggs could remain unincubated and still hatch within 5 days of parental absence. On Nukutepipi, a nest not included in this study contained an egg. After one parent’s incubation shift ended, the other parent was expected to return and resume incubation within 1 or 2 days. Instead, the egg remained unincubated for a prolonged period, and the newly hatched chick was later found wet and lifeless. A possible explanation for this extended parental absence could be difficulties in finding prey, leading to prolonged foraging trips which increase their chances of foraging success (Granadeiro *et al.*, 1998; Sommerfeld & Hennicke, 2010). Alternatively, the foraging parent could have been less experienced than its partner, resulting in a desynchronisation of incubation shifts (Howell & Bartholomew, 1962).

This incident highlights the critical role of parental presence in ensuring the survival of newly hatched chicks, which rely on parental brooding for thermoregulation. While red-tailed tropicbird eggs can hatch successfully after short periods of parental absence, newly hatched chicks on Nukutepipi require consistent parental care to survive during the early stages of their life.

Among the nests studied, all eggs hatched with at least one parent present, highlighting the importance of coordinated parental incubation shifts for offspring survival and reproductive success. Indeed, most red-tailed tropicbird parents breeding on Nukutepipi had well-synchronised incubation patterns, with one parent incubating while the other went to sea to forage (Figure 3-3). Although the study lacked data on the sexes of the parents, it was anticipated that the incubation shift durations would be similar in males and females. The within pair data from Nukutepipi are largely consistent with this, and align with observations by Fleet (1974) on red-tailed tropicbirds and Stonehouse (1962) on white-tailed tropicbirds. Similarly, Beard *et al.* (2023) reported that male and female red-billed tropicbirds performed incubation shifts of similar duration. However, they noted that when the first incubation shift was included, males tended to take longer shifts than their mates. This was attributed to females needing to replenish their energy reserves after egg-laying by foraging at sea, relying on their male partners to take on the first shift.

Beard *et al.* (2023) reported that, during incubation shifts, red-billed tropicbirds typically stay at the nest incubating and fasting while their partner is away foraging. In the present study, nests could not be monitored continuously and daily mass changes of incubating adults were not recorded to minimise disturbance and avoid the risk of nest abandonment. As a result, it was assumed that red-tailed tropicbird parents observed at the nest during consecutive visits did not interrupt their incubation shifts to feed. Furthermore, the duration of a parent's foraging trip was inferred to be equal to the incubation shift of its partner. On average, foraging trips lasted 250.4 hours (10.4 days), ranging from 148.3–360.9 hours (6.2–15.0 days) (Figure 3-3). Similar alternation patterns were recorded by Sommerfeld and Hennicke (2010) on Christmas Island and by Le Corre *et al.* (2003) on Europa Island. While both colonies exhibited biparental care during incubation similar to that observed on Nukutepipi, the durations of foraging trips differed markedly and were shorter. On Christmas Island, parents undertook much shorter foraging trips, averaging 152.9 hours (6.4 days) (range: 49.9–252.2 hours) (Sommerfeld & Hennicke, 2010). On Europa Island, trips were even shorter, averaging 96 hours (4 days) (range: 24–216 hours) (Le Corre *et al.*, 2003). The reasons for these differences remain unknown, though prey abundance may be a contributing factor, with low prey availability leading to longer foraging trips (Granadeiro *et al.*, 1998; Sommerfeld & Hennicke, 2010; Rishworth & Pistorius, 2015; Clay *et al.*, 2019). On Nukutepipi, it would be informative to equip tracking devices on the seabirds to identify where they forage. This would provide valuable data to assess whether these regions are, in fact, low in prey availability, thus helping to clarify the relationship between foraging areas and prey abundance, and ultimately providing insights into how prey distribution influences seabird foraging behaviours and success.

On Nukutepipi, the duration of foraging trips appeared to follow a more apparent trend when assessed at the individual level than at the population level (Figure 3-4). At the population level, the duration of foraging trips were variable. However, at the individual level, most red-tailed tropicbird parents performed progressively shorter foraging trips as the egg-hatching date approached. Similar observations have been recorded for various pelagic seabird species such as red-billed tropicbirds (Beard *et al.*, 2023), giant petrels (*Macronectes halli* and *M. giganteus*) (González-Solís, 2004), and northern fulmars (Gaston *et al.*, 2014). González-Solís (2004) suggested that pelagic seabird parents tend to reduce the length of their foraging trips toward the end of the incubation period to ensure that the attending parent has enough food to provision its chick when it hatches. He proposed three hypotheses that could explain how these changes in foraging trip durations are triggered: (1) seabird parents can predict the hatch date through endogenous timing; (2) they can assess the development of their unhatched chicks through various signals such as heart beat or bill tapping; and (3) the seasonal increase in prey availability. The first two hypotheses could not be tested in this study due to limitations in the data. Regarding the third hypothesis, the decreasing trend in foraging trip durations observed on Nukutepipi was consistent for pairs breeding both early and late in the season, suggesting that seasonal changes in prey availability may not have influenced the adjustments in foraging trip lengths on this island.

6.3 Parental behaviours during chick-rearing period

6.3.1 Brooding period and parental attendance

Parental attendance plays a crucial role in the early development and survival of red-tailed tropicbird chicks, particularly during the vulnerable post-hatching period. Seabird parents brood their chick under either their body or wing, providing warmth and protection against environmental stressors such as predators and harsh weather (Fleet, 1974; Amerson & Shelton, 1976). Furthermore, as hatchlings have limited capacity for swallowing and digesting, they require frequent, small meals, which can be achieved through parental attendance or brooding (Schaffner, 1990; Ramos & Pacheco, 2003). On Nukutepipi, the brooding period for chicks that survived this vulnerable stage lasted on average 14 days, with a range of 5 to 23 days (Figure 4-1). These observations align with those reported by Fleet (1974) on Kure Atoll. In contrast, on Johnston Atoll, the brooding period was significantly shorter, with parents brooding their chick for a maximum of 10 days (Amerson & Shelton, 1976). For chicks that did not survive this critical period on Nukutepipi, the average brooding duration was approximately 7 days, which was significantly shorter than that of the surviving chicks (Figure 4-1). This highlights the crucial role that parental brooding plays during the early stages of chick life.

On Nukutepipi, the absence of parents at the nest not only made chicks vulnerable to predation (discussed in Section 6.5.4), but also to intraspecific competition for food and nest sites (discussed in Section 6.5.5). Furthermore, the lack of parental attendance left chicks without food for extended periods, ultimately leading to starvation. For example, one hatchling on Nukutepipi was never observed being brooded after hatching, and its mass steadily decreased until it died from starvation on day 10. This case further underscores the crucial role that seabird parents play in early chick development.

Diamond (1975) studied the nest attendance of red-tailed tropicbird parents during chick development on Aldabra Atoll by calculating the proportion of nest visits during which at least one parent was present. His observations showed that seabird parents brooded their chick 100% of the time during the first week of life. Parental attendance declined slightly to 86% in the second week but rose again to 100% by the third week. These attendance rates were significantly higher than those observed in the present study. On Nukutepipi, parental attendance showed a steady decline as chicks aged: during the first 10 days post-hatching, red-tailed tropicbird parents were present at the nest 60% of the time, and this decreased further to 35% between 10 and 20 days old (Figure 4-2). The reasons for these differences remain unclear but may be attributed to several factors. One explanation is the presence of predators on

Aldabra Atoll such as rats and feral cats, which might necessitate constant parental attendance to protect chicks from predation (Harper & Cook, 2019a). In contrast, Nukutepipi is a predator-free environment, allowing parents to leave their chick unattended for longer periods. Alternatively, the differences may be attributed to Diamond's (1975) smaller sample size – specifically the number of nest visits – compared to the current study.

Once the brooding period finished, nest attendance of red-tailed tropicbird parents on Nukutepipi became more erratic as they returned solely to feed their chick (Fleet, 1974). In fact, between 20 and 30 days of age, chicks were attended by at least one parent 12% of the time. This rate of parental attendance further declined between days 40 and 90, ranging from 1% to 7% (Figure 4-2). Similar low levels of parental attendance were reported by Diamond (1975) on Aldabra Atoll. However, comparisons between both studies should be made with caution, as the sample sizes differ significantly. Interestingly, parental attendance on Nukutepipi gradually increased to 19% as the fledging period approached (Figure 4-2). This rise in attendance may be explained by the efforts of red-tailed tropicbird parents to ensure that their juvenile fledges successfully by provisioning it with food more frequently. Installing monitoring cameras at nests could provide valuable insights into parental feeding frequencies as fledging approaches. Alternatively, this observed trend may be due to the final age classes being based on small sample sizes, which could have affected the results.

6.3.2 Temporal patterns of foraging trips

During the chick-rearing period, much like the incubation phase, red-tailed tropicbird parents are required to regularly return to the nest to feed their chick. Because marine food resources are distributed in a patchy and unpredictable manner (Schreiber, 1996; Le Corre *et al.*, 2003; Beard *et al.*, 2023; Madden *et al.*, 2023), these pelagic seabirds must exhibit high levels of synchrony to ensure both their own survival and that of their growing chick. In this study, red-tailed tropicbird parents alternated between long foraging trips (LTs) and a series of short trips (STs).

Adults were not weighed on Nukutepipi to avoid disturbance, but it was assumed that STs were performed for the provisioning of chicks only, as observed in other red-tailed tropicbird colonies (Sommerfeld & Hennicke, 2010; Sommerfeld *et al.*, 2015) and many other seabirds species (e.g., wandering albatrosses (Weimerskirch *et al.*, 1993) and Cory's shearwaters (Granadeiro *et al.*, 1998)). Unlike the first incubation shift, which is typically performed by males to allow females to replenish their reserves after egg-laying (Stonehouse, 1962; Fleet, 1974; Beard *et al.*, 2023), the first series of STs on Nukutepipi seemed to be performed by whichever parent had been on incubation duty. Identifying the sex of the adults would help confirm this observation.

In this study, the durations of STs were estimated by calculating the time difference between the date when parents were last observed before embarking on a foraging trip and the date when they returned to the nest. On average, STs lasted for 26.8 hours (1.1 days), ranging from 6 to 129.6 hours (0.3 to 5.4 days) (Figure 4-3). However, due to limitations of the study design, the durations of STs may have been overestimated. Most parents were absent during the morning nest visit, present during the afternoon visit, and absent again during the following morning visit. Thus, it is unknown whether they left late afternoon or early the following morning. In contrast, the ST durations of some parents, averaging 9.6 hours (0.4 days), appeared to be more accurate, as these parents were observed in the morning, absent in the early afternoon, and present again later the same day. However, it is important to note that this estimate likely remains overinflated, as nests were not continuously monitored, and parents may have returned earlier than recorded. After completing their STs, seabird parents were not seen at the nest for an extended period, suggesting that they initiated an LT to forage for themselves (Sommerfeld & Hennicke, 2010; Beard *et al.*, 2023). The method used to assess ST durations was also applied to estimate the durations of LT. On Nukutepipi, red-tailed tropicbird parents performed LTs lasting an average of 271.4 hours (11.3 days), with durations ranging from 119 to 450.8 hours (5 to 18.8 days) (Figure 4-3).

The fact that red-tailed tropicbirds on Nukutepipi alternated between STs and LTs suggests that they adopted a bimodal foraging strategy. Sommerfeld & Hennicke (2010) argued that this foraging approach is typically adopted in seabird colonies whose surrounding waters have low prey abundance. Indeed, to ensure both their own survival and that of their offspring, members of pairs need to alternate roles in chick provisioning. One parent undertakes STs, performing one or two trips per day to nearby waters, where prey is typically scarce, to feed the chick. Meanwhile, the other parent embarks on an LT to more distant foraging areas (Sommerfeld & Hennicke, 2010; Campos *et al.*, 2018; Wojczulanis-Jakubas *et al.*, 2018). These distant areas generally have richer prey availability and lower competition, allowing the foraging parent to replenish its energy reserves (Booth *et al.*, 2000). After an extended period – approximately 11 days on Nukutepipi – the roles are exchanged: the ST-parent now undertakes an LT, while the LT-parent embarks on STs (Sommerfeld & Hennicke, 2010).

There are differing opinions about how pelagic seabirds determine when to switch from STs and LTs. Numerous studies (e.g., Weimerskirch *et al.*, 1993; Granadeiro *et al.*, 1998; Booth *et al.*, 2000) have demonstrated that adult body mass decreases during STs, as they prioritise provisioning for their chick, and then increases after completing an LT. Based on these findings, they have speculated that the alternation between STs and LTs is triggered when adults reach a critical body mass threshold. In contrast, others (Sommerfeld & Hennicke, 2010) have challenged this view. Although they also reported body mass loss in ST-adults, they argued that the key trigger is not body mass but rather the return of their partner from an LT, as ST-parents initiate an LT "almost immediately" after their LT-partner returns to the nest

(Sommerfeld & Hennicke, 2010). Although the present study cannot confirm this due to the limitations of weighing red-tailed tropicbird parents only once upon first encounter and the lack of continuous nest monitoring, it is plausible that the transition from STs to an LT is influenced by a combination of both factors. Indeed, in most nests, the ST-parent was not observed at the nest after the LT-parent had returned, suggesting an immediate turnover in duties, which aligns with the observations of Sommerfeld and Hennicke (2010) on Christmas Island. On the other hand, some chicks were left unattended and unfed for extended periods, suggesting that the ST-parent went on an LT to recover its body mass that it lost during STs, and did not wait for its LT-partner's return.

The bimodal foraging strategy has also been reported in another colony of red-tailed tropicbirds breeding on Christmas Island (Sommerfeld & Hennicke, 2010). However, the lengths of both STs and LTs differed significantly in both colonies. Indeed, on Christmas Island, red-tailed tropicbird parents performed STs of 3 hours (0.1 days) (range: 0.8–20.4 hours) and LTs of 57.4 hours (2.4 days) (range: 3.9–170.3 hours) (Sommerfeld & Hennicke, 2010). When comparing the durations of LTs between the two colonies – without accounting for STs, as those values were overestimated on Nukutepipi – it is evident that red-tailed tropicbird adults on Nukutepipi took longer LTs than those breeding on Christmas Island (11 days vs. 2.4 days). Sommerfeld and Hennicke (2010) argued that the length of foraging trips is primarily determined by prey availability, suggesting that seabirds on Nukutepipi may have had difficulties in finding food compared to those on Christmas Island. These findings are surprising because, unlike Christmas Island, Nukutepipi is in the middle of the Pacific Ocean, far from large land masses, and distant from industrial fisheries (McCabe *et al.*, 2025).

Industrial fisheries inflict considerable losses in marine biodiversity by outcompeting seabirds for marine food resources (Furness, 2003; Ramos & Pacheco, 2003; Danckwerts *et al.*, 2014). They do so by depleting fish stocks that seabirds rely on or by targeting higher-trophic-level species such as subsurface predators. In a healthy marine ecosystem, subsurface predators like tunas affect the behaviours of surface-dwelling fish (e.g., flying fish, squid, mahi mahi) by preying upon them from below. This drives prey to the surface making them more accessible to flying predators (i.e., seabirds) which forage from above. However, when industrial fishing reduces subsurface predator populations, surface-dwelling fish experience lower predation pressure, making them less likely to aggregate near the surface. As a result, seabirds struggle to locate their prey (Danckwerts *et al.*, 2014; Votier *et al.*, 2023). To compensate, seabirds extend their foraging trips, travelling further to more productive areas with higher prey availability (Sommerfeld & Hennicke, 2010; Bertrand *et al.*, 2012; Votier *et al.*, 2023). For example, industrial fisheries depleted local Peruvian anchovy (*Engraulis ringens*) stocks resulting in longer trips undertaken by Peruvian boobies (*Sula variegata*) (Bertrand *et al.*, 2012). Despite minimal fishing activity around Nukutepipi (McCabe *et al.*, 2025), red-tailed tropicbirds appear to face food limitations, as indicated by lengthy foraging trips. This suggests that other environmental factors may be at play. The most likely explanation, though yet to be confirmed, is low phytoplankton productivity in the tropics, which cascades through the food web, affecting higher trophic levels (Ballance & Pitman, 1999). Inter-annual investigations into this and other potential factors on Nukutepipi could provide valuable insights into why red-tailed tropicbirds struggle to find prey.

Adopting the bimodal foraging strategy appears to be an effective way to cope with low prey availability, as it is utilised by numerous pelagic seabird species such as little shearwaters (Booth *et al.*, 2000), Cory's shearwaters (Granadeiro *et al.*, 1998), and wandering albatrosses (Weimerskirch *et al.*, 1993). It has also been recorded in the red-tailed tropicbird's closely related species: the red-billed (Beard *et al.*, 2023) and white-tailed tropicbirds (Campos *et al.*, 2018). The latter species was observed to undertake significantly shorter foraging trips than the red-tailed tropicbird, with STs lasting 4 hours (0.2 days) and LTs lasting 16 hours (0.7 days) on Morro do Chapéu Island, north-eastern Brazil.

Le Corre *et al.* (2003) documented another foraging strategy observed in red-tailed tropicbirds on Europa Island, where seabird parents undertook foraging trips averaging 34 hours (1.4 days). This approach, known as the unimodal foraging strategy, is thought to be adopted by seabirds breeding in areas with abundant prey in nearby waters (Sommerfeld & Hennicke, 2010). Given the importance of understanding the foraging ecology of seabirds, further research is needed to assess the health of our marine ecosystems and the potential risks they face.

6.3.3 Amount of food delivered to chicks between consecutive weighings

The feeding frequency of red-tailed tropicbird parents could not be determined, as nests were not monitored continuously. However, other studies have shown a negative relationship between feeding frequency and chick age, with younger chicks being fed more often than older chicks (Schreiber, 1994; Ramos & Pacheco, 2003). Feeding frequency has been identified as a key factor influencing chick survival. In fact, multiple studies, including Ramos and Pacheco (2003) and Schaffner (1990) on white-tailed tropicbirds, and Ricklefs *et al.* (1985) on Leach's storm-petrels, have reported that non-surviving chicks received fewer meals than those that survived. In contrast, meal size did not affect chick survival, implying that this parameter is independent of feeding frequency (Ricklefs *et al.*, 1985; Schaffner, 1990; Ramos & Pacheco, 2003).

In the present study, meal sizes were estimated using the amount of mass gained by chicks between consecutive weighings. If a chick increased in mass, it suggested that one of its parents had returned and fed it; otherwise, it was assumed that no feeding had occurred. On

Nukutepipi, a positive correlation was observed between meal size and chick age during the first month of life, with meal sizes increasing from 18 g to 68 g. After this period, meal sizes plateaued to an average of 86 g per meal until fledging but varied considerably, with some meals weighing up to 346 g (Figure 4-4). These values were likely underestimated, as chicks were mostly not weighed immediately after they were feed, so they would typically had time to metabolise some of their meal before being weighed.

This increasing-plateauing pattern in meal size appears to be common among tropicbirds and other pelagic seabirds (Schaffner, 1990; Schreiber, 1996; Ramos & Pacheco, 2003). Tropicbird adults are known to forage for an "optimal payload size", which is determined by the digestive capacity and swallowing abilities of their chick, rather than foraging at their full potential (Ramos & Pacheco, 2003). For example, Ramos and Pacheco (2003) found that the optimal payload size in white-tailed tropicbirds was approximately 40% of the maximum payload size that parents could transport. This optimal payload size is shaped by natural selection, influenced by a combination of factors such as the digestive tract and swallowing capacities of chicks and energetic constraints on adults linked to flight, diving, prey availability, and weather conditions (Schaffner, 1990; Ramos & Pacheco, 2003).

Based on this, it can be argued that once chicks on Nukutepipi matured enough for their digestive tract and swallowing capacities to function fully, red-tailed tropicbird adults foraged for a target payload size of at least 86 g. Fleet (1974), in a study on red-tailed tropicbirds on Kure Atoll, calculated the amount of food delivered to chicks both between consecutive weighings and per day. Regardless of the calculation method, red-tailed tropicbird adults on Kure Atoll targeted a smaller payload size compared to those on Nukutepipi, with parents delivering an average of 66 g between consecutive weighings and 74 g per day to their chick. The underlying reason for these discrepancies remains unknown, and further investigations are needed to better understand the factors influencing payload size in different colonies.

Schreiber (1996) demonstrated the plasticity in red-tailed tropicbird parental feeding behaviour through four experiments: (1) increasing food demand by adding a large chick to a nest already containing a large chick; (2) inducing regurgitation in chicks to increase food demand; (3) altering food demand by swapping chicks of different ages between nests, and (4) reducing food demand by pre-feeding chicks. The study showed that parents could adjust to these experimental manipulations, suggesting that seabird adults can gauge the quantity and size of prey to catch based on the chick's food demand and swallowing capacity, both of which are correlated with age (Schaffner, 1990; Schreiber, 1996; Ramos & Pacheco, 2003). On Nukutepipi, a notable case involved a large chick that experienced significant weight loss. It moved to a nearby nest containing a smaller, unstudied chick, and its body mass subsequently recovered. Meanwhile, the smaller chick appeared to weaken daily and eventually died, suggesting that the larger chick may have been fed by the smaller chick's parents. Although the fate of the larger chick remains unknown due to the study's limited duration, this instance highlights the flexibility of red-tailed tropicbird parents in their provisioning behaviour. Flexibility in feeding behaviour has previously been reported in other avian species such as the masked booby (*S. dactylatra*) (Anderson & Ricklefs, 1992), Atlantic gannet (*Morus bassana*) (Nelson, 1964), and glaucous-winged gull (*Larus glaucescens*) (Henderson, 1975).

6.3.4 Prey types

Twenty-three prey items were collected from nests and regurgitations on Nukutepipi. The average mass of regurgitated prey was 61.8 g, while that of prey found near nests averaged 43.5 g. Overall, the mass of individual prey items ranged from 3 to 228 g (Table 4-1). However, these values may not accurately reflect the original prey mass caught by red-tailed tropicbirds, as regurgitated items may have been partially digested and prey found could have already decomposed. The most frequently occurring fish species were the Atlantic horse mackerel (see Appendix C-7), gray triggerfish (see Appendix C-6), trevally (see Appendix C-9), and flying fish (see Appendix C-10) (Table 4-1). In other colonies, studies have identified flying fish, mahi mahi, and squids as the most common prey for red-tailed tropicbirds (Fleet, 1974; Diamond, 1975; Le Corre *et al.*, 2003; Sommerfeld & Hennicke, 2010).

Red-tailed tropicbirds exploit diverse marine resources, with eight fish families documented in their diet on Nukutepipi, and 13 fish families and three cephalopod families (mainly squids) identified as being consumed on Europa Island (Le Corre *et al.*, 2003). A similar ratio of fish to squid was observed on Aldabra Atoll (Diamond, 1975). In contrast, Ashmole and Ashmole (1967) reported the opposite trend on Kiribati, which aligns with findings from Beard *et al.* (2024) in their study on red-billed tropicbirds breeding on St Helena. This variation in prey occurrence suggests that tropicbirds forage based on regional prey availability rather than prey preference (Beard *et al.*, 2024). However, Beard *et al.* (2024) also observed that red-billed tropicbird parents selectively forage for higher-quality prey to feed their chick compared to what they ingest themselves. This likely explains why fish, which are richer in protein and lipids than squid, constitute a larger portion of juveniles' diets, promoting chick growth, compared to the adults' diet. Similarly, Le Corre *et al.* (2003) reported that the mean mass of mahi mahi captured by red-tailed tropicbirds on Europa Island was 120 g, making it a highly profitable prey item. They noted that a single mahi mahi could meet the optimal payload mass needed to provision a mature chick. However, because mahi mahi are less abundant than cephalopods, Le Corre *et al.* (2003) concluded that red-tailed tropicbirds rely on a mixed diet, combining infrequent but highly profitable prey, like mahi mahi, with more common, less nutritious prey such as squid and small fish.

Although tropicbirds forage to achieve a target payload mass, they occasionally capture prey items that exceed this optimal payload mass. For instance, a red mullet weighing 228 g was found near a nest on Nukutepipi, indicating that red-tailed tropicbirds can transport prey weighing up to 30% of their body mass. Similarly, observations on Europa Island show that they can carry prey weighing 26% of their body mass (Le Corre *et al.*, 2003), while white-tailed tropicbirds on Aride Island have been reported to transport prey up to 40% of their body mass (Ramos & Pacheco, 2003). These findings demonstrate that tropicbird parents do not operate at full potential, at least during the chick-rearing period (Schaffner, 1990; Ramos & Pacheco, 2003).

6.4 Chick growth rate

6.4.1 Morphometrics of chicks

By conducting a series of weekly measurements, including head, culmen, tarsus-to-middle-toe, wing, and tail lengths, I documented the growth patterns of red-tailed tropicbird chicks on Nukutepipi, revealing distinctive developmental trends. For data analyses, chicks were classified into three groups based on their outcomes: surviving, non-surviving, and fledged. This classification enabled a comparative assessment of growth patterns among the groups. Additionally, the overall physical progression of the chicks can be visually represented in Appendix D, which presents a series of images illustrating their development over time.

Newly hatched chicks had a head length of approximately 5 cm, which increased rapidly by 0.19 cm/day during the first 40 days. After this period, growth slowed and stabilised at around 13.7 cm, matching the adult head size. A similar growth pattern was observed for culmen length, which started at approximately 1.3 cm, increased by 0.09 cm/day, and began to level off around day 40, reaching an average of 6.1 cm by fledging age. However, this remained slightly shorter than the adult average of 6.6 cm (Figure 5-2; Table 5-3). These observations align with those reported by Fleet (1974) on Kure Atoll and Diamond (1975) on Aldabra Atoll.

The tarsus-to-middle-toe length followed a comparable pattern, growing rapidly from 3 cm at hatching to about 8.2 cm by day 30, with a growth rate of 0.15 cm/day, before plateauing at around 8.7 cm (Figure 5-2; Table 5-3). Fleet (1974), who measured tibiotarsus and foot lengths separately, noted a similar trend and suggested that the rapid development of hind limbs aids thermoregulation. Interestingly, juveniles on Nukutepipi appeared to attain a pre-fledging asymptotic tarsus-to-middle-toe length that was 7.9% greater than that of adults. Ricklefs (1979) observed a similar phenomenon in common tern (*S. hirundo*) juveniles, where tarsal lengths exceeded adult measurements by approximately 15%, likely due to additional fleshy tissue. However, the short duration of the current study on Nukutepipi prevented a robust assessment of this trend in red-tailed tropicbirds, as only five chicks were observed reaching fledging age.

Wing and tail lengths exhibited exponential growth patterns. Wing length gradually increased from 3 cm at hatching, then accelerated after day 30, and reached approximately 32 cm by the fledging period, with a growth rate of 0.43 cm/day – slightly shorter than the adult wing length of 35 cm (Figure 5-2; Table 5-3). This chick-to-adult discrepancy has also been reported by Fleet (1974), Schreiber (1994), and Diamond (1975). Tail rectrices first appeared around day 25 and grew rapidly at a rate of 0.23 cm/day from day 40, reaching approximately 12.5 cm by fledging. Interestingly, fledgling tail rectrices were measured to be longer than those of adults, which averaged 11 cm (Figure 5-2; Table 5-3). This apparent difference arose because adult measurements were taken from their R2 rectrices rather than the central tail feathers (i.e., the long red tail streamers). Consequently, fledgling rectrices were significantly shorter than those of adults due to the absence of the elongated central streamers in juveniles, which corroborates Fleet's (1974) observations.

On Kiribati, Schreiber (1996) observed that red-tailed tropicbird chicks receiving more food exhibited faster wing growth than those receiving less. Similar findings were reported when comparing ENSO and non-ENSO years (Schreiber, 1994). Despite experiencing reduced food delivery, chicks were still able to fledge successfully, although it required more time. This indicates that juveniles are well adapted to fluctuating food supply (Schreiber, 1996). In contrast, on Nukutepipi, no significant difference in wing growth was observed between surviving, non-surviving, and fledged juveniles. This unchanged wing growth rate has also been documented in the black noddy (*A. tenuirostris*) and the common tern (Ashmole, 1962; LeCroy & Collins, 1972). To better understand these growth dynamics, inter-annual studies on Nukutepipi are needed to assess whether wing growth is influenced by periods of low prey availability such as those during severe ENSO years.

6.4.2 Mass of chicks

Unlike head, culmen, tarsus-to-middle-toe, wing, and tail growth rates which showed no significant differences across chick groups, the mass of red-tailed tropicbird juveniles on Nukutepipi varied significantly.

Starting with an average mass of 54 g at hatching, red-tailed tropicbird chicks experienced rapid mass gain during the first 50 days of their lives, with growth rates ranging from 7.1 g/day to 9.7 g/day. Following this initial phase of rapid mass gain, the daily mass change slowed significantly to -8.1 g/day but then increased to 3.8 g/day between 60 and 70 days of age. This resulted in a more gradual increase in mass, eventually reaching a peak of 688 g for surviving chicks and 723 g for those that successfully fledged. Notably, 24 juveniles exhibited an asymptotic mass that exceeded the average adult mass of 757 g by approximately 10%, on average. Surprisingly, despite surpassing adult mass, four of these juveniles did not survive. In three exceptional cases, juveniles exceeded adult mass by as much as 44% (Figure 5-3; Figure 5-4). A comparable average excess weight was reported by Diamond (1975) on

Ascension Atoll, where chicks reached an average asymptotic mass of 15% greater than adult mass. In contrast, Stonehouse (1962) recorded that red-billed tropicbird chicks exceeded adult mass by only 4%, while white-tailed tropicbird chicks exceeded adult mass by 33%. Despite the considerable variation in the percentage of excess weight, this growth pattern appears to be common among many bird species such as the violet-green swallow *Tachycineta thallassina*, merlin *Falco columbarius*, and southern rockhopper penguin *Eudyptes chrysocome* (Ricklefs, 1968). Ricklefs and Schew (1994) attributed this excess weight to fat accumulation resulting from parental overfeeding. They argued that this fat accumulation aligns with the energy insurance hypothesis, which states that overfeeding reduces "the probability that a chick will starve just by chance", as both meal sizes and provisioning rates can vary significantly due to the unpredictability of prey availability. For instance, in Leach's storm-petrels, fat reserves enable mature juveniles to endure periods of no food for up to 10 days (Ricklefs & Schew, 1994). Similarly, on Nukutepipi, a red-tailed tropicbird juvenile survived a fasting period of 9.8 days, highlighting the critical role of fat reserves in sustaining chicks during periods of reduced or infrequent feeding. During years of food shortage (i.e., ENSO events), however, Schreiber (1996) reported that tropicbird chicks often fail to reach a pre-fledging asymptotic mass. Instead, they exhibit a more gradual mass increase, ultimately achieving a mass comparable to those raised in non-ENSO years and successfully fledging despite the slower growth.

On average, chicks on Nukutepipi reached the adult mass by day 53, though the time required to achieve this varied significantly among individuals, ranging from as few as 35 days to as many as 83 days (Figure 5-3), largely depending on the frequency and amount of food they received. However, it is important to note that the juvenile requiring 83 days to reach adult mass was already a large, mature chick at the beginning of the study, suggesting that this observation may not accurately reflect typical mass gain patterns. The findings of the current study align with those of Diamond (1975), who reported that red-tailed tropicbird chicks on Ascension Atoll reached an adult mass of 762 g by day 50. In contrast, red-tailed tropicbird chicks on Kure Atoll required significantly less time (35 days) to reach an adult mass of 612 g (Fleet, 1974). Similarly, Schaffner (1990) documented white-tailed tropicbird juveniles taking a comparable number of days to reach an adult mass of 370 g.

As fledging period approached, juveniles gradually began losing mass, with daily mass changes ranging from -4.4 g/day to -16.4 g/day from 70 to 100 days of age (Figure 5-3; Figure 5-4). This mass recession prior to fledging is common among tropicbirds and other pelagic seabird species such as Leach's storm-petrels and northern fulmars. In these species, the loss of accumulated excess weight has been attributed to reduced parental provisioning rates and water loss (Ricklefs & Schew, 1994; Philips & Hamer, 1999). Notably, while chick body mass decreases, lipid reserves continue to increase. This sustained fat accumulation is thought to play a crucial role in the post-fledging activities of juveniles, as it provides the energy needed during the period when they must learn to forage independently and efficiently, even in unfavourable weather conditions (Philips & Hamer, 1999). However, Wilson's storm-petrel (*Oceanites oceanicus*) chicks experience a loss of both water and lipids during this period of mass recession, suggesting a different underlying mechanism in this species (Obst & Nagy, 1993). Water and lipid contents of red-tailed tropicbird juveniles on Nukutepipi were not measured, and no studies have examined these parameters in tropicbirds globally. Further research is required to understand the physiological changes they undergo during the fledging period.

Interestingly, during the final 10 days at the nest, the daily mass change of red-tailed tropicbird fledglings on Nukutepipi rebounded to 10.9 g/day (Figure 5-4). However, this observation may have been influenced by limitations in the analysis; the final age class (100–110) was based on a much smaller sample size, including only three juveniles, which could have skewed the results and contributed to the unusually high daily mass change observed in this group.

The daily mass change of red-tailed tropicbird chicks during their development at the nest has not been yet documented in other colonies. However, Ramos and Pacheco (2003) studied mass changes in white-tailed tropicbird chicks and found that during the first 35 days of life, the mass of surviving chicks increased at an average rate of 7.8 g/day, which slowed to 3.7 g/day by day 60. Prior to the fledging period, these chicks were observed experiencing mass recession, with their daily mass change dropping to -1.5 g/day (Ramos & Pacheco, 2003). These rates of daily mass change exhibited less fluctuations compared to those documented in the current study on red-tailed tropicbirds.

On Nukutepipi, only five red-tailed tropicbird juveniles were monitored until fledging due to the limited duration of the study. The average fledging age was 99 days, ranging from 94 to 106 days. In contrast, the fledging periods in other colonies were shorter, typically ranging from 83 to 90 days (Fleet, 1974; Diamond, 1975; Amerson & Shelton, 1976; Vanderwerf & Young, 2014). Notably, Fleet (1974) reported that a fledgling on Kure Atoll left its nest when just 65 days old, suggesting that this individual likely received more food than those that fledged at older ages. This suggests that the longer fledging periods observed on Nukutepipi may indicate that juveniles on the island received less food, resulting in slower growth rates. Furthermore, the mass of fledglings averaged 611 g, ranging from 532 to 660 g, suggesting that they were approximately 20% lighter than most of their adult conspecifics (Figure 5-3). In contrast, fledglings from other colonies were heavier than adults, with those on Kure Atoll and Christmas Island being 11% and 15% heavier, respectively (Fleet, 1974; Le Corre *et al.*, 2003). These findings suggest that juveniles on Nukutepipi may have experienced a reduced food supply, potentially linked to lower prey availability in their surrounding marine environment. Such limitations in food provisioning likely contributed to slower growth rates (longer fledging periods) and lower fledging masses compared to juveniles in other colonies, where food resources were presumably more abundant. These findings align with the longer foraging trips undertaken by red-tailed tropicbird parents on Nukutepipi compared to those in other colonies. As discussed in Section 6.3.2, longer foraging trips are often indicative of lower prey availability (Sommerfeld & Hennicke, 2010). Prolonged trips not only reduce the frequency of feedings but may also increase the energetic demands on parents, further limiting the food supply for their chicks and ultimately slowing their growth rates.

There may be a yet-to-be-determined threshold mass below which fledglings cannot successfully fledge. Indeed, two mature juveniles, aged 95 and 87 days old, showed morphometric readiness to fledge but ultimately failed to do so. One juvenile, weighing 416 g, was observed flying over the lagoon but was later found dead on the beach. The other, weighing 394 g, was last seen walking around the nest site before a corpse, presumed to be theirs, was discovered days later. Although DNA analysis could have confirmed their identities, their extreme lightness – approximately 50% lighter than the average adult mass – clearly hindered their survival. One possible explanation is that their parents failed to provision them adequately. Alternatively, the juveniles may have lacked the instinct to leave the nest to forage independently, resulting in prolonged fasting periods. This extended fasting likely led to the depletion of fat reserves and, eventually, critical protein loss, contributing to their inability to fly and survive (discussed in Section 6.4.3).

6.4.3 Fasting periods – duration and mass loss

Fasting periods typically consist of three distinct phases; however, those experienced by red-tailed tropicbird chicks have not yet been properly quantified.

Phase I begins immediately after a feeding event and lasts from a few hours to a few days. During this phase, immediate energy demands are met through the breakdown of carbohydrates, primarily glycogen (Jenni-Eiermann & Jenni, 2012). Phase I is characterised by a rapid mass loss due to the excretion of urine and faeces (Cherel *et al.*, 1987; Jenni-Eiermann & Jenni, 2012). Observations on Nukutepipi revealed that red-tailed tropicbird chicks lost an average of 92.3 g/day within the first day of fasting, with a slight positive correlation between mass loss and age (Figure 5-10). As discussed in Section 6.3.3, larger chicks have a greater capacity for digestion and swallowing than smaller chicks, enabling them to receive larger meals (Schaffner, 1990; Ramos & Pacheco, 2003). However, due to the unpredictability of prey abundance in marine ecosystems, parents may struggle to consistently provide optimally sized meals. This was evident on Nukutepipi, where significant variability in meal sizes contributed to substantial variation in chick mass loss during Phase I, which ranged from 5 to 204 g after 30 days of age (Figure 5-7). On average, chicks lost 13.5% of their initial mass during this phase, with some losing as much as 30.8% (Figure 5-8).

Phase II, also known as the "long phase of economy", begins once glycogen reserves are depleted (Cherel *et al.*, 1987). During this phase, fat stores become the primary energy source, leading to a slower rate of mass decline. The duration of Phase II is influenced by a bird's initial fat reserves and overall body condition (Jenni-Eiermann & Jenni, 2012). On Nukutepipi, Phase II lasted significantly longer than Phase I, with red-tailed tropicbird chicks fasting for an average of 3 days before being refed (Figure 5-6). When combining the durations of Phase I and Phase II, the findings from Nukutepipi align with Fleet's (1974) observations on Kure Atoll, where chicks rarely went unfed for more than 3.5 days. Remarkably, some juveniles on Nukutepipi endured Phase II for up to 8 days and still survived (Figure 5-11), suggesting that frequent, adequately sized meals prior to fasting allowed them to accumulate higher fat reserves, thus increasing their resilience (Ricklefs & Schew, 1994). Conversely, non-surviving chicks experienced an average Phase II duration of 4.2 days before succumbing to starvation (Figure 5-11). This chick group also exhibited greater variability in fasting durations, with one surviving up to 12 days (Figure 5-11), suggesting that the survival threshold for Phase II may lie between 8 and 12 days, assuming that the chicks were adequately fed beforehand. However, some chicks perished after fasting for as little as one day, likely due to insufficient meal sizes across multiple feedings resulting in smaller fat reserves and poorer body condition. The variability in Phase II durations was also reflected in chick mass loss, which ranged from 3 to 186 g (Figure 5-7). On average, chicks lost 10.7% of their initial mass during this phase, with a significantly lower daily mass loss compared to Phase I, averaging 27.3 g/day (Figure 5-8; Figure 5-10).

Among the five fledglings observed on Nukutepipi, three experienced fasting periods before leaving the nest. These juveniles fasted for 3 to 4 days prior to fledging (Figure 5-6), consistent with Fleet's (1974) findings on Kure Atoll, where chicks fasted for 5 days before fledging. Fleet (1974) attributed this phenomenon to chicks refusing food, a behaviour also documented in red-billed and white-tailed tropicbirds (Stonehouse, 1962; Schaffner, 1990). However, two fledglings on Nukutepipi gained mass on the day they fledged, suggesting that they were fed and did not refuse food. Monitoring cameras at nest sites would be essential to confirm parental feeding activity in such cases.

Finally, Phase III is the critical and final stage of fasting. At this point, the bird begins metabolising muscle protein to sustain itself, resulting in a rapid decrease in mass. Body condition deteriorates quickly during this phase, ultimately leading to death if the bird remains unfed (Cherel *et al.*, 1987; Jenni-Eiermann & Jenni, 2012). On Nukutepipi, the body mass of red-tailed tropicbird chicks exhibited a pattern of rapid decrease (Phase I) followed by a gradual decline (Phase II). However, the subsequent rapid decrease characteristic of Phase III was not observed, even among non-surviving chicks. This suggests that juveniles on Nukutepipi underwent only Phase I and Phase II of fasting. The absence of Phase III in red-tailed tropicbird chicks remains unexplained and warrants further investigations. It is also unclear whether red-tailed tropicbird adults similarly lack a Phase III, emphasising the need for comprehensive studies across all life stages of this species.

6.5 Success rates and factors contributing to nest failures

6.5.1 Success rates

On Nukutepipi, the hatching success rate – defined as the proportion of hatched eggs to total laid eggs – was 76.4%, the same as that reported on O'ahu, Hawaii by Vanderwerf and Young (2014). A slightly lower rate of 60.5% was recorded on Christmas Island (Sommerfeld *et al.*, 2015). Interestingly, both O'ahu and Christmas Island had a greater diversity of egg predators, including rats, feral cats, feral pigs, and mongooses, than Nukutepipi, where the primary predator was the strawberry hermit crab (discussed in Section 6.6.4). Despite this, they still achieved relatively high hatching success rates. In contrast, the colony inhabiting Raina Island, where relatively low levels of predation (only the buff-banded rail), was reported to have a much lower success rate of 39.3% (Richardson *et al.*, 2013). This suggests that the presence of predators does not necessarily result in lower hatching success rates, and conversely, the absence or low presence of predators does not always guarantee higher hatching rates.

Fledging success rate refers to the proportion of chicks that successfully fledge in relation to the total number of hatched chicks. In contrast to hatching success, calculating an accurate fledging success rate was not possible in this study. Indeed, due to its limited duration, the study concluded before 34 chicks had the opportunity to fully develop and fledge. Out of the 65 juveniles observed, 26 did not survive, indicating a minimum mortality rate of 40%.

Consequently, the maximum possible post-hatch survival rate, or fledging success, was 60%. However, since only five juveniles were observed to have fledged, the minimum fledging success rate was 7.7%. Therefore, based on these findings, the fledging success rate of red-tailed tropicbird chicks on Nukutepipi was estimated to lie between 7.7% and 60%. Surprisingly, the fledging success observed on Nukutepipi is the second to lowest recorded across comparable studies. The only other comparable low rate is the 54.7% fledging success rate on Christmas Island reported by Sommerfeld *et al.* (2015). In contrast, fledging success rates observed in other red-tailed tropicbird colonies such as Raine Island, O'ahu, Kiribati, Sand Island, and Johnston Atoll, are considerably higher, ranging from 76% to 98% (Schreiber, 1996; Amerson & Shelton, 1976; Vanderwerf & Young, 2014; Richardson *et al.*, 2023). The reason for these discrepancies in fledging success rates may be related to prey availability and is further discussed in Section 6.5.8.

On Nukutepipi, several factors were observed to contribute to egg and chick losses, including nest site inadequacies, poor coordination between red-tailed tropicbird parents, predators, intra- and interspecific competition, parasites, and human activity.

6.5.2 Nest site inadequacies

On Nukutepipi, red-tailed tropicbird nests were located on the ground beneath bungalows or vegetation. These nests were found under a wide variety of plant species, including pu'atea (pisonia), fara (pandanus), tāhinu (tree heliotrope), miki miki (bantigue), and 'aito (coastal she-oak). In addition to these specific plant species, other vegetation types such as molasses grass, beach naupaka, and salt bush, have also been associated with red-tailed tropicbird nests in different colonies (Fleet, 1974; Prys-Jones & Peet, 1980; Clark *et al.*, 1983; Morrell & Aquilani, 2000; Hennicke & Flachsbarth, 2009). On Rapa Nui, however, nests are located in cliff cavities (Flores *et al.*, 2017), a behaviour not observed on Nukutepipi, as its atoll structure, lacking cliffs, does not support such nesting. This suggests that red-tailed tropicbirds do not have a strong preference for specific nesting substrates. Instead, their primary requirement appears to be sufficient shade cover, which is vital for the survival of eggs and chicks, as red-tailed tropicbirds lack the ability to thermoregulate via gular fluttering, which is a cooling mechanism that promotes heat loss when temperatures rise. Without adequate shade, eggs are at risk of addling (cessation of embryo development due to overheating), and chicks are vulnerable to heat stress (Prys-Jones & Peet, 1980; Clark *et al.*, 1983; Morrell & Aquilani, 2000). Clark *et al.* (1983) observed that red-tailed tropicbird nests on Kiribati typically had at least 70% shade coverage. Similarly, other researchers have noted that these seabirds require full or partial shade for their nests, which underscores the critical importance of shade cover for red-tailed tropicbird nesting success (Howell & Bartholomew, 1969; Prys-Jones & Peet, 1980).

Red-tailed tropicbird parents may abandon their nest if the site is deemed unsuitable for the survival of their future chick (Howell & Bartholomew, 1962). On Nukutepipi, one of the studied nests contained an egg but was located in the middle of a road, where the sparse canopy provided little shade. During the first three visits, an adult was observed incubating the egg (see Plate E-1a in Appendix E). The nest was later abandoned (see Plate E-1b in Appendix E) and the egg left unattended for two weeks until it was accidentally stepped on by local staff. This abandonment behaviour suggests that the parents may have been inexperienced and realised that their nest site was unsuitable for the survival of their future chick (Howell & Bartholomew, 1962). Since the breeding season had just commenced, it is possible that they abandoned their offspring early in the season and attempted to replace it while food resources were still abundant. However, it is important to note that no monitoring devices such as GPS trackers or leg bands, were attached to red-tailed tropicbirds breeding on Nukutepipi, making these conjectures speculative. Sommerfeld and her colleagues (2015), who studied the breeding behaviours of red-tailed tropicbirds on Christmas Island, reported that producing a replacement egg is highly energy-demanding and becomes increasingly costly due to declining food resources as the breeding season progresses. Therefore, depending on whether the initial clutch fails during incubation or chick-rearing, females decide whether to produce a replacement clutch, with the likelihood of a female investing in another egg decreasing as the end of the breeding season approaches.

There was another case where, although the nest was situated under a bantigue shrub, it received limited shade cover due to its location at the edge of the plant cover. This lack of shade caused parents and their young chick to gradually retreat further under the vegetation, where slightly more shade was available. In addition, it was noticed from the first visit that the bill of the young was deformed, with its lower mandible not of the same length as the upper one (see Plate E-2 in Appendix E). Such deformities have been documented in various avian species, including yellow-eyed penguin (*Megadyptes antipodes*) (Buckle *et al.*, 2014), Scopoli's shearwater (*Calonectris diomedea*) (Roatti *et al.*, 2019). Several studies (e.g., Buckle *et al.*, 2014; Tattersall *et al.*, 2017) suggest that chicks are prone to teratogenesis if their eggs experience hyperthermia during incubation. In other words, exposure of a developing embryo to elevated temperatures increases the likelihood of hatchlings exhibiting bill malformations. However, the cause of teratogenesis observed in the red-tailed tropicbird chick on Nukutepipi remains uncertain. Other factors, such as genetic defects or inadequate food supply, can also lead to developmental abnormalities (Buckle *et al.*, 2014; Jones *et al.*, 2015; Roatti *et al.*, 2019). Furthermore, at just 13 days old, this chick developed a cloacal prolapse (see Plate E-2 in Appendix E), which ultimately led to its death. To date, there is no known reports of this condition in juvenile or wild birds in the available literature. In this instance, heat exposure is suspected to have indirectly contributed to the development of this lethal condition. However, studies on poultry (*Gallus gallus domesticus*) and pet birds (e.g., cockatoos *Cacatuidae* spp.) indicate that cloacal prolapse in adult birds can arise from various factors such as poor nutrition, reproductive stress, egg-laying difficulties, and bacterial or fungal infection (Johnson, 2009; DoveLewis, 2024; Ritzman, n.d.).

These observations on Nukutepipi underscore the crucial role of shade cover in the breeding success of red-tailed tropicbirds. However, breeding success is a complex process influenced by multiple interacting factors, which can ultimately determine reproductive outcomes.

6.5.3 Asynchrony between red-tailed tropicbird parents

As discussed in Section 6.3.2, red-tailed tropicbird adults on Nukutepipi exhibited a bimodal foraging strategy. During the breeding season, parents must balance between finding enough prey to sustain themselves, incubating their egg, and provisioning their chick with sufficient food (Sommerfeld & Hennicke, 2010; Sommerfeld *et al.*, 2015). To ensure successful hatching of their egg, they alternate between incubation shifts and LTs. In contrast, during chick-rearing period, parents switch between LTs and STs, allowing them to forage for themselves (LTs) as well as their chick (STs) (Sommerfeld & Hennicke, 2010; Sommerfeld *et al.*, 2015).

Poor coordination between members of pairs can have negative impacts on their breeding success. During the incubation period, if an LT-parent fails to return to resume incubation and its incubating partner has embarked on its own LT, their egg may be left unincubated for an extended period, making it vulnerable to predators (discussed in Section 6.6.4). Similarly, during the chick-rearing period, young chicks may be left unattended, becoming easy targets for predators. Additionally, Ramos and Pacheco (2003) observed that members of some white-tailed tropicbird pairs returned to the nest at approximately the same time to feed their chick. However, due to the limited digestive tract and swallowing capacity of their young, the second meal was often rejected and wasted. This not only leads to the loss of nutritious food for the chick but renders the parent's foraging effort essentially wasted. If this asynchrony persists, there would be periods when the chick would have to fast, which could lead to starvation and likely death. While no cases of double feeding were observed on Nukutepipi, some red-tailed tropicbird chicks were seen enduring prolonged fasting periods, with some lasting as long as 12 days.

On Nukutepipi, there were instances when chicks experienced intermittent fasting periods during which their mass exhibited unusual fluctuations, as shown in Plate F-1 in Appendix F. For example, one chick's body mass showed consecutive increases over approximately 7 days, followed by a gradual decrease lasting 5 to 10 days. This pattern suggests that while one parent was on ST duties, the chick was adequately fed. However, when this parent embarked on an LT, the other parent failed to return and resume food provisioning. These recurring on-and-off fasting periods weakened the chick, ultimately leading to starvation. This highlights the critical importance of biparental care in ensuring the survival of red-tailed tropicbird chicks.

Starvation of chicks from parental asynchrony was the primary cause of nest failures on Nukutepipi, accounting for 43.6% of all nest failures. Putting this another way, 65.4% of chick losses were caused by starvation. These high rates are striking when compared to other red-tailed tropicbird colonies. For instance, on O'ahu, starvation contributed to 7.2% of total nest failures (Vanderwerf, 2021), and on Christmas Island, it accounted for 8.3% of total chick losses (Sommerfeld *et al.*, 2015). These findings suggest that red-tailed tropicbird parents on Nukutepipi faced challenges in finding enough prey to sufficiently provision their chick. This proposition is supported by the duration of their foraging trips being lengthier compared to other colonies. As mentioned previously (Section 6.3.2), pelagic seabird parents tend to prolong their foraging trips when prey is scarce, thereby increasing their likelihood of encountering prey (Sommerfeld & Hennicke, 2010). This might indicate that prey abundance is low for red-tailed tropicbirds breeding on Nukutepipi. Further investigations, such as the attachment of tracking devices on the birds and the assessment of prey abundance, would help provide a deeper understanding of their breeding ecology, especially on where they forage. It could also provide an insight into the overall health of the marine ecosystems in this remote part of the Pacific Ocean (Piatt *et al.*, 2007).

6.5.4 Predators

Rats (*R. exulans*, *R. norvegicus*, and *R. rattus*) can contribute significantly to nest failures in red-tailed tropicbird colonies by preying on both eggs and chicks (Fleet, 1972; Flores *et al.*, 2017; Luna *et al.*, 2018). For instance, on Kure Atoll, *R. exulans* was responsible for the loss of over half the eggs and the death of all chicks in 1965 (Fleet, 1972). Interestingly, on Midway Atoll, nesting success did not improve following rat eradication, with success rates being 41% both before and after removal of rats (Tyler, 1991; Laniawe, 2008). In contrast, nest failures occurring on Nukutepipi could not be attributed to rat predation, as these predators had been eradicated from the island before this study. Instead, strawberry hermit crabs (*Coenobita perlatus*), which were highly abundant on the island and were observed scavenging on cracked eggs and seabird carcasses, as shown in Plate G-1 in Appendix G, were strong candidates for egg and chick predators. In fact, due to poor coordination between parents, four eggs that were left unincubated for extended periods of up to 7 days appeared to have been consumed by these arthropods. In addition, these hermit crabs were observed eating a 26-day-old chick that otherwise seemed healthy and had shown no signs of mass loss prior to death (see Plate G-2 in

Appendix G). The hermit crabs were also suspected to be the cause of the unexpected disappearance of a 7-day-old chick, whose carcass was never found. Numerous authors (e.g., Mejías, 2017; Morris, 1984; Marchant & Higgins, 1990; Leal *et al.*, 2016; Campos *et al.*, 2018) have observed arthropods such as the Caribbean hermit crab (*C. clypeatus*), land crab (*Johngarthia lagostroma*), mangrove root crab (*Goniopsis cruentata*), and coconut crab (*Birgus latro*) preying on unattended eggs and chicks of various seabird species, including white-tailed tropicbirds, red-billed tropicbirds, least terns (*Sternula antillarum*), and sooty terns.

In addition to rodents and arthropods, red-tailed tropicbirds face predation from a diverse array of predators. Feral cats, for example, have been documented preying on chicks in various colonies, including those on Christmas Island, O'ahu, Kiribati, and on Rapa Nui (Clark *et al.*, 1983; Vanderwerf & Young, 2014; Sommerfeld *et al.*, 2015; Flores *et al.*, 2017). A 2006 study indicated that these feline predators were responsible for the loss of 97.6% of red-tailed tropicbird chicks on Christmas Island (Sommerfeld *et al.*, 2015). Other predators, such as feral pigs (Clark *et al.*, 1983), mongooses (Vanderwerf & Young, 2014), chimango caracaras (Flores *et al.*, 2017; Luna *et al.*, 2018), buff-banded rail (Richardson *et al.*, 2023), and bristle-thighed curlews (Schreiber, 2003) have also been observed preying on unattended red-tailed tropicbird eggs and chicks. Although bristle-thighed curlews were present on Nukutepipi, they did not appear to target red-tailed tropicbird eggs, as they were never observed near the nests. However, it remains possible that predation events went undetected. Installing nest cameras for continuous monitoring would provide valuable insights into potential interactions between bristle-thighed curlews – or other predators – and red-tailed tropicbird nests, offering a clearer understanding of their impact on the colony.

6.5.5 Intraspecific competition

Due to poor coordination between some parents in provisioning their offspring, some chicks experienced prolonged periods of fasting. While most ultimately succumbed to starvation, two large chicks managed to survive by moving to a nearby nest that already contained a smaller chick (see in Plate H-1a and Plate H-1b in Appendix H). Being larger, they were able to outcompete the smaller chick for food, either by begging more insistently, which prompted the smaller chick's parents to feed them instead, or by pecking at the smaller chick. In both instances, these behaviours ultimately led to the death of the smaller chicks. The behaviour of wandering to nearby nests has also been observed on Johnston Atoll by Schreiber (2003), but no aggressive behaviours were recorded.

In addition to competing for food, some chicks also faced competition for nest sites. One instance involved an 18-day-old chick found dead while being pecked by an adult, as illustrated in Plate H-2 in Appendix H. Since the adult did not have markings on its head to indicate that it was one of the study birds, it was assumed to be unrelated to the chick. A similar incident occurred with another chick of approximately the same age from a different nest, though the identity of the pecking adult could not be determined, as this nest was not one of those being studied. Similar behaviour has also been documented in white-tailed tropicbirds by Campos *et al.* (2018), who reported that adults from previous breeding seasons exhibit strong fidelity to their nest sites, often engaging in "fierce fighting" behaviour. In their study, however, the chicks were at least 30 days old and survived the conflicts despite sustaining injuries. In a related observation on Nukutepipi, a 55-day-old chick was seen with head injuries (see Plate H-3 in Appendix H), possibly from a similar confrontation over its nest site, though continuous monitoring was not conducted that could have confirmed this.

6.5.6 Interspecific competition

Another contributing factor to parents not returning to the nest is interspecific competition with frigatebirds (Diamond, 1975; Padmakumar & Shanthakumar, 2023). On Nukutepipi, red-tailed tropicbird adults returning from foraging trips were often observed being chased by these kleptoparasitic foragers, sometimes in groups of up to three individuals. Brockmann and Barnard (1979) defined kleptoparasitism as “the theft of already procured food from one individual (the host) by another (the parasite)”. In this case, frigatebirds are the parasites, stealing food from a wide range of hosts, including boobies (*Sula* spp.), tropicbirds (*Phaethon* spp.), terns (*Sterna* spp.), gulls (*Larus* spp.), shearwaters (*Puffinus* spp.), and petrels (*Pterodroma* spp.) (Padmakumar & Shanthakumar, 2023).

Red-tailed tropicbirds generally manage to evade these attacks by either outrunning their pursuers or regurgitating their last meal, which frigatebirds catch mid-air. However, on Nukutepipi, two adults who did not sacrifice their meals were seen with wounds on their rumps and sides. One was found on the beach, panting severely and exposed to the sun during the hottest hours of the day. It appeared to be badly injured as there were flies swarming around it (see Plate I-5 in Appendix I) and no defensive behaviours were exhibited when approached. Unfortunately, this individual died later that day. The second wounded bird returned to its nest to brood its chick, as shown in Plate I-6 in Appendix I. However, the fate of this adult and its chick remains unknown due to the limited duration of the study.

6.5.7 Parasites

Invertebrate parasites also impacted the survival of red-tailed tropicbirds on Nukutepipi. A 66-day-old juvenile was observed with leeches on both eyes and inside its mouth, as shown in Plate J-1a and Plate J-1b in Appendix J. Despite being adequately provisioned by its parents, as indicated by its increasing body mass, the juvenile evidently succumbed to these blood-sucking parasites. This observation marks the first recorded instance of a host-parasite relationship between tropicbirds and leeches.

Leeches are commonly found in moist, humid environments (Davies *et al.*, 2008), which align with the conditions of the juvenile's nest on Nukutepipi. The affected nest was located in the southern part of the island in an area characterised by dense vegetation and high humidity. Similarly, a 77-day-old juvenile from area nearby nest was observed with a leech infestation in its eye. However, the fate of this individual is unknown due to the short duration of the study on the island.

Leeches have been documented to parasitise a wide variety of hosts, including ducks (Anatidae), herons (Ardeidae), procellariiforms (Procellariidae), penguins (Spheniscidae), passeriforms (e.g., eastern yellow robins *Eopsaltria australis*, Australian magpies *Gymnorhina tibicen*), and cassowaries (*Casuarius* spp.). They target various parts of the host such as eyes, nares, trachea, lungs, mouth, cloaca, legs, feet, and breast (Davies *et al.*, 2008; Nakano *et al.*, 2020).

Although a few samples of leeches from Nukutepipi were collected, preserved in 70% ethanol, and imported to New Zealand, they have yet to be identified. However, their dark brown appearance resembles that of the haemadipsid leech (*Chtonobdella palmyrae*), an avian-specific parasite described by Nakano *et al.* (2020). Nakano and colleagues (2020) demonstrated that the distribution of *Chtonobdella* is widespread throughout the Indo-Pacific region. They hypothesised that the occurrence of *C. palmyrae* on multiple distant islands may be due to seabirds, such as procellariiforms which migrate long distances and breed on these islands. Although no leech cases have been reported in the Hawaii Islands, Nakano *et al.* (2020) suggested that these islands are "potential candidates for undiscovered habitats of *C.*

palmyrae", as the ranges of Bonin petrels (*Pterodroma hypoleuca*) and Tristram's storm-petrels (*Oceanodroma tristrami*) include both Hawaii and islands where *C. palmyrae* has been documented (Nakano *et al.*, 2020).

Murphy's petrels, which also occur in the Hawaii Islands (Pyle & Pyle, 2009), were observed breeding on Nukutepipi. Therefore, it is possible that dispersal of leeches to Nukutepipi may have been facilitated by these birds' migratory routes. Additionally, red-tailed tropicbirds themselves may serve as parasitic hosts, as they also breed in the Hawaii Islands (Vanderwerf, 2021). However, this is speculation until the identification of Nukutepipi's leeches is completed.

In addition to leeches, parasitic flies were observed on both adults and chicks on Nukutepipi (see Plate J-2 in Appendix J). Due to the limited duration of the study, these parasites could not be identified under a microscope. However, they are suspected to belong to the family Hippoboscidae, commonly known as louse flies. These obligate ectoparasitic blood feeders have been documented to infest at least 18 avian orders (Luna *et al.*, 2020). Moreover, they are known to act as vectors for haemosporidian blood parasites in seabirds and have been linked to reduced breeding success in adults, as well as decreased body mass and survival rates in chicks (Luna *et al.*, 2020). Luna and his colleagues (2020) studied leukocyte levels – specifically eosinophil, lymphocyte, and monocyte involved in immune responses to infections – in red-tailed tropicbird colonies breeding on Rapa Nui, where louse flies are scarce, and on Salas and Gomez Islands, where louse flies are prevalent. They found higher leukocyte levels in the latter colony, suggesting that seabirds from this area had compromised body conditions. These findings raise questions about the potential impacts of louse flies on the red-tailed tropicbirds on Nukutepipi.

6.5.8 Human activity

On Nukutepipi, human activities, particularly the trimming of bushes and trees near nesting sites, frequently disrupted red-tailed tropicbird parents, leading to temporary abandonment of their egg. Although seabird parents generally returned after a few hours to resume incubation, the loss of shade cover from trimming often exposed the eggs to direct sunlight. As discussed in Section 6.5.2, such exposure can negatively impact embryo development and increase the risk of teratogenesis. This can also lead to accidental damage such as being stepped on by staff during vegetation trimming, as observed on Nukutepipi. Similar incidents have been reported by Schreiber (2003) and Amerson and Shelton (1976) on Johnston Atoll. Another human activity impacting red-tailed tropicbirds has been documented by Flores and colleagues (2017). On Rapa Nui, they observed that this species was exploited by local inhabitants for food and for their long red tail streamers, which were used for ornamental purposes.

Like many seabird species, tropicbirds are affected by industrial fisheries. Although no direct mortality has been reported, studies by Hagen and Wanless (2015) and Diop *et al.* (2018) highlight their potential impact. As discussed in Section 6.3.2, industrial fisheries contribute significantly to marine biodiversity loss by overexploiting resources and competing with seabirds for food (Furness, 2003; Bertrand *et al.*, 2012; Danckwerts *et al.*, 2014; Hagen & Wanless, 2015; Diop *et al.*, 2018; Egerton *et al.*, 2022). In addition to resource depletion, seabirds face the threat of bycatch – unintentional entanglement in fishing gear – which results in the deaths of hundreds of thousands each year (Furness, 2003; Croxall *et al.*, 2012; Dias *et al.*, 2019; Votier *et al.*, 2023). In the Cabo Verde Archipelago, handline fisheries have also been documented as a threat, with red-billed tropicbirds comprising 22% of recorded bycatch incidents (Montrond, 2020). Beyond direct mortality, fisheries discard vast amounts of fish – an estimated 25 to 30 million tons annually during the 1990s (Furness, 2003). While many seabird species take advantage of these discards, this behaviour increases their risk of bycatch by attracting them to fishing vessels and exposes them to nutritionally inadequate, non-targeted fish (Votier *et al.*, 2023). Indeed, discarded fish sometimes originate from deep waters – normally inaccessible to seabirds – and may contain high levels of heavy metals such as mercury or have lower lipid content, making them less suitable for chick growth (Furness, 2003; Votier *et al.*, 2023). Although Diop and colleagues (2018) found that tropicbirds do not rely entirely on fishery discards, it remains possible that they partially depend on them. However, red-tailed tropicbirds breeding on Nukutepipi may not be significantly affected by industrial fishing, as such activity is minimal around the island. Nonetheless, this cannot be entirely ruled out, and further studies are needed to assess potential direct and indirect effects of fisheries on the colony.

Climate change also poses a significant threat to red-tailed tropicbirds. Rising sea temperatures and shifting ocean currents alter the distribution and seasonality of prey species, further exacerbating foraging efforts (Hazen *et al.*, 2012; Diop *et al.*, 2018). Moreover, rising sea levels threaten nesting sites that are suitable for breeding red-tailed tropicbirds. This phenomenon has already been observed in various colonies, including on Tern Island, Midway Atoll, Laysan Island, and Kure Atoll (Hatfield *et al.*, 2011; Vanderwerf & Young, 2014; Egerton *et al.*, 2022). These challenges underscore the multifaceted interactions between human activities and red-tailed tropicbirds, highlighting the importance of comprehensive conservation strategies that address both their nesting habitats and foraging areas.

The increasing intensity and frequency of ENSO events due to climate change may further exacerbate challenges for seabirds, particularly by disrupting the availability and predictability of their food sources. As previously mentioned, ENSO events alter key oceanographic processes by modifying sea-surface temperatures, ocean currents, and weather patterns, all of which directly impact marine ecosystems and the distribution of prey species on which seabirds rely (England, 2000; Jaksic, 2004; Wang & Fiedler, 2006). Given that this study was conducted under El Niño conditions, it is likely that sea temperatures around Nukutepipi were anomalously warm. Such changes in oceanic conditions can lead to fluctuations in prey abundance, making food resources scarer and less predictable. As a result, many red-tailed tropicbird chicks on Nukutepipi may have succumbed to starvation, contributing to the island's notably low fledging success rate which ranged from 7.7% and 60%. Similarly, Schreiber and Schreiber (1984) documented breeding failures and declines in many seabird populations on Kiribati following the intense ENSO event of 1982–1983. Affected species included red-tailed tropicbirds, Christmas shearwaters (*P. nativitatis*), Phoenix petrels (*P. alba*), brown boobies (*S. leucogaster*), white terns, and brown noddies. Seabird populations gradually recovered post-ENSO event. While seabird populations gradually recovered after the event, Schreiber and Schreiber (1984) attributed these declines to reduced prey availability, highlighting the significant impact of ENSO-driven oceanographic changes on seabird breeding success and population dynamics. In contrast, Schreiber (1996) studied red-tailed tropicbirds on both Kiribati and Johnston Atoll during non-ENSO and the 1991–1992 ENSO event. Despite this El Niño being classified as relatively strong, fledging success remained consistently high, with only minor differences between ENSO years (80%–94%) or non-ENSO years (95%–98% fledging success). These findings contrast sharply with those from Nukutepipi and Kiribati in 1982–1983, despite all studies being conducted under El Niño conditions.

To better understand the factors driving these discrepancies, inter-annual assessments of breeding success, sea temperature variations, and prey availability on Nukutepipi are essential. Investigating how different ENSO events vary in intensity, duration, and regional oceanographic effects could help explain why some colonies, like those on Kiribati (1991–1992) and Johnston Atoll, maintained relatively stable fledging success (Schreiber, 1996), while others, like Nukutepipi and Kiribati (1982–1983), experienced high chick mortality (Schreiber & Schreiber, 1984). Additionally, studying adult foraging behaviour, prey composition, and the timing of food shortages during ENSO events would provide deeper insights into the mechanisms affecting chick survival. Such research would not only clarify the drivers of breeding success in red-tailed tropicbirds but also contribute to a broader understanding of how climate-driven oceanic changes impact tropical seabird populations.

7. Conclusion

7.1 Summary of findings

This thesis has investigated the breeding ecology of red-tailed tropicbirds on Nukutepipi, with a focus on parental behaviours during both the incubation and chick-rearing periods and chick growth rates.

On Nukutepipi, the breeding season of red-tailed tropicbirds was estimated to span approximately from November to May. The study monitored 80 nests, 55 of which contained a single egg. Of these, 13 eggs failed to hatch, resulting in a hatching success rate of 76.4%. One contributing factor to nest failure during the incubation period was nest sites that provided insufficient shade. Eggs that successfully hatched were typically found in nests located under trees or shrubs such as pu’atea (pisonia), fara (pandanus), tāhinu (tree heliotrope), miki miki (bantigue), and ‘aito (coastal she-oak), or beneath bungalows, which provided the necessary shade.

In addition to nest characteristics, parental behaviour during the incubation period was crucial for successful hatching. It was hypothesised that red-tailed tropicbird parents follow a specific pattern of nest attendance. This hypothesis was supported by observations on Nukutepipi, where seabird parents alternated between incubation shifts and foraging trips. This strategy ensured continuous incubation, with one parent attending the egg while the other foraged at sea. Incubation shifts lasted an average of 250.4 hours (10.4 days) and ranged from 148.3 to 360.9 hours (6.2 to 15 days). Desynchronisation of incubation shifts and foraging trips occasionally left eggs unattended, making them vulnerable to predation by strawberry hermit crabs. Such desynchronisation accounted for 30.8% of egg losses. Other contributing factors included accidental egg breakage by inexperienced parents and vegetation trimming by local staff.

Parental behaviours were also documented during the chick-rearing period, with a hypothesis that parental attendance would change as chicks developed. Observations on Nukutepipi supported this hypothesis. During early chick life, red-tailed tropicbird parents brooded their chicks beneath their body or wing. As the chicks matured and could be left alone at the nest, parents returned solely to provide food. On average, the brooding period ended when chicks reached 2 weeks of age, with a range from 5.4 to 22.6 days. Parental attendance was observed to decrease gradually, from 60% during the first 10 days of chick life to just 1% by the time the juveniles reached 80 days old. Interestingly, parental attendance gradually increased again, reaching 19% as they approached fledging.

It was also predicted that red-tailed tropicbird parents would exhibit a unimodal foraging strategy. However, observations on Nukutepipi revealed that parents adopted a bimodal strategy. This involved alternating between long trips (LTs), averaging 271.4 hours (11.3 days) and ranging from 119 to 450.8 hours (5 to 18.8 days), primarily for self-feeding, and short trips (STs), averaging 26.8 hours (1.1 days) and ranging from 6 to 95.8 hours (0.25 to 4 days), which were dedicated to provisioning chicks.

Meal sizes provisioned to chicks by parents were hypothesised to vary with chick age. This hypothesis was supported by the current study, as small chicks were observed to receive meals with an average mass of 18 g, while large chicks (from 30 days old and older) received meals averaging 86 g. Some individuals regurgitated prey items during handling, and prey remains were occasionally found near nest sites, facilitating an assessment of the red-tailed tropicbird’s diet. In total, eight fish families were identified, with Carangidae, Exocoetidae, and Balistidae being the most prevalent, alongside two unidentified cephalopods. The mass of regurgitated prey items averaged 61.8 g, ranging from 49 g to 69 g, while prey items found near nests averaged 43.5 g, with a range of 3 g to 228 g.

The growth rates of red-tailed tropicbird chicks on Nukutepipi were also studied from hatching to fledging. It was hypothesised that fledglings would leave the nest with morphometric measurements – head, culmen, tarsus-to-middle-toe, wing, tail lengths, and mass – comparable to those of adults. This hypothesis was partially supported. Fledglings departed the nest with head and tarsus-to-middle-toe lengths similar to those of adults, growing at rates of 0.19 cm/day and 0.15 cm/day, respectively. However, their culmen and wing lengths were slightly shorter than those of adults, with growth rates of 0.09 cm/day and 0.43 cm/day, respectively. Regarding tail length, fledglings lacked the distinctive long red tail streamers of adults, resulting in significantly shorter tail rectrices, which grew at a rate of 0.23 cm/day. The body mass of fledglings averaged 611 g. This was unexpectedly lower than that of adults, which weighed on average 757 g. Unlike their body parts, juveniles exhibited significant fluctuations in daily mass change. During early chick life (0–50 days old), their mass increased rapidly, with growth rates ranging from 7.1 g/day and 9.7 g/day. However, between 50 and 60 days of age, a decline in daily mass change was recorded at -8.1 g/day. This trend reversed between 60 and 70 days, as mass increased by 3.8 g/day. Beyond this stage, juveniles experienced a gradual decline in mass, with daily changes ranging from -4.4 g/day and -16.4 g/day until 100 days of age. Interestingly, during their final 10 days at the nest, juveniles gained mass rapidly, increasing by 10.9 g/day on average.

Finally, due to unpredictable availability of prey in marine ecosystems, red-tailed tropicbird juveniles experienced fasting periods averaging 3 days, with durations ranging from one to 10 days before feeding resumed. In contrast, chicks that succumbed to starvation endured longer fasting periods, averaging 5.2 days and ranging from 1.6 to 12.2 days. Fledglings, however, did not fast for more than 4 days before departing the nest. It was hypothesised that fasting periods in juveniles would consist of three distinct phases. This hypothesis was not supported, as only two phases were observed: Phase I lasted an average of 1.2 days, during which juveniles lost 13.5% of their initial mass, while Phase II lasted 2.6 days, with a mass loss of 10.7%.

A total of 65 chicks were monitored, of which four successfully fledged and 26 died. Due to the short duration of the study on Nukutepipi, the fledging success rate was estimated to range between 7.7% and 60%. Starvation was the primary cause of chick mortality, accounting for 65.4% of all chick losses. Additional contributing factors included predation by strawberry hermit crabs, nest site inadequacies, parasites such as leeches, and intraspecific competition for food and nesting sites.

7.2 Conservation implications

Predators, including rats, feral cats, and mongooses, have been identified as primary causes of chick mortality in other colonies of red-tailed tropicbirds such as those on Kure Atoll (Fleet, 1972), O’ahu (Vanderwerf & Young, 2014), and Christmas Island (Sommerfeld & Hennicke, 2010). In contrast, the absence of mammalian predators on Nukutepipi provided a unique opportunity to explore alternative environmental factors contributing to chick mortality. While predation by strawberry hermit crabs was responsible for a small portion (5.1%) of chick losses on Nukutepipi, the lack of mammalian predators highlighted other factors, such as food availability, as more prominent causes of chick mortality.

This study found that starvation accounted for 65.4% of chick losses on Nukutepipi, a significantly higher proportion than observed on other islands. For instance, starvation caused only 8.3% of chick losses on Christmas Island and 7.2% of nest failures on O’ahu (Sommerfeld *et al.*, 2015; Vanderwerf, 2021). This suggests that food availability, rather than predation, is a primary limiting factor for chick survival on Nukutepipi. Addressing this issue requires a deeper understanding of the foraging ecology of red-tailed tropicbirds and the broader ecological factors influencing prey availability.

Equipping red-tailed tropicbird adults with tracking devices such as GPS trackers and GPS tags could provide critical information about their foraging ecology, including the duration of foraging trips, foraging range and locations, and the types of prey targeted. Monitoring sea-surface temperatures may also be valuable, as warmer waters, particularly when reaching 27°C–28°C, are associated with an increase in prey species such as mahi mahi – a highly profitable food source for red-tailed tropicbirds during the chick-rearing period (Le Corre *et al.*, 2003). Additionally, the use of nest monitoring cameras could provide valuable insights into chick provisioning by recording the frequency and timing of food deliveries. Linking these environmental factors with parental behaviours and chick survival rates could enable researchers to predict fluctuations in prey availability and adjust conservation strategies accordingly.

Climate change poses a significant threat to red-tailed tropicbirds, both directly and indirectly. Rising sea levels reduce the availability of adequate nest sites – a phenomenon documented on Tern Island, Midway Atoll, Laysan Island, and Kure Atoll (Egerton *et al.*, 2022). Changes in sea-surface temperatures, ocean currents, and prey distribution may challenge this species' ability to locate sufficient food (Hazen *et al.*, 2012). Furthermore, ENSO events, which are known to influence oceanic conditions and increase in intensity and frequency, could further exacerbate these challenges (England, 2000; Jaksic, 2004; Wang & Fiedler, 2006; Einoder, 2009). Monitoring sea-surface temperatures, climate patterns, and their impacts on prey availability in the region could help anticipate shifts in foraging conditions and support the development of adaptive management strategies.

Another critical consideration is the impact of industrial fisheries on prey availability. Overfishing and unsustainable fishing practices can deplete fish stocks essential for seabirds (Bertrand *et al.*, 2012; Danckwerts *et al.*, 2014; Hagen & Wanless, 2015; Diop *et al.*, 2018; Egerton *et al.*, 2022). Although no direct mortality has been reported for this species and fishing activity around Nukutepipi is minimal, assessing its potential impact on local prey availability would be valuable. Additionally, identifying other environmental factors affecting prey abundance could help explain why red-tailed tropicbirds struggled to find food. This challenge was evident in the extended foraging trips undertaken by parents – suggesting low prey abundance – as well as slower chick growth, prolonged fledging periods, and high chick mortality due to starvation.

Protecting critical foraging and breeding grounds is essential for the long-term survival of red-tailed tropicbirds and other seabird species. Establishing Marine Protected Areas (MPAs) in the southern Pacific Ocean could help sustain prey populations and mitigate human-induced pressures. Additionally, collaborative research and conservation initiatives involving multiple red-tailed tropicbird colonies across the Pacific could enhance understanding and management of this species. Sharing data and insights from different colonies may help identify common threats, inform regional conservation strategies, and strengthen global efforts to safeguard seabird populations and their habitats.

7.3 Future research directions

More study is still needed to fully understand the breeding ecology of red-tailed tropicbirds and address the knowledge gaps highlighted in this study.

Although strawberry hermit crabs were identified as a minor predator of eggs and chicks, their impact on the red-tailed tropicbird population on Nukutepipi needs further investigation. Installing nest monitoring cameras could provide definitive evidence of predation events, including the frequency and conditions. This would also help identify any other undetected predators or disturbances that might influence nest success.

The fasting periods experienced by red-tailed tropicbird chicks included only two phases, instead of three (Cherel *et al.*, 1987; Jenni-Eiermann & Jenni, 2012), presenting another intriguing area for future research. Studying the physiological mechanisms underlying these fasting periods such as changes in water, lipid, and lean dry mass, could provide insights into the species' adaptations to food scarcity and infrequent parental provisioning.

Parasites, including leeches and louse flies, were observed on Nukutepipi, but not systematically studied. Future research should investigate the prevalence, diversity, and impacts of these parasites on adult and chick health and survival. Studies could also assess whether certain nest sites or environmental conditions are associated with higher parasite loads, offering guidance for habitat management.

Tracking studies on red-tailed tropicbird fledglings from Nukutepipi could provide valuable insights into their initial foraging behaviours and migration patterns. Equipping fledglings with GPS trackers or GPS tags could help determine whether their at-sea distribution overlaps with that of non-breeding adults, offering insights into intraspecific interactions or potential competition for food resources. Additionally, tracking adult birds during the understudied non-breeding season could help clarify behaviours and habitat use during a period associated with higher mortality rates in related species such as white-tailed tropicbirds (Mejías, 2017).

Finally, as food scarcity was identified as the major cause of chick mortality on Nukutepipi, long-term monitoring of climate change effects on red-tailed tropicbirds is essential. Research should explore how sea-surface temperatures, particularly during ENSO events, influence the abundance and distribution of key prey species like mahi mahi, on which seabirds rely on. Modelling the potential impacts of future ENSO events would further inform adaptive conservation strategies. The potential impacts of industrial fisheries and other environmental factors on prey availability should also be investigated to assess whether overfishing, along with other ecological changes, is contributing to food shortages. Addressing these research priorities will provide critical data to refine conservation efforts and support the long-term survival of red-tailed tropicbirds and other seabird species in a rapidly changing world.

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Appendix A – Summary of studies on red-tailed tropicbirds at different sites (abbreviations: Inc. = Incubation, ST = Short trip, LT = Long trip).

Table A-1. An overview of research conducted on red-tailed tropicbirds across various colonies.

Site	Breeding regime	Nesting success (%)	Hatching success (%)	Fledging success (%)	Inc. period (days)	Brooding period (days)	Fledging period (days)	References
Nukutepipi	seasonal	–	76.4	7.6 - 60.6	–	14.2	99.4	This study
Kure Atoll	seasonal	38 (in 1964), 17 (in 1965)	–	–	43.8	7 - 25	84.2	Fleet (1972, 1974)
Christmas Is.	seasonal	33.3	60.5	54.7	–	–	–	Sommerfeld & Hennicke (2010), Sommerfeld *et al.* (2015)
Europa Is.	seasonal	–	–	–	–	–	–	Le Corre *et al.* (2003)
Midway Atoll	–	41 (before and after rat eradication)	–	–	–	–	–	Tyler (1991), Laniawe (2008)
Aldabra Atoll	seasonal	4 - 45	–	–	51	–	90	Diamond (1975), Prys-Jones & Peet (1980)
Johnston Is.	seasonal	66 - 86	71.9	98, 85	42.7	10	83.7	Amerson & Shelton (1976), Schreiber (2003), Schreiber (1996)
Kiribati	–	–	–	80, 94, 95, 98	–	–	–	Clark et al.(1983), Schreiber (1996)
Raine Is.	seasonal	31	39.3	77.8	–	–	–	Richardson *et al.* (2023)
Easter Is.	–	37 (in 2014), 26 (in 2015)	–	–	–	–	–	Flores *et al.* (2017), Luna *et al.* (2018)
O'ahu	seasonal	63.1	79.2	77	44.3	–	82.4	Vanderwerf & Young (2014)

Table A-1 (cont.). An overview of research conducted on red-tailed tropicbirds across various colonies.

Site	Inc. shifts (hours)	ST durations (hours)	LT durations (days)	Foraging strategy	Main food items	Non-native predators	Native predators	Predator control	References
Nukutepipi	10.4	26.8 (overestimated)	5 (overestimated)	bimodal	Carangidae, Exocoetidae	none	strawberry hermit crab	rats eradicated before study	This study
Kure Atoll	8.12	–	–	–	Exocoetidae, Ommastrephidae	rats	–	–	Fleet (1972, 1974)
Christmas Is.	6.4	3.0	2.3	bimodal	–	rat, feral cat	–	–	Sommerfeld & Hennicke (2010), Sommerfeld *et al.* (2015)
Europa Is.	4	–	34	unimodal	Exocoetidae, Ommastrephidae	–	–	–	Le Corre *et al.* (2003)
Midway Atoll	–	–	–	–	–	rats	–	rats eradicated between studies	Tyler (1991), Laniawe (2008)
Aldabra Atoll	4 - 6	–	–	–	Exocoetidae, Ommastrephidae	–	–	–	Diamond (1975), Prys-Jones & Peet (1980)
Johnston Is.	–	–	–	–	–	none	bristle-thighed curlew	–	Amerson & Shelton (1976), Schreiber (2003), Schreiber (1996)
Kiribati	–	–	–	–	–	feral pig, feral cat	–	–	Clark et al.(1983), Schreiber (1996)
Raine Is.	–	–	–	–	–	–	buff-banded rail	–	Richardson *et al.* (2023)
Easter Is.	–	–	–	–	–	rat, chimango caracara	–	–	Flores *et al.* (2017), Luna *et al.* (2018)
O'ahu	–	–	–	–	–	rat, feral cat, mongoose	–	controlled	Vanderwerf & Young (2014)

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Appendix C – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
1		• Common name: Dolphin fish or Mahi mahi • Family: Coryphaenidae • Genus: *Coryphaena* • Species: *C. hippurus* • Mass: no data • Adult regurgitated
2		• Unidentified octopus and unidentified fish • Mass: no data • Adult regurgitated
3		• Common name: Surgeonfish • Family: Acanthuridae • Genus: unidentified • Species: unidentified • Mass: 13 g • Found at the nest

Appendix C (cont.) – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
4		• Common name: Trevally • Family: Carangidae • Genus : *Caranx* • Species: unidentified • Mass: 6 g • Found at the nest
5		• Common name: Hound needlefish • Family: Belonidae • Genus: *Tylosurus* • Species: *T. crocodilus* • Mass: 4 g • Found at the nest
6		• Common name: Gray triggerfish • Family: Balistidae • Genus: *Balistes* • Species: *B. capriscus* • Mass: 10 g • Found at the nest

Appendix C (cont.) – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
7		• Common name: Atlantic horse mackerel • Family: Carangidae • Genus: *Trachurus* • Species: *T. trachurus* • Mass: 82 g • Found at the nest
8		• Common name: Atlantic horse mackerel • Family: Carangidae • Genus: *Trachurus* • Species: *T. trachurus* • Mass: 80 g • Found at the nest
9		• Common name: Trevally • Family: Carangidae • Genus : *Caranx* • Species: unidentified • Mass: 68 g • Adult regurgitated

Appendix C (cont.) – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
10		• Common name: Flying fish • Family: Exocoetidae • Genus: *Exocoetus* • Species: *E. volitans* • Mass: 41 g • Found at the nest
11		• Common name: Gray triggerfish • Family: Balistidae • Genus: *Balistes* • Species: *B. capriscus* • Mass: 7 g • Found at the nest
12		• Common name: Flying fish • Family: Exocoetidae • Genus: *Exocoetus* • Species: *E. volitans* • Mass: 74 g • Found at the nest

Appendix C (cont.) – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
13		• Common name: Flying fish • Family: Exocoetidae • Genus: *Exocoetus* • Species: *E. volitans* • Mass: 28 g • Found at the nest
14		• Common name: Red mullet • Family: Mullidae • Genus: *Mullus* • Species: *M. barbatus* • Mass: 228 g • Found at the nest
15		• Common name: Atlantic horse mackerel • Family: Carangidae • Genus: *Trachurus* • Species: *T. trachurus* • Mass: 69 g • Chick regurgitated

Appendix C (cont.) – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
16		• Unidentified fish • Mass: 61 g • Chick regurgitated
17		• Common name: Atlantic horse mackerel • Family: Carangidae • Genus: *Trachurus* • Species: *T. trachurus* • Mass: 23 g • Found at the nest
18		• Unidentified squid • Mass: 3 g • Found at the nest

Appendix C (cont.) – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
19		• Common name: Trevally • Family: Carangidae • Genus : *Caranx* • Species: unidentified • Mass: 33 g • Found at the nest
20		• Common name: Scrawled filefish • Family: Monacantidae • Genus: *Aluterus* • Species: *A. scriptus* • Mass: 48 g • Found at the nest
21		• Common name: Hound needlefish • Family: Belonidae • Genus: *Tylosurus* • Species: *T. crocodilus* • Mass: 21 g • Found at the nest

Appendix C (cont.) – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
22		• Common name: Gray triggerfish • Family: Balistidae • Genus: *Balistes* • Species: *B. capriscus* • Mass: 15 g • Found at the nest
23		• Octopus hooks • Mass: no data • Chick regurgitated
24		• Unidentified fish • Mass: 49 g • Chick regurgitated

Appendix C (cont.) – Prey items regurgitated or found at the nests of red-tailed tropicbirds (note: electronic scale was tared after leaves and stone were placed). Photos by Aurélie Loussan in 2024.

N°	Photos	Name and additional information
25		• Unidentified fish • Mass: 67 g • Found at the nest

Appendix D – Growth stages of red-tailed tropicbird chicks on Nukutepipi. Photos by Aurélie Loussan in 2024.

Plate D-1. Hatchling of 3 days old.

Plate D-2. Chick of 19 days old.

Plate D-3. Chick of 25 days old.

Plate D-4. Chick of 37 days old (843 g).

Appendix D (cont.) – Growth stages of red-tailed tropicbird chicks on Nukutepipi. Photos by Aurélie Loussan in 2024.

Plate D-5. Juvenile of approximately 50 days old.

Plate D-6. Juvenile of 64 days old.

Plate D-7. Juvenile of 88 days old.

Plate D-8. Fledgling of 96 days old.

Appendix E – Inadequate nest sites on Nukutepipi. Photos by Aurélie Loussan in 2024.

Plate E-1a. An incubating red-tailed tropicbird nesting in the middle of the road.

Plate E-1b. A red-tailed tropicbird egg left unattended for two weeks before being accidentally stepped on.

Plate E-2 – A red-tailed tropicbird chick (13 days old) with an abnormal bill and a cloacal prolapse.

Appendix F – Different mass fluctuations recorded in red-tailed tropicbird chicks on Nukutepipi (provisioning by one parent versus both parents).

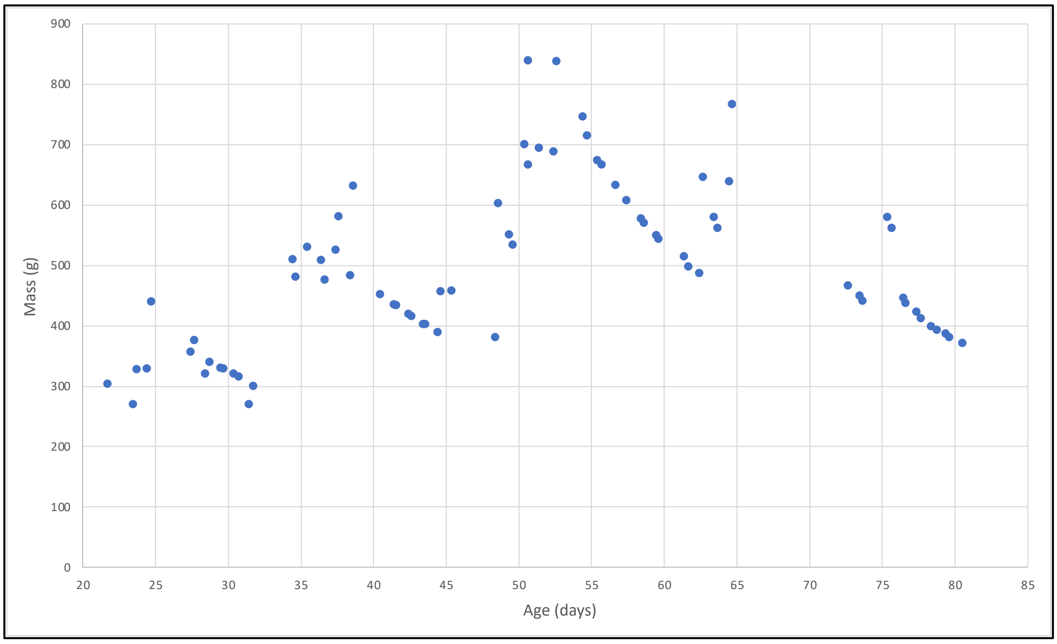

Figure F-1. Unusual body mass fluctuations of a red-tailed tropicbird chick suspected to be provisioned by only one parent.

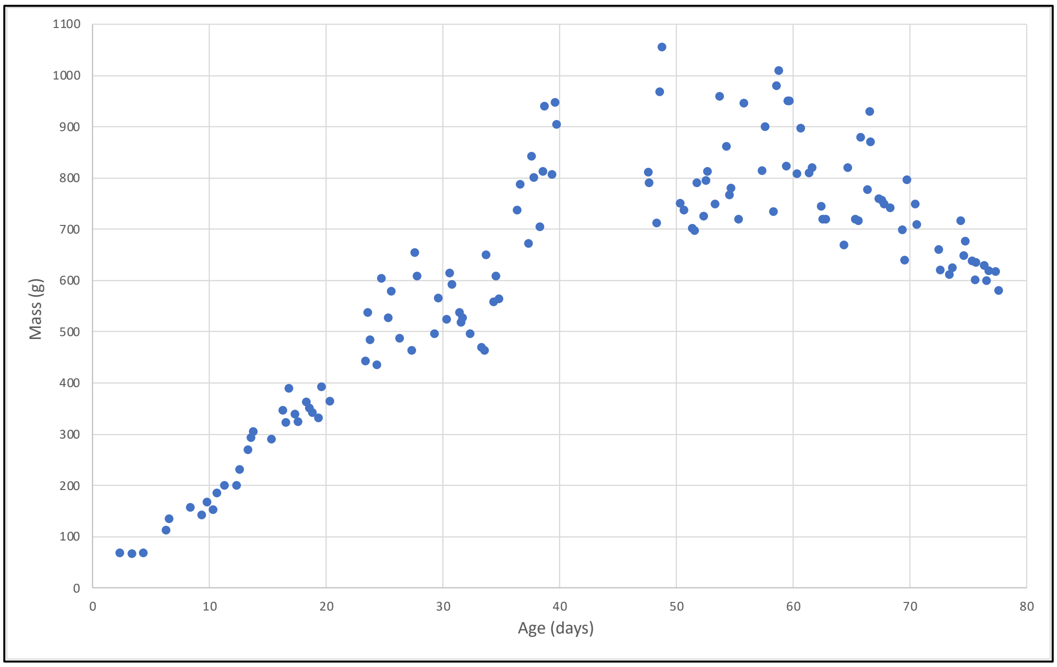

Figure F-2. Typical body mass fluctuations of red-tailed tropicbird chicks provisioned by both parents.

Appendix G – Strawberry hermit crabs as carcass scavengers and potential predators. Photos by Aurélie Loussan in 2024.

Plate G-1. Strawberry hermit crabs scavenging on a dead red-tailed tropicbird juvenile (70 days old).

Plate G-2. Strawberry hermit crabs suspected of preying on a healthy red-tailed tropicbird chick (25 days old).

Appendix H – Intraspecific competition experienced by red-tailed tropicbirds on Nukutepipi. Photos by Aurélie Loussan in 2024.

Plate H-1a. A large chick (72 days old) from a bungalow nest moved to a smaller chick's (6 days old) beach nest.

Plate H-1b. Smaller chick from beach nest found dead with blood in its mouth at 11 days old.

Plate H-2. A chick being pecked by an unmarked adult at 17 days old.

Plate H-3. Missing feathers on the forehead of a chick (66 days old).

Appendix I – Interspecific competition experienced by red-tailed tropicbirds on Nukutepipi. Photos by Aurélie Loussan in 2024.

Plate I-1. A brooding red-tailed tropicbird adult with a rump injury (fate unknown).

Plate I-2. An unstudied adult resting on the beach with a side injury and flies swarming around it (died shortly after).

Appendix J – Parasites observed on red-tailed tropicbirds on Nukutepipi. Photos by Aurélie Loussan in 2024.

Plate J-1a. Leeches on the left eye (also present on the right eye) of a juvenile (66 days old).

Plate J-1b. Leeches in the mouth (also present on the upper palate area) of a juvenile (66 days old).

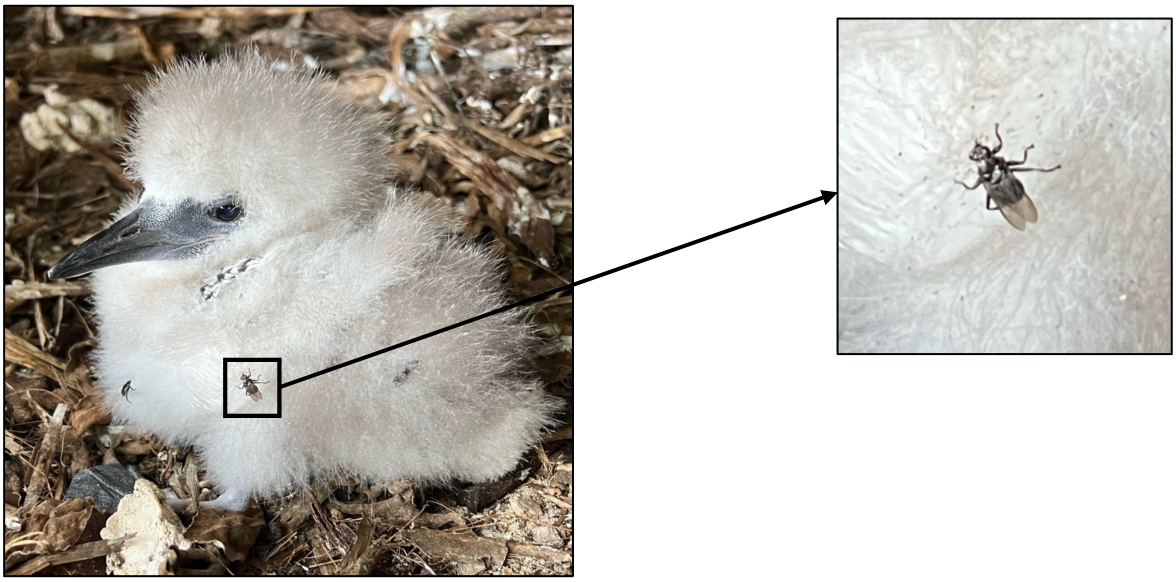

Plate J-2. Suspected louse flies on a chick (25 days old) (note: parasites also hidden in down feathers).