

Population dynamics of the Rodrigues fruit bat (*Pteropus rodricensis*): An analysis of long-term island wide bat count data.



Thesis submitted in accordance with the requirements of the University of Chester for the degree of Master of Philosophy by Amber Williams.

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Declaration

The material being presented for examination is my own work and has not been submitted for an award of this or another HEI except in minor particulars which are explicitly noted in the body of the thesis. Where research pertaining to the thesis was undertaken collaboratively, the nature and extent of my individual contribution has been made explicit.

Amber Williams

24 June 2024

Abstract

The Rodrigues fruit bat (*Pteropus rodricensis*) is an insular Old-World fruit bat endemic to the Island of Rodrigues. The Mauritian Wildlife Foundation implemented a population monitoring program in 1974 and an estimate of less than 80 individuals was recorded in 1979. Following conservation efforts of reforestation of native flora, the population has experienced a steady increase, subject to decreases in numbers after severe cyclones. A standardized methodology was applied in 2016 creating a dataset suitable for population modelling and statistical analysis. The most recent population census (2022) revealed that the population has remained stable at around 20,000 individuals for the last 5 years. This study uses Generalised Linear Mixed Models (GLMMs) to analyse 17 years of population monitoring data in order to identify the climatic factors potentially driving the population trend. We identified that the strongest factors driving changes in the population numbers were linked to resource availability. Most notable were annual precipitation levels, which had a positive relationship with population size ($\beta=1.745$, $P<0.001$), and cyclones, specifically relating to cyclonic strength, which was negatively related with the population size ($\beta=-0.205$, $P<0.0001$). This study also critically analyses the population count methodology and offers recommendations and suggestions for future research to be conducted on the species.

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Chapter 1 – Introduction

1.1. Island extinctions

Wildlife species have always faced pressures from the ever-changing environment. Such pressures include emerging diseases, inter- and intraspecific competition, pollution, anthropogenically induced climate change, and environmental stochasticity i.e., natural disasters (Frankham *et al.*, 2002). Following an examination of population trends for 29,400 vertebrate species, Ceballos *et al.* (2020) concluded that 1.7% of these species are on the brink of extinction, and more than 23,5000 regional populations of those species have been lost in the last 100 years. This acceleration of extinction events is recognized as the sixth mass extinction (Barnosky *et al.* 2011; Ceballos *et al.* 2020).

Such extinction rates are disproportionately accelerated on island habitats, which are hotspots of endemism (Major, 1988; Spatz *et al.* 2017). Endemic species are those which are confined to a singular geographic location and are prevalent on islands due to the isolation imposed by the physical restrictions on dispersal (Major, 1988; Whittaker, 1998). Due to endemism, island endemic species are at a greater risk of extinction than mainland species (Spatz *et al.* 2016). Island-dwelling, or insular, species are expected to be more inbred than those that reside on the mainland on account of having smaller population sizes, reduced ability of population expansion limited by resources, and low number of founders (Elgar & Cole, 2001). The effect of this inbreeding depression reduces population viability through decreased genetic variability making populations lack the ability to resist disease or withstand the demands of their changing environments (Loope, 1986).

1.2. Threat to insular fruit bats (*Pteropodidae*)

To date there are 1,400 species of bats (Order: Chiroptera) globally (Frick *et al.* 2020), inhabiting every continent, except within the Arctic and Antarctic regions (Wilson, 2015). All of which provide a degree of ecosystem services which aid in maintaining the stability of their environment (Kunz *et al.* 2011). Insectivorous species act as biological control in regulating the abundance of agricultural pests (Whitby *et al.* 2020) and mosquitoes (Puig-Monsterrat *et al.* 2020), which positively impacts food production and human health. Nectivorous and frugivorous bats play a vital role in seed dispersal, pollination and plant propagation (Muscarella & Fleming, 2007), in addition to facilitating nutrient dispersal through deposition of nitrogen-rich guano, aiding soil fertility (Kasso & Balakrishnan, 2013). Despite bats provisioning these critical ecosystem services, more than half of all bats species globally are considered threatened, or data deficient and require urgent conservation action (Frick *et al.* 2020).

More than half of all Chiroptera species reside on islands, with nearly 25% known to be island endemics (Jones *et al.* 2009a). On many island islands, such as Hawaii and New Zealand, bats are the only native mammal (Jones *et al.* 2009b). This can, in part, be attributed to their flight and dispersal ability and has allowed Old World fruit bats (Chiroptera: *Pteropodidae*) to colonise remote islands in the Indian Ocean (O'Brien, 2011).

Pteropodidae species have been recognized as the most threatened group of bats globally (Kingston *et al.* 2023). Of the 72 *Pteropodidae* species assessed by the International Union for the Conservation of Nature (IUCN), 59% are described as endemic, over 50% are considered to display a decreasing population size, and 71% are listed as Near Threatened or worse (Kingston *et al.* 2023). Within the *Pteropodidae*, the genus *Pteropus* includes 59 species, of which 96.5% have some or all of their distribution on islands, and 61.4.% are island endemics (McNab, 2009; IUCN, 2024). Insular species within the Indian Ocean include *P. livingstonii* residing on the Comoros Islands, *P. voeltzkowi* residing in Pemba, *P. niger* residing in Mauritius and *P. rodricensis* residing on Rodrigues Island (Mickleburgh *et al.* 1992; McNab, 2009). There are only nine *Pteropus* species found on Asian and Australian continental landmasses, and none in continental Africa (Mickleburgh *et al.* 1992). The reason behind the absence of *Pteropus* on continents is unclear, though theories have been posed that suggest this is perhaps due to the interspecific competition from frugivorous primates (McNab, 2009). More than six out of the eight recorded *Pteropus* extinctions to date were island endemics, including *P. subniger*, from the Mascarene islands (Bowen-Jones, 1997). Despite this, insular *Pteropus* species are considerably understudied in

comparison to their continental counterparts, such as the flying foxes of mainland Australia (Todd, 2019).

Hunting

Around half (92/183) of all *Pteropodidae* species have historically been, or continue to be, exposed to pressures from anthropogenic hunting for consumption (Mbetete *et al.* 2011), medicinal purposes (Tackett *et al.* 2022), or as a result of human-wildlife conflict (Mickleburgh *et al.* 2009; Ripple *et al.* 2016). The intensity of hunting pressure varies seasonally and by location. The hunting pressure depends on the opportunistic availability of bats in view of migration patterns, and situations of food scarcity in which bushmeat becomes a highly valued source of protein (Goodman, 2006; Jenkins & Racey, 2008). As a result of the advances in capture methods, unsustainable fruit bat hunting is a greater threat now than when reviewed historically, particularly when pressures are in conjunction with the threats outlined below (Bradshaw *et al.* 2009).

Changing climate

There has been an increase in extreme heat waves observed in the last decade, during which temperatures reach and sustain extremes of up to 42°C in the cases of South Asia and Australia (Welbergen *et al.* 2008). Such conditions cause significant physiological stress and result in mass mortality events of fruit bats (O'Shea *et al.* 2016). Most notable, however, is the threat of increased frequency and severity of natural disasters such as cyclones. Insular populations are vulnerable to these weather events as they cannot migrate to escape conditions and have limited options to shelter from high wind speeds (Pierson *et al.* 1996; McConkey *et al.* 2004). The warming climate elicits shifts in flowering and fruiting phenology, which limits resources for fruit bats and disrupts the ontogeny of reproduction (Scanlon *et al.* 2018).

Deforestation

Habitat loss driven by deforestation eradicates roosting and foraging resources for fruit bats and is a key cause of decline in *Pteropodidae* populations across their range e.g. Islands of Tonga (McConkey *et al.*

2004), Trinidad (Clarke *et al.* 2005), Nicobar (Aul, 2007), Rodrigues (O'Brien *et al.* 2007), Malaysia (Epstein *et al.* 2009), Pemba (Robinson *et al.* 2010), Kenya (Webala *et al.* 2014), Christmas Island (Woinarski *et al.* 2014), Southeastern Asia (Tsang *et al.* 2018), Australia (Westcott *et al.* 2018), Madagascar (Brook *et al.* 2019), Mauritius (Oleksy *et al.* 2019) and the Solomon Islands (Lavery *et al.* 2020). *Pteropodidae* are generally gregarious and show a high degree of roost fidelity, occupying roost sites for over 20 years in some cases (Parks, 2014). Favoured roosting sites are generally large trees that are greater in both height and diameter than the surrounding vegetation which provide optimum protection from unfavourable weather conditions (Popelka, 2006; Hahn *et al.* 2014). Therefore, dense, mature trees that can support aggregations of pups and mothers must be present in abundance to allow social learning and development to occur safely. In addition, males perform flight and vocal displays at their roosts, hence roosts are critical for mating and sexual selection behaviours as well as for raising offspring (Crichton & Krutzsch, 2000). Moreover, the absence of forests, and particularly the conversion of forests to agricultural land, increases fruit bat's dependency on harvested orchards for food. This exponentially increases human-wildlife conflicts, as farmers perceive fruit bats as pests and a threat to their livelihood if they are consuming their crops (Florens *et al.* 2017).

1.3. *The Rodrigues fruit bat*

The Rodrigues fruit bat (*P. rodricensis*), a medium-sized fruit bat (body size $\leq 20\text{cm}$, wingspan $\leq 90\text{cm}$) with dark brown fur and golden shoulders, is endemic to the Island of Rodrigues in the Indian Ocean, (Tatayah *et al.* 2017). Rodrigues fruit bat have been listed on the Bat Conservation International's worldwide priority conservation list since 2014 (Bat Conservation International, 2014), and are classified as Endangered, subject to criteria B1ac(iv)+2ac(iv), by the IUCN (Tatayah *et al.* 2017). The classification relates to the Rodrigues fruit bat's area of geographical distribution totaling less than $5,000\text{ km}^2$, the area of occupancy within that zone totaling less than 500 km^2 , being endemic to one single location, and experiencing extreme fluctuations in the total of mature individuals (IUCN, 2012).

The Mauritian Wildlife Foundation (MWF) provide the IUCN with the updated minimum population count every five years to reassess the Rodrigues fruit bat conservation status in accordance with the IUCN Standards (2019) (R. Jhangeer-Khan, personal communication, 30 November 2023). The Rodrigues fruit bat was downlisted from Critically Endangered to Endangered in 2017 when the minimum population estimate was reported as 20,000 (Tatayah *et al.* 2017). This census count is a significant increase from the bottleneck of less than 100 individuals recorded in 1979 (Tatayah *et al.* 2017). There are numerous reasons that led the population to reach this bottleneck (outlined below in 1.5. Threats to the Rodrigues fruit bat). Given the historical near extinction of the Rodrigues fruit bat, it is critical that the status of the population be subjected to long-term monitoring to allow for the driving factors to be regularly assessed.

1.4. Importance of the Rodrigues fruit bat to the island ecosystem

Globally, fruit bats are vitally important species due to the ecosystem services they provide including pollination, seed dispersal and fertilization (Ramírez-Fráncel *et al.* 2022). Though there are no direct studies that quantify the ecosystem services of Rodrigues fruit bats, Muscarella & Fleming (2007) reported that *Pteropodid* bats significantly contribute to the pollination of canopy trees in Old World forests. In addition to this, Rodrigues fruit bats are valued for their ability to retain large loads of seeds in their digestive tract and subsequently disperse propagules (Fleming *et al.*, 2009). Based on data collected on continental species, it is assumed that traversing the entire island (108 km²) during foraging bouts is well within the Rodrigues fruit bat's capability (Todd, 2019). This enables them to defecate seeds enclosed in nutrient-rich guano far from the parent tree (Seltzer *et al.*, 2013). As a result, Rodrigues fruit bats are responsible for the succession of many native fruits, flowers, and leafed plant species on the island (Cox *et al.* 1991; Fujita & Tuttle, 1991; Powell, 2005; Kunz *et al.* 2011). A great degree of the island's flora relies heavily on this action of seed dispersal; thus, the Rodrigues fruit bat's decline threatens the integrity of Rodrigues' plant biodiversity (Brautigam & Elmqvist, 1990; Vale *et al.* 2023). This was observed on the Marianas Island of Guam, as pollination failure and reduced fruit set was apparent following the extinction of the island's native fruit bat, *Pteropus tokudae* (Cox *et al.*, 1991).

1.5. Threats to the Rodrigues fruit bat

Hunting

Though not formally recorded, Vinson (1964) observed Rodrigues fruit bat populations being severely depleted by overhunting for bushmeat (Cheke & Dahl, 1981), an activity which likely increased because of resource scarcity following a cyclone such as Cyclone Celine II in 1979 (Jones, 1980; Mickleburgh *et al.* 2009). Hunting of Rodrigues fruit bats has ceased since the implementation of Part V (Protection of Flora and Fauna) of the Wildlife and National Parks Act (1993), which lists Rodrigues fruit bat as a Fourth Schedule protected species and making it an offence to hunt, possess or trade any part of the animal (Tatayah *et al.* 2017).

Global warming and cyclones

The changing climate, particularly global warming, poses a threat of an increase in frequency and severity of detrimental and stochastic weather events such as cyclones (Cheke & Dahl, 1981; Rahmstorf & Coumou, 2011). There is growing concern over the increase in intense cyclones over the Indian Ocean due to the warming climate (Deo & Garner, 2014). Cyclone formation requires sea surface temperatures above 26°C (Lighthill, 1994), which are being observed more frequently than before as a consequence of global warming (Smith & Reynolds, 2005; Deo & Garner, 2014). An increase of approximately 3°C in sea surface temperatures were recorded from 1982 – 2015, a trend which is expected to continue (Sakalli & Başusta, 2018).

It is known that cyclones cause direct mortality to Rodrigues fruit bats by the high wind speeds displacing individuals from unsheltered areas (Kingstone *et al.* 2021). This is evident in bat corpses being littered across the island following a storm (C. Jones, personal communication, 19 June 2023). Indirect mortality is assumedly caused by the stripping of vegetation from the forested areas that withstand the storm, which further eradicates roosting and foraging resources (Kingston *et al.* 2021). As fruit bats have a high basal metabolic rate, which can increase up to 16 times during flight (Speakman *et al.* 2003), their calorific demand is high, thus, shortages of food can lead to limited recruitment or reproduction success, and even mass starvation events (Diengdoh *et al.* 2022). In addition to starvation, Rodrigues

fruit bats obtain most of their hydration from the fruit that they consume and consequentially the destruction of fruit resources also causes fatal dehydration (Jones, G. *et al.* 2009; Diengdoh *et al.* 2022).

Following a severe cyclone, Rodrigues fruit bats can suffer mortality events up to 50% of the population (Powell & Wehnelt, 2003). Though reportedly, the population can recover at a subsequent rate of 12-15% per year if not hit with further storms (Powell, 2005). To make effective conservation considerations, it is necessary to identify if cyclones do drive changes in the population as this increase in frequency, duration and intensity of the storms would be of concern to Rodrigues fruit bat conservation.

Deforestation

The Rodrigues fruit bats' roosting sites are stands of mature trees, notably *Ficus spp.*, *Mangifera indica* and *Cassine orientalis* on sloping gradients (Powell, 2005; Popelka, 2006; Gottschalk, 2016).

Unfortunately, anthropogenically led deforestation removed copious mature fruiting and roosting trees from the Rodrigues island which degraded the quality of roosting habitat for the bats (Cheke & Dahl, 1981; Fujita & Tuttle, 1991). As a consequence of reducing the vegetative buffer, remnant patches are left susceptible to destruction by frequent tropical cyclones (Jones, G. *et al.* 2009; IUCN, 2017). The removal of vegetation from these trees reduces the availability of shade for Rodrigues fruit bats, making them vulnerable to overheating in high temperatures (Downs *et al.* 2012; Korine *et al.* 2016).

Overheating is a serious risk when considering that Rodrigues fruit bats have an inability to dissipate body heat owing to their lack of sweat glands (Diengdoh *et al.* 2022). Whereas mainland *Pteropus spp.* would migrate to escape unfavourable conditions, the Rodrigues fruit bat is confined to Rodrigues. Further, Powell (2005) observed intense roost fidelity in Rodrigues fruit bats when individuals were seen congregating at areas around the roosts, as opposed to migrating to new sites, when space within the roost was insufficient because of overcrowding. This behaviour makes bats increasingly vulnerable to the stresses of weather exposure that would be less intense in dense forests.

Low recruitment rates

Rodrigues fruit bats are K-selected, meaning they produce one pup per female per year and do not reach maturity until at least their second year (Todd *et al.* 2018). This hinders their recovery from

population declines (Cox *et al.* 1991; Jones *et al.* 2003; Gottschalk, 2016; Daniel *et al.* 2017). Pups are born during the summer after a gestation period of around 6 months (Popelka, 2006). Pups are altricial and will remain attached to the mothers for 30 days until they are too heavy to carry during flight, at which point they are left at the roost (Popelka, 2006). Pups begin to explore the roost and experiment with wing flapping at around 50 days old, at this stage social interaction with conspecific pups is critical to develop social skills and encourage flight development (Popelka, 2006). At 3 months old, pups are weaned and are capable of flight, although are not fully independent until around 1 year old (Crichton & Krutzsch, 2000). The reproductive ecology of the Rodrigues fruit bat emphasises the importance of tall, dense trees for a secure hibernaculum for pup rearing. Additionally, pups weigh 20-30% of mothers body weight at birth (Popelka, 2006). Thus, due to the high maternal investment committed during gestation, birthing, lactation and rearing of the pups, mothers require a reliable and continuous source of food to accommodate the energy that they exert during this time (Korine *et al.* 2004).

Genetic diversity

Considering that the Rodrigues fruit bat population has recovered from a bottleneck, there are concerns relating to eroded genetic variability (Luikart & Cornuet, 1998; Vilas *et al.* 2006). Small population sizes increase the chance of individuals mating with genetically similar conspecifics, known as inbreeding (Frankham *et al.* 2002). Inbreeding reduces the heterozygosity of the population and increases the chance of recessive lethal gene expression (O'Brien & Hayden, 2004). Inbreeding negatively impacts the fitness of the population by reducing the success of offspring survival potentially leading to extinction (Keller & Waller, 2002). Taki *et al.* (2021) investigated the genetic diversity of the Ryukyu flying fox (*Pteropus dasymallus*), a closely related insular species. The population residing on the isolated Yonaguni Island had low genetic diversity resulting from no gene flow between neighboring islands and, consequently, a high inbreeding coefficient (Taki *et al.* 2021). This population was noted to be extremely vulnerable and at high extinction risk when compared with the populations residing on the neighboring islands, which have high levels of gene flow and display a degree of inter-island movements (Taki *et al.* 2021). As the Rodrigues fruit bat's range resembles the Ryukyu flying fox, and both have been subject to the founder effect because of bottleneck recovery, their genetic diversity could be comparable.

O'Brien *et al.* (2007) assessed the genetic diversity of Rodrigues fruit bats and revealed that despite recovering from a small number, the population retains genetic variability which indicates a healthy

level of within-population gene flow. However, the genetic status of the Rodrigues fruit bat has not been assessed for nearly two decades, during which the population has been subjected to mortality events at the hand of severe cyclones, such as 2019's Cyclone Gelena (C. Jones, personal communication, 19 June 2023), and thus may require reassessment. It is therefore essential to maintain a long-term population census to monitor the population's size with genetic integrity in mind.

Anthropogenic disturbance

The influence of anthropogenic disturbance on the Rodrigues fruit bat has not yet been formally studied. It is assumed that the Rodrigues fruit bats are well adapted to human presence due to their continued population growth alongside the island's urban growth and development. There are, however, some studies on closely related species such as *P. niger* and *P. giganteus* suffering mortality due to electrocution following individuals landing on power lines in Mauritius and Sri Lanka (Krystufek, 2002). Though there are no formal records of Rodrigues fruit bats suffering the same deaths it is not unreasonable to assume that they occur due to the island being of similar infrastructure to that of Mauritius.

1.6. Population monitoring of Pteropodidae

Long-term monitoring is crucial when attempting to understand what drives a population to fluctuate over time (Lindenmayer *et al.* 2022). As ecological processes will take prolonged periods to unfold, the effects will not be apparent in short-term studies which depict a snapshot in time (Hughes *et al.* 2017). Similarly, short term studies are unable to document species responses to various threats, such as habitat loss or invasive species, which are vital to inform conservation strategy (Lindenmayer *et al.* 2012). In addition to long-term data, large-scale monitoring is also critical as it incorporates an entire population's habitat and resources. This enables an understanding of the populations range over space and time, which, again, cannot be accomplished through short term monitoring (Hughes *et al.* 2017).

Count methods

Due to their dispersal ability, expansive distribution, and crypticity, fruit bats are notoriously difficult to monitor and globally understudied (Welbergen *et al.* 2020). Common methods employ ground counts; in which bats are counted at their roost site during the day using binoculars (Craig *et al.* 1994; Sewall *et al.* 2003; Cousins & Crompton, 2005; Palmeirim *et al.* 2007; Sugita *et al.* 2009; Robinson *et al.* 2010; Carpenter *et al.* 2014; Neupane, 2015; Daniel *et al.* 2017; Wu *et al.* 2022) and dispersal counts; in which bats are counted as they depart from a roost in the evening (Wiles, 1987; Stinson *et al.* 1992; Bowen-Jones *et al.* 1997; McConkey *et al.* 2004; Forsyth *et al.* 2006; Epstein *et al.* 2009; Ravon *et al.* 2014; Dey *et al.* 2015; Brook *et al.* 2019; Hayes & Engbring, 2020). An alternative method includes disturbance counting; though not widely adopted, this involves exposing daytime roosts to sudden loud noises causing the bats to disperse, upon which they are then counted, or photographed and subsequently counted (Powell, 2005). Other noteworthy methods include the use of drones or radar (Chaiyes *et al.* 2017; Meade *et al.* 2019; McCarthy *et al.* 2021), thermal imaging (Hristov *et al.* 2008) and population estimates generated from molecular genetic studies (O'Brein *et al.* 2007; Phalen *et al.* 2017; Ibouroi *et al.* 2021; Taki *et al.* 2021; Wu *et al.* 2022). The latter methods are less adopted due to the cost of obtaining the required equipment and subsequent training of observers (Westcott *et al.* 2011).

Advantages and disadvantages of methods

Notable disadvantages of ground count methods are associated with the ephemerality of day roosts resulting in a lack of definitive knowledge of hibernacula location and status required to conduct these counts (Utzurum *et al.* 2003). Even once roosts are located there is the issue of imperfect detection which renders count based data as a biased representation of the population due to constraints associated with observer bias (Nichols *et al.* 2000), species crypticity (Gu & Swihart, 2004) and the obstruction of the study species by surrounding vegetation (Kellner & Swihart, 2014). However, Westcott & McKeown (2004) reported that if a true count is conducted i.e. observers walk within roosts and exhaustively count all individuals, the scope for precision is greater than at a dispersal count. This comes down to individuals being relatively static at a day roost during ground counts and thus reducing double counting. It is also feasible to obtain data on demographics from a ground count as it is relatively easy to sex fruit bats through binoculars from moderate distances when the genitals are exposed (Westcott *et al.* 2011). Though this data is not essential for modelling abundance, it is certainly beneficial to collect as it can be utilised in more in-depth modelling such as a population viability analysis (Beissinger, 2002).

There is debate on the accuracy of dispersal counts. Kunz *et al.* (2009) and Westcott and McKeown (2004) highlighted that for species forming large colonies, dispersal counts with a single human observer, i.e., the absence of a simultaneous second count or video recording of the emergence for later verification, can be unreliable in view of the speed in which aggregations from large colonies disperse from the roost. Errors can comprise of observers failing to count emerging individuals or failing to observe streams of numerous bats in directions not easily visible from the selected vantage point, as well as failure to observe main roosting sites altogether. Inaccurate monitoring causes errors in establishing the population status and is therefore ineffective in determining the impact, or success, of current management actions (Wiest *et al.*, 2018). Ultimately, this can lead to the potential incorrect allocation of resources for management strategies (Rodhouse *et al.* 2012)

Furthermore, ground counts incur less labour cost than dispersal counts. In a review of survey methods of fruit bats, Murphy *et al.* (2008) stated that the estimated cost of ground counts is one-quarter of those of dispersal counts. This is because of the closed population assumptions of dispersal counts stipulating that all known roost sites be surveyed simultaneously and on multiple recurring evenings which demands the involvement of large numbers of observers. However, these costs are often reduced

by the utilization of volunteers, which adds value to monitoring by creating opportunity for citizen science (Eby, 2004).

Ultimately, there is no 'one size fits all' approach to monitoring fruit bat populations. This is emphasized by their gregarious nature, ease of dispersal and by them occupying a variety of habitats globally which incur an array of location-specific or habitat-specific challenges (Kunz *et al.* 2009). Devising robust methodological approaches to population monitoring is essential so that populations are not over- or under-estimated leading to ill-informed conservation strategies. Arguably of the most importance, is consistency in the data methodology to create a long-term time series of counts that can be used to analyse trends in population within space and time. The longer the time series, the sounder the conclusions on population trends that can be elucidated (Woinarski, 2018). Long-term datasets including multiple climatic variables, can help to elucidate the driving factors of population trends, and their degree of impact on these trends (Butchart *et al.* 2010). As many relevant environmental covariates should be collected as possible alongside the population count. Obtaining these metrics is core to defining the status of the population and identifying any evidence of decline which would trigger proactive conservation efforts (Shea & Mangel 2001; Marsh & Trenham, 2008).

The Rodrigues fruit bat has been subjected to consistent annual monitoring since 2006 using a combination of both dispersal and ground count estimates, creating a long-term dataset. Such population census has created a heterogeneous dataset that, when appropriately modelled, can give an estimate of population abundance (Kidwai *et al.*, 2019).

1.7. Aims

In this study I assess the long-term time series population count data for the Rodrigues fruit bat from 2006-2022. I investigate how the survey-specific and climatic, both daily and annual, variables affect the population count.

The aims are:

1. To understand the factors driving the trends in population of the Rodrigues fruit bat over time, with a particular focus on the impact of cyclones. This will be achieved through synthesis and subsequent analysis of the data collected by the MWF from 2006 – 2022 against climatic variables using generalized linear mixed models.
2. To provide an insight into what extent the conditions on the day of surveying influence the population count. This will be achieved through statistical modelling of data against climatic variables.
3. To use published literature to critically analyse the data collection methodologies and make suggestions to improve the survey techniques in the future.

Chapter 2 - Materials and Methods

2.1. Seasonality on Rodrigues Island

Rodrigues is an island of volcanic origin within the Republic of Mauritius (19.7245° S, 63.4272° E) and is known as the most eastern land of the African continent. At 226m above sea level, and only 109 km² in size (18km x 8.5km), this small Mascarene Island is located in the Indian Ocean around 574km east of Mauritius (Powell & Wehnelt, 2003), see Fig. 1a and Fig. 1b. Rodrigues island has a central ridge, which peaks at 398m, and cascades into deep valleys within which bat roosts are located (Middleton & Burney, 2013), see Fig. 2.

A

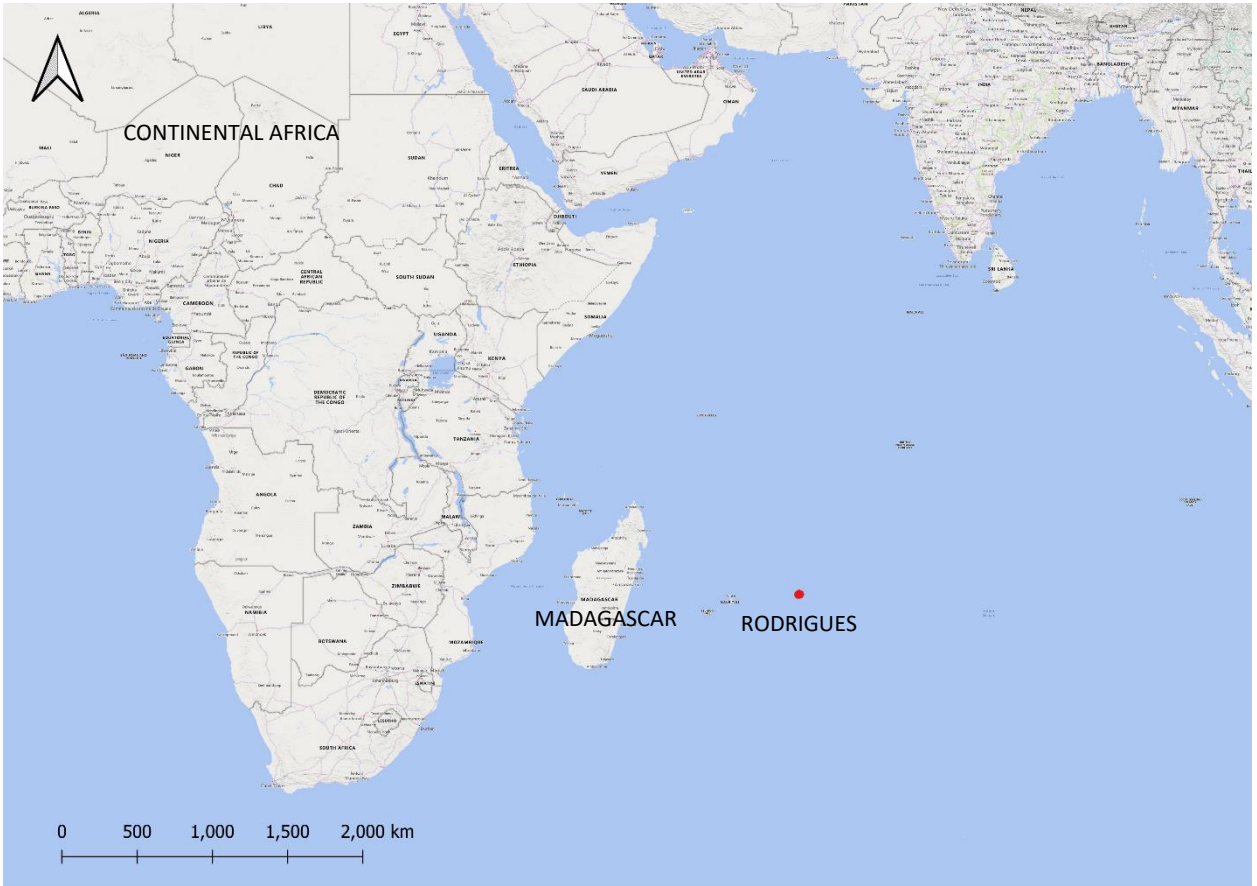




Figure 1

- A) Map showing location of Rodrigues (red boundary) in relation to larger landmasses, such as Madagascar and continental Africa.
- B) Map of Rodrigues. Lower right-hand image shows the location of the island in relation to Mauritius, Mascarenes.

Map created using QGIS version 3.30.1 (Appendix.I).

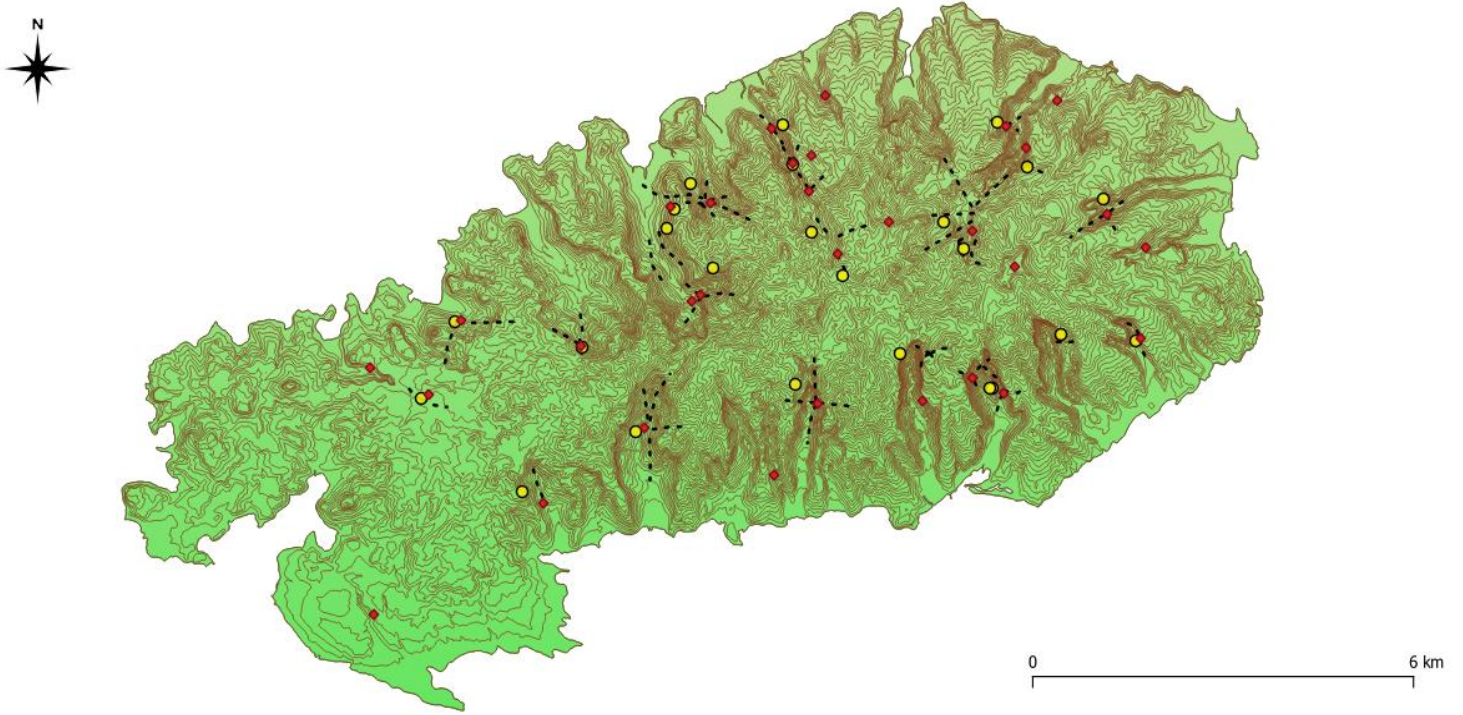


Figure 1

Map of Rodrigues fruit bat roost areas and vantage points

Red markers represent the location of both permanent and temporary roosts on the island.

Yellow dots represent vantage points.

Black dashed lines illustrate the general flight paths of the bats based on anecdotes from observers.

Contour lines represent 10m in elevation difference.

Map created using QGIS version 3.30.1 (Appendix. I).

2.2. *Seasonality on Rodrigues Island*

The sub-tropical climate of Rodrigues has two broad seasons; the 'dry', or winter season (May-October), and the 'wet', or summer season (November-April) during which the island is susceptible to experiencing cyclones as a result of the shift in trade winds (Strahm, 1989). During the winter, average humidity level is 73%, which increases to 81% during the summer (Cheke & Dahl, 1981). The temperature range during the winter is 19-26°C, and 23-29°C during the summer (National Oceanic and Atmospheric Administration, 2023).

2.3. History of deforestation on Rodrigues Island

By the late 1960s the majority of the forests on Rodrigues had been converted to agricultural land and the remaining fragments were severely degraded (Fox, 2006). This was further exacerbated by anthropogenically led burning and woodcutting, that occurred during the 1960s to convert the land to terraced farmland, and by drought that occurred during the 1970s (Gade, 1985; Fox, 2006). Prior to this, Rodrigues was abundant with endemic and native forests comprising *Arecaceae sp.*, *Ebenaceae sp.*, *Lecythidaceae sp.*, *Ficus spp.*, *Pandanaceae sp.* and *Rubiaceae sp.*, amongst others. Now the island is relatively barren, mainly vegetated with invasive plant species introduced during the 1980s by the Mauritius Department of Forestry. Fast-growing exotic species, such as *Fabaceae sp.* and *Myrtaceae sp.* were planted to replace the lost indigenous forests and provide commercial timber and fruit for locals, and as canopy cover for the remaining endangered vertebrates (Fox, 2006). These reforestation efforts were effective in providing roosting and foraging resources for the Rodrigues fruit bat, particularly the fruiting species *Tamarindus indica*, *Carica papaya* and *Mangifera indica*.

Exotic tree species are not as able to withstand cyclones as natives and are more susceptible to uprooting which increases forest fragmentation (Kueffer & Mauremootoo, 2004). Other negative consequences of invasive flora relate to the greater uptake of water than the native flora, notably *Acacia nilotica* (Morris *et al.* 2011) and *Eucalyptus robusta*. This increases soil erosion and reduces the available water budget within the ecosystem, which bears negative consequences for the production of Rodrigues fruit bat foraging resources (Kueffer & Mauremootoo, 2004; Funk, 2013). In addition, species such as *Furcraea foetida* dominate the forest floors and outcompete native species for space and nutrients making reforestation efforts of native tree species difficult (Keuffer & Mauremootoo, 2004). Despite this, the MWF and the Rodrigues Forestry Service have made great efforts in the last two decades to restore the native flora by removal of invasive species and the planting of over 170,000 seedlings of 43 species in 14.5 hectares within the island's nature reserves, Grand Montagne and Anse Quitor (Mauritian Wildlife Foundation, 2023).

2.4. *Roost site location*

Most Rodrigues fruit bat roosts occur between 21-319m above sea level, on sloped gradients within valleys in dense forest areas of *Ficus spp.* or *Cassine orientalis* (Fig. 3a and Fig. 3b). Roost sites are particularly prevalent on the eastern side of valleys with slopes facing north, northwest and west as these areas offer protection from Southeastern trade winds, see Fig. 2 (Powell, 2005; Gottschalk, 2016).



A

B

C

D

Figure 2

Photographs of fieldwork on Rodrigues

A+B) Photograph of the view from Anse Ally's vantage point observing permanent roost for dispersal count.

C) Rodrigues fruit bats observed at roost during ground count.

D) Photograph of bats within roost.

2.5. Survey methodology

On the days prior to the annual census counts, preliminary site visits are conducted at all roosting sites to confirm the presence/absence of bats. If bats are not present at permanent roost sites they are declassified from permanent status to temporary and surveyed as such. It should also be noted that temporary roosts observed to host colonies of over 50 bats for over 5 years are then reclassified as permanent roosts and surveyed using the evening dispersal count (EDC) method accordingly (detailed below). After a site has been re-classified to a permanent roost site, a suitable vantage point is identified. Vantage points have been selected based on surveyor accessibility and view of roost emergence e.g., if the roost was within a valley, the vantage point would ideally be elevated above the roost and provide a 180° vision of the valley to observe bats leaving in multiple directions. Data relating to the elevation of the vantage points and distance of said vantage point from the focal roost is not available for analysis (see 4.7. Monitoring recommendations).

Evening dispersal count

A large group of volunteers and experienced roost observers from the MWF (>50 volunteers and 17 staff members) are employed yearly to conduct EDCs. When conducting a population count, the manner in which animals distribute themselves in space and time needs to be accounted for (McCarthy *et al.*, 2021). As *Pteropus sp.* can traverse up to 500km within 48 hours (Roberts *et al.* 2012), it is assumed a significant proportion of the Rodrigues fruit bat population can disperse from roost to roost within a short time (Westcott, 2004; Westcott *et al.* 2011). Therefore, to satisfy the assumption of population closure, a census count should assess all known roosts at the same time (Westcott & McKeown, 2004). Thus, to obtain the most accurate estimation of the island's population and account for the dispersive nature of fruit bats, synchronous surveys take place at all known permanent roosts across the entire island (Eby *et al.* 1999).

Each survey was conducted by one experienced member of MWF and at least one volunteer. Counts are conducted concurrently from the vantage points, (Fig. 2 and Table. 1) observing all known permanent roost sites across the island for three consecutive evenings during the last week of November.

November has been selected for the census as this has historically been the time of year when the greatest aggregations of bats are recorded including females with pups (Jhangeer-Khan, R, personal

communication, November 19, 2023). The surveys started at around 16:00 hours, as this is the time the bats are known to begin emerging from the roosts, until around 19:00 hours or until no daylight was remaining. The start and end times of the survey were recorded to control variation in survey length in statistical models. Bats leaving and returning to roosts were counted by hand-tallying the number of bats exiting the roost in 5-minute intervals. The count of bats returning was subtracted from the count of bats exiting to eliminate double counts of individuals that do not immediately leave the roosting area. In addition to counting the bats exiting, bats that were observed entering from other valleys were also accounted for. This method assumes that all bats within the roost emerge within the survey's duration and that all bats that emerge are counted. However, in practice, these assumptions are not always reasonable. As a consequence of surveys discontinuing when light levels are deemed insufficient and not when bats are no longer emerging, a percentage of bats remain uncounted at roost sites (A. Williams, personal observation, 2023).

In-situ direct bat estimation

Direct count methods are conducted at all temporary roost sites during the day on the three consecutive days in which the EDCs take place. Sites are surveyed using the ISE method in which experienced observers return to the same assigned site to estimate the number of visible bats. Depending on the site, some temporary roosts are subjected to physical counts in which bats are exhaustively counted, whilst some sites are estimated. This estimate involves observing the distribution of the clusters of bats per tree within the roosting site and deciding if this is relatively equal across the roost (A. Williams, personal observation, 2023). If this is deemed the case, the number of bats on one tree branch is then counted and multiplied by the number of branches within one roosting site. If the distribution within the site is not deemed equal, the number of bats is roughly estimated. There is, however, great variation in temporary roost size accessibility, and so the methodology cannot be fully standardized. There are multiple independent observers at each temporary site, each estimation is reached individually and discussed amongst the observers until a final estimate is agreed upon (A. Williams, personal observation, 2023). It should be noted that Montagne Cimetiere is a permanent roost surveyed using the ISE method on account of the roost being located within the same area as Jardin Mamzel, (Fig. 4), thus an EDC of this roost would likely double count bats moving between two sites. In addition, visibility and access are a constraint of the site making the identification of a suitable vantage point difficult.

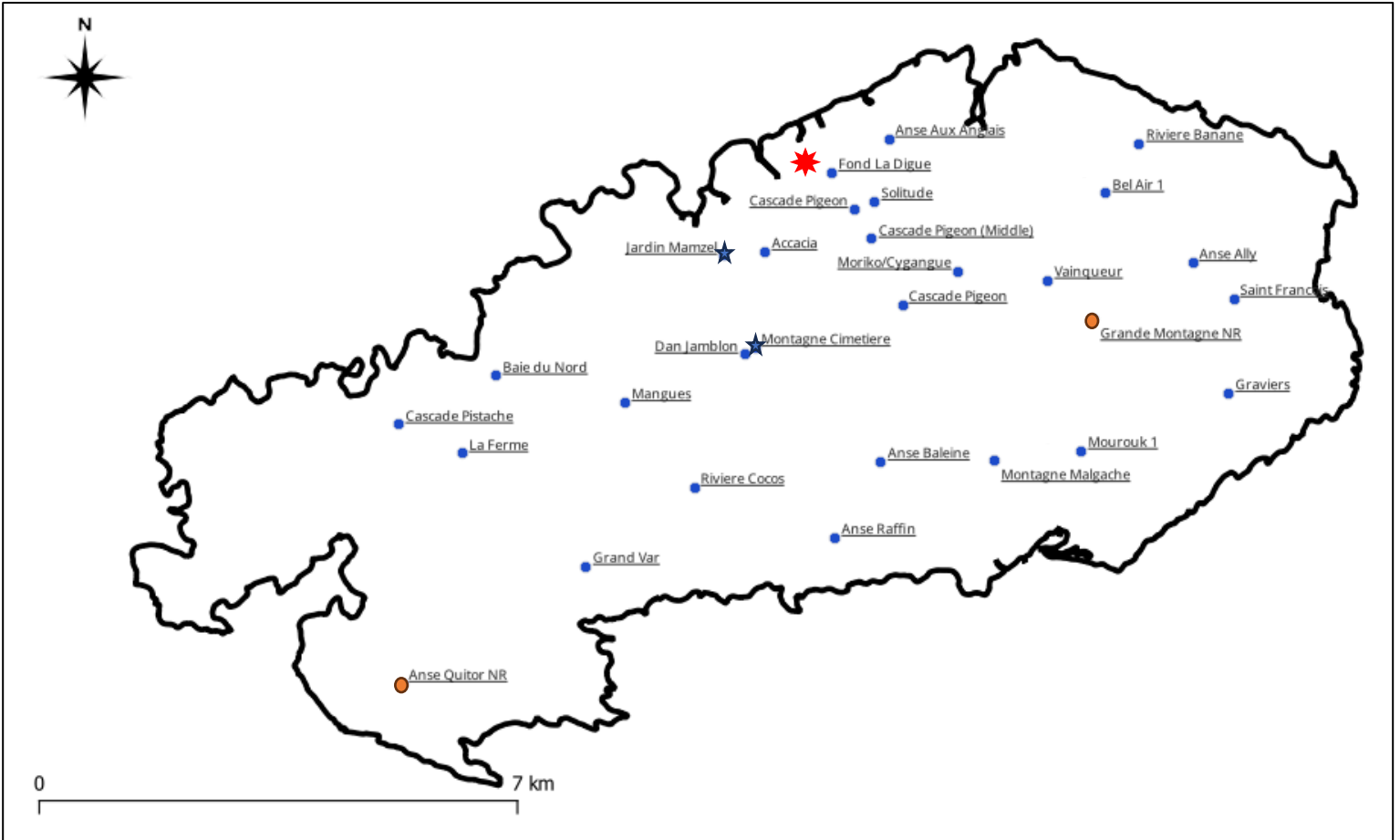


Figure 3

Map of Rodrigues showing locations of Rodrigues fruit bat roosting sites

Locations referred to within the text are represented by a star marker.

Pointe Canon meteorological station is represented by red sun marker.

Note that Grand Montagne Nature Reserve and Anse Quito Nature Reserve are not bat roosts and are thus represented by an orange marker.

Map created using the Free and Open Source QGIS version 3.30.1 (Appendix. I).

2.6. *Environmental and observational covariates*

Climatic data was obtained from one single weather station on the island; Point Canon, located to the northeast of Rodrigues (Fig. 4), accessed through the meteomanz.com web site. Due to the small size of the island, it is assumed that this single weather station provides a true representation of the weather conditions at all the roost sites. All daily weather conditions are calculated by the arithmetic mean of the minimum and maximum value of the relevant unit over the 24 hour period starting from 00:00. Average annual weather conditions are calculated by dividing the sum of all average daily observations of the relevant unit by the total number of observations (i.e. days in a year).

2.6.1. Variables related to detection probability

Survey effort

The length of time that the survey was conducted varied depending on the individual observers' perception of when light levels were deemed insufficient to continue counting bats. Therefore, the start and end time of the survey were recorded for all counts so that duration (in hours) could be included in the models to account for the effect that survey effort has on the abundance of individuals detected. Additionally, not all sites are equal in terms of the level of survey effort required during surveying (A. Williams, personal observation, 2023). Some sites have vantage points that offer a clear view of the emergence whilst other sites' vantage points are looking down into the valley to observe the emergence (Fig. 2). At the latter sites, a proportion of bats are obscured by vegetation or rockface, thus potentially eliciting a false negative error (Meyer *et al.* 2011). For these reasons, roost sites were included as a random effect in statistical models to control for error incited by the between-site variations, and to avoid pseudo replication caused by repeated surveys at the same roost.

Observer expertise

Observer expertise was included as an index score calculated by the number of surveys that the individual had conducted up to that date. This is known as an index of observer expertise and was included in models to account for the potential bias that survey experience could introduce to the count (Kelling *et al.* 2015). For example, it is assumed that naive observers could under or overestimate the population more than an experienced observer (Erwin, 1982). Under the assumption of the count being initially underrepresented, as time progresses and observers gain competence in survey methods a positive bias would be observed in the population trends (Kelling *et al.* 2015). This could lead to a false assumption of population growth, thus, to account for this, observer expertise was included as an explanatory variable in statistical models (Link & Sauer, 1997).

Daily cloud cover

Though not assumed to influence Rodrigues fruit bat emergence, it is assumed that survey days subjected to increased cloud cover would impose limitations on observer visibility. Thus, to account for

this, cloud cover (in oktas) was included as a covariate in statistical models. Okta is a universal measurement representing the percentage of cloud cover when the sky is divided into eights as measured by the weather station (Jones, 1992).

Average daily temperature

High heat levels induce physiological stress for Rodrigues fruit bats which could hinder their motivation to depart from the shaded areas within the roost (Welbergen *et al.* 2008). Therefore, on days of high heat, it is possible that they may wait until it is cooler to emerge or evade emergence entirely. To investigate if this has a significant effect on emergence, daily temperature (in °C) was included as a covariate in statistical models.

Average daily precipitation

Though fruit bats will fly during rain, precipitation increases the metabolic cost of flight for Rodrigues fruit bats due to the constraints associated with rainwater collection on the patagium and pelage (Voigt *et al.* 2011). Thus, average daily precipitation (in millimetres) was included as a covariate in statistical models.

Average daily wind speed

As with precipitation, there is an increased metabolic cost of flying during high wind speeds (O'Mara *et al.* 2019). This would lead to the assumption that increasing wind speeds on the day of the survey would deter bats from emergence, though this has not yet been formally clarified for Rodrigues fruit bats. To investigate if this has a significant effect on emergence, wind speed (in km/h) was included as a covariate in statistical models.

Survey type

It is recognized that the ISE method violates the assumption of population closure, as bats can, and most likely do, move from temporary roost sites to permanent sites within the time before EDCs are

performed. To account for the variation in the census survey methods, survey type was included as a factor in statistical models.

2.7. Annual climatic variables

Average annual temperature

In addition to extreme heat events causing mass mortality, the prolonged physiological stress induced by increased temperatures significantly reduces individual fitness and could be driving population decline (Dey *et al.* 2015; Diengdoh *et al.* 2022). To investigate if this has a significant effect on population numbers, annual temperature (in °C) was included as a covariate in statistical models.

Average annual precipitation

Annual precipitation levels are used as a metric to measure drought events. Significantly low levels of rainfall severely decrease the availability of foraging resources for Rodrigues fruit bats (Lučan *et al.* 2016). Further, as they obtain most of their hydration from their foraging items, they are very susceptible to mortality by dehydration (Jones, G. *et al.* 2009). To investigate if this has a significant effect on population numbers, annual precipitation (in millimetres) was included as a covariate in statistical models.

Cyclones

Cyclonic data was accessed through the International Best Track Archive for Climate Stewardship (IBTrACS; Knapp *et al.*, 2010). Only data from cyclones that passed within a 275km radius of Rodrigues and exceeded a minimum wind speed of 100 knots (51mps) during 2006-2022 were included (Evan & Camargo, 2011). The threshold of 275km was selected as this is considered the 'local scale' that a cyclone would influence the Mascarene Islands (Nicoll *et al.* 2017). The accumulated cyclonic energy index (ACE) was utilised (Bell, 2003). This index uses the square sum of the maximum sustained wind speed of the storm in 6-hour periods (00:00, 06:00, 12:00, 18:00) divided by 100 to quantify the intensity of the storm during its lifetime as a continuous variable (Camargo & Sobel, 2005; Nicoll *et al.* 2017). The greatest value of ACE per year was selected as this metric quantifies the severity of a cyclone.

2.8. Data analysis

All data analysis was performed using R Statistical Software (v4.3.2; R Core Team, 2023) (see Appendix. I).

Generalised Linear Mixed Models

Continuous covariates were standardized using the function 'scale' in R, and Generalised Linear Mixed Models (GLMM) were applied via the "lme4" R package (v1.1-26; Bates *et al.* 2015).

EDC and ISE datasets were combined because separate analysis was deemed ineffective as these outputs yielded results for only a proportion of the population and thus would not have provided an effective insight to what degree cyclones are driving population numbers. There are several studies that have combined data from direct and dispersal counts when assessing Old World fruit bat population (Utzurum *et al.* 2003; Cousins & Compton, 2005; Jenkins *et al.* 2007; Dey *et al.* 2015; Oedin *et al.* 2019; Hayes & Engbring, 2020).

GLMMs with a Poisson distribution were used to model the driving trends in the population, with population count as the response variable and the following covariates as the explanatory variables; T: average daily temperature (°C) on survey day (OSD), R: average daily rainfall (mm) OSD, C: cloud cover (Okta) OSD, W: average daily wind speed (km/h) OSD, At: average annual temperature (°C), Ap: average annual precipitation (mm), A: value of ACE for survey year, Ty: survey type, S: survey effort, I: index of observer expertise, Y: year (17 levels) and Ro: roost (35 levels). These variables were selected for the models based on the potential influence that variations in climatic conditions, both annual and daily, have on the result of the population count. All possible combinations of variables within the model were tested manually and model fit was checked visually using q-q plots. The purpose of the GLMM was to determine to what extent each of the selected variables influenced the result of the count. It was assumed that annual climatic variables would have a stronger effect on the population count due to their influence on resource availability, which in turn drives recruitment and mortality. Whereas daily climatic variables were assumed to have more influence on the emergence trends, i.e. motivation to emerge, observer visibility and timing of peak emergence. Exploratory analysis demonstrated a possible quadratic effect of annual precipitation representing a positive relationship with moderate values (i.e.

years that the island was not subject to drought or flooding); thus, a quadratic term was added for this covariate. To avoid pseudo-replication, year and roost location were added as random effects as both variables contain repeated levels within the dataset. To account for the differences in methods, an interaction effect was added between ACE, annual temperature, annual precipitation, and survey type to identify any differences in the impact of the strength of climatic variables at permanent and temporary sites. Multiple competing models were then created containing different combinations of independent covariates. Subsequently, the best fitting model was selected based on the Akaike information criterion (Akaike, 1973; Symonds & Moussalli, 2011), see Table. 1. Models with a delta AIC <2.0 were considered to be equivalent (Richards, 2005). Effect size for fixed effects were calculated by converting the regression coefficients into odds ratios (OR). Plots were created using the “ggplot2” (v.3.3.3; Wickham, 2016) and “ggeffects” (v.0.3.1.; Lüdtke, 2018) R packages.

Missing data imputation

After appropriate formatting of the data, it was noted there was missing data in the following covariates: survey effort (number of missing data entries = 3), and index of observer expertise (number of missing data entries = 63). The missing data was imputed using two of the methods described in Lopucki *et al.* (2022). For missing data from ‘survey effort’, from the arithmetic mean was calculated from the rows for a site over the years (Lopucki *et al.* 2022). This method was chosen based on the knowledge that the same observer is deployed at each site every year; therefore, we can assume the individual observer would have conducted each survey with the same effort i.e., consistent duration of the survey. For missing data for the ‘index of observer expertise’, the arithmetic mean was calculated from the column for a given year (Lopucki *et al.* 2022). This method assumes that the observers across sites will have on average, a similar degree of expertise for any given year.

Collinearity

Before modelling the data, a test for multicollinearity was conducted using the variance inflation factor (VIF) function via the car R package (v3.1.2; Fox & Weisberg, 2019). This produces a measure of the correlation between predictor variables; if the degree of correlation is too high, this can reduce the validity of the linear models' output. If the output is equal to or greater than 5 there is a severe correlation between variables and thus should be assessed and highly collinear variables removed from analysis (Freckleton, 2011).

2.9. *Statement of ethics*

This project was granted approval by the Chair of the Science & Engineering Research Ethics committee from the Faculty of Science, Business & Enterprise at the University of Chester on 4th March 2023 (see Appendix. III).

Chapter 3 – Results

The data analysed comprised of 17 years of Rodrigues fruit bat population count data collected during the last week of November every year. From 2006-2022 the roost locations increased from 8 to 31. Based on the 2022 census there were 17 temporary roosts subject to ground counts and 14 permanent roosts subject to evening dispersal counts. During the annual population census there was a total of 51 ground counts and 39 evening dispersal counts conducted on Rodrigues Island. Due to new roost locations being added every year the variance of these counts cannot be determined as there is no variability from a single year of surveys. Figure. 5 shows the median count and range of bats at each roost across the survey period. Details of each roost including number of years the site was subject to surveys and mean counts can be found in Appendix. V.

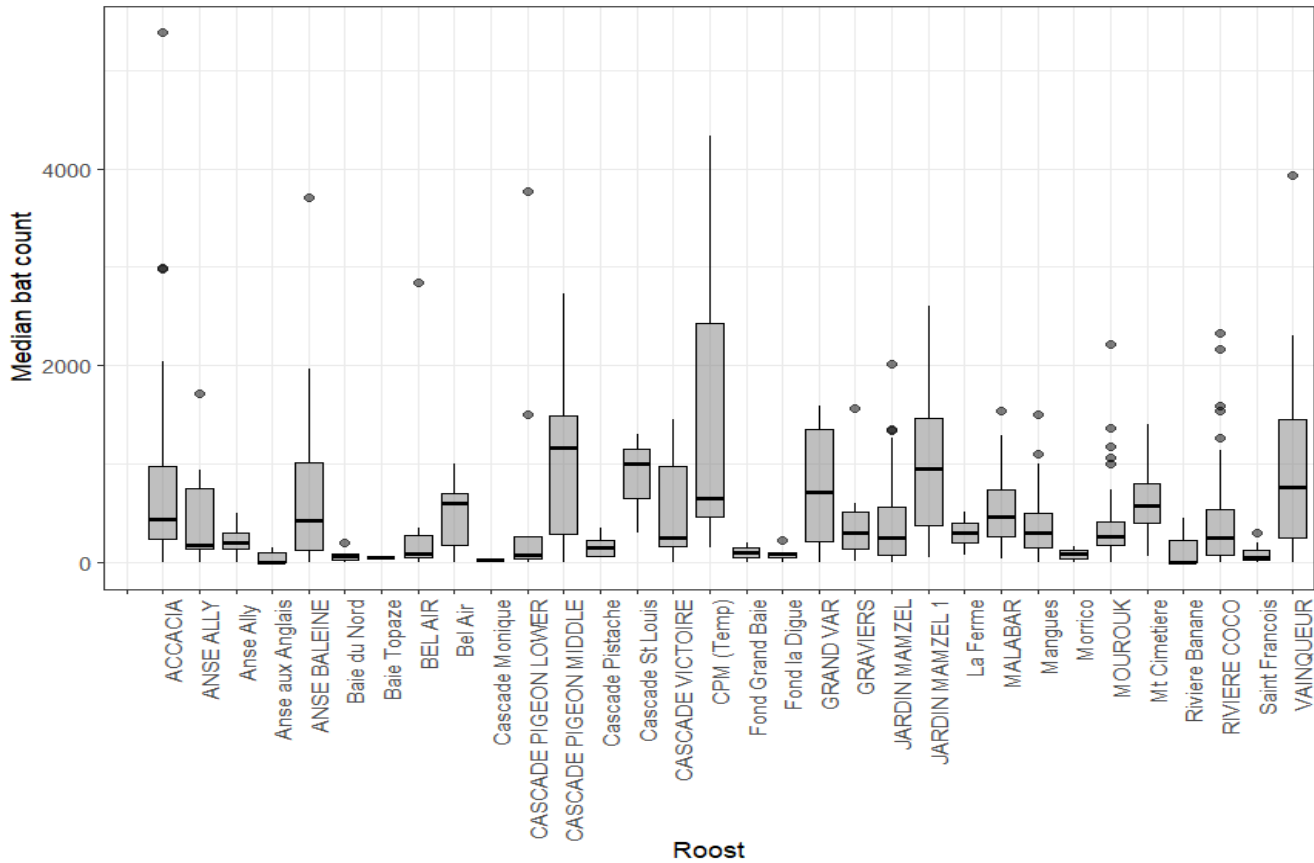


Figure 5

Box plot showing median count of bats at each roost site across survey period.

Roost locations capitalised represent EDC survey sites and those not capitalised represent ISE survey sites.

CPM (Temp) = Cascade Pigeon Middle subject to ISE survey method.

The Rodrigues fruit bat population count underwent several fluctuations in numbers but broadly increased across the study period from 6032 in 2006 to 15327 individuals counted in 2022 (see Fig. 7). This population trend is formed from summing up all the data from the minimum counts at all roosts across the island. The selection process for the GLMM used to analyse this data is presented in Table. 1, and the subsequent results can be found in Table. 2. The best model explaining population count included year and roost location as random effects, temperature, precipitation, cloud cover, wind speed, annual temperature, annual precipitation as predictors with additional interaction effects between accumulated cyclonic energy and roost type and annual precipitation and roost type (Table 1). None of the competing models were within delta AIC <2.

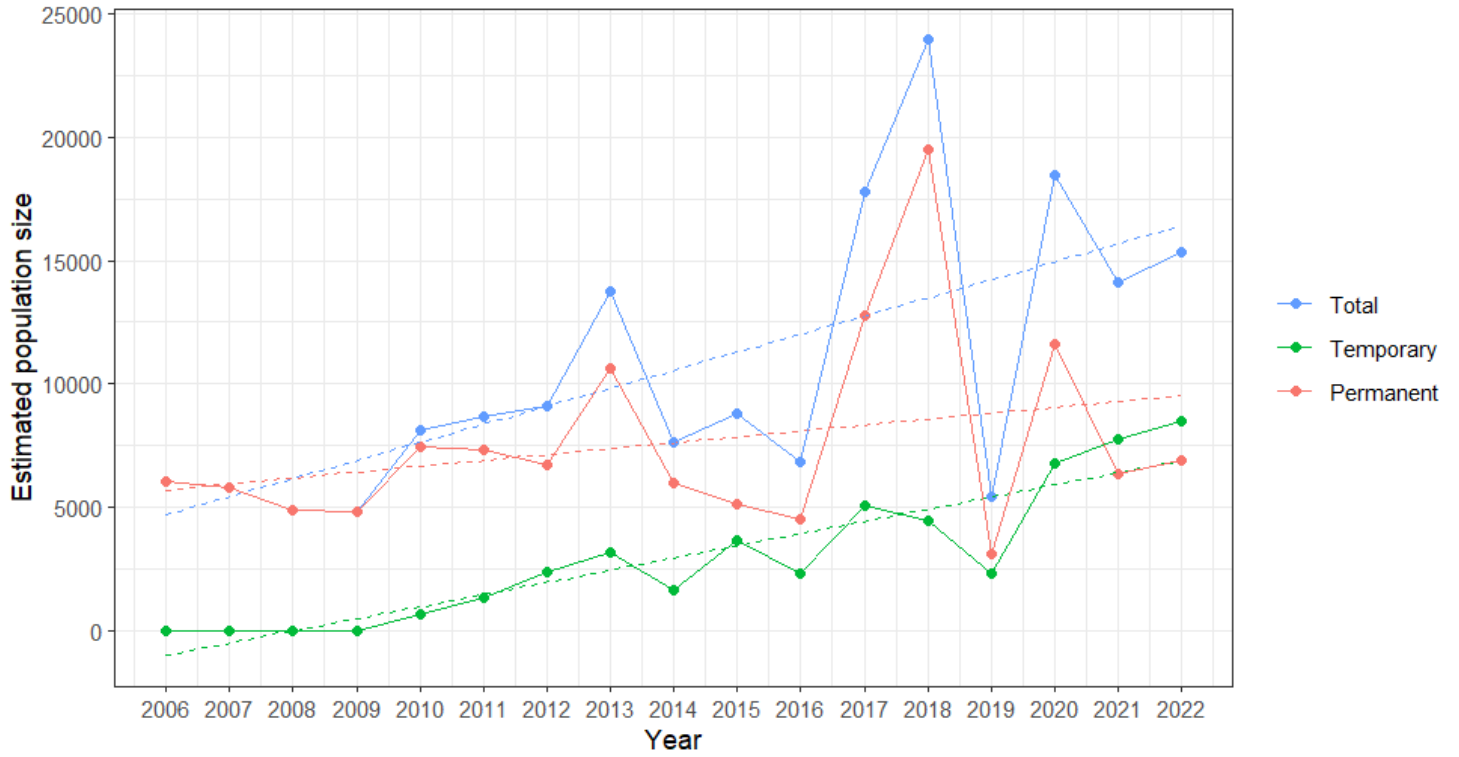


Figure 6

Time series plot of minimum estimated size of sum of Rodrigues fruit bat population at all roosts (2006-2022)

Total count is a sum of counts at permanent and temporary sites.

Table 1

Model selection of competing GLMMs to find the model of best fit for the influence of explanatory variables on population counts of the Rodrigues fruit bat. Only the top ten competing models are shown.

<u>Model</u>	<u>Candidates</u>	<u>K</u>	<u>AIC</u>	<u>ΔAIC</u>
6	T+R+C+W+At+Ap+I(Ap ²)+S+I+A*Ty+At*Ty+(Ap+I(Ap ²))*Ty+(Y)+(Ro)	20	220016.8	0
5a	T+R+C+W+At+Ap+I(Ap ²)+S+I+A*Ty+At*Ty+Ap*Ty+(Y)+(Ro)	19	220281.2	264.4
5	T+R+C+W+At+Ap+S+I+A*Ty+At*Ty+Ap*Ty+(Y)+(Ro)	18	220292.1	275.3
4a	T+R+C+W+At+Ap+I(Ap ²)+S+I+A*Ty+At*Ty+(Y)+(Ro)	17	220824.7	807.9
4	T+R+C+W+At+Ap+S+I+A*Ty+At*Ty+(Y)+(Ro)	16	220835.1	818.3
3a	T+R+C+W+At+Ap+I(Ap ²)+S+I+A*Ty+(Y)+(Ro)	15	221272.7	1255.9
3	T+R+C+W+At+Ap+S+I+A*Ty+(Y)+(Ro)	14	221283.1	1266.3
2a	T+R+C+W+At+Ap+I(Ap ²)+A+Ty+S+I+(Y)+(Ro)	15	221497.0	1480.2
2	T+R+C+W+At+Ap+A+Ty+S+I+(Y)+(Ro)	14	221507.1	1490.3
1	T+R+C+W+At+Ap+I(Ap ²)+A+S+I+(Y)+(Ro)	14	221508.4	1491.6

Table 2

Estimates of the best fitting model following AIC model selection

<u>Effects</u>				
<i>Random effects:</i>	<u>Variance</u>	<u>Std. Deviation</u>		
<i>Roost</i>	0.7688	±0.8768		
<i>Year</i>	1.12872	±1.1345		
<i>Fixed effects:</i>	<u>β</u>	<u>Std. Error</u>	<u>Statistic-Z</u>	<u>P value</u>
<i>Intercept</i>	6.899	±0.397	17.397	<0.0001
<i>Survey type (ISE as base level)</i>	-1.234	±0.298	-4.140	<0.0001
<i>Survey effort (hours)</i>	0.059	±0.002	29.298	<0.0001
<i>Observer expertise</i>	0.020	±0.005	3.973	<0.0001
<i>Cloud cover (okta)</i>	0.022	±0.003	6.280	<0.0001
<i>Average daily temperature (°C)</i>	0.035	±0.004	8.059	<0.0001
<i>Average daily precipitation (mm)</i>	0.033	±0.003	10.326	<0.0001
<i>Average daily wind speed (km/h)</i>	-0.017	±0.004	-4.835	<0.0001
<i>Average annual temperature (°C)</i>	-0.174	±0.035	-4.931	<0.0001
<i>Average annual precipitation (mm)</i>	1.577	±0.165	9.556	<0.0001
<i>I(Average annual precipitation²)</i>	-0.765	±0.190	-4.036	<0.0001
<i>ACE</i>	-0.108	±0.019	-5.667	<0.0001
<i>ACE: Survey type (ISE as base level)</i>	-0.113	±0.007	-16.305	<0.0001

<i>Average annual temperature (°C): Survey type (ISE as base level)</i>	-0.164	±0.008	-20.364	<0.0001
<i>l(Average annual precipitation^2) (mm): Survey Type (ISE as base level)</i>	0.083	±0.005	16.365	<0.0001

Results from GLMM investigating the relationship of explanatory variables and population count. Interaction effects in the models are represented by a colon.

Explanatory variables

Results from the GLMM confirm that average annual precipitation, cyclone strength, survey effort, average daily windspeed, and average annual temperature all have a significant relationship with Rodrigues fruit bat population counts.

Average annual precipitation has a significant positive relationship with Rodrigues fruit bat population counts until the rainfall levels reach 1300mm, at which point this variable becomes a limiting factor (see Fig. 7). For every one unit increase in average annual precipitation the expected log count of Rodrigues Fruit bat increases by 1.577 (OR= 4.84, CI= 3.501, 6.690), see Table. 2 and Fig. 7. Cyclone strength has a significant negative relationship with Rodrigues fruit bat population counts. For every one unit increase in storm severity the expected log count of Rodrigues Fruit Bat decreases by 0.108 (OR= 0.90, CI= 0.87, 0.93) see Table. 2 and Fig. 8a. Survey effort has a small but statistically significant positive relationship with Rodrigues fruit bat population counts. For every one unit increase of survey effort the expected log count of Rodrigues Fruit Bat increases by 0.059 (OR= 1.06, CI= 1.0001, 1.126), see Table. 2 and Fig. 8b. Average daily windspeed and average annual temperature both have a small but statistically significant negative relationship with Rodrigues fruit bat population counts. For every unit increase of average wind speed the expected log count of Rodrigues Fruit Bat decreases by 0.017 (OR= 0.98, CI = 0.976,0.99), see Table. 2 and Fig. 8c. For every one unit increase in annual temperature the expected log count of Rodrigues Fruit Bat decreases by 0.174 (OR= 0.84, CI= 0.784, 0.900.) see Table. 2 and Fig. 8d.

Observer expertise (OR=1.02, CI= 0.9424, 1.1047), daily cloud cover (OR = 1.02, CI =0.8899,1.1731), average daily temperature (OR = 1.04, CI =0.7814, 1.3737) and average daily precipitation (OR=1.03, CI= 0.7353, 1.4537) all had an insignificant relationship with the Rodrigues fruit bat population counts and are discounted from further discussion.

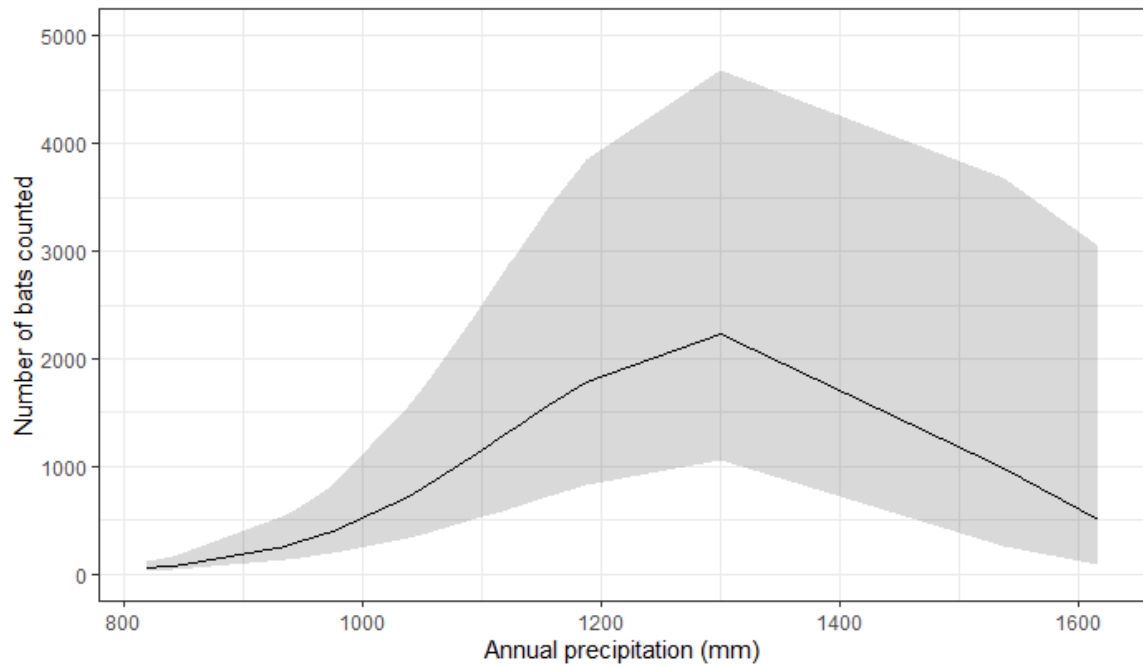


Figure 7

Marginal effects of annual average precipitation on predicted Rodrigues fruit bat count at any single vantage point

Grey band represents upper and lower 95% confidence intervals.

The y-axis has been back transformed to the original scale.

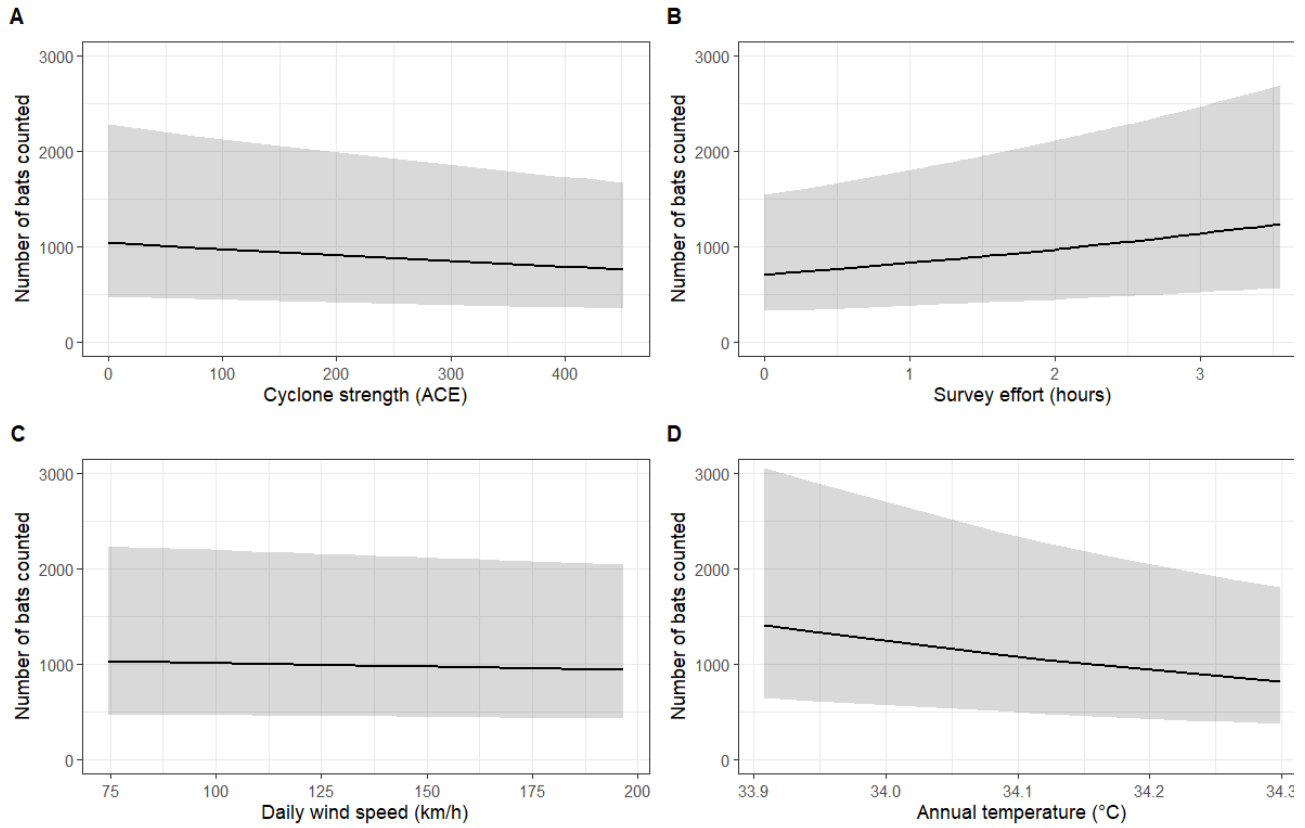


Figure 8

Marginal effects of climatic variables with statistically significant relationships with the predicted Rodrigues fruit bat count at any single vantage point

Grey band represents upper and lower 95% confidence intervals.

The y-axis has been back transformed to the original scale.

Chapter 4 – Discussion

The results from this study suggest that Rodrigues fruit bat population has undergone an increase in population over time (6032 in 2006 to 15327 individuals counted in 2022) which is significantly affected by climatic variables relating to resource availability such as annual average precipitation and ACE. Increased levels of annual rainfall enable population increases as the rain facilitates ample resources to support a healthy growing population (Kingston *et al.* 2023). Contrastingly, low levels of annual rainfall would yield low resource availability, which appears to have a limiting effect on the Rodrigues fruit bats' ability to survive. However, there is a tipping point in which high levels of rainfall begin to impede the population due to the onset of flooding which would reduce resource availability. Similarly, following a storm with high ACE, the Rodrigues fruit bat's resources and roosting sites are damaged which also restricts their ability to survive and reproduce in addition to the storm causing direct mortality (Kingston *et al.* 2023).

4.1. *Influence of climatic variables on population*

Though an effect was observed, daily cloud cover, observer expertise, average daily temperature and average daily precipitation all had a small effect on the Rodrigues fruit bat population counts and thus are discounted from further discussion. As annual climatic variables drive the productivity of foraging resources, the annual variables are more likely to have consequences on mortality and productivity of the population than the daily climatic variables relating to the day of the survey (Eby *et al.* 1999).

Average annual precipitation

Of all the climatic variables measured in this study, annual precipitation had the strongest effect on the population count based on the results in Table. 2. Increases in average annual precipitation levels have a significant positive correlation with the number of bats counted (Fig. 7). Increased annual precipitation aids in the production of fruit and flowering resources for Rodrigues fruit bats, thus foraging efforts are increased accordingly (Almeida-Neto *et al.* 2008; Presley *et al.* 2009). Our results are consistent with findings on fruit bats in Malaysia (Hodgkison *et al.* 2004), the Amazon (Ramos Pereira *et al.* 2010), Malagasy (Ramanantsalama *et al.* 2022), the Neotropics (Corro *et al.* 2021; Ligo *et al.* 2023), and Mexico (Montiel *et al.* 2011). This result is noteworthy in view of the frequent months of insufficient rainfall which leave Rodrigues in periods of drought, usually from January to March (Gade, 1985). These prolonged periods of drought cause intense food shortages for Rodrigues fruit bats (Welbergen *et al.* 2008).

However, when average annual precipitation exceeds 1300mm the effect becomes negative (see Fig. 7). This is presumably due to damage that flooding incurs on the Rodrigues fruit bat's feeding resources, flowering and fruiting flora (Ramos Pereira *et al.* 2010). Particularly as the fruiting resources are non-native and have not evolved to withstand waterlogged conditions, in addition to the status of soil erosion on the island (Funk, 2013). High levels of rainfall also coincide with the occurrence of a strong cyclone (see below).

The effect of annual precipitation is stronger at temporary sites than at permanent sites (Table. 2). This can be explained by the abundance of island wide resources inciting increased levels of dispersal to these areas, and subsequently, the increased requirement to utilize temporary 'stopover' sites during island wide migrations. Additionally, this could support the theory of an increase in population resulting

in overcrowding at permanent sites which requires individuals to utilize alternative temporary sites as 'overflow'. Conversely, if there are ample resources, inferred by increases in annual precipitation levels, it would make sense that more individuals would be observed at temporary roost sites.

Accumulated cyclonic energy (ACE)

Accumulated cyclonic energy has the second most significant effect on the Rodrigues fruit bat population. An increase in ACE has a negative influence on the number of bats counted, (Fig. 7a). This can be corroborated by several other studies which suggest insular bat species suffer population declines as a consequence of cyclones and tropical storms (Pierson *et al.* 1996, Shilton *et al.* 2008; Fleming & Murray, 2009; Gannon & Willig, 2009; Sergio *et al.* 2018). This may be linked to the direct mortality from exposure to the high wind speeds which destroy roosting areas and cause lethal injuries to the bats (Trehwella *et al.* 1998). Though these mortality rates have not yet been quantified for Rodrigues, the influx of injured and deceased bat corpses found littered over the island immediately after a storm would indicate that this effect is very apparent (C. Jones, personal communication, 19 June 2023). However, the larger mortality rates occur as a secondary result brought on by the detrimental destruction of foraging and roosting areas (Rodríguez-Durán, 2009). McConkey *et al.* (2004) reported that on Vava'u Islands after Cyclone Waka in 2001, 80% of the trees identified as food resources for *Pteropus tonganus* were devastated. This effect was observed to increase to 90% for Western Samoa following Cyclone Ofa in 1990 (Elmqvist *et al.* 1994).

Further, Rodrigues fruit bats have been observed displaying abnormal foraging behaviours post-storm such as licking dew off the ground and eating unripe fruit, suggesting they were suffering from starvation (McConkey *et al.* 2004; R. Jhangeer-Khan, personal communication, 20 November 2023). Other studies have reported a similar phenomenon in which *Pteropus* species were observed ground foraging and consuming leaves, which were the only remaining food source available post-storm as a consequence of canopy loss (Pierson *et al.* 1996; Gannon & Willig, 2009).

The results from this study suggest that the negative influence of cyclones on population counts is stronger at temporary sites than permanent ones (see interaction effect between ACE and Survey type in Table. 2). This makes logical sense if we consider temporary sites as 'stopover' sites for bats during foraging bouts (Morrison, 1987). If there is a reduction in available foraging resources, there would be little requirements to travel or rest at temporary 'stopover' sites during said travel, to resources

(Bonaccorso *et al.* 2007). This also supports the theory that permanent roosts are favoured in terms of proximity to resources. It is reasonable to assume that bats would prefer to reside here to conserve energy when needing to travel to forage (Morrison, 1978).

Furthermore, if the population is decreased there would remain less pressure to leave permanent roosting sites because of overcrowding. If temporary sites are used as ‘overspill’ areas when permanent sites reach carrying capacity, this would become null when populations decrease as room in permanent sites would be created. Fruit bats are gregarious for many well-documented reasons such as roost security (Kunz *et al.* 2003), thermoregulation (Dechmann *et al.* 2004), cooperation (Emlen, 1994), and safety from predators (Fenton *et al.* 1994). Though not a current problem on Rodrigues, severe storms historically led people to depend upon bat meat for protein sources (Mickleburgh *et al.* 2009). Thus, bats may congregate at larger sites rather than spreading out across the island, using gregarious behaviour as protection from predation by humans (Hamilton, 1971). Thus, if the population decreases individuals may migrate to areas where other conspecifics would be. If this were true, then during population depressions following storms temporary sites would become vacant as there is an assumed preference of permanent sites, suggesting a source-sink dynamic (Dias, 1996).

Survey effort

As expected, the number of bats counted increases with survey effort (Fig. 8a). This is unsurprising as surveys of a longer duration will inevitably be witness to more bats than shorter surveys. This has been witnessed in other bat monitoring programs (Skalak *et al.* 2012) and in other species groups such as bird species in Quintana Roo, Mexico (Lynch, 1995). As duration of the count significantly affects the number of bats counted, it is essential to include survey effort as a confounding effect in population monitoring studies. Failing to do so could lead to inaccurate results with a positive bias associated with sites in which observers conduct the survey for more hours than at other sites (Fig. 8a).

Average daily windspeed

Though only a small effect size, increases in average daily wind speed were negatively correlated with bat emergence (Fig. 7c). This can be explained by the high metabolic costs associated with flying in high wind (O’Mara *et al.* 2019). Rodrigues fruit bats residing at roost sites within valleys need to ascend to exit the cascade for evening foraging (Personal observation, 2023). They do this by utilizing the

orographic lift, which allows them to gain elevation with very few wingbeats, thus expending as little energy as possible (O'Mara *et al.* 2019). One can assume that this act is challenging under conditions of high wind speeds causing Rodrigues fruit bats to delay or evade emerging (Koch *et al.* 2023).

An explanation for reduced numbers detected at temporary sites could be that the bats move down to lower branches, or further into the clustered vegetation, to protect from the high wind speed. This behaviour would make detection difficult, particularly at temporary sites that are surveyed from a distance using binoculars (Campbell *et al.* 2006). Furthermore, bats may cluster together as a mechanism to protect against gusts (Sugita & Ueda, 2013). This behaviour could increase the difficulty of distinguishing individual animals from surrounding clusters from a distance (McCarthy *et al.* 2021). To assess these hypotheses further, site specific wind speed data would need to be collected from each vantage point using an anemometer, as opposed to daily wind speed across the whole island.

Average annual temperature

Our results suggest that an increase in average annual temperature leads to decreases in the number of bats counted (Fig. 7d). This is to be expected as, unlike the trend observed with daily temperature, long bouts of high temperatures induce severe physiological stress (Dey *et al.* 2015) and reduces fitness and recruitment in Old World fruit bats (Welbergen *et al.* 2008). This is primarily attributed to the vulnerability to heat exhaustion and dehydration as Rodrigues fruit bats lack sweat glands to thermoregulate (Diengdoh *et al.* 2022). Instead, thermoregulatory behaviours include wing fanning to induce convection (Laburn & Mitchell, 1975; Ochoa-Acuña *et al.* 1999), urine bathing (Ochoa-Acuña *et al.* 1999), licking of the wrist and wing membrane (Nelson, 1965), flying over water to cool their stomachs (Thanapongtharm *et al.* 2015) and, as a last resort, panting (Downs *et al.* 2015). However, these activities are insufficient in counteracting high heat stress (Kingstone *et al.* 2023). This is particularly true of species with thick dark fur, such as Rodrigues fruit bats (Kingstone *et al.* 2023).

Additionally, high temperatures have a negative correlation with fruit production (Al-Yahyai, 2011). Therefore, it is reasonable to assume that during years of increased annual temperature, recruitment may be reduced due to the associated energetic costs of reproduction that cannot be replenished. These costs incorporate gestation, milk production and lactation, flight during pregnancy and post-pregnancy with pup attached, and extended maternal care which can last up to a year (Racey & Entwistle, 2000). As the energetic investments associated with flight are high, Rodrigues fruit bats may

preserve energy by aborting emergence when resource availability is low, resulting in a low EDC value (Speakman *et al.* 2003).

4.2. *Roosting sites*

Larger aggregations of individuals were observed at permanent roost sites than at temporary ones (Table. 2). An explanation for this could be that these sites are generally larger than the temporary sites, and therefore have a capacity for a greater number of individuals (Morrison, 1980). An alternative explanation could be that permanent sites have been occupied for several years longer than temporary sites and greater aggregations of bats are exhibiting roost fidelity to the longer-standing hibernacula (Parsons *et al.* 2011). Permanent sites could also be located closer to high-value fruiting resources (Rothenwöhrer *et al.* 2011) or offer greater refuge from unfavorable weather conditions (Fleming *et al.* 1998), thus posing as a more energy-efficient choice for roosting than temporary sites. Alternatively, the temporary sites may be used as day roosts or ‘stopover’ sites between permanent roosts during foraging bouts (Senthikumar *et al.* 2012; R. Jhangeer-Khan, personal communication, 22 November 2023). To confirm this theory, further studies need to be conducted in which the movement ecology of Rodrigues fruit bats were assessed by radio tagging a sample of the population (Palmer & Woinarski, 1999; Oleksy *et al.* 2019).

It has been reported that some species of fruit bats display inter-individual spacing to counteract the negative effects of overcrowding in roosts (Respicio *et al.* 2023). These effects include increased levels of stress, in conjunction with a decrease in the population’s health which is ascribable to the higher susceptibility to disease and parasite transmission associated with overcrowding (Hayman *et al.* 2013; Webber *et al.* 2015). Thus, an alternative theory could be that individuals migrate to temporary sites when permanent sites reach maximum capacity, resulting in temporary sites being used as ‘overflow’.

Additionally, in light of the large number of animals congregating at permanent sites, it is reasonable to assume that these sites may be the location in which important reproductive events, such as mating displays and subsequent mate selection, harem protection and mating (Campbell *et al.* 2006a), and rearing of young occurs (Lewis, 1995). To investigate this further, behavioural studies would need to be conducted, I recommend this be carried out using camera traps to remove any influence of human

presence on behaviour (Rodrigues *et al.* 2023) and to allow for nocturnal or cryptic behaviour patterns to be observed (Krivek *et al.* 2022).

4.3. *Implications for conservation management*

Current in-situ conservation management is focused on the eradication of invasive flora and restoration of native habitat (Tatayah *et al.* 2017). As our results showcase the variables with the strongest effect on the population count are related to the availability of foraging resources, this study supports the continuation of this conservation management. However, as the foraging resources of the Rodrigues fruit bats are not exclusive to native flora (e.g. *Mangifera indica* and *Carica papaya*) I suggest efforts focus on the removal of invasive species that have negative consequences for the soil quality and hydrology of the island such as *Furcraea foetida*, and not those which provision foraging resources. This study also stresses the importance for the continued long-term monitoring of the species with potential implementations to the methodology (see 4.7. Monitoring recommendations) and/or additional studies (see 4.8. Future research).

4.4. *Monitoring recommendations*

The length of the dataset has provided a historical record which significantly aids the underpinning of the population trends. Whilst the methods described are valid and cost-effective, below I propose some suggestions to the methodology which could be enforced provided there is feasibility (Corso *et al.*, 2010).

Additional variables

A factor not considered in the data collection is the site-specific variation in distance from the vantage point to roost site being observed. It is a general assumption in population monitoring that detection is negatively correlated with distance of observer from the focal animal (Buckland *et al.* 2001; Focardi *et al.* 2005). Additionally, the probability of false positive error is increased by distance from the roost site (McClintock *et al.* 2010). Therefore, I recommend adding the distance of the vantage point from the roosts being observed, measured with a rangefinder, as a covariate in the dataset to control this variation in the data collection and improve repeatability. To improve the accuracy of the influence of climatic variables, it would be beneficial for observers to note the temperature, precipitation status and cloud cover at their exact location at the precise time of the survey using anemometers (Owen *et al.* 2023).

Double observer approach

As aforementioned, observers are assigned to sites which create a bias as individual observer methods deviate from one another. When combined with the site-specific challenges, it is difficult for a single observer to keep an accurate tally of the bats leaving and returning (Kunz *et al.* 2009). Therefore, I recommend at least two observers be assigned to each site, one to observe bats leaving and the second to see them returning and entering (Nichols *et al.* 2000). This way observers do not have to keep a mental note of both sets of bats and subtract the total during the survey. Instead 'leaving' observers can count bats crossing a transect and 'returning' observers can count the bats crossing in the other direction. When the emergence is complete, the observers can combine their tallied sheets and have a total for bats leaving, returning, and entering every 5 minutes as well as a total at the end of the survey.

However, it is recognized that the utilization of this method at all vantage points simultaneously would demand an increased number of trained staff and volunteers.

Independent observer approach

Monitoring could be made increasingly more robust and accurate by employing two independent observers to monitor the same emergence simultaneously but without any communication between each other (Forcey *et al.* 2006). A joint detection probability can then be calculated using the data from the independent observers (Nichols *et al.* 2000). This was done by Forcey *et al.* (2006) for migrating bird species using the program DOBSERV. Forcey *et al.* (2006) found that this returned a more accurate estimation of species abundance than the single observer approach. For more accuracy, the double and independent observer approach could be adopted, i.e. the double independent one. This would demand two sets of two observers per site, each set counting independently. Alternatively, a video camera could be deployed in place of the second pair of observers to record the emergence whilst the manual count is occurring simultaneously (O'Shea *et al.* 2003). This medium can be referred to and reanalyzed later, increasing the reliability of count outputs, and reducing human error, of which the likelihood is increased with larger colonies such as that of the Rodrigues fruit bat (Kunz *et al.* 2003; Meretsky *et al.* 2010; Carpenter *et al.* 2014).

4.5. Future research

Fortnightly data

Alongside the annual population census, EDCs are conducted fortnightly at the Malabar permanent roost. This site has been subjected to more frequent observation than the remaining roost sites since the 1970s as it historically hosted the greatest colony aggregation island wide (Personal communication, R. Jhangeer-Khan 22 November 2023). With the exception of average daily precipitation, the daily climatic variables were not assessed as having a large effect size on the annual Rodrigues fruit bat population count. However, on account of the dataset accumulated by the fortnightly EDC at Malabar having a greater volume of surveys, there would likely be more variation in climatic conditions allowing for a more thorough analysis of the influence of weather conditions on EDC results. It would be valuable to subject this data to the same GLMM analysis presented in this study to compare the seasonal trends with the annual trends as has been conducted in the Malaysian (Hodgkison *et al.* 2004) and Amazonian (Ramos Pereira *et al.* 2010) rainforests for local fruit bat species. Although the considerable climatic seasonal variation in the aforementioned locations is not reflected in Rodrigues' climate, identifying seasonal shifts in the Rodrigues fruit bat population would open the gap in the research for further assessment (Kunz *et al.* 2009). Analysis of this dataset would elucidate the within-year population trends and fluctuations, such as seasonal variation within breeding, as opposed to across several years. This could also provide insight as to which, if any, climatic variables have an influence on the emergence times of the colony from this roost which would, in turn, support the analysis presented in this study.

Patterns in emergence

The circadian phenomenon of bat colony emergences from their hibernacula is known to be in sync with the time of sunset (Erkert, 1978), though weather conditions and light levels have also been shown to have an influence (Frick *et al.* 2012). Long-term monitoring of emergence events allows investigation of covariate influence on the activity, in particular how this has changed over time and differs between roost sites across the island.

Additionally, an understanding of the emergence pattern will aid the planning of bat ecotourism for Rodrigues. Bat tourism exists in Austin, Texas where tourists gather at Congress Bridge to watch the nightly emergence of the Mexican free-tailed bat (*Tadarida brasiliensis*). This activity attracts 240,000

tourists each year and generates an annual 6.5 million USD in revenue (Bagstad & Wiederholt, 2013). In addition to wildlife tourism benefiting the local economy, it can be designed to educate and change any negative attitudes people may have towards focal species and their conservation (Bixler *et al.* 2002). Further, applying monetary value to wildlife increases the chance of conservation success as it highlights the value of the species to locals via incoming funds (Duffus & Deardon, 1990; Smyth, 1998). Having documented the emergence of a colony from Malabar every fortnight, there is knowledge of the emergence pattern throughout the year. A GLMM, as presented in this study, to underpin the trends in emergence times and the influence of climatic variables is required for the implementation of successful non-consumptive wildlife tourism.

Emergence times also provide an insight into behavioural ecology (Frick *et al.* 2012). Changes to the emergence pattern can be caused by alterations in resource availability i.e. earlier emergences occurring post-cyclone could infer a scarcity in resources causing alterations in behaviour on account of increased intraspecific competition (Frick *et al.*, 2012). By observing the timing of emergence at different vantage points, resource use across the island could be mapped and monitored, highlighting areas which need priority protection. This would be more effective in conjunction with radio-tagged individuals (Mildenstein, 2002).

Population viability analysis

To underpin the stability of the population, data would be subjected to population viability analysis (PVA) which predicts how the remnant populations' persistence and dynamics could be impacted by numerous processes, both intrinsic and extrinsic, over time (Beissinger, 2002). This would give a prediction of how the Rodrigues fruit bat population will respond to the expected increase in cyclone activity and strength (Sakalli & Bařusta, 2018). These processes include demographic (birth rate, growth rate etc.), genetic, and environmental, as well as stochastic variables, all of which have complex and interacting effects (Dobson *et al.*, 2013). The output aids the construction of species-specific conservation management plans in a more effective manner than that of general landscape management applied to a habitat to conserve several species assemblages (Groves *et al.* 2002; Noon *et al.* 2012). A more effective proposal of conservation management would combine general and species-specific approaches, the latter obtained via PVA. By continuing general habitat management and adopting targeting conservation strategies for Endangered species and those that provide significant ecosystem services such as Rodrigues fruit bat (Noon *et al.*, 2012).

Movement ecology and radiotelemetry

Despite no radio tagging studies ever been conducted for this species, anecdotally it is observed that inter-roost movement occurs island wide for Rodrigues fruit bats (R. Jhangeer-Khan, personal communication, 19 November 2023). Understanding the movement ecology of the focal species is essential for designing a comprehensive conservation strategy so that locations encompassing important resources can be identified and considered in habitat management plans (Trehwella *et al.* 2001; Mildenstein, 2002). Conservation efforts for *Pteropus* species are generally concentrated solely at the roost and surrounding vicinity (Palmer & Woinarski, 1999). However, identifying new temporary sites or other areas of resource could highlight areas that need protection i.e. are not suitable for anthropogenic development, such as the land surrounding the temporary roost at Fond La Digue which is close to settlements (Palmer & Woinarski, 1999; Vardon *et al.* 2001).

Also, mapping the movement of Rodrigues fruit bats would allow their island-wide seed dispersal capacity to be quantified. Currently the level of this action has not yet been formally assessed for this species and has only been inferred from other *Pteropodidae* studies across the globe, such as *Pteropus conspicillatus* (Richards, 1990), *Cynopterus brachyotis* (Tan *et al.* 2000), *Eidolon depreanum* (Picot *et al.* 2007), and *Pteropus dasymallus inopinatus* (Nakamoto *et al.* 2009). A similar methodology could be adopted to Rehm *et al.* (2018) which utilised radiotelemetry and mean gut passage time to calculate the seed dispersal ability of frugivorous avian species in Guam. This would elucidate to what degree Rodrigues is reliant upon the bat for promoting reforestation. A study of such regard could also provide insight into what capacity Rodrigues fruit bats are facilitating the succession of invasive flora. This is important because Rodrigues' main conservation focus is reinstating the native flora and removal of invasive plant species, and it is known that Rodrigues fruit bats are not exclusively foraging on native fruit (Powell, 2005). Therefore, it may be beneficial to underpin this phenomenon to identify if mitigation strategies are necessary, and subsequently design them appropriately.

Furthermore, Rodrigues fruit bats are assumed to travel directly to fruiting resources following emergence, though without radio tagging of individuals this movement is inferred from observations alone (Widmann, 1996). Considering fruit bats' capacity to traverse great spatial scales in a short time this assumption is not well grounded (Brooke, 2001). Tagging and mapping the movements of the bats would improve the ability to monitor and follow the direction of dispersal from the permanent roosts and would improve the accuracy of EDC, as was done by Walton & Trowbridge (1983) for *Pteropus*

giganteus. In addition, this information would enable a better understanding of the purpose of the permanent and temporary roosting sites (see later section on behavioural ecology).

Further genetic assessment

Investigation into the population's genetic diversity is necessary. O'Brien *et al.* (2007) documented adequate genetic variability in both in- and ex-situ populations of Rodrigues fruit bat. Ensuring this status is preserved is of great importance for conservation efforts, particularly since the Rodrigues fruit bat's populations documented recovery from near extinction (Frankham *et al.* 2002). This makes it more important because recurring declines are known to hinder a population's genetic health, which can lead to inbreeding depression and lineage extinction through genetic drift (O'Brian, 2007). Species residing on islands are fundamentally susceptible to lineage extinction by the nature of biogeography, small evolutionary niches, and increased likelihood of genetic drift attributed to stochastic weather events (Loehle & Eschenbach, 2012).

A study on the Mauritian pink pigeon (*Nesoenas mayeri*) used computer simulations to predict the future of genetic variation in the wild population (Jackson *et al.* 2022). This study found that the population's genetic variation was expected to decline in the absence of continued conservation efforts, despite the present rebound in population numbers. Therefore, before the Rodrigues fruit bat population can be considered truly secure in the continual future, monitoring practices should adopt demographic and genetic measures (Staples *et al.*, 2005; Jackson *et al.* 2022). This should be in the form of long-term collection of quantifiable data of both in- and ex-situ populations.

Additionally, considering the Rodrigues fruit bat's status of Endangered it may be constructive to assess the populations' landscape genetics to understand the level of island wide geneflow (Igawa *et al.* 2013). If there are roosting regions that host genetically fragmented populations, they could potentially be susceptible to eradication following localized damage from a severe cyclone. However, due to the island's small size and the dispersibility of the Rodrigues fruit bats it would be unlikely for the population to be fragmented. This may explain why the genetic variability of the population remains relatively high despite the bottleneck the population incurred in the 1970s (O'Brien, 2011; Welbergen *et al.* 2020). Despite this, I still propose combining landscape genetics, radiotelemetry and analysis of the long-term monitoring data to identify if there is a sympatric gene pool (Frei *et al.* 2016).

Behavioural ecology

The social and behavioural ecology of Old-World fruit bats is largely understudied to date because of their mobility and cryptic nature. Documented behavioural monitoring of the Rodrigues fruit bat has been conducted on captive populations or closely related species e.g. report of allomaternal care in captivity (Kunz *et al.* 1994). Thus, very little is known about their behavioural ecology in the wild as there is speculation about the transference of information obtained from captive animals to wild populations (Rees, 2015). This is because captive individuals have significant alterations in their behaviour ascribable to the confinement of captivity, as well as the reduced enrichment and frequent exposure to close human presence (Rees, 2015).

To observe the behaviour without invasive methods or human presence alterations, we recommend installing wildlife camera traps at permanent roost sites (Rydell *et al.* 2022). Camera traps are a relatively low-invasive method (Sollmann *et al.* 2013; Krivek *et al.* 2022) and would provide insight into their sexual selective behaviour, such as mating displays (Moore *et al.* 2021). It is known that males perform wing displays, but these have not been visually documented (Pierson & Rainey, 1992). It would be of interest to know if the onset of mating displays is affected by climatic variables and cyclonic strength, as this could provide insight into whether the decreases in abundance post-cyclone are linked to stunted copulation attempts or whether the energetic requirements of gestation and lactation are too demanding during bouts of low resource availability to induce the inception of recruitment. These studies would help to confirm inferences made from the present study. However, it is acknowledged that there are obvious difficulties associated with costs and the mounting of camera traps within roosts without visibility being obscured by vegetation, and the likelihood of capturing behaviours involving flight (Moore *et al.* 2021).

Chapter 5 - Conclusion

This study analysed 17 years of annual population monitoring data on the Rodrigues fruit bat and identified factors driving the changes in population. As this is the first long-term dataset for *Pteropus* species in the Indian Ocean, there is the potential for inferences to be made to other island fruit bat species, particularly those on neighboring islands such as *Pteropus niger* on Mauritius and La Réunion.

These results provide evidence to support the hypothesis that Rodrigues fruit bat populations are driven by variations in resources. Rodrigues fruit bats depend on the continuous year-round supply of ample foraging resources (Kingston *et al.* 2023). This reliance makes them severely vulnerable to devastation imposed by habitat loss from climate-related drivers (Kingston *et al.* 2023). Specifically, the results highlight the strongest factors driving the population trends, which are annual precipitation and ACE, both of which are linked to the provisions of food availability (Kingston *et al.* 2023).

I highlighted the importance of continued population monitoring and provided justification for the continued collection of survey-specific covariates during surveys, such as observer and survey effort, which have confounding effects on the final population count. I stress the importance of modelling populations against these metrics to take account of how variations in survey duration and individual observer expertise can influence the final population estimate.

Additionally, I provided recommendations for improvements to the methodology which could aid in standardizing the survey methods. I identified areas for future studies which would require more in-depth data collection and analysis, such as demographic data for PVA to better underpin the population's ecological dynamics. Further research would aid in predicting the future of the Rodrigues fruit bat's population and improve their current conservation status.

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Appendices

Appendix. I – Software and scripts

Software

- QGIS: Data file available at:

<https://qgis.org/en/site/>

- R

<https://www.r-project.org/>

- RStudio

<https://posit.co/download/rstudio-desktop/>

Map data file is available at:

QGIS

Script for statistical analysis is available at:

R Script

Appendix. II – Data sharing agreement

Relevant forms which approve the access to the data collected by Mauritian Wildlife Foundation for the purpose of this research can be found at: [Data sharing agreement](#)

Appendix. III – Project approval letters

Relevant forms granting approval for the commencement of this project can be found at: Research approval

Appendix. IV – Cyclone

Data on cyclones included in data analysis and models can be found at: [Cyclone information](#)

Appendix. V – Roost details

<u>Roost</u>	<u>Type</u>	<u>No. Years</u>	<u>Mean Count</u>	<u>Min</u>	<u>Max</u>
Accacia	Permanent	17	795	3	5383
Anse Ally	Temporary	10	326	0	1714
Anse aux Anglais	Temporary	4	50	0	150
Anse Baleine	Permanent	17	689	0	3703
Baie du Nord	Temporary	5	75	0	200
Baie Topaze	Temporary	1	50	50	50
Bel Air	Permanent	12	412	0	2845
Cascade Monique	Temporary	2	28	20	35
Casdcade Pigeon					
Middle	Permanent	7	1308	6	4330
Cascade Pistache	Temporary	11	160	45	350
Cascade St Louis	Temporary	3	867	300	1300
Cascade Victoire	Permanent	3	513	1	1454
Cascade Pigeon					
Lower	Permanent	3	661	0	3768
Fond Grand Baie	Temporary	2	102	3	200
Fond la Digue	Temporary	6	92	5	225
Grand Var	Permanent	3	809	1	1591
Graviers	Temporary	12	379	11	1568

Jardin Mamzel	Permanent	17	612	0	2601
La Ferme	Temporary	6	300	75	515
Malabar	Permanent	17	519	44	1542
Mangues	Temporary	12	450	0	1500
Morrigo	Temporary	2	85	0	170
Mourouk	Permanent	17	387	3	2215
Mt Cimetiére	Permanent	17	589	67	1400
Riviere Banane	Temporary	4	136	0	450
Riviere Coco	Permanent	17	438	0	2333
Saint Francois	Temporary	10	91	0	300
Vainqueur	Permanent	17	920	1	3934

Appendix. VI – Output of variables with effect size less than 0.05

