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Assessing the past and future impacts of conservation management on the population biology of the endangered Mauritius Fody *Foudia rubra*

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Declaration

I confirm that this is my own work and that the use of all materials from other sources has been properly and fully acknowledged.

Signed

Date: December 2022

For Tom and Leo, who have given me roots and wings.

“But then science is nothing but a series of questions that lead to more questions.”

Terry Pratchett, 1948 – 2015

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Abstract

Earth is experiencing an anthropogenic biodiversity crisis driven by habitat loss, climate change, invasive predators, and over-exploitation. Islands have high levels of unique biodiversity but are simultaneously more susceptible to these threats, and consequently species declines and extinctions are more common on islands. Practical conservation interventions are therefore vital, but fully assessing their outcomes requires detailed datasets which can only be created by long-term monitoring, and which remain rare for tropical species of conservation concern.

This thesis uses one such dataset to explore impacts of conservation management on demography of the endangered island endemic Mauritius fody *Foudia rubra*. Results demonstrate that individual productivity is primarily driven by breeding phenology, as birds who initiate breeding early have higher nest productivity and higher re-nesting rates; these components of fitness contribute to higher seasonal reproductive success. Within this population, birds on territories nearer to feeding stations initiate breeding earlier than their peers further away, and this demonstrates that management has a positive but indirect impact, mediated by the influence of territory quality on breeding phenology.

Various stochastic and climatic processes influence productivity both negatively and positively, and there is an interesting interaction between pre-seasonal rainfall and the within-season relative start of breeding. Finally, demographic modelling determines that access to supplemental feeding improves population growth and persistence, and reduces risk, across a range of potential management scenarios, demonstrating that management can reconcile the dual roles of this population as both a refuge and as a source for new populations.

These results allow management recommendations to be made for this species to improve efficiency; and a greater understanding of the scale of and mechanism by which supplemental feeding can improve outcomes will be relevant to other species facing similar threats. As such, this study can answer calls within conservation for a greater emphasis on fully evaluated practical interventions in addition to conservation science limited to assessment of threats.

Contents

1. General introduction

1.1. Global biodiversity crisis

The Earth is currently experiencing a sixth mass extinction event (Baumsteiger & Moyle, 2017); this is, however, the first where the cause is largely, if not entirely, anthropogenic (Dirzo et al., 2014). There is an 'evil quartet' of human impacts driving extinctions: habitat loss and degradation (including anthropogenic climate change), overexploitation, invasive species, and the cascading community level effects caused by these (Ewen et al., 2012). Many species face complex interactions of several factors on their route to extinction; hunting and persecution drastically reduced the numbers of passenger pigeons *Ectopistes migratorius* and its extinction, from formerly being one of the most numerous birds in the world, was finally driven by disease and the breakdown of social structure (Loehle & Eschenbach, 2012).

Populations of monitored vertebrates have declined by 68% since 1970 (Almond et al., 2020); previously, the largest driver of these losses has been habitat loss for agriculture (Jaureguiberry et al., 2022), but climate change is predicted to shortly overtake land use change as the biggest threat to biodiversity (Newbold, 2018). When species decline or disappear, there can be cascading extrinsic impacts because of missing ecosystem services. Many birds function as pollinators (Ford et al., 1979) and the loss of this function can impact entire habitats through reduced fruit set and consequential reduction in plant density (Anderson et al., 2011). Biodiversity loss and extinctions are not randomly distributed, and island birds are at particular risk of extinction because of human activities, specifically the accidental or deliberate introduction of exotic predators, and hunting (Blackburn et al., 2014). Of the 129 bird species which have gone extinct since 1500 (Butchart et al., 2004), 90% have been island species (Impey et al., 2002).

Globally, there are multifaceted approaches for confronting biodiversity loss. Frameworks for tackling this crisis have been set out in the Convention on Biological Diversity's Aichi targets (2010), which were agreed by 196 member states and came into effect in 1993; and within the Sustainable Development Goal 15 (Life on Land) of the United Nations Sustainable Development Goals (UN, 2015). 2010-2020 was designated as the United Nations Decade of Biodiversity with a goal of reducing biodiversity loss and involving considerations of biodiversity into economic development and planning. The Paris Agreement is a legally binding international treaty intending to ameliorate the growing threat of the anthropogenic climate crisis, and was signed by 196 nations at COP21 in 2015 (UNFCC, 2015). However, the Aichi targets were not met and progress towards the Paris Agreement is slow. Subsequently, 2021-2030 was designated the UN Decade on Ecosystem Restoration; the goals of this decade are to 'prevent, halt and reverse the degradation of ecosystems on every continent and in every ocean', and recognises that a key aspect of such programmes is to tackle poverty and income disparity, and to empower people everywhere to assist (United Nations General Assembly, 2019). The Convention on Biological Diversity's COP-15 meeting in December 2022 will see all signatory members adopt the post-2020 global biodiversity framework, which aims to halt biodiversity loss by 2030 and display net improvement by 2050. As they stand, these targets are voluntary, but they demonstrate the increasing awareness that urgent action must be taken to halt these losses, not least because reducing biodiversity loss is essential for global and human wellbeing (Sandifer et al., 2015; Waldron et al., 2017). Meeting such goals via effective conservation management will depend on understanding the impacts of these drivers on biodiversity loss and endangered species, and also how drivers may interact, and impacts be cumulative (Jaureguiberry et al., 2022).

Given the scale of global ecosystem loss, and the ongoing and intensifying threat of anthropogenic climate change, practical conservation management of endangered species and ecosystems is critical. Conservation seeks to both identify and mitigate against threats to species, and to restore ecosystems of various scales to previous functionality. Given the amount of natural habitat lost globally, understanding the function of species in restored ecosystems will be vital for protecting biodiversity in the future. Conservation interventions typically aim to alter the behaviour and demography of the target species, either intrinsically by directly increasing reproductive or survival rates, or extrinsically by improving habitat, and by managing or removing invasive species.

The most significant threat currently faced by endangered species is habitat loss (Hale et al., 2020), which can be driven by clearance for agriculture and by climate change altering fundamental habitat structure, water availability, and rainfall patterns. Given the likelihood that global emissions will not be limited to 1.5 degrees as the Paris Agreement requires (Estrada & Wouter Botzen, 2020), much conservation in the coming decades will need to focus on mitigating the impacts of anthropogenic climate change. Restoration ecology at large scales can restore full ecosystem function by providing food resources and breeding and sheltering sites (Hale et al., 2019), and is an effective tool for reducing biodiversity loss (Loch et al., 2020) because conserving entire ecosystems has the potential to protect all species which use that system and may therefore be more beneficial than actions targeted at single species. Entire habitat restoration proved key in supporting the only remaining population of the critically endangered Seychelles warbler *Acrocephalus sechellarum*; preferred trees were planted in beneficial locations and the outcome was an increase in reproductive success (Komdeur & Pels, 2005). Bateman et al (2020) emphasise the need for both protective management for current bird habitats and the need to safeguard projected future habitats as safeguards, as habitat connectivity and wildlife corridors can play a vital role in protecting birds by enabling them to alter distribution as necessary to remain within their preferred climate windows (Stralberg et al., 2019).

1.2. Island biodiversity

As a result of their geographical isolation, islands tend to harbour a higher number of endemic species and an increased level of globally valuable biodiversity than mainland areas (Soorae, 2008). Island biodiversity is determined by firstly the size of the island and secondly its isolation from continental landmasses (J. Liu et al., 2020). Increasing island size increases biodiversity, while both spatial and temporal isolation from larger landmasses decreases it; colonisation rates decrease with increasing distance from mainland areas, and speciation rates increase with size and geographical isolation (MacArthur & Wilson, 1963). Islands also provide a huge variety of geographical types, sizes, degrees of isolation, and ecological niches, but are usually comparatively simpler than mainland equivalents (Triantis et al., 2016). The small scale of many island populations means that they can provide model systems to learn valuable lessons about evolution, the formation and function of biological communities, population ecology, and density dependence, which have had vital wider applications within ecology (MacArthur & Wilson, 1963; Triantis et al., 2016; Warren et al., 2015). Islands can therefore play an important role in biogeographical and ecological studies which can illustrate larger conservation issues as well as directly assisting the species and systems involved.

However, the same features that result in islands harbouring a disproportionate amount of biodiversity, make them also particularly susceptible to extinction and therefore they also contribute disproportionately to global biodiversity loss (Bombaci et al., 2018). Because of their closed nature which limits movement of terrestrial individuals, the smaller size of populations, and their geographic distribution, islands are more susceptible to invasive species and habitat loss than mainland areas (Converse et al., 2013; L. J. H. Garrett et al., 2007a). Island endemics have suffered severe population declines and extinctions (Triantis & Matthews, 2020); as well as more than 90% of recorded avian extinctions being island species, a similar proportion of endangered birds are restricted to islands (Impey et al., 2002). As a result, many conservation efforts have focused on islands and island species (Laws & Kesler, 2012), with a variety of approaches and tactics considered. Island populations historically would have had lower numbers than continental equivalents, and as many are now declining, they can illustrate Caughley's (1994) small population and declining population paradigms; firstly, why small populations can persist despite their limited size, and secondly the causes and drivers of population decline. While the small population paradigm has offered theoretical explanations as to the persistence of such populations, conservation is most able to act on the declining population paradigm, which has led to the recent focus on natural and anthropogenic threats to wild species (Norris, 2004).

Anthropogenic climate change is also leading to range shifts of continental species to both higher latitudes and higher elevations, as such shifts allow species to track the sometimes very narrow window of climatic conditions that they prefer (Rushing et al., 2020). The potential range of montane birds is shrinking, and several species have become locally extinct as their preferred climate moves upslope and eventually disappears (Freeman et al., 2018). An analysis of 329 temperate species across 16 taxa (including birds) showed that 84% of these species shifted their range northwards by an average of 31-60km (Hickling et al., 2006). However, such range shifts present specific and major problems for tropical island species. Because the relative steepness of temperature gradients in temperate zones allows species to move short distances to remain in their preferred climate, in the tropics such gradients are much shallower, meaning that species would have to move a much greater distance to stay within their climate window. Island species have limited latitudinal space and potentially no altitudinal space, and this inflexibility of range creates further pressure when habitats are impacted by climate change.

1.3. Conservation on islands

Island birds particularly have been a focus of conservation in recent decades, as they are both particularly susceptible to threats and relatively easy to study. The most famous extinct bird is the dodo *Raphus cucullatus*; endemic to Mauritius, the last dodo died only 70 years after human colonisation of the island in 1598 (Cheke & Hume, 2010). Its demise was unsurprisingly due to habitat loss and the pigs, rats, cats and other exotic animals which arrived with humans. Since then, many other island bird species have also become extinct, and habitats are being fragmented into smaller and smaller pieces which can change both availability and function of the habitat. Habitat loss can be due to land use change for agriculture but also to the impacts of anthropogenic climate change which may render habitat unsuitable via droughts, extreme storms, and phenological mismatches (Burgess et al., 2018).

Invasive predators rendering habitat unsuitable is a form of habitat loss, and introduced predators such as rats *Rattus rattus* and cats *Felis catus*, are potentially responsible for more island extinctions than any other single issue except for human hunting and over-exploitation (Blackburn et al., 2014; Bombaci et al., 2018). Rats are a major reason for the decline of the Mauritius olive white-eye *Zosterops choronothos*, and trapping experiments alongside demographic models demonstrated that removal of predation pressure could offer a 6-fold increase in productivity of this critically endangered species (Maggs et al., 2015). Similarly, the range of the South Island snipe *Coenocorypha iredalei* decreased after human colonisation of New Zealand and the species went extinct when the final two islets hosting the species were invaded by rats (Miskelly, 2012). The introduction of the brown tree snake *Boiga irregularis* to Guam caused the extinction of 12 species and dramatic declines in 10 others (Wiles et al., 2003). The Guam rail *Hypotaenidia* *owstoni* declined until it was declared extinct in the wild, but a population was maintained in captivity and has since been reintroduced onto an offshore islet of Guam where its numbers are stable (Trask et al., 2019).

Translocations and reintroductions are a very commonly used conservation tool used to support endangered species in recent decades, but have met with mixed success and failure rates are high (Taylor et al., 2017). A large review of translocation projects by Bubac et al. (2019) determined that the main drivers of unsuccessful projects was a lack of post-release monitoring, and a failure to adequately determine and address the causes of the initial species decline. However, there are also some conservation success stories involving species which have been brought back from near extinction to far larger populations, using a variety of conservation techniques. The Mauritius kestrel *Falco punctatis* reached a low of 4 wild individuals in the 1970s but now numbers in the hundreds thanks to intensive conservation efforts by the Mauritian Wildlife Foundation and the Durrell Wildlife Conservation Trust (Jones et al., 1995). This effort involved many different approaches including hand rearing of several generations of birds, and the ongoing provision of nest boxes to provide appropriate sites in degraded habitats. Similarly, Hihi *Notiomystis cincta* have been reintroduced to a range of offshore islands and fenced mainland 'islands' in New Zealand and numbers have increased (Hare et al., 2019), but the populations remain dependent on the management of invasive species and supplemental feeding.

1.4. Current conservation issues

The evidence for and assessment of conservation interventions needs to improve for the impact of interventions to be fully realised and for biodiversity targets to be reached, but the solutions to this problem are not straightforward. Ideally all conservation interventions would be formally planned, with risks and their mechanisms fully assessed, desired outcomes stated, and the mitigating management assessed before application. However, limitations of budgets, skills, and especially time, mean that conservation for such species is frequently ad-hoc and not planned in a way which enables formal assessment of outcomes. In addition, there are serious ethical questions around experimentation on endangered species particularly when this might influence the persistence of such species whose numbers may already be critically low (Robinson et al., 2020).

In addition to the analysis of threats and actions taken to mitigate them, conservationists also need to evaluate the effectiveness of actions taken, as outcomes can be counter intuitive. For example, provision of supplementary food to the critically endangered Seychelles magpie-robin *Copsychus sechellarum* increased conflict over high-quality territories to the extent that the reproductive success of individuals on these territories was negatively impacted, because these birds were spending so much effort and time on competition (López-Sepulcre et al., 2010). The solution in this case was to switch conservation efforts to habitat restoration, which improved mean habitat quality, reduced conflict, and improved the reproductive rates of all individuals.

Despite an increasing understanding of the range and severity of threats to biodiversity, there have been recent criticisms that conservation is too focused on the analysis of threats, and that effective conservation is dependent on not only describing these threats and their mechanisms, but crucially also designing, applying and testing management plans which mitigate against them (Reid et al., 2021). However, the number of studies which attempt to develop formal species management plans is low and not increasing over recent decades (Ewen et al., 2013; Scheele et al., 2018; Taylor et al., 2017; Williams et al., 2020). More recently there have been attempts to formalise the structure of conservation science, to improve rigor and enable better and easier sharing of skills, methods, and outcomes. Such frameworks were historically conceptual but increasingly also feature practical tools and frameworks to enable conservation decisions to be made efficiently and rapidly. Adaptive management (Williams, 2011), structured decision making (Hemming et al., 2022) and the formal Conservation Standards (CAML, 2021) are examples of such strategies, each with slightly different emphases and strengths and weaknesses. There is currently no consensus within conservation about which, if any, of these formalised approaches to adopt, and uptake appears to be slow (Hemming et al., 2022).

An essential part of producing impactful progress is conservation decisions which are based on sound ecological evidence, but both planning and assessment require long term monitoring datasets which support ecological inferencing, modelling, and prediction (Cook et al., 2017). Such datasets remain rare for species of conservation concern and especially so for tropical species (Chauvenet et al., 2012; Reid et al., 2021).

1.5. Mauritius

The Indian Ocean island of Mauritius is a system which can illustrate all the issues typical to islands. Geographically isolated, it once hosted a high degree of biodiversity and endemism, but since human habitation began has lost more than 95% of its natural habitat (Safford, 1997c), and a combination of this and introduced predators means that at least 11 endemic bird species, and many others from different taxa, have been lost since human inhabitation began (Triantis & Matthews, 2020). The Dodo *Raphus cucullatus* is the most emblematic extinct species of all and is responsible for the understanding that extinction is possible, as before its disappearance species were considered immutable and safe from all possible human interference.

Despite these past and current threats, Mauritius still has more than 300 endemic species overall (Senapathi et al., 2010) with some bird species, such as the Mauritius Kestrel *Falco punctatus,* Echo Parakeet *Psittacula eques,* and Mauritius Pink Pigeon *Nesoenas mayeri*, having recovered from critically low numbers as a result of intensive conservation efforts including supplementary feeding and habitat restoration (Bunbury et al., 2009; Senapathi et al., 2011; T. D. Taylor & Parkin, 2010). These iconic success stories mean that despite great ecological devastation Mauritius is also home to some spectacular conservation successes. In fact, globally there are three areas where biodiversity indices are increasing rather than decreasing: Hawaii, New Zealand, and Mauritius, which have all suffered huge species losses but, because of intensive study and conservation, have brought numerous species back from the brink of extinction. There are, therefore, many lessons which can be learned from the conservation work in these locations which may be relevant to other species under pressure from many of the same threats.

1.6. This study

In this study, extensive individual-based demographic data on a little-studied endangered Mauritius endemic the Mauritius fody *Foudia rubra* is used to determine whether conservation management contributes to individual and population productivity, and to project future scenarios to suggest future management regimes. The population is offered supplemental food ad libitum, and as such this study may answer some of the calls for rigorously evaluated conservation interventions to support the extensive literature on threat assessment. The central hypothesis of the study is that access to supplemental food may increase productivity of individuals and the population, though this effect may be mediated by intrinsic factors such as the distance of a birds' breeding territory from a feeding station, and by extrinsic factors such as climate. Studies such as this are fundamental to understanding the ecology and conservation of island endemics, and results may also support research into other similar populations, as well as contributing towards the mitigation of global biodiversity loss. These analyses are based on several detailed datasets which are outlined in the General Methods.

In Chapter 3, the detailed longitudinal data available for this species gives us the opportunity to unpack links between individual variables (including any impact of supplemental feeding) and demography; this can be difficult against the background of natural processes which also impact the same vital rates. Chapter 4 seeks to understand whether stochastic events drive variation in productivity for the full population; such events are largely climatic, but also relate to intrinsic measures of productivity and population density.

Chapter 5 includes population viability analysis in VORTEX to forecast the outcome of a variety of potential future management scenarios. The data used for these analyses were primarily the outcomes of analyses of reproductive rates within Chapters 3 and 4, and a summary of survival rates for adults and juveniles. An R package called CMRCT (Capture Mark Recapture Continuous Time) was used to generate these estimates, because the fody dataset features a resighting rate of <1 and continuous time monitoring rather than discrete periods of monitoring and therefore Program MARK was not appropriate.

2. General Methods

2.1. Mauritius

Mauritius is a small island in the western Indian Ocean between latitudes 19°58.8' and 20°31.7' south and longitudes 57°18.0' and 57°46.5' east; it is 2,040km^2 and surrounded by numerous tiny islands and islets. It is a geographically isolated, 2,000 km from the eastern coast of Madagascar; it has never been connected to any other landmass and as a result has a high degree of endemism. Arab explorers first encountered the island around 850 and was mapped by Portuguese explorers in the 16th century. Dutch ships arrived in 1597 and the island was permanently colonised by 1637. Historically Mauritius supported many endemic species including 40 endemic bird species (Temple, 1974) and thus displayed the diversity and distinctiveness of many island systems; however it has lost more than 95% of its native habitat since human colonisation in 1638 (Jones & Safford, 1998), mainly due to forest clearing for agriculture. Sugar cane was introduced as a crop by the Dutch in 1680 (Parnell et al., 1989) and now covers more than 50% of the island area. Eleven endemic bird species[1] have gone extinct since human colonisation of Mauritius, reflecting the high rate of extinction typical of geographically small islands (Triantis & Matthews, 2020), and of the remaining avian endemics, eight are threatened (Safford & Jones, 1998). Threats to endemic species are ongoing; very little suitable habitat remains, rats *Rattus rattus* and crab-eating macaques *Macaca fascicularis* are pervasive, and climate change is altering both temperatures and rainfall patterns (Doorga, 2022; Senapathi et al., 2010).

2.2. Île aux Aigrettes

Ile aux Aigrettes is a small (27 ha) coralline islet around 800m off the south-east coast of Mauritius. While too small for permanent human habitation its proximity to the coast and its canopy of the now critically endangered ebony *Diospyros egrettarum* made it a target for logging; by World War II little canopy remained and the islet was used as a gun emplacement. The Mauritian Wildlife Foundation lease the island, and since the 1970s they and the National Parks and Conservation Service have been working on intensive habitat restoration; all invasive predators have been removed except for a very small number of shrews, and the forest canopy is good and increasing as the habitat develops. Aldabra giant tortoises *Aldabrachelys gigantea* has been introduced to the islet as a functional ecosystem replacements for Mauritius' extinct giant tortoises, and these aid habitat restoration by partially digesting tree seeds and encouraging germination. As a result of this restoration the islet is now used as a safe harbour for several endangered plants and animals, including the Mauritius pink pigeon *Columba mayeri* and the

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[1] Dodo, Blue Pigeon, Broad-billed Parrot, Mascarene Grey Parrot, Mascarene Coot, Mauritian Teal, Mauritius Owl, Mascarene Sheldgoose, Mauritius Night Heron, Red Rail, Mauritius Starling.

Mauritius olive white-eye *Zosterops chloronothos*. There is intensive fieldwork ongoing on Île aux Aigrettes; all species translocated there are monitored daily in addition to the supplemental food offered. Île aux Aigrettes is used as a test case for a form of conservation which, in the future, could allow self-sustaining populations of many endangered species to be moved between it and other islets around Mauritius (Jones, C. personal communication).

2.3. Mauritius Fody

The Mauritius Fody *Foudia rubra* (henceforth 'fody') is a small (14cm) weaver in the Ploceidae family; it is one of seven extant species in the genus *Foudia* and is endemic to Mauritius. Males in breeding plumage have a bright orange-red head and upper chest, with a patch of red on the rump and a black bill (Fig 2.1). The lower chest, back, and wings are olive-green with white wing bars. Females, juveniles and males in non-breeding plumage are cryptic, mostly olive-green, with a bone or brown bill (Fig 2.2). Ecologically it is a generalist and may previously have existed in high densities at seabird colonies and similar locations (Cheke & Hume, 2010).

Since human colonisation of Mauritius in 1610, the island has lost >95% of its natural habitat (Safford, 1997c) and at least 11 endemic birds have become extinct (Cheke & Hume, 2010). Several of the remaining endemic species are endangered and the Mauritius fody, which was once common and widespread (Safford, 1997c), declined to no more than 120 pairs in around 1990, when it was classified as Critically Endangered (IUCN, 2019). It was limited in range to some very small areas of native forest in the Black River Gorges National Park; many Mauritius endemics use native habitat preferentially and this is one remaining area of relatively pristine habitat remaining (Bunbury et al., 2009). There is, however, evidence that the fody and the pink pigeon preferentially nest in the Japanese Red Cedar *Cryptomeria japonica*, which is exotic but not invasive, probably because it appears to provide better protection for nests against invasive predators such as rats *Rattus rattus* and crab-eating macaques *Macaca fascicularius* (Safford, 1997a) which destroy nests and eat eggs and fledglings and were a main driver of the species' initial decline. The fody appears to prefer stands of *Cryptomeria* adjacent to native forest, and Safford (1997) has suggested planting more *Cryptomeria* near to patches of native forest to support the small populations of endemic birds which remain on mainland Mauritius. A new plantation of *Cryptomeria* was planted in early 2004 (Cristinacce, 2004) but it is unknown how long it will be before these young trees are mature enough to be of use to the mainland bird populations.

Figure 2.1: Male Mauritius fody Foudia rubra *in breeding plumage on Île aux Aigrettes.*

Figure 2.2: Female Mauritius fody Foudia rubra *on Île aux Aigrettes.*

The Mauritius Wildlife Foundation and the National Parks and Conservation Service created a Species Recovery Plan for the fody, with one of the most important strategies being a reintroduction of fodies to act as a safeguard (Garrett et al., 2007b). Between 2002 and 2005, 93 harvested and captive bred individuals were released onto Île aux Aigrettes Nature Reserve (20.23° S, 57.44° E), a 27 hectare partially restored offshore islet home to the best remaining example of endemic coastal ebony forest (Ferriere et al., 2018). A majority of invasive predators have been successfully removed from the island and restoration work on the habitat is ongoing (Cristinacce et al., 2009). This population rapidly increased to a current carrying capacity of around 350 adult birds (Fig 2.3), and as a result the species has been downlisted to Endangered by the IUCN (Birdlife International, 2019). Similar intensive conservation work has allowed several species such as the Mauritius kestrel *Falco punctatus* and pink pigeon *Nesoenas mayeri* to recover from critically low numbers (Cheke & Hume, 2010; Jones et al., 1995).

The Île aux Aigrettes population is provided with supplementary food at two aviaries which also functioned as release sites. All fodies are captured either at the nest or within these aviaries after fledging, and ringed with an ID ring and a unique combination of two or three colour bands that enable visual identification (Figure 2.1). Many birds within this population attend the feeding aviaries daily, where field staff can monitor their health and social behaviour. Any pair exhibiting nesting behaviour is followed, nest locations mapped by GPS (Garrett et al., 2007b), and the nest monitored (Cristinacce et al., 2010). Start and end dates for nests are either known from these field observations or, when a nest is discovered in progress, dates are estimated from the stage the nest was found (early nest building, late nest building, eggs, chicks, or fledglings) and stage timings as recorded in Safford (Safford, 1997b). Observations of breeding pairs allows social parentage of almost all nests (>99.9%) to be known.

Fodies are multiple brooded, with some individuals in this population having more than ten nesting attempts within a season. They build a domed nest within concealing vegetation and nests are not re-used. Little is known about pair bond formation except that fodies use nest building as part of this process and as a result many nests do not have eggs laid in them. Both sexes participate in nest building; females incubate eggs and brood chicks, and both parents feed chicks and fledglings until independence (Safford, 1997b). In some seasons, nest fly and larvae and nest mites were a problem, and nests were treated with Carbaryl (Garrett & Jones, 2008).

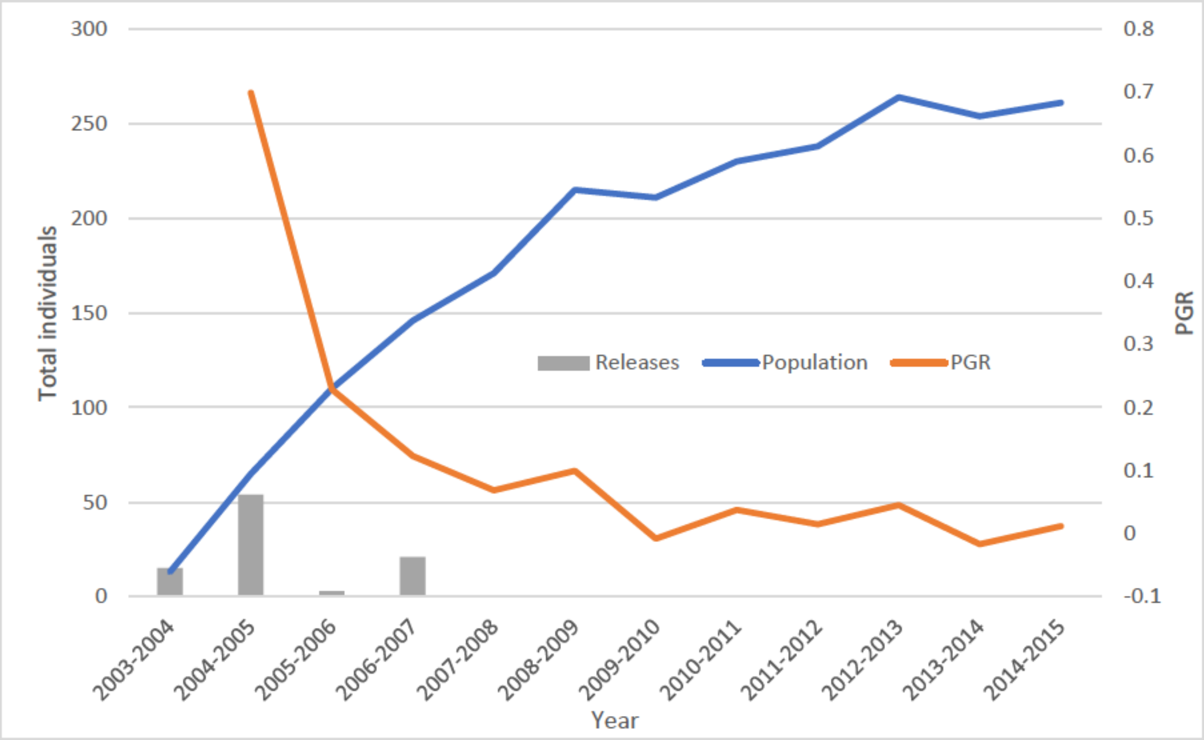

Figure 2.3: Reintroductions, total population size and population growth rate of the Mauritius fody Île aux Aigrettes population from 2003-2015.

2.4. Study system

2.4.1. Fieldwork

This population of fodies is offered supplemental food within the release aviaries; until 2012 only the aviary near to the field station was provisioned in this way but in September 2012, as a result of the rapid population increase, food began to be offered at the second aviary much nearer to the centre of the islet (Fig 2.4).

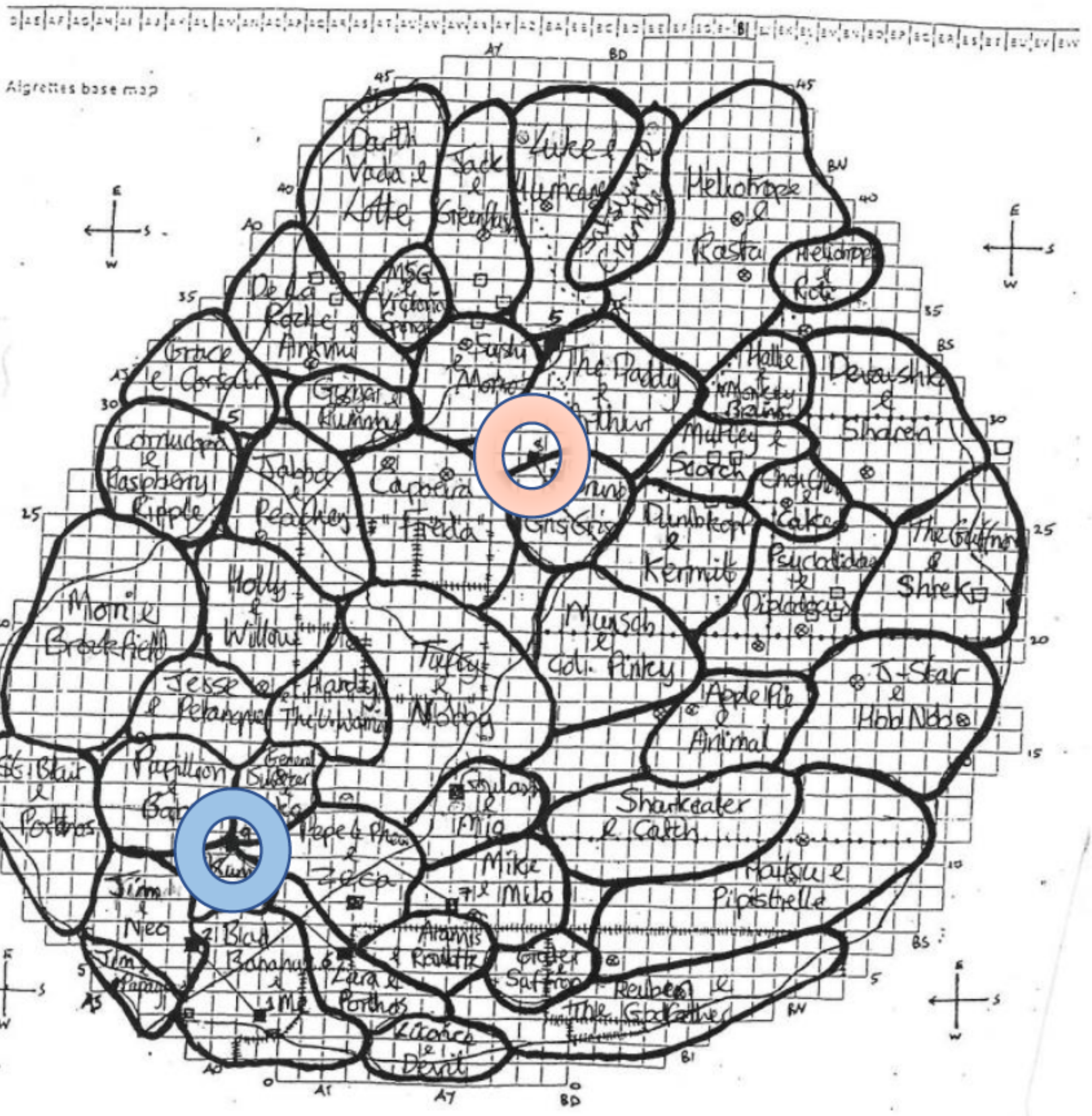

Figure 2.4: Outline map of Île aux Aigrettes showing feeding aviary near to field station (blue) and the second feeding aviary added in 2012 (red).

Until 2006-2007, the food offered was a labour-intensive mix of chopped fruit, grated hard-boiled egg, grated carrot, and oats mixed with insectivorous bird food, which was made fresh daily. Since then, this was changed to duck starter mix, ground up with prunes and honey, and mixed with insectivorous bird food as before. This mixture can be prepared in bulk and therefore reduces staff workload (Garrett & Jones, 2008). The fodies are provided with enough of this mix to last for

around 3 days, to minimise disturbance, and all feeding equipment is sterilised when the food is replenished. Water is provided in drip feeder bottles, and water baths are also provided.

2.4.2. Datasets

Individuals attending either of the feeding stations are identified by their colour rings; re-sightings are recorded at feeding stations twice per day every day, and all re-sightings across the islet are also recorded. Any birds exhibiting pair bonding or nesting behaviour are followed, and any nests found monitored until their conclusion. Nest watches occur every 3-5 days and parental behaviour enables the nest stage to be determined; stages are defined as early nest building, late nest building, eggs, or chicks (from Safford, 1997b). Fledglings are ringed either in the nest which makes their social parentage certain, or they are trapped within a feeding aviary in which case their parentage is determined by the behaviour of adult birds nearby. In early seasons, if nests were accessible then chicks were ringed on the nest but in later seasons more fledglings were ringed in the feeding aviaries to prevent nest disturbance, although accessible nests are still checked for numbers of eggs and chicks (Ferriere & Coutee, 2016).

This fieldwork has resulted in three large datasets which span the duration of this study. Firstly, observations and ringing has created a studbook of more than 650 individuals including birth and death dates when known or estimated from resighting when unknown, and social parentage. Daily attendance recording across the islet has built into a resighting database of more than 70,000 daily observations of these individuals. Finally, nest observations result in a record of nearly 2000 nesting attempts with start and end dates, parents, and nest outcomes. From this, a derived dataset was created which summarise a breeding season for a bird; for example F32119_2005-2006 would contain a wide range of specifics of breeding behaviour of bird F32119 during the season 2005-2006, including the bird’s age during the focal season, the number of partners, nests, and fledglings, the proportion of the total nests within each defined mating systems, territory quality, and the climatic and seasonal variables as described in Chapter 4.

Analyses presented here draw together these datasets to build an overall picture of fody ecology and the impact of conservation management. However, as is commonly the case, limitations of fieldwork and data collection limited the approaches taken in some cases. For example, territory maps were not created for all breeding seasons, and as the main hypotheses of this thesis examines the impact of conservation management mediated by territory distance from a feeding station, this resulted in the exclusion of some breeding seasons from these analyses. Table 2.1 summarises the datasets used, the limiting factors for each, and the resulting seasons included. Datasets named Nest, Individual, and Seasonal will be referred to as such throughout subsequent analyses for clarity.

This study therefore covers 12 breeding seasons from 2004-2016. Within this population, nesting attempts per season range from 0 – 10 (mean 2.61 ± 1.73); clutch sizes from 1 – 5 (mean 2.03 ± 0.88); brood sizes from 0 – 4 chicks (mean 0.61 ± 0.98), and the number of fledglings from 0 – 4 fledglings per nest (mean 0.32 ± 0.78). Occasions where nest building was initiated but not completed and no eggs laid were excluded from subsequent analyses; fodies appear to use nest building as a social and pair bonding activity (Safford, 1997b) so only nests where one or more eggs were laid are included. As a result, the minimum nest count for any individual included here is 1. Breeding attempts where either parent was unknown, and where this would impact on the social mating system assigned, were excluded (n=11). The remaining data represented 1133 nests over the 12 years of the study. All analyses were performed within the statistical software R (R Core Team, 2021) and VORTEX (Lacy & Pollak, 2018).

The climatic variables used in this study are collected automatically by synoptic weather stations at Plaisance (20°26’S, 57°41’E, 50 m above seas level) and consist of daily rainfall measures and daily maximum temperatures; data from this weather station has been demonstrated to be an accurate proxy for conditions on Île aux Aigrettes (Taylor, 2018). These data were consolidated into seasonal summaries of average daily rainfall, rain days, and average temperatures; these data were also used to calculate storm days and drought events following methods in Taylor (2018). These seasonal predictors were used for the analyses that form Ch 4 of this thesis, which also contains full methods and the calculations used.

Table 2.1: data availability and structure for analyses included. Crosses indicate where data is unavailable, due to changes in fieldwork methodology, specifically lack of territory mapping or resighting data. Three datasets used within these analyses are NEST, INDIVIDUAL and SEASONAL. Green indicates full span of named datasets, but slashes indicate seasons excluded. INDIVIDUAL is limited by lack of territory mapping; SEASONAL limited by availability of climate metrics and an accurate density measure, and NEST by both factors as while basic nesting data is available until 2015-2016, predictors within NEST models are from INDIVIDUAL and SEASONAL datasets.

Season	2003-2004	2004-2005	2005-2006	2006-2007	2007-2008	2008-2009	2009-2010	2010-2011	2011-2012	2012-2013	2013-2014	2014-2015	2015-2016
Nests	×	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Territory	×	✓	×	✓	✓	✓	✓	✓	×	✓	×	×	✓
Unpaired	×	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	×	×
Climate variables	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	×
Density	×	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	×	×
NEST		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩 /	🟩			
INDIVIDUAL		🟩	🟩 /	🟩	🟩	🟩	🟩	🟩	🟩 /	🟩			
SEASONAL		🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩				

2.4.3. Territory quality

A key focus of this study was to determine whether access to conservation management in the form of the provision of supplementary food was a driver of increased reproductive success. Detailed individual territory occupancy data is available for the breeding seasons indicated in Table 2.1, and for each of these years the distance between the nearest edge of each birds' territory to the closest feeding station was measured in cm on seasonal territory maps (Fig 2.5), which are all to the same scale. 1cm measured distance on these maps equals 36.9m and for simplicity this unit was maintained throughout the analyses. As fodies are territorial and despotic, this metric may be informative in determining whether access to food enables higher reproductive effort and success.

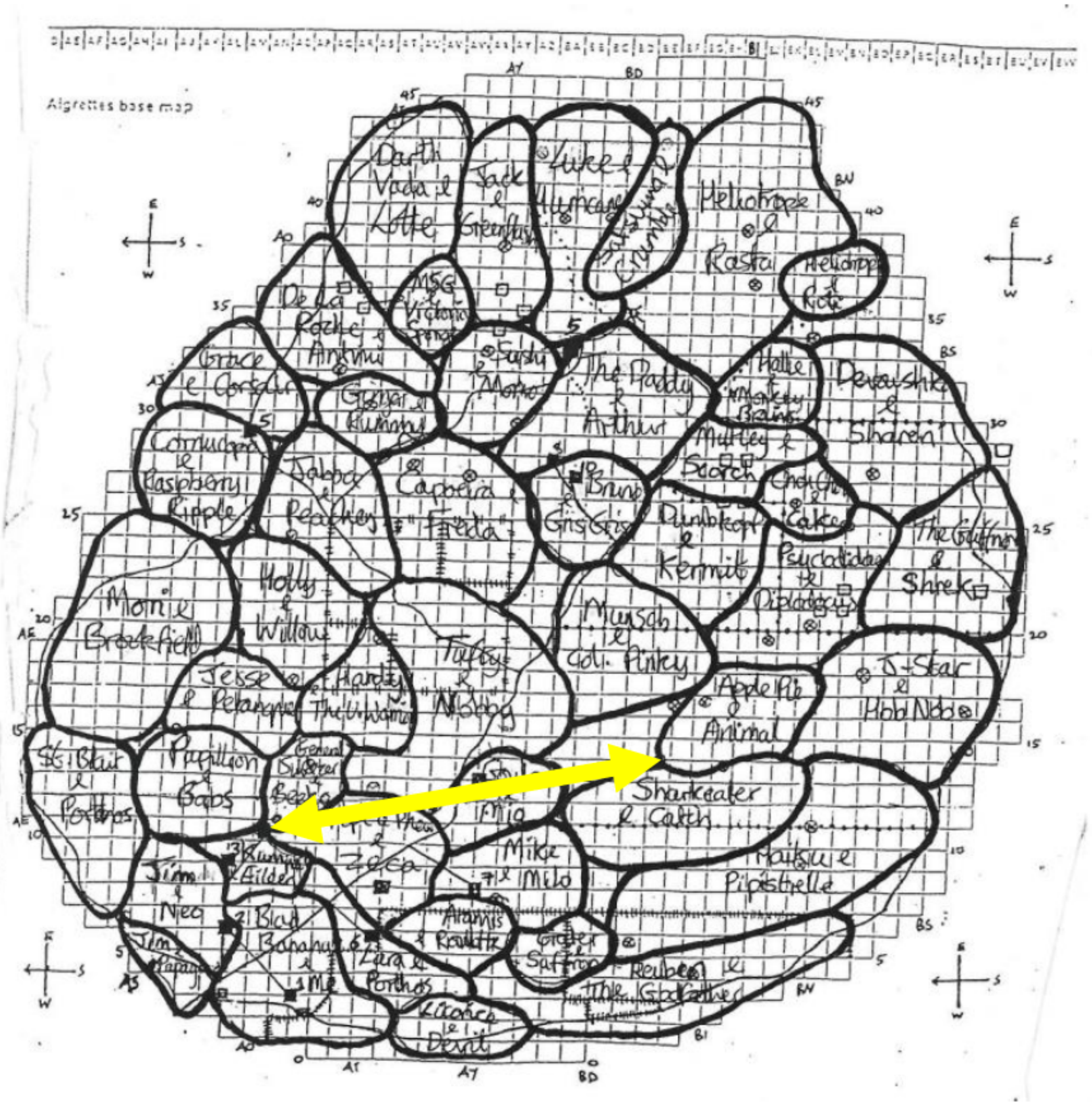

Figure 2.5: Method for calculating the territory distance metric. The distance was measured in cm along the yellow line, with the nearest edge of the territory marked 'Apple Pie & Animal' at right, and a feeding station at left.

2.4.4. Breeding seasons

Breeding behaviour was noted year-round and fodies can nest multiple times in a season (Jones et al., 2005; Safford, 1997b); so to accurately determine seasonal individual seasonal productivity, first it was necessary to define the duration and limits of the breeding seasons. A period of two weeks in April was the only time with no breeding activity recorded in any year (Figure 2.6, years 2004-2015 inclusive). Therefore, for all subsequent analyses it was assumed that the breeding season runs from the end of this consistent gap in April to the following March, although several breeding seasons within the span of the data start considerably later than April, and finish earlier than March. The duration of each season was calculated as the number of days between the start date of the first recorded nesting attempt after this gap and the end date of the latest recorded nest before the following gap.

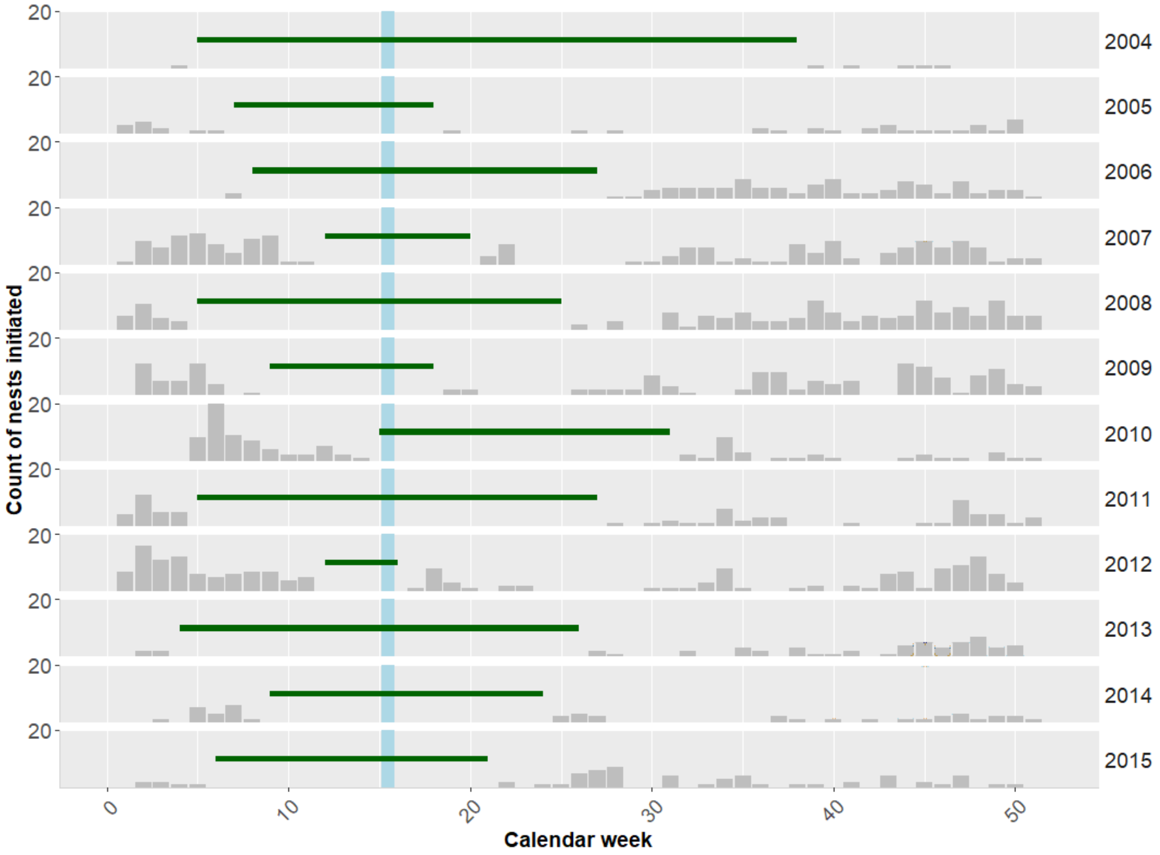

Figure 2.6: Count of nest initiations by calendar week, faceted by breeding season. Light grey vertical bars indicate a count of nests initiated in specified week; dark green horizontal bars indicate non-breeding seasons; vertical blue areas indicate consistent non-breeding period across all years.

Season relative start dates were determined as the number of days between the earliest recorded nest across all seasons and the first nest within the focal season, and relative end dates as the number of days before the earliest of all end dates. These data were correlated with the season duration to investigate the relationship between season position and duration. Breeding season start dates varied from April to September, spanning 149 days; end dates were less variable and fell between January and March, spanning 71 days. Overall season durations ranged from 122 days to 325 days. Seasons that started earlier were longer overall than those which started later (Pearson's correlation r = 0.921, p < 0.05); similarly seasons that ended later were longer than those that ended earlier (Pearson's correlation r = 0.686, p = 0.01).

2.4.5. Mating systems

Varied mating systems are a feature of this population; here these are described by nest, so a nest that is discrete in time is defined as monogamous even if parent birds have more than one partner per season. Safford (1997b) describes a pair of fodies on mainland Mauritius which built a nest and then deserted it while feeding chicks in a previous nest; this may suggest that such varied mating behaviour is not specific to the Île aux Aigrettes population but is more easily observed and recorded there as a result of intense fieldwork and population density.

Start and end dates for nests are either known from field observations or, when a nest is discovered in progress, dates are estimated from the stage the nest was found (early nest building, late nest building, eggs, chicks, or fledglings) and stage timings as recorded in Safford (Safford, 1997b). These dates were used to define and quantify four mating systems used by the Île aux Aigrettes population (2.2), based on which nests overlapped with the chronologically previous or next nest of either parent. While polyandry is noted, the sample size of such nests which contained eggs was very small (n=2) and therefore this mating system was excluded from the following analyses.

Table 2.2: Mating system definitions

System	Description	% of nests (total 1133)
Monogamy	Neither parent overlaps the nest with any other	85.4%
Polygyny	The male parents overlaps either the start, or the end (or both) of the nest with another, with a different female	11%
Multi	The same parents have multiple concurrent (overlapping) nests	3%
Polyandry	The female parents overlaps either the start, or the end (or both) of the nest with another, with a different male	0.6%- *excluded from following analyses*

Tukey's Honestly Significant Difference test was performed on an analysis of variance model to determine whether any significant differences in fledglings per season existed between sexes, systems, or the interaction between sex and system. This pairwise comparison of means across sexes and mating systems showed that male non-monogamous males had more fledglings per season than their monogamous peers; however, no such difference exists for females (Fig 2.7).

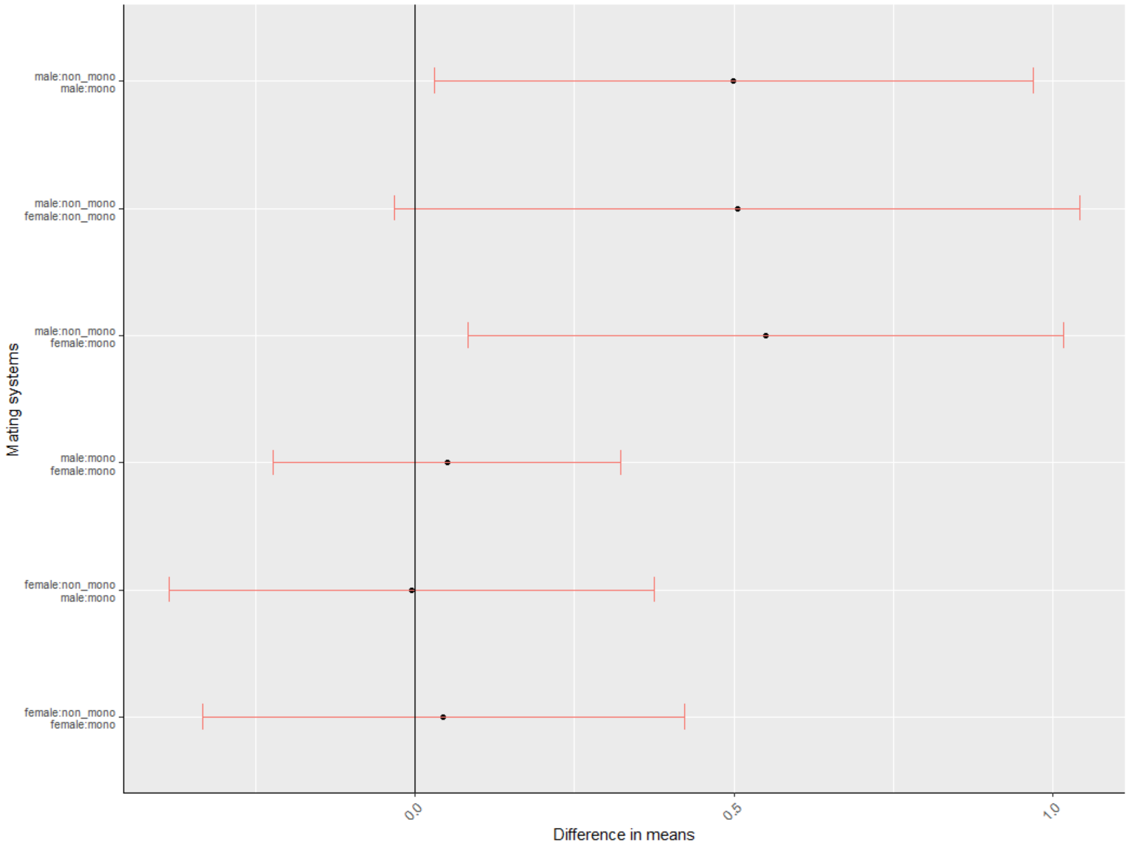

Figure 2.7: Pairwise comparison of means and SE fledglings per season for sexes and mating systems. Means (SE) of: mono females = 0.77 (0.07); non-mono females 0.81 (0.12); mono males 0.82 (0.08); non-mono males 1.32 (0.20).

2.4.6. Annual Reproductive Success

It is clear from available data that there is significant variation in productivity (measured as fledglings per season), both between individuals within breeding seasons, and between seasons. The drivers of these two levels of variation may well be different and ideally to explore this models would include both individual and cohort covariates. However, as the data is unbalanced and not all metrics were available for all breeding seasons, a comprehensive analysis of cohort-level and individual-level predictors was impossible. As a result, the analyses have been approached in parts, and the purpose of the analyses presented here is to understand drivers of variation in productivity between individuals and between seasons.

As the fody has multiple broods, preliminary analyses explored the extent to which seasonal productivity is influenced by nests per season versus the productivity of individual nests. Linear mixed effects models (LME4, Bates et al., 2015) were created with the centred productivity metric as the response variable; predictor variables were these two components of productivity and the bird ID included as random effect. Sexes were analysed separately. These models indicate that for both sexes, both nests per season and fledglings per nest are significant in predicting fledglings per season (Figure 2.8, A and B). Analyses in this study will clarify management impacts on each of these components.

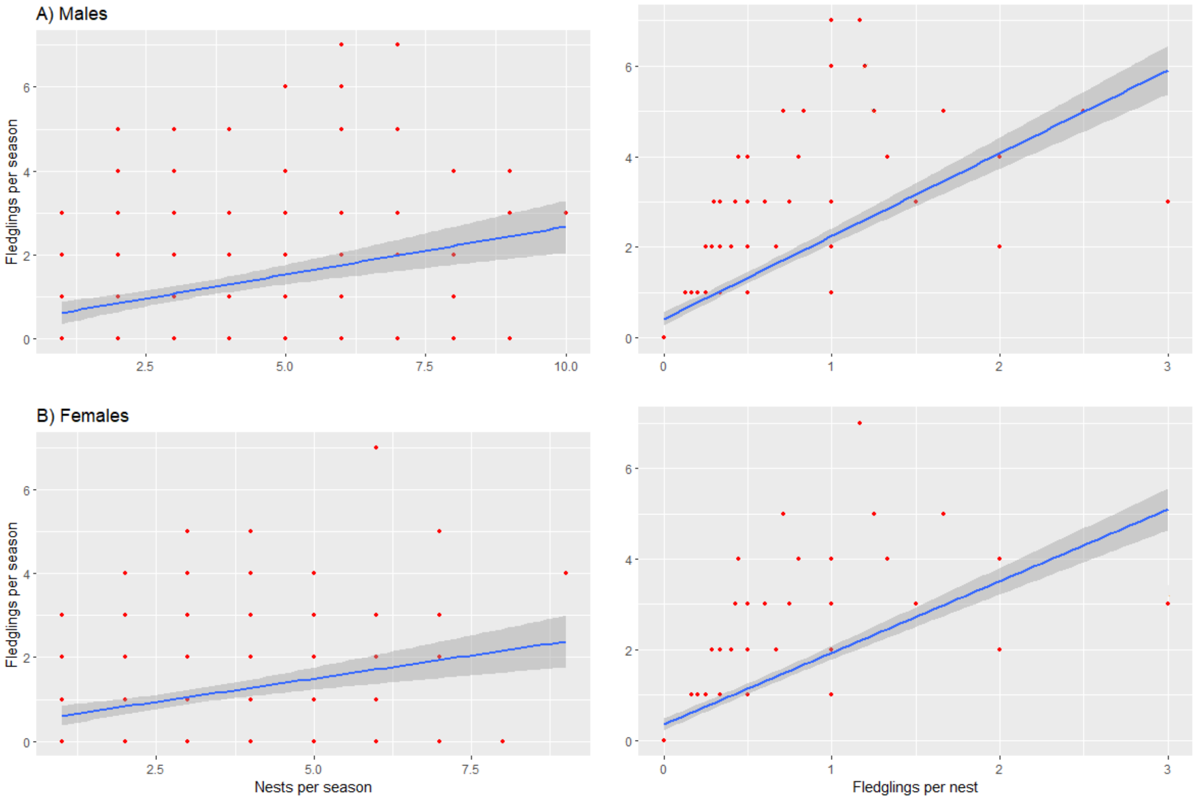

Figure 2.8: Annual reproductive success components for A) male birds and B) female birds including the influence of nests per season and fledglings per nest. Red dots indicate data points and lines are linear model estimates with standard errors. P values for males: nests per season $p < 0.005$, fledglings per nest $p < 0.005$; females nests per season $p < 0.005$, fledglings per nest $p < 0.005$.

3. Proximity to supplemental food has a positive but indirect impact on reproductive success in an endangered tropical wild bird

3.1. Abstract

Current conservation research is insufficiently focused on designing and testing management interventions for species of conservation concern. Such interventions usually result in habitat improvements which in turn improve key vital rates such as productivity or survival. Due to practical limitations and difficulties of experimenting on small and endangered populations, testing the impacts of conservation interventions is frequently retrospective, and can be challenging because of concurrent influences of background natural processes on vital rates.

Here, long-term individual-based data on the endangered island endemic Mauritius Fody *Foudia rubra*, is used to explore the impacts of a management intervention, supplementary feeding, on demography. This study tests two competing hypotheses; firstly, that access to supplemental feeding (mediated by territory proximity) may increase productivity; and secondly that conflict over such high-quality territories can dampen vital rates such that individuals on these territories may not fully realise their potential.

The population was split into growth and stable phases to determine whether drivers of variation in overall seasonal productivity, fledglings per nest, and re-nesting probability vary as the population reaches density dependence. Results indicate that while there is some evidence that the social environment may dampen productivity, this is largely independent of territory quality. Early breeding and repeat breeding both increase productivity, and these are positively influenced by access to supplementary feeding. Impacts vary between the growth and stable phases of the population and indicate that territory proximity to feeders may be more important when the carrying capacity has been reached.

This study demonstrates how long-term data on endangered species can be used to assess the impact of management interventions and hence contribute to population recovery and management; and demonstrates that a greater focus on conservation interventions can only be delivered if species recovery programmes invest in long-term monitoring which generates such data.

3.2. Introduction

In recent decades, conservation science has focused on analysing and quantifying threats to endangered species, with the theoretic goal of preventing species extinction and thereby slowing or even reversing global biodiversity loss. This leads to an increasing understanding of how issues such as habitat loss (Buckley et al., 2016), climate change (Taylor et al., 2021a), invasive species (Jones et al., 1998) and overexploitation (Kyne & Adams, 2017) are affecting species of conservation concern. Meeting the biodiversity criteria set out in the Convention on Biological Diversity's Aichi targets (Aichi Biodiversity Targets, 2010) and within the Sustainable Development Goal 15 (Life on Land) of the United Nations (UN, 2015) will be dependent on not only describing these threats and their mechanisms, but crucially also designing, applying and testing management plans which mitigate against them (Reid et al., 2021). However, the number of studies which attempt to develop species management plans in this way is low and not increasing at the same rate as studies which examine threats (Ewen et al., 2013; Scheele et al., 2018; Taylor et al., 2017b; Williams et al., 2020).

Such species management plans identify key interventions, such as supplemental feeding, which are designed to have positive impacts on survival and productivity which in turn increase population growth and viability (Ewald & Rohwer, 1982; Jones et al., 1998; Tollington et al., 2019a). However, conservation interventions are frequently ad-hoc and not implemented as formal experiments, due to limitations of time, budget, or staffing (Scheele et al., 2018); as well as ethical and practical concerns around experimenting on small and endangered populations (Chauvenet et al., 2012b). This makes assessment of their impacts complex and necessarily retrospective, and such studies must also allow for the background noise of natural variation in climate or environment which similarly impact on the vital rates in question.

Supplemental food effectively causes environmental change, which influences individual behaviour (Robb et al., 2008) and links the management of endangered species to their demography and to population growth and persistence. As access to food can be a limiting factor for avian reproduction, proving *ad-libitum* supplemental food can result in changes to reproductive rates; previous studies and meta-analyses have shown that birds offered food reproduce more, and more successfully than their peers (Newton, 1998; Ruffino et al., 2014). They may also have increased clutch sizes (Clifford & Anderson, 2001); increased rates of polygyny (Ewald et al., 2018); altered breeding phenology (Smith & Smith, 2013); increased rates of repeat breeding (Dhondt, 2010); or increased fledgling body mass (Dzielski et al., 2021). Other behavioural changes resulting from the provision of supplemental food include changes to territory quality and defence (Strain & Mumme, 1988); choice of mating systems (Václav et al., 2003); and spatial distribution, dispersal, and migration (Kennedy & Ward, 2003). In addition, as endangered species numbers recover, there may be density-dependent changes in demographic rates (Carrete et al., 2006) and a consequential change in the impacts of conservation efforts.

The range of potential outcomes of supplemental feeding has led to criticisms that supplemental feeding can be offered as a default measure with little consideration of consequences (Ewen et al., 2015) as there is the potential for marginal or negative outcomes. These include higher rates of disease transmission at feeding stations (Tollington et al., 2015; Wilcoxen et al., 2015), and concerns around inferior individuals breeding or interfering with conspecifics (Carrete et al 2006). In addition, the impacts of supplemental food are frequently not experienced equally through space and time; better outcomes are seen when food is offered permanently rather than only during some phases of reproduction (Schoech et al., 2008), and the accessibility of food will often vary especially for territorial species (Kaiser et al., 2015). For territorial species, the provision of highly clumped food resources can drive an increase in conflict on territories close to feeding stations such that that the benefit of breeding on such territories can be removed entirely (López-Sepulcre et al., 2009), due to the energy and time demands of defence. In such situations the solution can be to decrease habitat heterogeneity, to reduce the gradient of territory quality and therefore conflict between those territories (López-Sepulcre et al., 2010).

Understanding the mechanism and full range of impacts of conservation on target species is therefore a key issue, and will include the impacts of population trajectory, individual demography including mating systems, territoriality and conflict, and breeding phenology. A detailed understanding of population dynamics is required when considering both population modelling (Morandini et al., 2019) and practical interventions, as marginal outcomes may not be supported by cost / benefit analyses. Including a wide range of potential covariates may also reveal complex interactions which would otherwise not become obvious, and will allow managers to focus efforts more effectively. Such analyses depend upon datasets generated by ongoing monitoring of the species in question; but such datasets remain rare for species of conservation concern (Chauvenet et al., 2012b; Reid et al., 2021).

Here, 12 years of longitudinal, individual-based monitoring data on a reintroduced population of the endangered tropical island endemic Mauritius Fody *Foudia rubra* are used to unpack the drivers of individual variation in productivity, focusing on the impacts of supplemental feeding, as well as territory quality, mating systems and other covariates which may also drive variation in this key metric. The data was split into growing and stable phases to enable the analyses to determine whether potential benefits and drawbacks of territory quality vary as the population reaches a carrying capacity. As the population grows, conflict over high quality territories would increase and this may result in territory quality increasing productivity in the growth phase but its positive impacts being dampened by conflict when the population is stable. Therefore, this study aims to assess two competing hypotheses:

1. Access to supplemental food, mediated by territory proximity to a feeding station, may increases productivity along a spatial gradient. This would result in birds on such territories having a higher annual reproductive success than their peers across the time series of the data.

2. Increased conflict over territory and food resources may dampen vital rates for birds occupying these territories and may reduce or entirely remove their benefits. This may be evidenced by reduced hatching or fledging rates for such territories even if effort is higher for these birds, meaning that annual reproductive rates would be similar across territory gradients, and such impacts may emerge when the population is at the carrying capacity.

3.3. Methods

This study aimed to investigate the impact of a range of intrinsic demographic factors on reproductive effort and success; the detailed long-term data available for this species enables components of fitness as well as overall annual reproductive success to be analysed. While the specific causes of density dependence can be hard to pinpoint, the study also aimed to determine whether the impact of such factors alters under different population growth trajectories; specifically, before and after the carrying capacity of the population was reached. Territory defence may be energetically more demanding when density dependence has been reached and more birds are competing for available space; in this context the outcomes of breeding on a high-quality territory would vary across these population growth phases. In addition, for multiple breeding species annual reproductive success is a composite measure, contributed to by the number of fledglings raised from each nest as well as re-nesting rates, which may both be highly variable. Many species show a trade-off between current and future reproduction, within breeding seasons or across them (Senécal et al., 2021; Weggler, 2006) and therefore here re-nesting probability and the success of individual nests are both included.

To encompass the range of potential impacts on reproductive success, some analyses were based on bird performance and some on the performance of individual nests; the datasets used were therefore Individual, and Nest. For analyses examining breeding performance across a season, derived datasets were created summarising key reproductive metrics. Male and female birds may respond in different ways to the same factors, and therefore all analyses based on individual breeding season performance were separated by sex. Unless otherwise specified, models were generalised linear mixed models built using the 'LME4' package (Bates et al., 2015) in R Studio version 2023.03.0 (RStudio Team, 2020) and R version 4.2.1 (R Core Team, 2021).

The ID of the parent bird, or the female parent for nest-based analyses, was included as a random effect to prevent pseudoreplication. In all models, the response variable and numeric predictors were scaled to improve model fit and interpretation. Models were replicated for each growth phase and sexes modelled separately. When analysing datasets with correlating predictors, multiple models containing each correlating predictor were created and the models ranked using AIC scores.

3.3.1. Population growth phases

To determine the point at which a carrying capacity was reached and the population growth rate stabilised, the 'segmented' package (Muggeo & Muggeo, 2003) was used to generate a linear model with the population growth rate as the response variable and breeding season as the single predictor. Such models indicate the point at which the slope of a line significantly changes, and in this case indicates the point in time at which the population growth rate flattens as the carrying capacity is reached.

3.3.2. Fledglings per season

To determine overall annual reproductive success (fledglings per season), models were built with seasonal fledgling production as the response variable, and predictors as outlined in Table 3.1. These models used the ‘Individual’ data (see General Methods section 2.4.2). Mating systems were summarised differently for the sexes as within many species with facultative polygyny, a polygynous males do better than monogamous peers, but females in such pairings do less well. These data encompass all ecological metrics available for this population within the Individual dataset, although some breeding seasons were excluded due to missing territory data (see General Methods). Predictors were tested for autocorrelation using the Hmisc package within R (Harrell Jr, 2023); however, none correlated significantly and therefore all predictors were included.

Table 3.1: Metric, ecological reasoning, and sex included for individual predictors of nests per season.

Variable	Definition	Sex included
Age	Age in years of parent bird and is an accurate correlate of experience in this population. Older birds can frequently have higher productivity than their younger peers.	M, F
Relative Start	The number of days between the 1st April of the focal season and the start date of the bird’s first nest within that season. This aspect of spring phenology has been shown to be a vital component of overall reproductive success in many passerine species. For the IAA fody population this is either known from direct observation of parent birds, or if the nest is found in progress dates are calculated based on nesting stage timings in Safford (1997).	M, F
Territory	Territory distance of nest to closest feeder; unit is cm as measured on territory maps for the focal season where 1cm measured distance = 36.9m (see General Methods section 2.4.3). Hypothesis 1 links this metric of quality to reproductive effort and success.	M, F
Social network	The number of birds the individual has paired with before which remain alive in focal season and is an indication of the available mating pool for each individual.	M, F

Non-monogamous	The proportion of nests which are not categorised as monogamous: neither parent overlaps this nest with any other. Male birds of several species have increased reproductive success if they are non-monogamous, while the reverse can be true for females.	M
Proportion 'multi'	The proportion of nests which are categorised as 'multi' – the same pair of birds have at least one overlapping nest. Pair familiarity may increase reproductive success.	F
Proportion polygynous	The proportion of nests which are categorised as polygynous. In many species with facultative polygyny, females in such pairings do less well than their monogamous peers.	F
Unpaired	The number of the opposite sex which have never paired before. This metric is designed to evaluate the potential mating pool available to members of the opposite sex but also represents conflict with birds attempting to gain a territory or mate. Hypothesis 2 offers a potential link between this metric and reproductive success.	M, F

3.3.3. Fledglings per nest

To investigate factors that increase the productivity of individual nests, a range of potential ecological predictors which might influence fledgling production were considered (Table 3.2). These metrics are specific to nests, rather than to birds and therefore the Nests dataset was used to build a detailed picture of the success rates of nests over the growth stages of the population.

Table 3.2: Predictors included for nest-based productivity analyses.

Variable	Definition
Nest interval	Number of days between conclusion of male parent's previous nest and initiation of current (can be negative for overlapping nests)
Age	Age in years of parent bird
Switch	Did parent switch partners before this nest Y/N
Pair count	Count of experience of parent pair as total recorded nests before current
New / Previous	Whether current pair is new or familiar
Mating system	Mating system categorisation of nest
Relative start	The number of days between the 1st April of the focal season and the start date of the nest

Territory	As above, measured from territory edge as nest-specific locations were not available

Male and female nest intervals showed significant correlation and so two linear mixed effect models were compared using an information theoretic approach wherein each model contained all non-correlating predictors and then either male or female intervals; these were compared using AIC scores. Again, the fledgling per nest metric was centred around the seasonal mean to remove cohort effects, and models included this metric as the response and the variables in Table 3.3 as predictors. The identity of the female parent was included as a random effect to prevent pseudoreplication.

3.3.4. Nests hatched and fledged

To determine whether the nest-based predictors in Table 3.3 determined whether the nest survived incubation or survived to fledge, using the ‘Nest’ data binomial generalised linear mixed models were built with a response variable of 0/1 indicating whether the nest survived the focal stage, and the identity of the female bird as a random effect to prevent pseudoreplication. Limitations of data meant that survival of the brood phase could not be included (see General Methods).

3.3.5. Re-nesting probability

The impact of multiple nesting attempts on overall seasonal productivity is complex to estimate because birds which are unsuccessful in early nesting attempts may compensate by re-nesting more frequently than their successful peers. To model re-nesting probability, determined as the likelihood of a bird making another nesting attempt after the conclusion of the current nest, using the ‘Nest’ data generalised linear mixed models with binomial errors were built where the response variable was a binary indicating the presence or absence of a subsequent nest. Predictors included covered nest bird, and social information to determine which of these may influence the decision to re-nest (Table 3.3).

Table 3.3: predictors included for modelling re-nesting probabilities.

Variable	Definition
Pair count	The number of times the parent birds have nested together. A metric of experience and familiarity.
Relative Start	The number of days between the 1st April of the focal season and the start date of the current nest.
Territory	Territory distance of nest to closest feeder.
Social network	The number of birds the individual has paired with before which remain alive in focal season.
System	The mating system definition of the nest (see Table 2.2)

Fledglings	The total fledglings from the current nest
New / previous	Whether the partner bird is new, or has been paired with previously. A metric of experience and familiarity.
Age	The age of the parent bird in years.
Unpaired	The number of the opposite sex which have never paired before.

3.3.6. Breeding phenology

It is common for an earlier relative start of breeding increase seasonal productivity for passerines (Siikamäki, 1998). Therefore, the same predictors were used as for determining the number of nests and number of total fledglings, to investigate whether any of these enable a bird to initiate breeding earlier. The relative start of each bird's breeding season was the response variable with the remaining predictors included as in section 3.2.

3.4. Results

3.4.1. Population growth phases

The ‘segmented’ analysis of the overall population growth rate indicated that a significant break point occurred at 2.392 (±0.129) seasons. This shows that the population approaches a carrying capacity part way through the 2006-2007 breeding season; therefore, this season and those before were defined as ‘growing’, and all after that point as ‘stable’. The following analyses determine whether the impact of available predictors varies across these phases.

3.4.2. Fledglings per season

Results show no direct influence of territory quality on annual reproductive success but conversely also no disproportionate impact of conflict on such territories.

During the growth phase, overall annual reproductive success for males is reduced by the presence of more unpaired females (Table S3.1A); this may indicate competition between unpaired and paired female birds for access to males, resources, and territory. In the stable phase, male productivity is positively influenced by an earlier relative start and negatively by the presence of unpaired female birds (Table S3.1B).

For females, in the growth phase there are no significant predictors in these models; however, there is a trend towards increasing numbers of unpaired male birds reducing their productivity (Table S3.2A). In the stable phase, this trend becomes significant and negative, and there is a positive influence of an earlier relative start enabling greater reproductive success (Table S3.2B).

3.4.3. Fledglings per nest

The models containing the nesting interval of the male bird had the lowest AIC scores, and these show that there is no direct positive or negative influence of access to supplementary food. In the growth phase of the population, a shorter nesting interval for the male parent, and an earlier relative start date for the nest, both increase nest fledgling production (Table S3.3A). In the stable phase, an earlier relative start is again important, and as female birds age they produce fewer fledglings per nest (Table S3.3B).

3.4.4. Nests hatched and fledged

The models determining which predictors influence whether a nest survives incubation show that for the growth phase, there are no significant predictors of survival past this stage. There are trends towards increasing male age and the male parent remaining with his previous partner being beneficial, and towards a territory close to a feeder increasing the likelihood of the nest failing to hatch any eggs (Table S3.4A). This trend could indicate some influence of competition on closer territories as fodies are known to destroy other fody nests, but hatching rates are not significantly reduced.

In the stable phase, an earlier relative start and a shorter interval for the male bird both increase the likelihood that a nest will survive past incubation, and if the male bird remains with his partner from his previous nest this is also beneficial (Table S3.4B). There is a trend towards older females enabling their nests to survive incubation.

The models examining survival of the nest to fledging indicate that during the growth phase, a shorter male nest interval and an earlier relative start date both increase the likelihood of fledging (Table S3.5A). In the stable phase, an earlier relative start is again beneficial and there is a trend towards older females enabling their nests to fledge (Table S3.5B).

3.4.5. Re-nesting probability

In the growth phase, males are more likely to re-nest if they are familiar with their partner bird, and if the nest had an early start. In the stable phase, a male is more likely to re-nest if the current nest is polygynous, if his territory is close to a feeder, and if the nest has an early start. He is less likely to re-nest if there are more unpaired birds, or if the current nest successfully fledges more chicks (Table S3.6A). In addition, there is a significant interaction between territory and relative start; males on nearby territories are more likely to re-nest after an early start than their more distant peers (Table S3.6B, Fig 3.1A).

In the growth phase females are more likely to re-nest as they get older, or if the current nest started early, and they are less likely to re-nest if the current nest fledged more chicks (Table S3.7A). In the stable phase, an early relative start again increases the re-nesting probability, as does territory quality. Increasing numbers of unpaired birds and more fledglings from the current nest decrease renesting probability (Table S3.7B, Fig 3.1B).

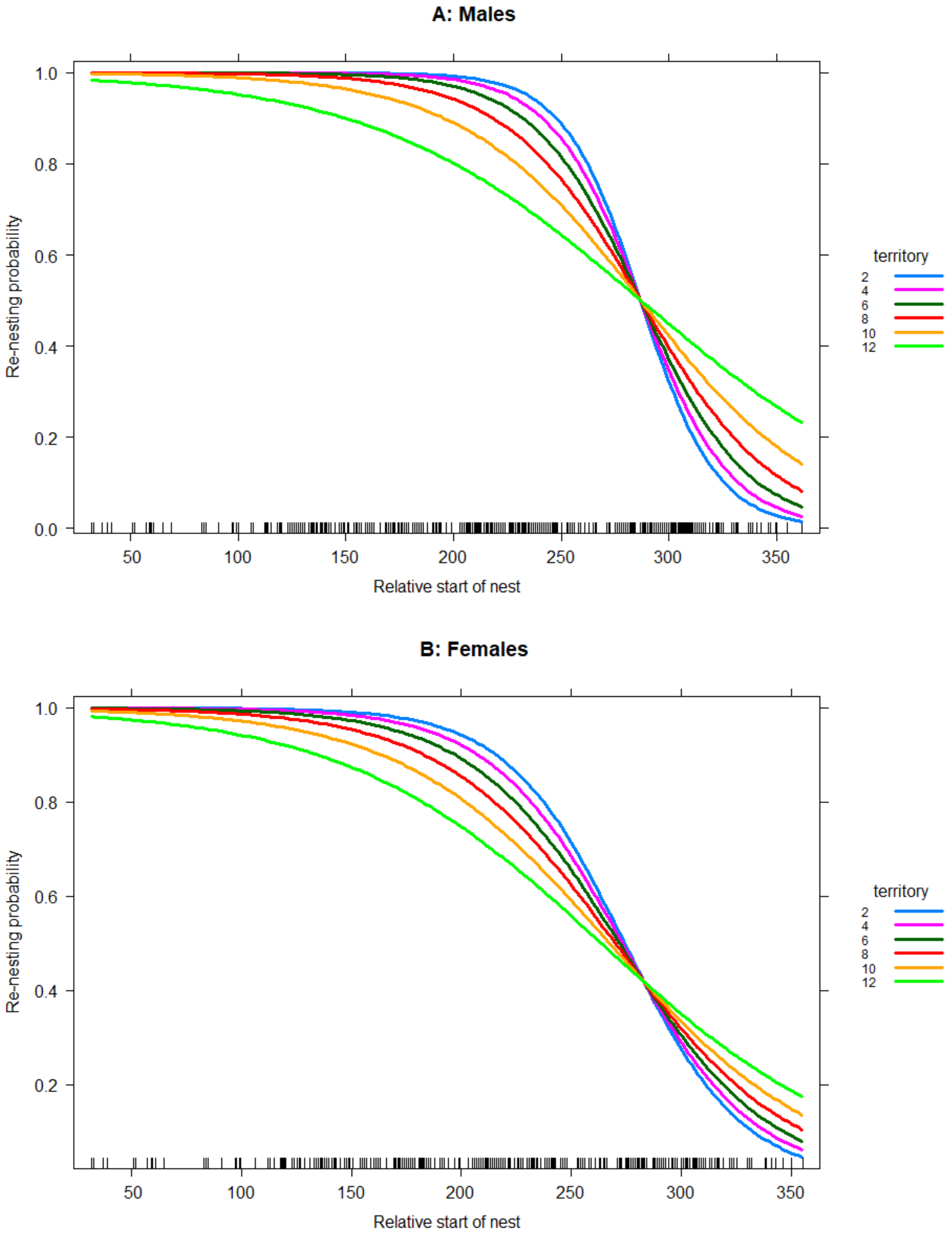

Figure 3.1: Impact of territory distance from a feeding station on re-nesting probability for A: males and B: females in the stable phase of the population. X axis indicates relative start of current nest; y axis is re-nesting probability. Coloured lines indicate re-nesting probability curves for 6 levels of territory quality. Analyses in section 4.3 demonstrate that birds on more distant territories are less likely to re-nest as the season progresses, while the probability of a bird on a nearby territory re-nesting remains high for longer. However, re-nesting likelihood for birds on nearby territories reaches zero while for those on more distant territories does not; this may indicate that nearby birds stop earlier as they have been successful earlier.

3.4.6. Breeding phenology

It is clear from the previous results that an early initiation of breeding is the most important influence on the metrics of annual reproductive success analysed here, and therefore any factor which itself enables an earlier start of breeding is also vital. In the growth phase, there are no included predictors which enable males to have an earlier start of breeding, although there is a trend towards older males being able to initiate breeding earlier (Table S3.8A). However, in the stable phase male birds on a territory nearer to a feeding station can initiate breeding significantly earlier than their more distant peers (Table S3.8B; Fig 3.2).

For females, in the growth phase a larger social network enables an earlier relative start (Table S3.9A); and in the stable phase social network size and territory proximity to a feeder both enable an earlier start (Table S3.9B).

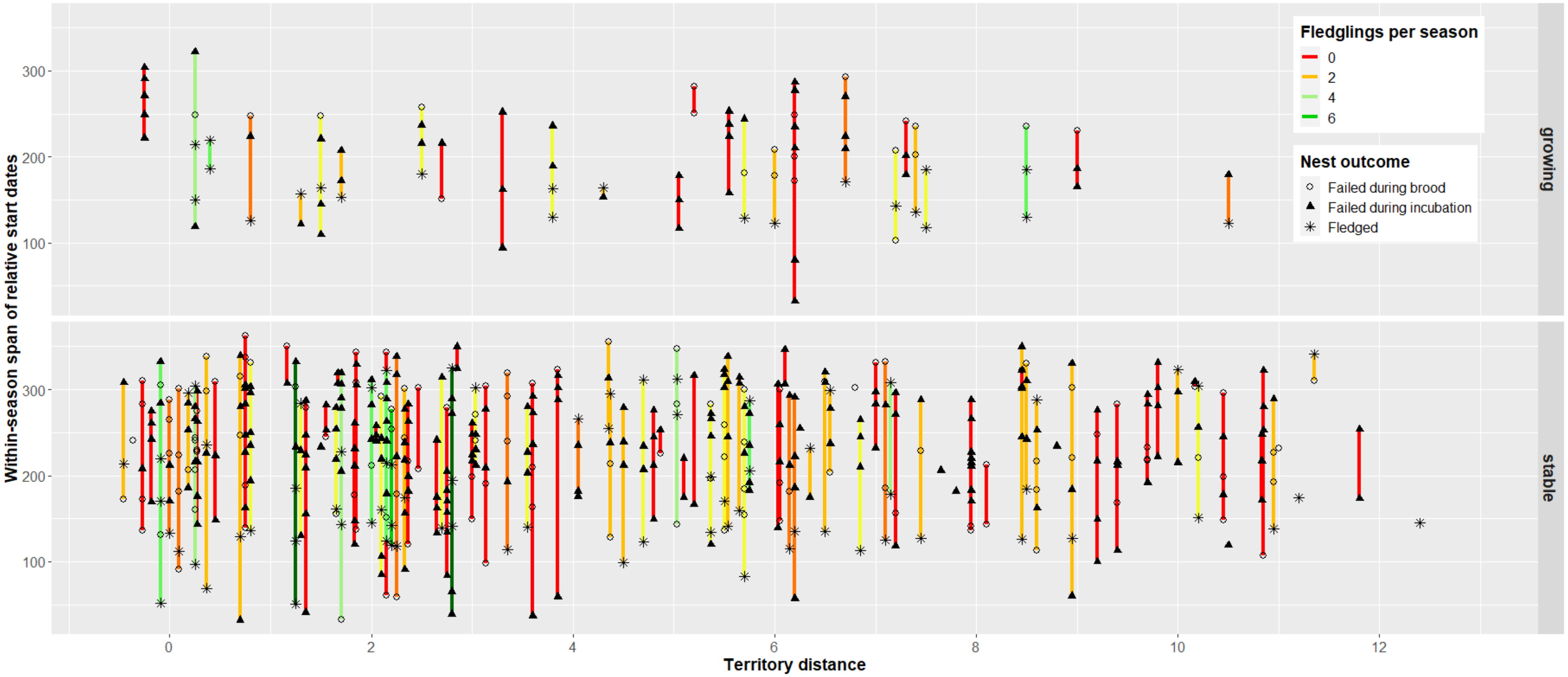

Figure 3.2: The interaction of x: territory distance from a feeder and y: relative nest start date, including nest outcomes and overall ARS for male Mauritius fodies, faceted by the growing and stable phases of the Île aux Aigrettes population. Vertical lines indicate the span of all nest initiations for each bird and therefore represent a breeding season; symbols indicate nest initiation timings and outcomes, and line colour indicates total annual reproductive success. Analyses show that in the stable phase of the population male fodies start breeding earlier if they have a territory closer to a feeding station (section 4.4); and that an earlier relative start increases both productivity of nests and overall ARS for the parent bird (section 4.2).

3.5. Discussion

In this study, results demonstrate that reproductive success of both sexes within this population is driven by a wide range of factors which influence re-nesting rates, fledglings per nest, and total fledgling production. Birds able to initiate breeding early produce more fledglings per nest and have higher annual reproductive success; and birds on territories closer to the feeding stations start breeding earlier than others. This impact is weaker during the growth phase of the population, indicating that distance from a feeding station may matter less while the population has more space and competition for territories is therefore less intense. Proximity to feeding stations also modifies the probability of re-nesting, as this remains higher for most of the season for birds on these territories. The benefit of nesting close to a feeding station is therefore largely indirect and is expressed through enabling an earlier start of breeding, but these analyses suggest that this management intervention, alongside extensive habitat restoration, has played a significant role in supporting high numbers of this species as it recovered from critically low numbers.

As with many endangered species management plans, the supplemental feeding offered to this population of fodies is ad-hoc and was not planned in a way to enable formal assessment of its impacts. Consequently, conclusions made here are correlative, and depend upon the quality of the long-term datasets generated by the monitoring effort. These data are generated by re-sightings of marked individuals in the field, and assigning of offspring to parents. Birds attending either feeding aviary are recorded daily, and when an adult pair is observed displaying nesting behaviour, they are tracked until the nest is found and the nest is then monitored until its conclusion. In addition, the island is searched following a grid layout (Figure S1), which means that nesting efforts at a distance from the aviaries are equally likely to be found. The addition of the second feeder partway through the study, and the similar impacts it had on nesting proximity, suggests that conclusions are unbiased with respect to pair and nest detection.

Chicks are ringed on the nest or within the aviaries after fledging, which they typically visit as a family group with their parents. Some individuals are ringed as older fledglings or adults, and their parentage is unknown as a result (118 of 643 total individuals over the course of the study). These cases probably reflect nesting attempts that went undetected or in which a nest was inaccessible making the counting and marking of chicks impossible. While misidentification of offspring or parents could introduce noise into the data, this noise would apply across all individuals and breeding seasons and therefore relative differences in productivity are likely to remain ecologically meaningful. Île aux Aigrettes is too small for variations of climate across the islet to be significant, and water is provided ad libitum at feeding stations and in concrete troughs installed across the islet, intended for giant tortoises but also used by fodies. Therefore, access to fresh water is unlikely to be a limiting factor in reproductive effort or success.

The main finding of this study is that once the carrying capacity has been reached, management appears to influence breeding phenology and re-nesting rates, and consequently improves reproductive effort and success of this species. A pattern of decreasing reproductive success as a season progresses is commonly seen in many passerine species (Grüebler et al., 2010) and is a key component in individual fitness as birds able to initiate breeding earlier usually have increased productivity (Both et al., 2004; Porlier et al., 2012). In many species this benefit is due to synchronicity with ideal climatic conditions and food resource availability (Lv et al., 2020), and early nests often have increased productivity (Siikamäki, 1998) because of this. Multi-brooded species can also breed more frequently after an early start (Senécal et al., 2021). Results here confirm that this tropical island endemic follows the same patterns in that birds which initiate breeding earlier in the season produce more fledglings than their peers through highly productive early season nests and through higher re-nesting rates. Territory proximity to a feeding station enables significantly earlier initiation of breeding for both sexes and has a direct and positive impact on re-nesting rates; re-nesting rates on such territories reach zero sooner than more distant territories but this likely indicates that these birds have been successful earlier in the season. Many bird species demonstrate a trade-off between reproductive effort and success, in terms of nests per season versus fledglings per nest (Senécal et al., 2021), and these results demonstrate that access to food may release such constraints for fodies on high quality territories.

The results in this study linking access to supplemental food to territory distance from a feeder are consistent with other studies which demonstrate that not all individuals within supported populations have equal access to food, and that this can be mediated by proximity (Tollington et al., 2013). This could be due to the direct impacts of food availability, or to higher quality individuals being better able to defend such territories (Tollington et al., 2019b). Food can be a limiting factor for multiple brooded species, and when food is limited individuals may trade-off between current and future reproductive efforts (Senécal et al., 2021; Verhulst et al., 1997). Alleviating this limitation by the provision of supplemental food can alter reproductive decisions such as the frequency and timing of breeding (Veiga, 1996); and this consequently can increase individual productivity (Nagy & Holmes, 2005; O’Brien & Dawson, 2013; Verboven et al., 2001). Multiple breeding is common among bird species with extended breeding seasons, and in such species, productivity is higher among individuals that nest frequently compared with their peers who nest less frequently (Morrison 1998). Such speeding up, or ‘fast track’ life histories may be particularly beneficial for opportunistic breeders in rapidly changing environments (Vedder et al., 2013). In turn, individual productivity impacts on the total reproductive success of populations and therefore on population viability and persistence (Senécal et al., 2021).

Females with a larger social network are also able to achieve an earlier start of breeding. While little is known about the process of pair bond formation in fodies, this is likely to be a time-saving measure in that these females have a wider pool of existing pairs to mate with, while others may need to use time within the breeding season to form such bonds before they can initiate a nest. Positive links between mate retention and reproductive success observed in other species have been linked to time management (Dubois & Cézilly, 2002). Zebra finches *Taeniopygia guttata* which remain in continuous pairs gain higher productivity, because pairs can produce multiple clutches in succession without needing to spend time creating a new pair bond (Adkins-Regan & Tomaszycki, 2007). This suggests a cost in time or energy of forming new pair bonds. Surprisingly, there are no obvious benefits of any form of polygyny on these metrics of reproductive success; however, there are indications that a male retaining his previous partner is beneficial in terms of nest hatching and fledging rates which would suggest a similar benefit from pair familiarity.

The results presented here appear to support hypothesis 1, that the provision of supplemental feeding increases productivity, albeit indirectly by enabling an earlier relative start of breeding. There appears to be little evidence of conflict disproportionately impacting birds on territories near to feeding stations; while results here indicate that the presence of unpaired birds dampens productivity for both sexes, these do not consistently follow the expected patterns of increased conflict for high quality territories when the population is stable, and there is no significant evidence within these analyses that such territories fare less well on any of the available metrics.

Taken together, these results indicate that supplemental feeding may remove some density-dependent limits on reproduction and therefore may be supporting a higher number of birds than the habitat would otherwise allow. For a species recovering from critically low numbers, this maintenance of the population at a high level demonstrates a key benefit of supplemental feeding (Zhang et al., 2021), especially as the ultimate aim for this population is to provide individuals for future translocations. Other studies have similarly demonstrated that the provision of supplemental food can be essential for population maintenance (Academia & Watts, 2023; Arcese & Smith, 1988). The lack of a direct effect of territory quality on annual reproductive success may be a consequence of the complexity of ecological datasets and the high level of variation in territory quality, relative start dates, and nest outcomes between individuals. Future analyses on seasonal impacts on breeding which impact all members of a population may clarify some of these interactions.

While assessing the impact of ad-hoc conservation interventions against a background of varying natural processes is a crucial challenge for conservationists, the detailed longitudinal data which this requires are rarely available, particularly for tropical species of conservation concern (Hidalgo Aranzamendi et al., 2019a). These analyses demonstrate how species recovery plans can be informed by such detailed datasets, and how these analyses can increase understanding of the complex interactions of processes driving observed variation.

Formal, assessable conservation planning remains difficult especially for endangered species or those with a very small range; ad-hoc management is therefore vital and will continue to be so during the ongoing biodiversity crisis and with increasing threats of climate change and habitat loss. Studies which enable the assessment of such management interventions similarly remain vital. This study shows that ad-hoc management can alter the behaviour of individuals, lead to increased reproductive success, and support the total population of a species of conservation concern. Complex multivariate studies such as this can generate useful insights into species ecology and conservation, and this analytical approach may inform other species management projects. However, the data is unbalanced; this emphasises the importance of continuity of data collection and of integrated data management for long-term monitoring programmes. While recommendations have been made previously for such monitoring to be standard for all bird reintroductions (Sutherland et al., 2010a), datasets on this scale remain rare and studies which assess practical conservation interventions remain the minority (Taylor et al., 2017b; Williams et al., 2020). The methods used in this study may enable similar retrospective analyses for such species where datasets do exist; and all reintroduction and conservation intervention projects should be encouraged to invest in consistent ongoing monitoring which generates such data.

3.6. Supplementary materials

Table S3.1: Predictors of overall annual reproductive success for males

A: MALES, growth only						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.2922	0.2908	10.7135	1.005	0.3372	
Relative start	-0.1156	0.3623	12.9882	-0.319	0.7546	
Territory	-0.2853	0.3307	16.2267	-0.863	0.4009	
Age	0.1902	0.3675	18.5029	0.518	0.6108	
Unpaired	-0.816	0.301	16.4352	-2.711	0.0152	*
Social	0.2775	0.3555	18.0757	0.781	0.4452	
Non-mono	-0.1725	0.2931	19.9230	-0.588	0.5629	
B: MALES, stable only						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	-0.10184	0.15483	37.12622	-0.658	0.514747	
Territory	-0.0937	0.16071	40.90475	-0.583	0.563065	
Age	-0.07026	0.17695	51.62307	-0.397	0.692975	
Unpaired	-0.55885	0.1504	100.86193	-3.716	0.000333	***
Social	0.25274	0.17297	92.34574	1.461	0.147361	
Non mono	0.05224	0.1523	94.17568	0.343	0.732359	
Relative start	-0.55184	0.15114	100.67253	-3.651	0.000416	***

Table S3.2: Predictors of overall annual reproductive success for females

A: FEMALES, growth only						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.39565	0.32198	14.2616	1.229	0.239	
Age	-0.19033	0.42862	13.2231	-0.444	0.6642	
Unpaired	-0.65826	0.33244	17.9984	-1.98	0.0632	.
Social	0.47285	0.47373	17.9664	0.998	0.3315	
Proportion of nests polygynous	0.08764	0.35216	17.9757	0.249	0.8063	
Proportion of nests ‘multi’	-0.04523	0.36582	17.6295	-0.124	0.903	
Relative start	-0.17961	0.41059	15.4483	-0.437	0.6678	
Territory	-0.19983	0.3418	14.8278	-0.585	0.5676	
B: FEMALES, stable only						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	-0.125004	0.138459	43.0211	-0.903	0.3716	
Relative start	-0.604462	0.140879	107.571	-4.291	3.91E-05	***
Territory	-0.046712	0.141109	56.9782	-0.331	0.7418	
Age	0.051736	0.169889	72.8002	0.305	0.7616	
Unpaired	-0.389586	0.161007	103.548	-2.42	0.0173	*
Social	-0.006302	0.152728	80.4796	-0.041	0.9672	
Proportion of nests polygynous	0.038795	0.135364	107.948	0.287	0.775	
Proportion of nests ‘multi’	0.169528	0.133175	105.426	1.273	0.2058	

Table S3.3: Model outcomes of predictors of fledglings per nest

A: Fledglings per nest, growth						
	Estimate	**Std. Error**	**df**	**T value**	**Pr(>|t|)**	
(Intercept)	0.08005	0.27188	66.0245	0.294	0.76936	
Male nest interval	-0.31576	0.11149	69.23481	-2.832	0.00605	**
Male age	0.06413	0.14309	26.32404	0.448	6.58E-01	
Pair switch	-0.31216	0.37758	72.92349	-0.827	0.41109	
Female age	-0.14389	0.13335	19.7363	-1.079	0.29356	
Pair count	0.03663	0.13758	10.07399	0.266	0.7954	
Nest 'multi'	-0.23901	0.34676	70.87101	-0.689	0.49291	
Nest polygynous	-0.08192	0.4374	73.34261	-0.187	0.85195	
Previous partner	0.15544	0.30065	71.10172	0.517	0.60676	
Population density	-0.15698	0.14526	16.44864	-1.081	0.29543	
Relative start	-0.5487	0.12711	64.99505	-4.317	5.52E-05	***
Territory	-0.14375	0.11198	10.59418	-1.284	0.2266	
B: Fledglings per nest, stable						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	-0.030979	0.116996	390.361851	-0.265	0.7913	
Male nest interval	-0.054646	0.043593	441.981457	-1.254	0.2107	
Relative start	-0.204818	0.044655	436.988799	-4.587	0.00000589	***
Male age	0.017065	0.049839	76.5289	0.342	0.733	
Pair switch	-0.166368	0.117323	428.878409	-1.418	0.1569	
Female age	0.104223	0.048331	193.715155	2.156	0.0323	*
Pair count	-0.051746	0.052949	57.594805	-0.977	0.3325	
Nest 'multi'	-0.236002	0.215732	384.488637	-1.094	0.2747	
Nest polygynous	0.088698	0.124104	441.97035	0.715	0.4752	
Territory	0.003703	0.038132	86.962251	0.097	0.9229	
Previous partner	0.032657	0.11943	441.676066	0.273	0.7846	
Population density	-0.019278	0.043691	370.181873	-0.441	0.6593	

Table S3.4: Outcome of binomial GLMER predicting nest survival past incubation

A: Survival past incubation, growth					
	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	0.69304	0.71263	0.973	0.3308	
Male nest interval	-0.53787	0.33594	-1.601	0.1094	
Relative start	-0.12556	0.30772	-0.408	0.6832	
Male age	0.64408	0.36628	1.758	0.0787	.
Pair switch	-2.5152	1.2865	-1.955	0.0506	.
Female age	0.09021	0.3292	0.274	0.7841	
Pair count	-0.10026	0.3384	-0.296	0.767	
Nest 'multi'	-0.31828	0.80629	-0.395	0.693	
Nest polygynous	1.0019	1.44384	0.694	0.4877	
Territory	0.5233	0.27691	1.89	0.0588	.
Previous partner	-0.70031	0.78771	-0.889	0.374	
Population density	-0.20107	0.35631	-0.564	0.5725	
B: Survival past incubation, stable					
	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	0.047799	0.332259	0.144	0.88561	*
Male nest interval	-0.25439	0.124413	-2.045	0.04088	**
Relative start	-0.37916	0.126191	-3.005	0.00266	
Male age	0.092501	0.1553	0.596	0.55142	*
Pair switch	-0.68208	0.336419	-2.027	0.04261	.
Female age	0.236228	0.143447	1.647	0.0996	
Pair count	-0.02608	0.16323	-0.16	0.87305	
Nest 'multi'	-0.80008	0.65362	-1.224	0.22092	
Nest polygynous	0.00103	0.349646	0.003	0.99765	
Territory	-0.04489	0.11507	-0.39	0.69645	
Previous partner	-0.13563	0.334822	-0.405	0.68541	
Population density	-0.00671	0.123789	-0.054	0.95676	

Table S3.5: Outcome of binomial GLMER predicting nest survival past fledging

A: Survival past fledging, growth					
	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	-2.6719	1.0966	-2.437	0.01483	
Male nest interval	-1.536	0.7327	-2.097	0.03604	*
Relative start	-2.1363	0.5922	-3.607	0.00031	*
Male age	0.777	0.4775	1.627	0.10369	***
Pair switch	-0.7854	1.5914	-0.494	0.62163	
Female age	-0.6803	0.6294	-1.081	0.27975	
Pair count	-0.4367	0.5029	-0.868	0.38517	
Nest ‘multi’	0.1303	1.0966	0.119	0.90539	
Nest polygynous	-0.6409	1.7925	-0.358	0.72067	
Territory	-0.1913	0.3311	-0.578	0.56342	
Previous partner	0.9701	1.042	0.931	0.35186	
Population density	-0.7411	0.521	-1.423	0.15488	
B: Survival past fledging, stable					
	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	-1.623	0.4169	-3.894	9.88E-05	***
Male nest interval	-0.1832	0.1477	-1.24	0.215	
Relative start	-0.6774	0.1574	-4.303	1.69E-05	***
Male age	-0.01481	0.1967	-0.075	0.94	
Pair switch	-0.5755	0.4814	-1.195	0.2319	
Female age	0.344	0.176	1.955	0.0506	.
Pair count	-0.0716	0.1999	-0.358	0.7202	
Nest ‘multi’	-30.97	3560000	0	1	
Nest polygynous	0.1798	0.4745	0.379	0.7047	
Territory	0.02922	0.1455	0.201	0.8408	
Previous partner	-0.07859	0.421	-0.187	0.8519	
Population density	-0.09885	0.1529	-0.646	0.518	

Table S3.6: model outcomes for predictors of re-nesting probability for male birds

A: growth	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**	
(Intercept)	3.98E+00	3.52E+00	1.132	0.257443	
Pair count	1.28E+00	6.05E-01	2.116	0.03433	*
Nest ‘multi’	1.74E+00	1.39E+00	1.253	0.21025	
Nest polygynous	3.25E+01	1.36E+07	0	0.999998	
Territory	-3.20E-01	4.38E-01	-0.729	0.465785	
Relative start	-2.73E+00	7.04E-01	-3.876	0.000106	***
Social	-1.56E+00	9.38E-01	-1.66	0.096903	.
Unpaired females	3.28E-02	9.37E-02	0.351	0.72582	
Age	-3.28E-01	5.20E-01	-0.63	0.528419	
Fledglings from previous	-4.82E-01	4.39E-01	-1.098	0.272241	
Previous partner	-2.07E+00	1.50E+00	-1.378	0.168322	
Territory * relative start	-5.03E-01	4.34E-01	-1.16	0.24603	
B: stable	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**	
(Intercept)	5.18673	1.10028	4.714	2.43E-06	***
Pair count	0.34271	0.22296	1.537	0.124276	
Nest ‘multi’	1.24638	0.84253	1.479	0.139052	
Nest polygynous	1.33559	0.45194	2.955	0.003124	**
Territory	-0.8036	0.21799	-3.686	0.000227	***
Relative start	-3.40766	0.3886	-8.769	<0.0002	***
Social	0.55415	0.21392	2.59	0.009584	**
Unpaired females	-0.08718	0.02006	-4.345	1.39E-05	***
Age	-0.15717	0.14427	-1.089	0.275982	
Fledglings from previous	-1.02522	0.26666	-3.845	0.000121	***
Previous partner	-0.1312	0.58537	-0.224	0.822657	
Territory * relative start	0.96906	0.25256	3.837	0.000125	***

Table S3.7: model outcomes for predictors of re-nesting probability for female birds

A: growth	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**	
(Intercept)	31.06992	528.79137	0.059	0.95315	
Pair count	0.90368	0.53669	1.684	0.09222	.
Nest ‘multi’	1.11709	1.22856	0.909	0.36321	
Nest polygynous	-2.21289	1.66872	-1.326	0.18481	
Territory	-0.88977	0.46586	-1.91	0.05614	.
Relative start	-2.63131	0.90741	-2.9	0.00373	**
Social	1.62086	0.99951	1.622	0.10488	
Unpaired males	-0.08075	0.15812	-0.511	0.60955	
Age	-2.24228	0.90132	-2.488	0.01285	*
Fledglings from previous	-1.00082	0.49838	-2.008	0.04463	*
Previous partner	-24.23007	528.81392	-0.046	0.96345	
Territory * relative start	-0.07259	0.35613	-0.204	0.83849	
B: stable	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**	
(Intercept)	2.92469	1.12917	2.59	0.00959	**
Pair count	0.32246	0.19311	1.67	0.09495	.
Nest ‘multi’	0.51387	0.88299	0.582	0.56059	
Nest polygynous	-0.30958	0.42222	-0.733	0.46342	
Territory	-0.38431	0.17243	-2.229	0.02583	*
Relative start	-2.37988	0.29192	-8.152	3.57E-16	***
Social	0.33968	0.2647	1.283	0.19939	
Unpaired males	-0.05679	0.02818	-2.015	0.04388	*
Age	-0.22586	0.16072	-1.405	0.15994	
Fledglings from previous	-0.55802	0.23822	-2.342	0.01916	*
Previous partner	0.40112	0.54772	0.732	0.46396	
Territory * relative start	0.49458	0.21306	2.321	0.02027	*

Table S3.8: predictors of relative start date of breeding for male birds

A: MALES, growth						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	3.61E-16	1.77E-01	2.00E+01	0	1	
Territory	-1.68E-01	1.99E-01	2.00E+01	-0.845	0.408	
Age	-3.94E-01	2.08E-01	2.00E+01	-1.897	0.0723	.
Unpaired	-1.13E-01	1.84E-01	2.00E+01	-0.613	0.5468	
Social	-2.57E-01	2.11E-01	2.00E+01	-1.216	0.238	
Nests non-monogamous	-1.80E-01	1.84E-01	2.00E+01	-0.976	0.3406	
B: MALES, stable						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	8.79E-17	9.45E-02	1.03E+02	0	1	
Territory	2.54E-01	9.74E-02	1.03E+02	2.602	0.0106	*
Age	2.69E-02	1.12E-01	1.03E+02	0.239	0.8112	
Unpaired	-3.62E-02	9.65E-02	1.03E+02	-0.375	0.7088	
Social	-5.26E-02	1.12E-01	1.03E+02	-0.47	0.6392	
Nests non-monogamous	1.36E-01	9.78E-02	1.03E+02	1.387	0.1683	

Table S3.9: predictors of relative start date of breeding for female birds

A: FEMALES, growth						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	-2.10E-16	1.72E-01	2.10E+01	0	1	
Territory	-1.52E-01	1.82E-01	2.10E+01	-0.838	0.4113	
Age	1.08E-01	2.24E-01	2.10E+01	0.48	0.6359	
Unpaired	-5.46E-02	1.83E-01	2.10E+01	-0.298	0.7685	
Social	-5.80E-01	2.24E-01	2.10E+01	-2.594	0.0169	*
Nests non-monogamous	-3.19E-01	1.83E-01	2.10E+01	-1.742	0.0961	.
B: FEMALES, stable						
	Estimate	**Std. Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	1.95E-02	9.49E-02	4.04E+01	0.205	0.8383	
Territory	2.46E-01	9.48E-02	6.03E+01	2.59	0.012	*
Age	1.90E-01	1.16E-01	7.87E+01	1.633	0.1066	
Unpaired	-5.62E-02	1.04E-01	1.10E+02	-0.539	0.5912	
Social	-2.09E-01	1.03E-01	8.55E+01	-2.023	0.0462	*
Nests non-monogamous	1.20E-01	9.02E-02	1.11E+02	1.327	0.1874	

4. Potential drivers of temporal variation in the productivity of a managed tropical wild bird

4.1. Abstract

Stochastic and directional environmental change can impact breeding behaviour and reproductive success of individuals and populations, and have the potential to reduce population growth and viability. Small and endangered populations can be particularly vulnerable to such effects. Environmental change, including anthropogenic climate change, may alter the frequency and severity of stochastic events such as storms and heatwaves; this can severely impact island species which are limited in their ability to migrate. Conservation management intended to support endangered populations may ameliorate the impacts of such stochasticity, but impacts can be complex to discern.

This study uses long-term monitoring data of a species of conservation concern, the endangered tropical island endemic Mauritius Fody *Foudia rubra*, to illustrate the impact of a variety of climatic and population variables on the productivity of both sexes. Individual productivity and re-nesting probability, as well as the success of individual nests, are improved in warmer and stormier years; but increasing population density has a negative effect on these metrics and fledging rates are reduced in wetter seasons. Previous work has demonstrated that birds which breed early are more successful; the ability to initiate breeding early is improved by conservation management (mediated by territory distance from a feeding station), but reduced by pre-seasonal rainfall, which in Mauritius is increasing, driven by anthropogenic climate change.

Studies of this type depend on long-term monitoring data which are not frequently available for species of conservation concern, and require repeated measures of seasonal productivity alongside relevant demographic predictors. This study demonstrates that management and climate variables both impact on the reproductive success of the population, and these results will inform future management for this species.

4.2. Introduction

Stochastic events such as storms and rainfall have the potential to reduce population growth rates (Hilton et al., 2003; McLaughlin et al., 2002; Reiertsen et al., 2021) and therefore can modify extinction risk, even within populations which would otherwise be stable (Mangel & Tier, 1994). Extreme events are predicted to increase in frequency and intensity with anthropogenic climate change (IPCC, 2012), and their effects can interact with other pressures on endangered species such as habitat loss (Fisher et al., 2015; Latimer & Zuckerberg, 2021), and directional climate change. The occurrence of stochastic events varies across space and time, and their effects are unpredictable and under-researched (van de Pol et al., 2010); but will be experienced by all individuals within a population, especially if the species has a limited distribution (Reiertsen et al., 2021). The IUCN considers that small and geographically isolated populations are particularly susceptible to stochastic events (Le Breton et al., 2019), and as a result range size can be used as a correlate of extinction risk (Runge et al., 2015). Endangered species from tropical islands have restricted range sizes and small or declining populations, and their window of climatic suitability may be very small because their environment tends to be less variable than temperate equivalents (Colwell et al., 2008). Therefore, even a small shift in prevailing climate conditions may render the environment unsuitable and have a significant impact on vital rates. Small islands are also disproportionately vulnerable to the effects of climate change; prevailing conditions on geographically isolated islands such as Mauritius are changing in terms of temperature increases (Doorga, 2022), and changes in rainfall patterns (Senapathi et al., 2010) as well as their increasing risk of severe cyclones and other extreme events (Descamps et al., 2015; Thompson et al., 2021).

Climate factors such as rainfall patterns can both increase (Mares et al., 2017) and decrease (Burant et al., 2022) reproductive success, with mechanisms including direct impacts on survival (Bourne et al., 2020), and indirectly via altering reproductive decisions (Husby et al., 2009; Mares et al., 2017), including the timing of breeding (Hidalgo Aranzamendi et al., 2019b; Senapathi et al., 2011), and the frequency and success of second or multiple broods (Weggler, 2006). Conservation interventions aim to improve population growth and viability by mitigating a specific threat, such as the provision of supplemental food to increase recruitment and survival rates; and changes to vital rates resulting from management have the potential to dampen the influence of stochastic events on individual demography (Bowgen et al., 2022; Husby et al., 2009; Scridel et al., 2018; Senapathi et al., 2011).

Understanding the specific mechanisms by which environmental stochasticity influences the vital rates of individuals and populations are therefore key questions for conservationists (Frederiksen et al., 2014), and will allow more accurate predictions of the responses of populations and species to future climate change scenarios (Conradie et al., 2019). Statistical approaches which model both the proximate impacts of management and stochastic events, and whether these have a population level impact are key to answering these questions (Barbraud et al., 2011), but require repeated measures of each climatic, population, and individual criterion over multiple years (Frederiksen et al., 2014). However, such datasets juxtaposing relevant climate and individual data remain rare, especially for tropical species of conservation concern (Chauvenet et al., 2012a; Reid et al., 2021).

This study examines the population consequences of stochastic events on a population of the endangered Mauritius Fody *Foudia rubra* on Île aux Aigrettes, a 27-hectare islet 800m off the coast of Mauritius at (20.23° S, 57.44° E), which has been partially restored and is managed as a reserve by the Mauritian Wildlife Foundation. Intensive fieldwork efforts on the islet have resulted in extensive long-term individual-based datasets summarising demography and reproductive behaviour for 600 individuals and 1133 nesting attempts over the duration of the study. There is also relevant climatic and environmental data for the region across the time period of the study. These data therefore provide an opportunity to explore stochastic processes including extreme weather events and their impacts on this population. Previous work on this population demonstrated an early relative start of breeding enables greater individual productivity, and that access to supplemental food, mediated by territory distance, enables an earlier relative start. Here, in determining important seasonal predictors of reproductive success across the population, this study hypothesises that aspects of breeding behaviour and productivity will vary with environmental conditions, including anthropogenic climate change, in multiple ways which may be positive and negative. The management of this and similar species will be informed by a better understanding of such links.

4.3. Methods

The goal of this study was to determine seasonal drivers of the high variance in seasonal productivity demonstrated by this population (Fig 4.1), which displays no obvious trend over time.

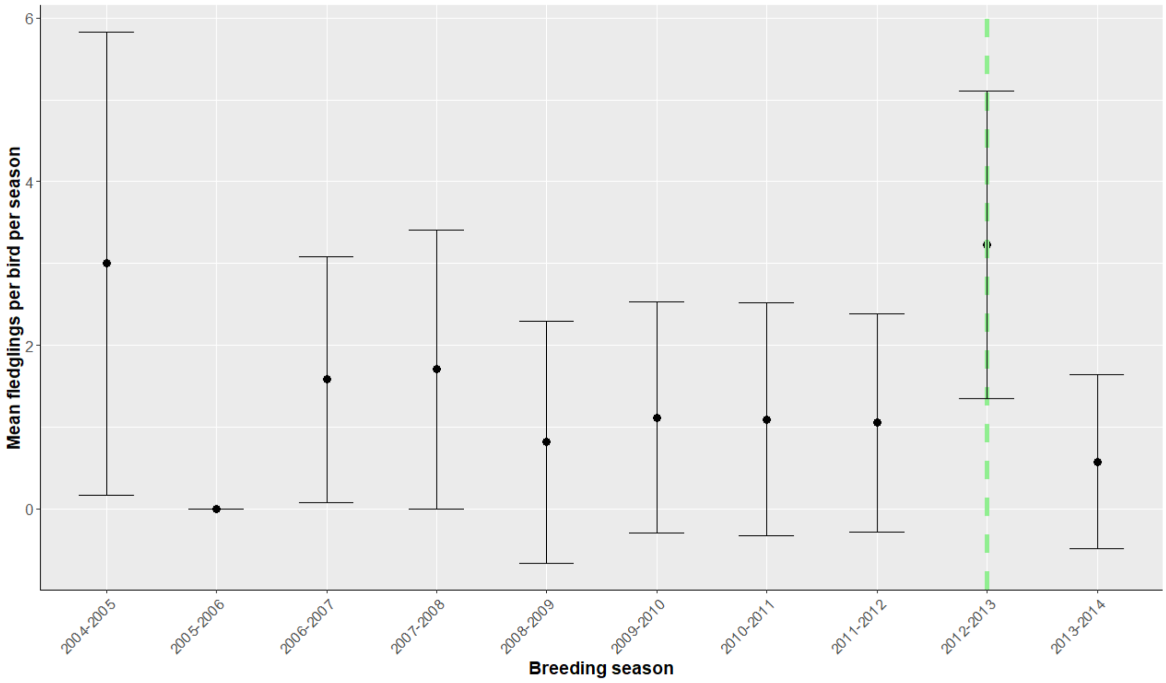

Figure 4.1: Means and SDs of mean fledglings per season per bird. One feeder was available throughout the study; timing of the addition of a second feeding station marked by vertical green dashed line (see Figure S4.1). For definition of breeding seasons see section 2.4.4.

The modelling framework was similar to that in Chapter 3; models were built to determine the impact of seasonal predictors on overall annual reproductive success, re-nesting probability, the productivity of individual nests, and the likelihood of nests surviving to hatching and to fledging. For an explanation of how nesting attempts and breeding seasons are defined, see General Methods, sections 2.4.2 and 2.4.4. These data span 2004-2005 to 2011-2012 inclusive (Seasonal dataset, see General Methods), during which all seasonal predictor data are available (Table 4.1). Each of these seasonal metrics can influence avian reproduction; pre-seasonal rain days have been shown to reduce female reproductive effort because of reduced foraging time and a consequential reduction in body condition; population fledglings represents the overall effort within the previous season which may have a hangover effect on the focal season; density indicates the size of the population and may reveal density-dependent effects; rain days and storm days can both increase and decrease reproductive effort via their impact on habitats and energetic demands, and average temperatures can also have similarly unpredictable outcomes.

Table 4.1: Seasonal predictors and definitions. All data are relevant to the focal breeding season.

Factor	Measure
Rain days FMA	The total number of days in February, March, and April with > 1 mm rainfall
Population fledglings	Total fledgling production by the population in the season prior
Density	The size of the current population at start of season
Rain days	The total number of days > 1 mm rainfall
Average temperature	The average daily max temperature
Storm days	The number of days at or greater than the 95th percentile of all rain days 1950-onwards

A model matrix was built to determine the influence of seasonal predictors on these metrics of reproductive success. Candidate predictors of seasonal variability (which affect all individuals within a population equally) for which data are available are defined in Table 1; these also show considerable variance over the time series (Fig S4.1). As these analyses are already temporal in nature the data were not split into growing and stable phases of the population; however, simple linear models were built to establish any trends in these variables over the time series of the data. These models demonstrate that storm days are decreasing significantly, average daily temperature is increasing significantly, and there is a marginal decrease in rain days (Table S4.1). To allow inter-annual trends to be separated from potentially spurious changes in these climatic variables and productivity as both vary over time, climate predictors were de-trended by breeding season, by subtracting predicted from observed values, leaving isolated climate anomalies of greater and less than these predicted values. For consistency, this process was applied to all climate metrics; however, as the overall productivity metric as shown in Figure 4.1 shows no significant directional trend, response variables were not modified in the same way. Sexes were analysed separately to determine whether males and females responded differently to the predictors included here.

Climate data are generated by weather stations in Plaisance, 5km from Île aux Aigrettes and shown in other Mauritius studies to be an accurate proxy for climate on the islet (Taylor, 2018). These data contained no correlations, so in all cases maximal models were built. Predictors were rescaled to aid in model fit, and all models were built in R Studio version 2023.03.0 (RStudio Team, 2020) and R version 4.2.1 (R Core Team, 2021).

4.3.1. Fledglings per season

A modelling framework was built to determine the impacts of these seasonal and population predictors on annual reproductive success, using the Seasonal dataset (see General Methods). These data are in the form of summaries of breeding seasons for each bird, and a maximal model was built with annual reproductive success in fledglings per season as the response variable and all metrics from Table 4.1. Initial models were generalised linear mixed models with poisson errors but were overdispersed, so the final model forms were generalised linear mixed models with negative binomial errors. All models included the bird ID to prevent pseudoreplication, and sexes were modelled separately.

4.3.2. Fledglings per nest

We followed a similar procedure to investigate the impact of these climate variables on the productivity of individual nests, using the Nest dataset (see General Methods). Firstly, the same set of seasonal predictors were used to determine whether any of these influenced the success rate of individual nests. The model used was a zero inflated generalised linear mixed model based on the AD Model Builder (Fournier et al., 2012), with negative binomial error distributions and a log-link. The response variable in these models was the productivity of individual nests, and the female ID and breeding season were included as random effects to prevent pseudoreplication.

4.3.3. Nests hatched and fledged

The same data and approach was used to determine the influence of these seasonal metrics on the proportion of nests which reach hatching, and fledging. Models were binomial generalised linear mixed models, with a response variable of 0/1 indicating whether the nest survived the focal stage, and the identity of the female bird as a random effect to prevent pseudoreplication.

4.3.4. Re-nesting probability

Finally, the Nest data was used to determine whether the same set of seasonal variables influenced the probability of a bird making a repeat nesting attempt. Models were generalised linear mixed models with binomial errors, where the response variable was a binary indicating the presence or absence of a subsequent nest.

4.4. Results

4.4.1. Fledglings per season

An increasing number of storm days within a breeding season has a marginal positive impact fledgling production, presumably because of positive impacts on habitat such as availability of nesting material or natural food resources. Full results of the model investigating the impact of seasonal variables on overall reproductive success for males are in Table S4.2; Table 4.2A summarises all individual reproductive success models.

For females, storm days have a significant positive influence and there is a marginal negative impact of increasing numbers of pre-seasonal rain days (Table 4.2A, Table S4.3). The impact of more pre-seasonal rain days may be due to a decrease in body condition because of less foraging time before breeding begins, and the impact of rain during this period on breeding phenology.

4.4.2. Fledglings per nest

The model investigating the impacts of seasonal variables on fledglings per nest has no significant terms, indicating that none of these metrics influence nest productivity (Table S4.4). Table 4.2B contains a summary of nest-based productivity models.

4.4.3. Nests hatched and fledged

Increasing numbers of storm days and average temperature both increase the likelihood of a nest surviving to hatch (Table 4.2B, Table S4.5), while population density decreases it. Nest survival to fledging is negatively influenced by rain days and by increasing population density (Table 4.2B, Table S4.6).

4.4.4. Re-nesting probability

Males are more likely to re-nest after seasons with high fledgling productivity, in seasons with more storm days and higher average temperature; but are less likely to re-nest as the population density increases (Table 4.2A, Table S4.7).

The picture for females is similar; storm days and average temperature increase the re-nesting probability while population density decreases it (Table 4.2A, Table S4.8).

Table 4.2: Effect size and SE of metrics within models of seasonal reproductive success. A) is models from sections 4.4.1 and 4.4.2 based on Seasonal data and B) is models from sections 4.4.3 and 4.4.5 using Nest data. Effect and SEs in red ***bold*** *indicate a significant and negative impact; in green* ***bold*** *a significant positive impact, and* ***bold*** *a marginal effect.*

A)	**Males, ARS**		**Females, ARS**		**Males, re-nest**		**Females, re-nest**	
Metric	Effect	SE	Effect	SE	Effect	SE	Effect	SE
Rain days	0.00	0.01	0.00	0.01	0.01	0.01	0.02	0.01
Population fledglings	1.39	1.22	1.10	1.04	**1.34**	**0.46**	**1.09**	**0.42**
Storm days	**1.14**	**0.62**	**1.20**	**0.58**	**0.47**	**0.22**	**0.56**	**0.21**
Average temperature	8.40	6.66	7.06	5.94	**5.08**	**1.84**	**4.01**	**1.70**
Rain in Jan, Feb, Mar	-0.10	0.08	**-0.14**	**0.08**	**0.14**	**0.08**	0.07	0.07
Population density	-0.02	0.01	-0.01	0.01	**-0.04**	**0.01**	**-0.04**	**0.01**

B)	**Nest productivity**		**Likelihood of hatching**		**Likelihood of fledging**	
Metric	Effect	SE	Effect	SE	Effect	SE
Rain days	-0.01	0.01	0.00	0.01	**-0.04**	**0.02**
Population fledglings	0.11	0.08	0.38	0.36	3.30	2.44
Storm days	1.20	0.83	**0.67**	**0.19**	2.05	1.37
Average temperature	11.16	8.13	**3.16**	**1.45**	18.47	13.58
Rain in Jan, Feb, Mar	-0.06	0.07	-0.01	0.06	-0.09	0.12
Population density	-0.01	0.01	-0.01	0.01	**-0.03**	**0.01**

4.5. Discussion

This study demonstrates that a range of extrinsic factors including stochastic and directional climate events can influence individual productivity within a breeding season. Largely, the included metrics of reproductive success increased with increasing average temperature and storm days but were negatively impacted by increasing population density.

This study relies on the quality of the data used in the analyses. Data used for individual predictors are based on intensive fieldwork and the individual marking of all birds within the population, and inferences made here are likely to be sound. However, due to limitations and changes to data collection methods during the study, as well as the ad-hoc addition of the second feeder, it was not possible to resolve the population level impacts of this second feeder, but for the breeding seasons included, all data are available and complete. These analyses are not intended as a detailed examination of the impacts of fine-scale climate variation on this species, but as a broad indication of the influence of seasonal metrics on this population. Pre-seasonal rain days was included to determine whether climate outside the breeding period impacts reproductive performance; and a potential avenue for future research would involve a more detailed analysis of the influence of such climate metrics across variable time windows.

Results here and in Chapter 3 indicate that that anthropogenic climate change and conservation management have opposing impacts on this population, both mediated by their impact on the relative start of breeding. While there is no direct impact of pre-seasonal rain days on these metrics of productivity, in years with higher rainfall in these months the mean onset of breeding is delayed significantly (Fig 4.2). Anthropogenic climate change is altering rainfall patterns in Mauritius, with increasing sea surface temperatures in the western Indian Ocean driving increased numbers of rain days in both rainy seasons (June – November, December – May; (Senapathi et al., 2010). Pre-seasonal rainfall levels have been demonstrated in other species to reduce the reproductive success of females through limiting their ability to forage and gain body condition for repeated breeding attempts (Crick, 2004) and the marginal impact on female breeding performance may suggest similar processes. Nests initiated later are less productive, probably due to phenological mismatches with ideal conditions for nesting as well as a lack of body condition; but birds breeding on territories nearer to feeding stations can start breeding earlier and have more fledglings per nest than their more distant peers (see Chapter 3). This benefit of access to supplementary food indicates that ongoing conservation management may go some way to ameliorating negative impacts of climate change on this species.

This aligns with other studies (Buckley et al., 2018; Liu et al., 2018), which demonstrate that supplemental food can relieve limiting factors for species undergoing cyclones (Prugh et al., 2018), habitat loss (Maron et al., 2015), and severe storms (McLaughlin et al., 2018). While there appear to be some benefits to this species at current levels of these stochastic effects, tropical species tend to have narrower windows of climatic suitability than temperate because their environment is much less variable. Despite the decrease in the occurrence of storm days over the relatively short time series of data used here, Indian Ocean tropical storms are expected to increase in severity and frequency (Thompson et al., 2021), driven by anthropogenic climate change in Mauritius (Doorga, 2022). Results in these analyses suggest that this could have a significant impact on the fledging rate of individual nests, as nests during the monsoon season are less successful than those at other times of year. The future therefore remains uncertain, and if negative impacts become apparent the provision of supplemental feeding to this population may become even more vital.

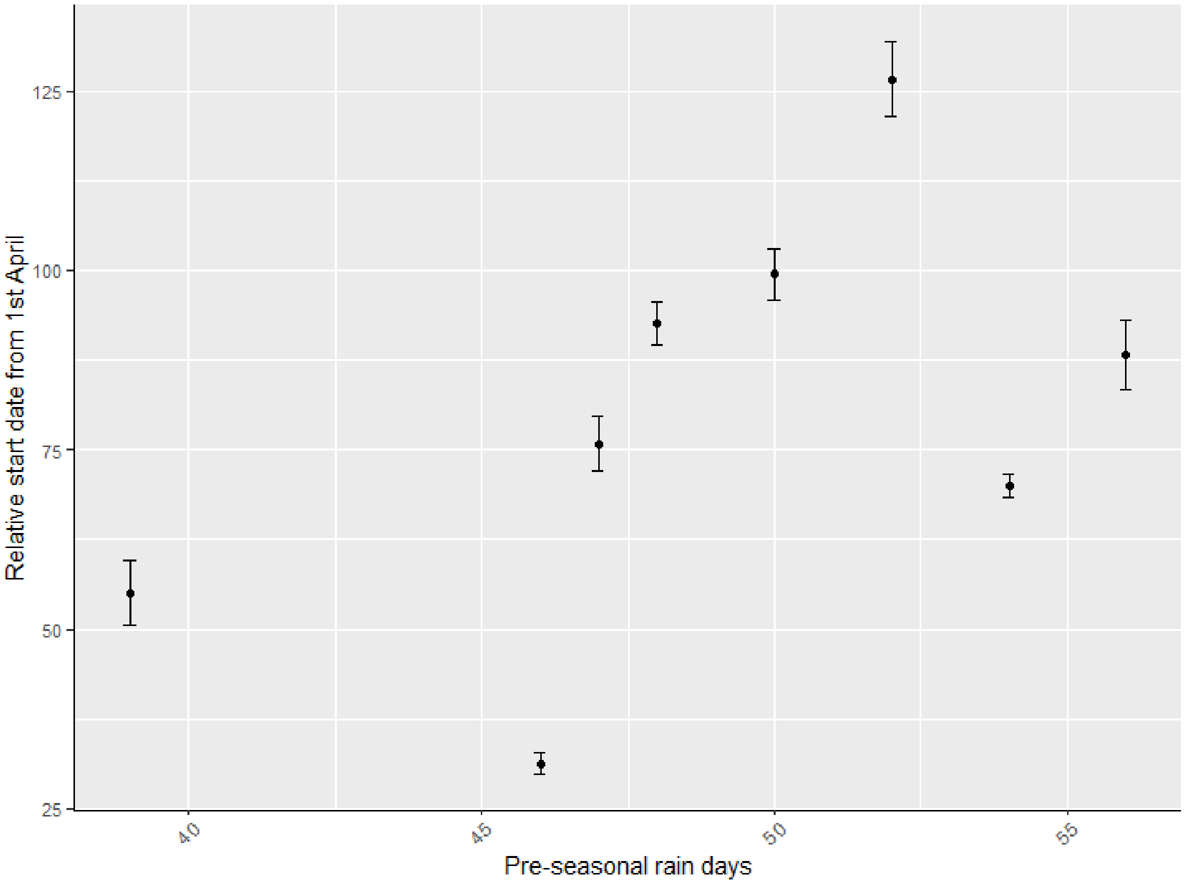

Figure 4.2: Effect of pre-breeding season rainfall on means and SEs of nesting initiation dates of all birds. X axis is count of rain days during February, March, and April; Y axis is the relative start date of breeding initiation expressed as days between 1st April of the focal year and observed breeding initiation. Generalised linear mixed model with negative binomial errors, described by y=-39.55 + 2.44x, where y = pre-seasonal rain days and x = relative start date, p value = 0.009. This model indicates that that birds begin nesting later in years with higher rainfall during February, March, and April.

Interestingly, these results also show that while within-season storm days can be beneficial, within-season rain days decreases the likelihood of nests surviving to fledging. Other studies have shown that increasing rainfall can have impacts on nesting success, including reduced fledging success and reduced juvenile and adult survival (Öberg et al., 2015), likely driven by reduced visitation rates by parent birds during inclement conditions as well as direct thermoregulatory impacts on chicks (Schöll & Hille, 2020). However, increasing total rainfall is also likely to increase natural prey abundance (Lv et al., 2020a), and storms may provide similar benefits while disrupting foraging and natural behaviour less due to their patchier distribution in time in comparison with daily rainfall. Storms may also physically alter habitats in ways which benefit fodies, by opening forest canopy and creating additional nesting sites (Leuenberger et al., 2021).

Results also demonstrate a positive impact of increasing average maximum daily temperatures on re-nesting rates and nest hatching rates for this species. The mechanism by which warmer seasons are beneficial is currently unknown but it may relate to increased habitat for nesting and to a reduction in time and energy demands for incubation. Historically, fodies were much more widespread across Mauritius and would likely have lived near to and depended upon seabird colonies which may themselves be unpredictable in occupancy and productivity (Jones, C; personal communication). This makes it likely that fodies would have evolved to be flexible breeders themselves; and their positive responses to the various climatic changes investigated in this study may be further demonstration of this. However, suitable climate windows for tropical species can be narrow, and relatively small shifts in prevailing conditions may present major obstacles for island species. Globally, many species are shifting their distributions to more polar latitudes (Sheldon, 2019) and to higher elevations (Saracco et al., 2019), to track their preferred temperature windows; but these solutions are frequently unavailable to island species which have limited ranges (Colwell et al., 2008). Therefore, it may be unwise to assume that any future alterations in any of rainfall, storm events or temperature would continue to be beneficial as further climate warming may have impacts on the population which are not currently discernible; thermal stress can alter avian behaviour with negative consequences for reproduction and survival (James et al., 2020).

Much of the previous work examining climate change impacts on birds has focused on temperate regions because these are expected to experience the greatest level of warming (Sheldon, 2019); this work has indicated that such species face highly complex and interacting selection pressures on breeding and phenology (Lv et al., 2020). There is a lack of detailed studies examining the impacts of environmental change on tropical species, but these emergent results suggest that similar pressures occur for this tropical species.

Given this lack of similar studies on tropical bird species, and the rarity of datasets which enable such analyses (Barbraud et al., 2011; Chauvenet et al., 2012a; Reid et al., 2021), this work is therefore a vital part of the emerging understanding of links between stochastic environmental impacts, climatic conditions, conservation management, and population demographics for tropical species.

4.6. Supplemental materials

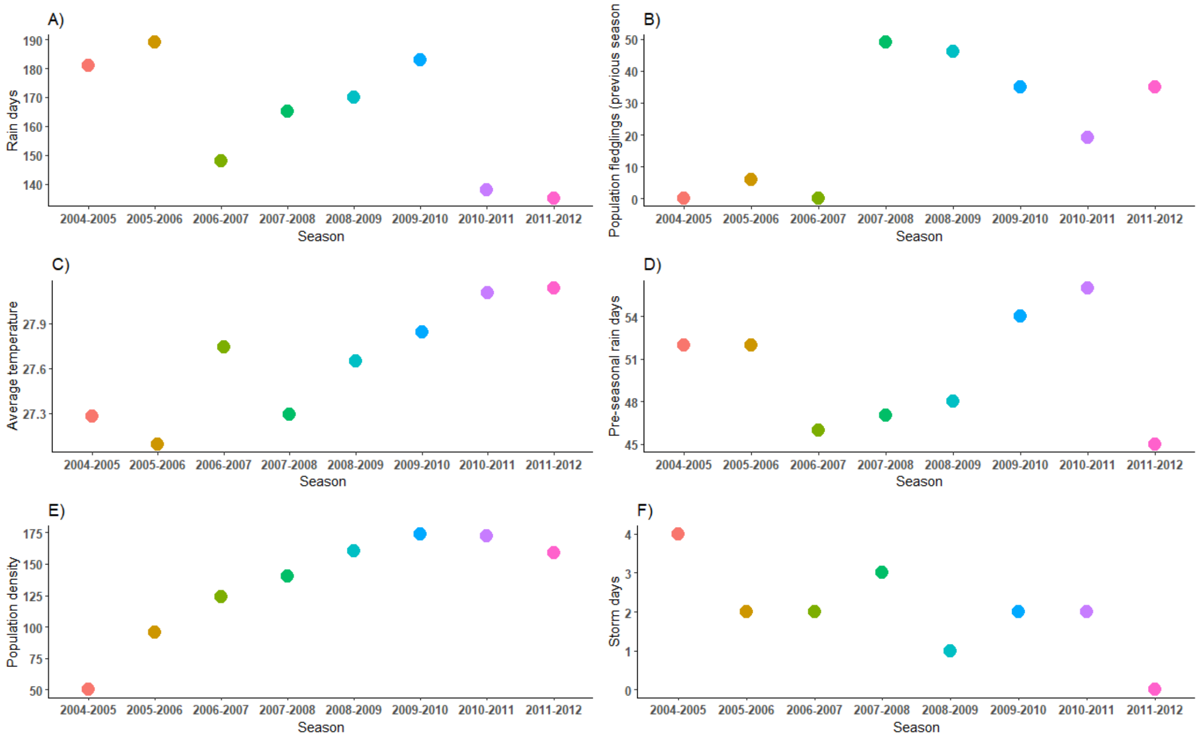

Figure S4.1: seasonal distribution of A) rain days, B) fledglings produced in the previous breeding season, C) average temperatures, D) Pre-seasonal rain days, E) population density and F) storm days. For definitions of these metrics see Table 1. The addition of a second feeding station partway through the study may have allowed us to compare population productivity in time periods with 1 and then with 2 feeders available. However, due to limitations in data collection relating to demography and to climatic conditions, data is restricted after the addition of the second feeding station (Fig 4.1). Preliminary analyses exploring impacts of the second feeder were equivocal and confounded by population density (Table S4.2) and it was therefore concluded that these models would examine the time period with one feeder available.

Table S4.1: Outcomes of models establishing trends in climatic predictors over the time series of available data.

	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	
Mean productivity					
(Intercept)	1.8547	0.6782	2.735	0.034	*
Season (numeric)	-0.1243	0.1343	-0.926	0.39	
Rain days					
(Intercept)	188.643	13.442	14.033	8.17E-06	***
Season (numeric)	-5.56	2.662	-2.088	0.0818	.
Average temperature					
(Intercept)	27.01802	0.15683	172.271	2.58E-12	***
Season (numeric)	0.13887	0.03106	4.471	0.00423	**
Rain days FMA					
(Intercept)	50.21429	3.39501	14.791	6.01E-06	***
Season (numeric)	-0.04762	0.67231	-0.071	0.946	
Storm days					
(Intercept)	3.6071	0.6854	5.263	0.0019	**
Season (numeric)	-0.3571	0.1357	-2.631	0.039	*

Table S4.2: model estimates for overall ARS for male birds.

	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	
(Intercept)	2.304192	1.912402	1.205	0.2283	
Rain days	-0.002018	0.013961	-0.145	0.8851	
Population fledglings	1.392038	1.218196	1.143	0.2532	
Storm days	1.13909	0.620549	1.836	0.0664	.
Mean temperature	8.398067	6.663424	1.26	0.2076	
Rain days Jan, Feb, Mar	-0.099777	0.075924	-1.314	0.1888	
Population density	-0.016617	0.013063	-1.272	0.2034	

Table S4.3: model estimates for overall ARS for female birds.

	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	
(Intercept)	1.6398464	1.807325	0.907	0.3642	
Rain days	0.0006918	0.013164	0.053	0.9581	
Population fledglings	1.0960459	1.043469	1.05	0.2935	
Storm days	1.2035556	0.577485	2.084	0.0371	*
Mean temperature	7.056223	5.944974	1.187	0.2353	
Rain days Jan, Feb, Mar	-0.13698	0.080716	-1.697	0.0897	.
Population density	-0.012921	0.012349	-1.046	0.2954	

Table S4.4: model estimates for fledglings per nest.

	Estimate	Std. error	z value	Pr(>|z|)	
(Intercept)	-1.50195	1.5999	-0.94	0.35	
Rain days	-0.01392	0.01334	-1.04	0.3	
Population fledglings	0.11172	0.08289	1.35	0.18	
Storm days	1.20256	0.82911	1.45	0.15	
Mean temperature	11.16228	8.1254	1.37	0.17	
Rain days Jan, Feb, Mar	-0.05761	0.07287	-0.79	0.43	
Population density	-0.01284	0.00921	-1.39	0.16	

Table S4.5: Model estimates for seasonal impacts on the probability of a nest surviving to hatching.

	Estimate	Std. error	z value	Pr(>|z|)	
(Intercept)	1.38E+00	1.03E+00	1.332	0.18272	
Rain days	-1.20E-06	1.05E-02	0	0.99991	
Population fledglings	3.85E-01	3.56E-01	1.081	0.27986	
Storm days	6.69E-01	1.92E-01	3.489	0.00049	***
Mean temperature	3.16E+00	1.45E+00	2.175	0.02964	*
Rain days Jan, Feb, Mar	-7.14E-03	6.21E-02	-0.115	0.90845	
Population density	-1.16E-02	7.09E-03	-1.631	0.1029	

Table S4.6: Model estimates for seasonal impacts on the probability of a nest surviving to fledging.

	Estimate	Std. error	z value	Pr(>|z|)	
(Intercept)	2.42144	2.01665	1.201	0.2299	
Rain days	-0.03532	0.01771	-1.994	0.0461	*
Population fledglings	3.29877	2.44021	1.352	0.1764	
Storm days	2.05181	1.37054	1.497	0.1344	
Mean temperature	18.47082	13.57607	1.361	0.1737	
Rain days Jan, Feb, Mar	-0.08618	0.11567	-0.745	0.4563	
Population density	-0.02836	0.01405	-2.019	0.0435	*

Table S4.7: model estimates for re-nesting probability for male birds.

	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	
(Intercept)	6.56817	1.60332	4.097	4.19E-05	***
Rain days	0.01393	0.01187	1.173	0.24061	
Population fledglings	1.33888	0.4561	2.936	0.00333	**
Storm days	0.47377	0.22488	2.107	0.03514	*
Mean temperature	5.07838	1.84328	2.755	0.00587	**
Rain days Jan, Feb, Mar	0.13597	0.07689	1.768	0.07698	.
Population density	-0.03846	0.01092	-3.523	0.00043	***

Table S4.8: model estimates for re-nesting probability for female birds.

	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	
(Intercept)	5.736041	1.456651	3.938	8.22E-05	***
Rain days	0.016748	0.010824	1.547	0.12178	
Population fledglings	1.093813	0.420717	2.6	0.00933	**
Storm days	0.563098	0.20689	2.722	0.00649	**
Mean temperature	4.009199	1.700965	2.357	0.01842	*
Rain days Jan, Feb, Mar	0.071243	0.071629	0.995	0.31992	
Population density	-0.035893	0.009956	-3.605	0.00031	***

5. Supplementary feeding reduces risk and improves outcomes of translocations in a tropical wild bird

5.1. Abstract

Conservation management of endangered species aims to mitigate specific threats, to enhance survival and reproductive rates of individuals and thereby improve population growth and persistence. Demographic and population viability analyses enable a range of biotic and abiotic factors to be varied so that their aggregate impacts on populations can be determined; for example, a range of different conservation management regimes can be simulated, and their outcomes forecast. Experimentation on endangered species can be difficult, risky, and unethical; and while such demographic modelling can therefore be of primary importance in conservation planning, it requires detailed longitudinal individual-based datasets which remain rare for tropical species of conservation concern.

Here, such data on the endangered Mauritius Fody *Foudia rubra* is used to make assessments of reproductive and survival rates, including the impact of conservation management, and these estimates are then used to inform a range of demographic models. VORTEX is used to model scenarios including harvests and new populations established from these harvested birds to determine whether previously demonstrated benefits of increasing access to supplemental food have population level impacts in these situations.

Results indicate that intense management can be used as a tool to aid in population recovery from major perturbations such as after a harvest, or as new populations are being established. The study population has a dual function as both a refuge from ongoing threats and a source from which new populations will be established in the future, and these scenarios confirm that management enables this population to fulfil both roles. Such insights will feed into decision-making for this species, enabling future conservation to be cost-effective while remaining highly effective in supporting the recovery of the species from critically low numbers.

5.2. Introduction

When deciding on management priorities for their target species, conservationists need an understanding of the full context of variation in vital rates of their target species. The causes of such variation can relate to individual factors such as territory quality (Shutt et al., 2021), or to climatic factors such as rainfall and temperature patterns (Bowgen et al., 2022). Frequently, wild populations will show high variance in productivity and survival as these factors interact. Conservation intends to improve the growth and viability of threatened populations; the specific aim of management will vary depending on the needs of the species and is generally intended to mitigate a specific threat, for example reducing the impact of invasive predators through trapping regimes (Maggs et al., 2015) or nest site limitation through the provision of nest boxes (Stojanovic et al., 2022).

Demographic modelling and population viability analyses (PVA) enable managers to explore impacts of intrinsic and extrinsic factors, including management, by varying vital rates including birth and survival and building this variation into a projection of full population outcomes. Demographic models can be used in conservation in a variety of ways; the impacts of conservation interventions, stochastic events, and climatic variables can be included, and the process can thereby clarify which drivers of variation in vital rates may have the greatest impact on future population size. Studies have used demographic modelling to identify juvenile mortality as a key driver of population decline (Stojanovic et al., 2022); to compare the impacts of multiple differing management interventions on reproductive rates of an ex-situ breeding programme (Franklin et al., 2021); and to examine the outcomes of a specific intervention, predator removal, for an island species (Fantle-Lepczyk et al., 2018).

Virtual tests of intervention impacts are particularly useful when managing endangered species, as limitations of time, budget or staffing may not allow experimental approaches which can also be risky and unethical when numbers are critically low or declining (Chauvenet et al., 2015; Fantle-Lepczyk et al., 2018). For example, Haig et al. (1993) were able to estimate the population viability of a remnant population of four red-cockaded woodpeckers after a severe bottleneck, and to determine that supplementation with translocated individuals was the most appropriate and effective conservation technique. Translocations are a commonly used conservation tool (Cade & Temple, 1995; Safford et al., 1998) which can be used to augment existing populations or to establish new populations, usually in sites which are either part of the species' historical range or are suitable due to available habitat and protection status. However, historically translocations do not have a high success rate (Berger-Tal et al., 2020; Mitchell et al., 2009), and involve significant risk to both the remaining individuals of the source population and to the individuals translocated (Fischer et al., 2022). The IUCN guidelines on translocations (IUCN & SSC, 2013) state that the impacts of harvests on the existing population must be considered to ensure that these are not destabilised, or the remaining individuals impacted detrimentally, and should also include accurate projections of how the new population may establish and what management interventions are required. Demographic modelling enables these questions to be answered with no risk to existing populations, and has been used to forecast the long-term outcomes of translocations in a huge range of taxa including mammals (Lee et al., 2020), birds (Freifeld et al., 2016) and reptiles (Glavas et al., 2022). These analyses require a thorough understanding of demographic processes for the target species, alongside longitudinal individual-based data and relevant climate and environmental data. Such datasets remain rare for tropical species of conservation concern (Chauvenet et al., 2012a; Reid et al., 2021) and therefore there are few studies which use PVA to assess the future of such species (but see Nicoll et al., 2021).

This study offers a rare opportunity to use quality long-term data on an endangered tropical bird the Mauritius fody *Foudia rubra*, to assess a range of biotic and abiotic factors as well as their aggregate impacts on population growth and persistence. The target population has dual objectives: firstly, as a refuge; it has been marooned on a restored offshore islet reserve (Ferriere et al., 2018) to protect it from threats of invasive species and habitat loss which persist on the mainland, and this population is likely to be the only viable remnant of this species. Secondly, because this population increased rapidly to the apparent carrying capacity of the islet and appears resilient, resulting in the down-listing of the species from Critically Endangered to Endangered (Birdlife International, 2019), the population will function as a source for planned future reintroductions. These objectives are potentially at odds, in that a key goal is removal of significant numbers from the only functional and protected population of an endangered species. The analyses presented here attempt to determine whether management can reconcile these objectives; specifically, whether the availability of supplemental food maintains population numbers and can be used as a targeted aid in population recovery and establishment after major perturbations such as harvests.

The Mauritius fody is endemic to Mauritius and its population declined to no more than 200 pairs in around 1995, due to concurrent pressures of habitat loss and introduced predators. The Mauritian Wildlife Foundation created a species management plan, with a reintroduction to a protected area a key goal. Île aux Aigrettes is a 27-hectare islet 800m off the coast of Mauritius at (20.23° S, 57.44° E), which has been partially restored and is managed as a reserve, with invasive predators removed. The study population of Mauritius fodies was released onto the islet between 2002 and 2004, with the initial birds being released in 2002 and smaller supplements in each of the subsequent two years, totalling 93 individuals. The population increased rapidly and reached a carrying capacity of around 200 adult birds, where it has remained largely stable. The population was offered supplementary food initially at one feeding aviary; a second feeding aviary was added part-way through the study. Almost all birds on the islet access this food, and daily monitoring of the feeding aviaries has resulted in the resighting data used to generate survival estimates in this study. In addition, birds are monitored for presence and breeding activity, leading to a large longitudinal individual-based dataset relating to nesting attempts and their outcomes. The annual reproductive success metrics used in this study are based on 1133 nesting attempts from 600 individuals over 12 years 2003 – 2015.

We use this monitoring data alongside relevant demographic analyses within VORTEX (Lacy & Pollak, 2018) to determine the impacts of management and on three key population scenarios. Firstly, the population growth rate and extinction risk of the current population which appears to be stable at a carrying capacity of around 200 adults; secondly, the impact of a harvest on the individuals remaining in this population; and thirdly the establishment of a new population formed from the harvested individuals. As previous work on this population has demonstrated the positive impact of management on individual reproductive rates of the fody (mediated by breeding phenology), it is hypothesised that management might also improve population growth and viability within these scenarios.

5.3. Methods

The population viability analyses aimed to address three key questions. Firstly, to determine the impact of supplemental food on the population growth and viability of the current Île aux Aigrettes fody population; secondly to determine impacts on the remaining population after a harvest of individuals for translocation, and lastly to forecast the establishment and development of a new population formed from such translocations. These scenarios were modelled within VORTEX (Lacy & Pollak, 2018), and the demographic model implemented was in the form:

$N_{t+1} = cbs_0N_t + sN_t$

where N = the number of adult individuals; c = proportion of adult females breeding; b = offspring per female per season; s_0 = the annual survival rate of birds from birth to 1; s = annual survival rate of adults ages 1+; and t = time (years). *b* has two components:

$b = o*p$

where *o* = mean offspring per female per brood and *p* = nesting attempts per season; detail of the calculation of these variables is outlined below.

b, the measure of offspring per female per season, is built from two components. *o*, the mean fledglings per female per brood, was calculated across the timespan of the Individual data as 0.4 ± 0.55 fledglings per brood. While earlier results show an impact of relative start on this metric, there is no impact of territory and therefore this value was constant across all scenarios.

The remaining component *p*, the distribution of broods per season, is observed from the same Individual data; while nesting rates measured in this way are not a focus of the earlier chapters of this thesis, this metric was chosen for these purposes as nesting rates depend on re-nesting probabilities which were analysed in Chapter 3. Results there indicated three key effects: firstly, re-nesting rates are higher if the nest has an earlier relative start; secondly re-nesting rates decrease more rapidly at greater distances from feeding stations; and thirdly the relative start of nests is determined by territory distance from a feeding station. However, re-nesting probability is not a metric available within VORTEX and therefore here the observed number of nests per female per year by distance from feeding stations is used as both representative of, and the natural outcome of, re-nesting probabilities and how these vary with access to supplemental food.

To enable the impacts of varying management intensity to be determined, the full range of territory distances were divided into 6 bins (Table 5.1). Future management plans for this species would consider available territory space and from this determine the number of feeding stations required to enable a specified mean territory distance from the nearest available feeder. The distribution of nests per season by female within each bin were varied in the Reproductive Rates tab of VORTEX; scenarios for bin 1 represent a population with intense management where the mean territory distance is less than 71.5 metres from a feeder; and those for bin 6 represent low intensity management where the mean territory is more than 357.51m from a feeder.

Table 5.1: Minimum and maximum of each distance bin as applied to the Île aux Aigrettes population. Bin 6 includes all remaining territories further than the stated distance.

Distance bin	Min distance of bin (m)	Max distance of bin (m)
1	0.00	71.50
2	71.51	143.00
3	143.10	214.50
4	214.51	286.00
5	286.10	357.50
6	357.51+	

The demographic model as outlined above was implemented in VORTEX, and population scenarios primarily use the distribution of nests per season, driven by both territory proximity and the relative start of breeding, to vary *n*. The proportion of females breeding within each season (*c*) was determined on a seasonal basis by expressing the number of females associated with nests with eggs with a season as a proportion of the total adult females observed within that season; the Individual dataset was used for this analysis. The final value used for VORTEX was the mean of these seasonal means at 68%. Fodies use nest building as part of pair bonding and as a social activity (Safford, 1997b), and therefore only nests with eggs which represent a serious reproductive effort were included in these analyses. While there is considerable mating system variation in this population, monogamous nests are 85% of the total analysed here, with rates of other mating systems varying between individuals and over time. As none of the available options within VORTEX better represent this system, the reproductive system selection was monogamy. Density dependence was modelled within these scenarios by imposing a carrying capacity of 200 adult birds, which approximates the true population. All other VORTEX inputs which were altered from the default are outlined in Table S5.1.

For each scenario described below, VORTEX ran 1000 iterations over 25 years and from these the mean projected population size for each year was determined. Mean population growth rates (lambda, λ) were estimated year-on-year for each iteration of each scenario ($\lambda = N_{t+1}/N_t$). The mean of these means is the overall scenario growth rate, and confidence intervals were obtained by ordering each iteration mean and taking the 25th and 975th values.

5.3.1. Survival estimates

Accurate population viability analysis (PVA) requires robust estimates of age-specific annual survival rates, and a bespoke survival analysis was performed to determine s_0 and s. To generate these, the package Capture Mark Recapture (Continuous Time) (CMRCT; Fouchet et al., 2016) was used within the R statistical environment (R Core Team, 2021). This package offers continuous time monitoring and therefore is suitable for the available data, which is generated by ongoing daily observations; packages which enable analysis of data in this form are not yet widely used. To create the models within CMRCT, 11 years of resighting data which were used, which were summarised into presence or absence of a bird within a specific month; this amounted to more than 17,000 records.

CMRCT requires the creation of separate formulae for survival and recapture estimates, and the initial approach was to follow a formal model selection process following a matrix of 45 models which varied age classes, sex, the number of feeding stations available and social network size and which allowed survival rates to change over time. While CMRCT does not include automated processes for formal model selection, it was possible to extract log-likelihoods from model output elements within R and from this AIC scores were calculated. From this model matrix the best supported models were those including constant survival and constant recapture with no variation between adults and juveniles, which are vital for further analyses in VORTEX (Table S5.2). As a result, it was decided to base the survival and recapture formulae on ecological reasoning around a priori knowledge of similar passerines, in which juvenile survival is reduced in relation to adult survival (Armstrong et al., 2021). The survival formulae therefore included the constant and age across the two classes which allows survival to vary between juveniles and adults. The age classes used were <1, indicating juveniles, and >=1 indicating adults; it was not possible to ungroup further into chicks and fledglings as for the majority of the study duration chicks were not monitored in the nest. The recapture formula included the interaction of age and time to allow for differences in effort and therefore resighting over the duration of the study. This approach smooths out time-based effects such as the impacts of the number of feeders or disease, and gives a single point estimate for juveniles (s_0) and adults (s) across the duration of the study.

5.3.2. Sensitivity analyses

A baseline scenario including the distribution of nesting rates across all distance bins, and other values as outlined above, was created to perform sensitivity analyses which clarify the main sources of uncertainty within the VORTEX scenarios.

For these sensitivity analyses, metrics otherwise kept stable in VORTEX were varied by ±10% (Table 5.2) to determine the influence of these metrics in relation to the baseline model. These scenarios followed a new population profile (see Section 5.3.5) to allow maximum variation in population growth rates over time and prevent the density-dependent dynamics of the carrying capacity overpowering other processes.

Table 5.2: Metrics varied in VORTEX for sensitivity analysis including baseline, decreased and increased values.

VORTEX input	Value	90%	110%
% adult females breeding	68.00	61.20	74.80
Offspring per female per brood	4.00	3.60	4.40
Mortality rates for adults	35.00	31.50	38.50
Mortality rates for juveniles	15.00	13.50	16.50

5.3.3. Current management

The initial goal of this study was to model the impact of supplemental feeding on the trajectory and viability of the current Île aux Aigrettes population, and distance bins as described were used to simulate six populations with differing levels of management intensity. Therefore, there were 6 initial scenarios which assumed a carrying capacity of 200 adult birds, approximating the true population.

5.3.4. Harvested populations

Because the species management plan for the fody includes the creation of new populations from harvests of the Île aux Aigrettes birds, the second goal of the study was to determine the impacts of such harvests on the IAA population. Using the initial scenarios above as baselines, 6 new scenarios model the outcome of harvesting 15 birds of each sex in years 4, 5 and 6 of a population at carrying capacity; these numbers were chosen to closely mimic the initiation of the Île aux Aigrettes population and to forecast the likely extent of a future harvest. All other variables remained the same.

5.3.5. New population establishment

Finally, the third goal of the study was to forecast the population growth and establishment of a new population formed from these harvested individuals, and to determine the importance of supplemental feeding on such translocations. New population scenarios were created to mirror the harvests outlined above; 15 birds of each sex released in year 1 and then a supplement of 15 birds of each sex released in each of years 2 and 3. This is comparable to the IAA population and future translocations are likely to follow a similar release schedule. All other variables remained the same.

5.4. Results

5.4.1. Survival estimates

The survival analysis conducted in CMRCT resulted in single point estimates of annual survival of 0.65 for juveniles and 0.84 for adults. These were inverted to generate the mortality rates included in VORTEX, which were 35 (SE +/- 10) for juveniles and 15 (+/-3) for adults. The empirical data required to generate accurate standard errors of these estimates were not available, and therefore notional values were included to introduce stochasticity; these mortality rates remain static across all scenarios within VORTEX.

5.4.2. Sensitivity analyses

Sensitivity analysis indicates that the baseline model is most sensitive to variation in input parameters relating to fecundity (Fig 5.1), which would be expected for a relatively short-lived passerine.

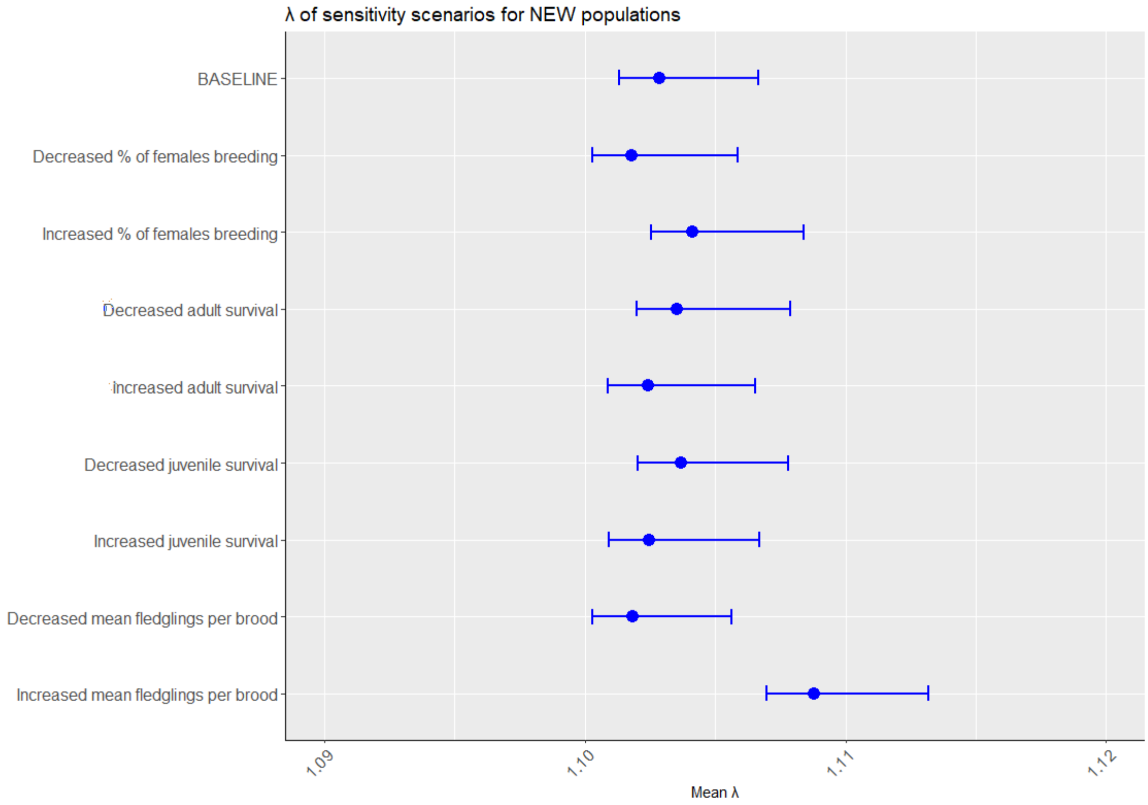

Figure 5.1: the impact of +10 and -10 of key demographic parameters on mean population growth rates across 1000 iterations of new and supplemented populations.

5.4.3. Current management

While the extinction risk of all 6 scenarios was 0 for this timescale of 25 years, there is considerably increased uncertainty within the bin 6 scenarios, and the growth rate and total size of this simulated population is reduced in comparison with the others (Fig 5.2, A and B). This indicates that the supplementation of food at low density may be inadequate to maintain the population at the current carrying capacity and therefore may be unable to fulfil the goal of maintaining this marooned population.

5.4.4. Harvested populations

Scenarios including the harvesting of individuals for translocation indicate that the population would recover rapidly (~4 years) when management intensity remains high (Fig 5.2, A and B). In contrast, the population size fails to recover to the carrying capacity on this timescale when under low intensity management and again the population growth rate is more variable. These results suggest that high intensity provision of food ameliorates the negative impact of harvesting on this population.

5.4.5. New population establishment

The results of scenarios examining the establishment of a new population suggests again that supplementary feeding improves population growth rates (Fig 5.2, A and B). Populations of birds under high intensity management increase rapidly, but under low intensity management population 6 increases much more slowly and does not reach the carrying capacity on this timescale.

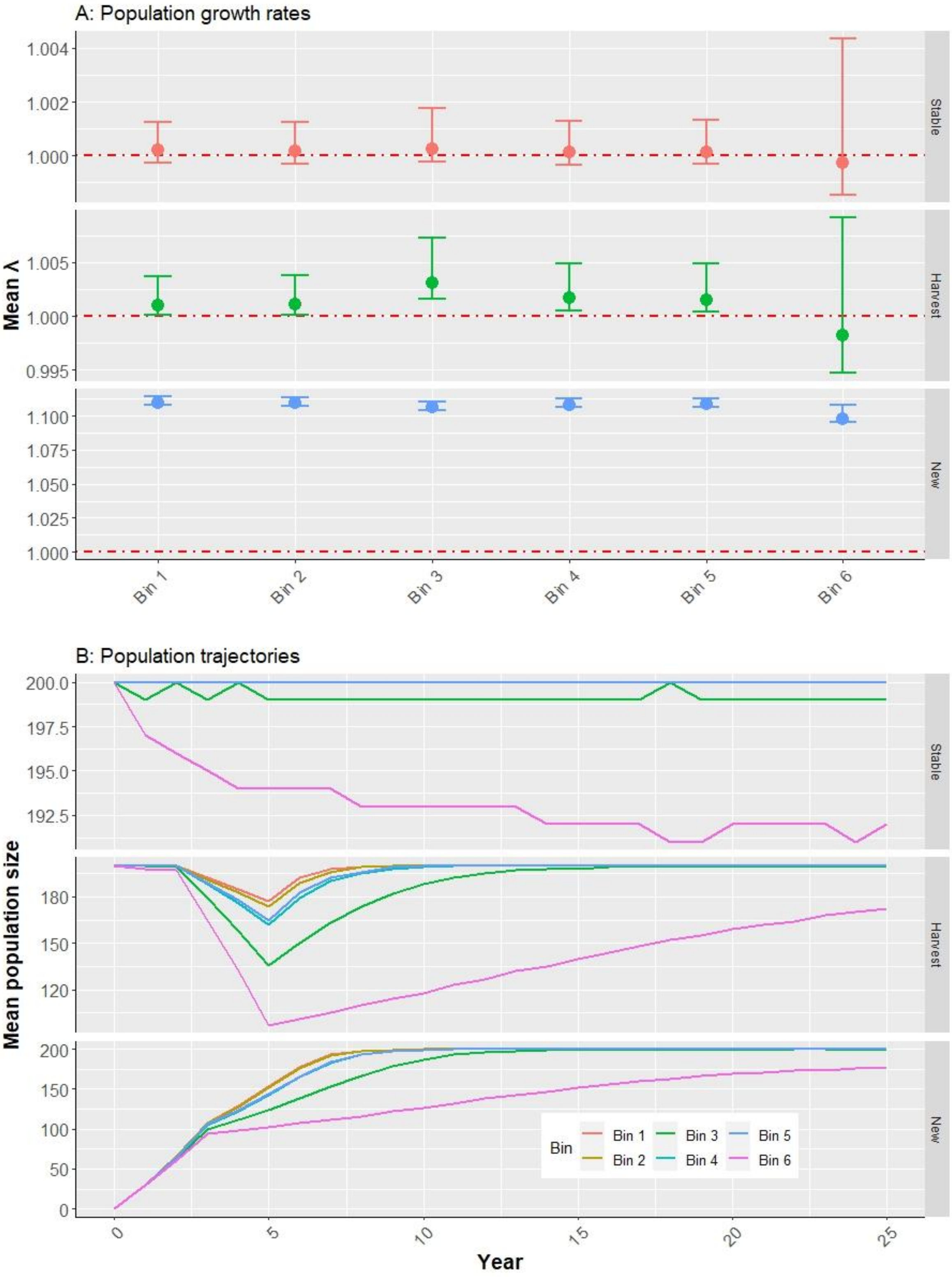

Figure 5.2: A: Mean population growth rates (λ); and B: mean total estimated population size B, over 1000 iterations of each scenario (Stable, Harvest, New), by distance bin from feeder. See Table 2 for details of distance bins. Red dotted line in A indicates λ of 1 which is necessary to maintain a stable population. Values shown in A, bins 1-6, Stable scenarios: 1.0001, 1.0001, 1.0002, 1.0001, 1.0001, 0.9998; Harvest scenarios: 1.0009, 1.0011, 1.0030, 1.0016, 1.0014, 0.9989; New scenarios 1.1050, 1.1046, 1.0977, 1.1038, 1.1039, 1.0943. Note that in the stable panel in B lines 1, 2, 4, and 5 are overwritten at K.

5.5. Discussion

This study demonstrates that conservation management can reconcile the dual goals of this population of fodies, in that access to supplemental feeding can be used as a tool to ameliorate negative impacts of translocations on remaining birds and new populations. Modelling of these scenarios in VORTEX demonstrates how PVA software can play a key role in the conservation of endangered species and can inform decision making and conservation planning. The sensitivity analyses performed here indicate that the model is most sensitive to fecundity, as would be expected for a small and relatively short-lived passerine.

The first aim of this study was to determine the impact of supplemental feeding on the maintenance of the current population at the carrying capacity of the habitat. Results suggest that only populations simulated with the lowest intensity management, where the mean territory distance is high, perform less well and with a reduced total population size. All other populations maintain at or very close to the carrying capacity.

The second aim of the study was to predict the impact of a harvest of birds from this population, in line with the species management plan which aims to create new sub-populations elsewhere to further increase total numbers and safeguard the species. The harvest scenarios were created to mimic the formation of the Île aux Aigrettes population in terms of the numbers of birds removed and the timescale of the harvest; future translocations would likely follow a similar pattern. The outcome of these scenarios suggests that management would be essential for the recovery of the remaining population after the harvest; populations simulated with the lowest intensity management failed to recover to the carrying capacity within 25 years whereas the scenarios in which all individuals had easy access to feeding stations (high intensity management) returned to carrying capacity within around 5 years.

Finally, birds taken from the harvest scenarios were used to simulate creation of new populations. Again, scenarios under high intensity management increased to the simulated carrying capacity rapidly, as the Île aux Aigrettes population did; while those with minimal management increased very slowly and did not reach the carrying capacity over the timescale of these scenarios. For these purposes it was assumed that any new release site will have similar climatic conditions as Île aux Aigrettes; and as Mauritius has no pristine habitat remaining even on restored islets, any new population is highly likely to require similar management during its establishment.

The survival estimates used within these scenarios were generated using a bespoke analysis because specifics of available data did not allow a more standard analysis to be performed, and it was not possible to create survival estimates which varied over time within different age classes. There is a lack of evidence for demographic rates of tropical species (Shogren et al., 2019), particularly for juvenile age classes, but tropical species appear to have higher survival rates than temperate (Scholer et al., 2020). The point estimates of annual survival generated for these two age classes (juveniles 0-1 years 0.65; adults 1+ 0.84) are in line with similar passerine species in which juvenile survival is lower than for adults (Dierickx et al., 2019), and were adequate for the survival estimates required by VORTEX scenarios which focused on variations in breeding rates due to management.

The outcomes of each scenario type suggest that birds at the greatest distance from a feeding station have a small but significant reduction in reproductive rates, and populations simulated from these rates have reduced growth and viability and increased uncertainty. It is currently unknown whether birds with territories in distance bin 6 access supplemental feeding at reduced rates or not at all, and only an experimental removal of food would clarify this. This uncertainty has implications for the management of this species; if these individuals remain reliant on food, removing it would impact their demographic rates, and the viability of the simulated populations would be similarly affected. This suggests that reducing or removing supplementary feeding would carry risk; overall the current population remains viable, but declines may result from a higher proportion of birds displaying the demographic rates of those at the highest territory distances. While prior results link nest productivity to the relative start date of the nest in that earlier nests are more productive, mean nest initiation dates across the distance bins used here are similar (see section 6.2) and this suggests that management may have little impact on this metric. Similarly, feeder density will also need to be considered when planning a translocation to a new site as the forecast of new populations suggests that access to food is key to rapid population increase.

Supplemental feeding is a commonly used management tool (Chauvenet et al., 2012a) and its efficacy has been previously demonstrated for the IAA fody population, with individuals with closer access to feeding stations having more nests per season than their peers. Previous work on endangered populations have also demonstrated a proximity effect of feeding stations (Tollington et al., 2019c), with the mechanism of such effects due to easing of time constraints for foraging as well as resource availability, although there are also concerns regarding feeding around disease transmission (Lawson et al., 2018; Robb et al., 2008). This study shows that supplemental feeding can be used as a highly focused tool and not just as an ad-hoc default response when supporting endangered populations; the scenarios analysed here demonstrate that this metric of food accessibility has specific benefits for population growth, and that accessibility could be reduced when the population is stable. These analyses demonstrate that, under appropriate management regimes this population will be able to fulfil its dual purpose as a refuge and a source.

Such questions around the provision and intensity of management are a part of the ongoing analysis of conservation efforts for endangered species, which may include a cost / benefit analysis of management and whether a reduction in intensity is feasible with minimal risk to the target species (Ferrière et al., 2014). Historically much conservation work has been ad-hoc and based largely on deterministic assumptions about the target species, and more formalised decision-making remains rare for species of conservation concern. Approaches such as Structured Decision Making (Panfylova et al., 2019)enable management alternatives to be compared before decisions are made and aims to reduce uncertainty, but requires detailed projections such as made here in order that alternatives can be ranked, and objectives achieved. Similarly, the formalised Conservation Standards (conservationstandards.org) emphasise that appraisal of outcomes is a key aspect of the ongoing cycle of assessment, planning, implementation, analysis, and sharing of conservation best practice. PVA, using systems like VORTEX as demonstrated here, can be a key part of such decision processes and enables evidence-based and cost-effective management to benefit species of conservation concern.

Taken together, these results indicate that intensive management is key for harvested and new populations, but that a static population of this species could be kept stable with a reduction in the current management intensity. These results demonstrate that intensive management can be targeted to situations where it is most needed and reduced in others, and this will feed into future management plans for this species and illustrate how long-term monitoring data and modelling can be used to clarify conservation priorities amid the complexity of threat mitigation.

5.6. Supplementary Materials

Table S5.1: VORTEX parameters varied from default settings. For details of values in bold see relevant Methods section.

Parameter	Value
Scenario settings	
Number of iterations	1000
Number of years	25
Extinction definition	N < 1
Reproductive system	
Reproductive system	Monogamy
Age of first offspring females	1
Age of first offspring males	1
Maximum age of reproduction females	20
Maximum age of reproduction males	20
Maximum lifespan	20
Maximum broods per year	11
Maximum progeny per brood	4
Sex ratio at birth -- in % males	50
Reproductive rates	
% of adult females breeding	67
SD in % breeding due to EV	0
Distribution of broods per year	**See Methods**
Offspring / female / brood (normal distribution)	Mean 0.29, SD 0.76
Mortality rates	
Mortality from 0-1 (both sexes)	**See Methods**
SD in 0-1 mortality due to EV (both sexes)	**See Methods**
Annual mortality after age 1 (both sexes)	**See Methods**
SD in mortality after age 1 (both sexes)	**See Methods**
Mate monopolization	
% of males in breeding pool	100
Initial population size	
Initial population size	**See Methods**
Carrying Capacity	
Carrying Capacity	200
SD in K due to EV	0
Harvest	
Population harvested	**See Methods**
First year of harvest	5
Last year of harvest	6
Number of females from after age 1	30
Number of males from after age 1	30
Supplementation	

Population supplemented?	**See Methods**
First year of supplement	2
Last year of supplement	3
Number of females from after age 1	15
Number of males from after age 1	15

*Table S5.2. Model form, calculation criteria and ultimate Akaike weight of formal model selection structure for initial CMRCT model matrix. S(.) indicates constant survival; P(.) indicates constant recapture effort. Age(*) indicates the number of age classes included (0,1+ or 0, 1-2 and 2+). Upper case T is time as a categorical variable; lower case t indicates time as a continuous variable; F indicates time represented by the number of available feeders. The calculations used were: AIC = -2(log-likelihood) + 2K; relative likelihood = exp (-0.5 * Δ AIC); Akaike weight = relative likelihood divided by the sum of relative likelihood across all models. The sum of all relative likelihoods as used for this calculation was 1.171967.*

Model	Log-likelihood	Parameters (K)	AIC	Δ AIC	Relative likelihood	Akaike weight
S(.)P(.)	**-22364**	**2**	**44732**	**0**	**1**	**0.853266**
S(t).P(.)	-22365	3	44736	4	0.135335	0.115477
F	-22367	3	44740	8	0.018316	0.015628
S(.)P(t)	-22367	3	44740	8	0.018316	0.015628
Recap(F), null	-22378	3	44762	30	3.06E-07	2.61E-07
Age(2)	-22397	3	44800	68	1.71E-15	1.46E-15
Age(2) + t	-22397	4	44802	70	6.31E-16	5.38E-16
Age(2) + t + age(2) * t	-22398	5	44806	74	8.53E-17	7.28E-17
Age(2) + F	-22400	4	44808	76	3.14E-17	2.68E-17
Age(2) + F + age(2) * F	-22400	4	44808	76	3.14E-17	2.68E-17
Recap(t) + age(2)	-22401	4	44810	78	1.15E-17	9.85E-18
Age(3)	-22402	4	44812	80	4.25E-18	3.62E-18
Recap(t), age(2) + t	-22401	5	44812	80	4.25E-18	3.62E-18
Age(3) + t	-22403	5	44816	84	5.75E-19	4.91E-19
Recap(t) + age(2) + F	-22403	5	44816	84	5.75E-19	4.91E-19
Recap(T), null	-22396	12	44816	84	5.75E-19	4.91E-19
Age(3) + F	-22404	5	44818	86	2.12E-19	1.8E-19
Age(3) + t + age(3) * t	-22403	7	44820	88	7.78E-20	6.64E-20
Recap(t), age(3)	-22406	5	44822	90	2.86E-20	2.44E-20
Age(3) + F + age(3) * F	-22405	7	44824	92	1.05E-20	8.99E-21
Recap(t), age(3) + t	-22406	6	44824	92	1.05E-20	8.99E-21
Recap(t), age(3) + F	-22408	6	44828	96	1.43E-21	1.22E-21
Recap(F), age(2)	-22412	4	44832	100	1.93E-22	1.65E-22
Recap(F), age(2) + t	-22412	5	44834	102	7.1E-23	6.05E-23
Recap(F), age(2) + F	-22414	5	44838	106	9.6E-24	8.19E-24
Recap(F), age(3)	-22417	5	44844	112	4.78E-25	4.08E-25
Recap(F), age(3) + t	-22417	6	44846	114	1.76E-25	1.5E-25
Recap(F), age(3) + F	-22419	6	44850	118	2.38E-26	2.03E-26
Recap(T), age(2)	-22430	14	44888	156	1.33E-34	1.14E-34

Recap(T), age(2) + t	**-22430**	**15**	**44890**	**158**	**4.91E-35**	**4.19E-35**
Age(2) + T	**-22434**	**14**	**44896**	**164**	**2.44E-36**	**2.08E-36**
Recap(T), age(2) + F	**-22433**	**15**	**44896**	**164**	**2.44E-36**	**2.08E-36**
Recap(T), age(3)	**-22435**	**15**	**44900**	**168**	**3.31E-37**	**2.82E-37**
Recap(T), age(3) + t	**-22435**	**16**	**44902**	**170**	**1.22E-37**	**1.04E-37**
Recap(t), age(2) + T	**-22438**	**15**	**44906**	**174**	**1.65E-38**	**1.4E-38**
Recap(T), age(3) + F	**-22438**	**16**	**44908**	**176**	**6.05E-39**	**5.17E-39**
Age(3) + T	**-22444**	**15**	**44918**	**186**	**4.08E-41**	**3.48E-41**
Recap(F), age(2) + T	**-22449**	**15**	**44928**	**196**	**2.75E-43**	**2.35E-43**
Recap(t), age(3) + T	**-22448**	**16**	**44928**	**196**	**2.75E-43**	**2.35E-43**
Age(2) + T + age(2) * T	**-22449**	**25**	**44948**	**216**	**1.25E-47**	**1.06E-47**
Recap(F), age(3) + T	**-22459**	**16**	**44950**	**218**	**4.59E-48**	**3.92E-48**
Recap(T), age(2) + T	**-22469**	**25**	**44988**	**256**	**2.57E-56**	**2.19E-56**
Recap(T), age(3) + T	**-22479**	**26**	**45010**	**278**	**4.3E-61**	**3.67E-61**
Age(3) + T + age(3) * T	**SINGULAR FIT**					
T	**SINGULAR FIT**					

6. General discussion

6.1. Summary of results

This study investigates the impacts of a management intervention, specifically supplemental feeding, on a population of the endangered island endemic Mauritius Fody *Foudia rubra*. The main aim was to determine whether long-term monitoring datasets can be used to evidence the benefit of conservation interventions even in ecologically complex situations where natural processes can confound the impacts of such interventions; and whether analyses of such datasets can support the recovery of species from critically low levels.

The supplemental feeding that this study assesses was not planned or initiated as part of a formal conservation management programme. Ad-hoc management of this kind is common within conservation programmes, as when threats to endangered species are ongoing and populations are declining, the time necessary for a fully planned and assessed management programme is a luxury not always available. In addition, such planning requires time, money, and effort from managers at a time when rapid practical interventions are required. Thus, at present such analyses are frequently retrospective and depend on long-term monitoring programmes which generate the data necessary.

In the analyses performed here, results show that this management influences individuals and the population, albeit indirectly, and that it will remain important for future conservation scenarios for this species. The annual productivity of individuals in this multiple-brooded species is determined by both numbers of fledglings per nest, and total nests per season. Results indicate that the key metric influencing both factors is the relative start date of the nest, but also that some birds on territories with closer access to feeding stations can initiate breeding earlier and therefore benefit from an increase in both components of individual productivity.

When discerning potential impacts of conflict on this population, some inference is required as there is no direct data available on conflict. The metric of unpaired members of the opposite sex was initially included as a measure of potential mating opportunity, but analyses show that the presence of higher numbers of unpaired birds dampens productivity for both sexes. This is likely to be due to the territoriality of this species and intra-sexual competition for territory and mating opportunities. However, results do not fully support the alternative hypothesis that productivity on high quality territories is dampened disproportionately as the proportion reaches carrying capacity within the ‘stable’ phase of these data. The presence of unpaired members of the opposite sex does reduce fledgling production, but there is only a temporal pattern linked to productivity for females, and no such pattern for males who are the primary territory holders.

Results then show that a range of stochastic factors such as rain days and average seasonal temperature impact the productivity of the entire population. The specific mechanism of the benefits here remains unknown, although they likely relate to habitat suitability for repeat nesting, and for females to a reduction in the energetic demands of brooding. The influence of a reduction in the number of pre-seasonal rain days may be linked to both increased time for foraging and therefore better body condition, and to the potential for an early start to breeding.

The Île aux Aigrettes fody population has a dual role as both a refuge for the species from ongoing mainland threats, and as a source from which individuals for new populations will eventually be harvested. VORTEX scenarios including a range of survival and reproductive rate parameters were used to determine whether the management in place for this population can reconcile these conflicting roles by promoting population growth rates and maintaining the population once the carrying capacity has been reached. As repeat nesting attempts are the outcome of higher re-nesting probability, VORTEX scenarios included the distribution of nests per season across the span of territory distances. These scenarios demonstrate that proximity to food is vital for the maintenance of current numbers, the recovery of the population after a harvest, and for the rapid establishment of a new population formed from harvested individuals.

Productivity is reduced in individuals furthest from feeding stations, but it is not possible given the data available to determine whether these individuals access supplemental food less than their peers, or not at all. If productivity rates as seen on these territories is fully independent of food, this provision could be removed with no population impact. However, if these birds do rely on food, removing it entirely may reduce productivity further and the population may decline as a result. Only an experimental removal of food would establish which applies, and this may suggest a potential future research focus for this species.

While the overarching conclusions drawn from these analyses are strong, the experimental design was limited by some aspects of the data available, and the data is unbalanced as a result. The second feeding station was added to the study system part-way through a breeding season with only one full season after this falling within the scope of this study. This paucity of data meant that it was not possible to separate the impacts of the second feeder from those of increasing population density. In addition, not all data included within the analysis were available for all seasons; territory mapping was not conducted across all years of the study and as a result analyses directly including this metric did not include all breeding seasons. The link between territory proximity to feeders and relative start is strong, however, and it is highly unlikely that the small number of missing years within this dataset would alter or reverse the relationships demonstrated.

Taken together, these results appear to support the main hypothesis of this thesis, that supplemental feeding is effective at improving reproductive effort and success and population persistence, mediated by its impact on the relative start of breeding which is the proximal driver of increased fledgling output for birds seasonally and for individual nests.

6.2. Passerine breeding phenology

The timing of breeding events is commonly a key driver of productivity for breeding birds. Accurate timing of nesting events synchronises both ideal climatic conditions and resource availability, and in species that have repeat nesting attempts early breeding can maximise the duration of their breeding effort and therefore enables more nests. Here, results demonstrate that access to supplemental feeding increases individual productivity via both routes, in that birds on high quality territories have more early nests which are more productive, and have higher re-nesting rates. Mean nest initiations are similar across all distance bins used in the VORTEX analyses (Fig 6.1); however, Fig 3.8 and analyses in Chapter 3 show that territory proximity enables some birds to initiate breeding earlier than their peers. Taken together, this suggests that the impact of territory distance from a feeder is specific to the birds which able to defend these territories; it may be that these individuals are of particularly high quality and therefore that the impact of management is mediated via both territory and individual quality enabling an earlier start of breeding. There is however no body condition data available on this population to enable inclusion of these metrics in these analyses.

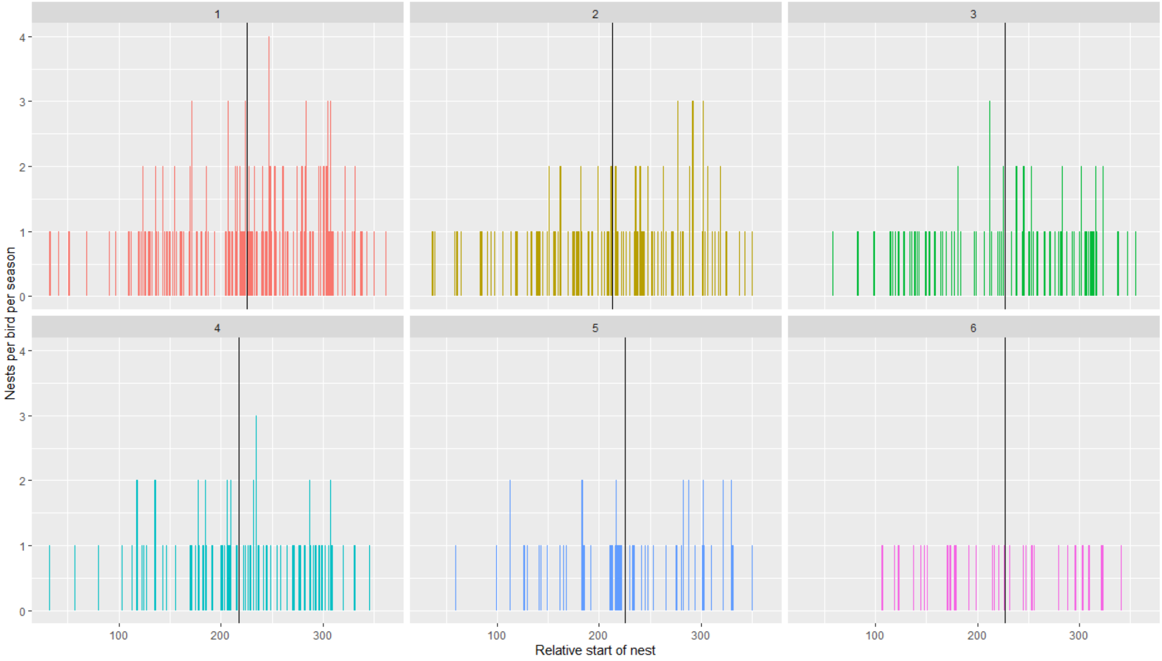

Figure 6.1: Distribution of the relative start of breeding and nests per season for distance bins as used in VORTEX analyses (Chapter 5). Vertical lines within each panel indicate mean nest start date for that distance bin; no significant difference exists between these mean dates (AOV F 0.102, p = 0.749).

6.3. Climate change

Climate change is impacting Mauritius through these changing rainfall patterns and in increasing temperatures. For the fody, a certain amount of climate warming is beneficial to annual reproductive success, although the specific mechanism of this benefit is currently unclear. Fodies built nests from dry leaves and warmer years may increase the availability of suitable nesting materials; one male participated in 16 nesting attempts within one season and such behaviour requires a large amount of nesting material as fodies are not known to reuse nests. Additionally, warmer ambient temperatures release females from the requirement to brood eggs and young chicks. This reduces time constraints which may enable the female to start another nesting attempt or to improve her body condition in preparation. For many temperate species, the ‘climate window’ within which a species can function is well understood (Taylor et al., 2021b); but for the fody it is not, and many species demonstrate a ‘thermal cliff’ of physiological performance in which increasing temperatures optimises performance but only as far as a peak after which performance declines rapidly (Cunningham et al., 2021). The maximum temperature of the fody climate window may be reached at any point, and therefore it cannot be assumed that further anthropogenic warming will continue to be beneficial.

Climate change driving asynchrony between avian reproductive effort and ideal conditions of climate and foraging, and therefore is an increasing concern for conservationists as this can destabilise populations (Simmonds et al., 2020; Youngflesh et al., 2023). Climate change in Mauritius may also interact with the most important metric shown in these analyses, which is breeding phenology and specifically the relative start of breeding within each breeding season. In breeding seasons with more pre-seasonal rain days, breeding is initiated later (Fig 4.2); previous work has shown that rain days during this period are increasing in Mauritius with anthropogenic climate change (Senapathi et al., 2010). This may impact on individual annual reproductive success, as birds may take longer to gain breeding condition during the pre-season and as nest initiation is pushed later into the breeding season. The results demonstrated in Chapter 3, that access to supplemental feeding enables an early relative start of breeding, suggests that management may enable birds on high quality territories to mitigate some of the impacts of these changing rainfall patterns. This indicates that management of endangered populations can increase individual productivity and improve population persistence despite negative impacts of the changing climate.

6.4. Management recommendations

The Mauritius fody has previously been little studied, and these results increase understanding of several aspects of its ecology and demography which may feed into management decisions. The Île aux Aigrettes population appears healthy and resilient; Vortex modelling of static populations in Chapter 5 shows that populations modelled on distance bins 1-5 are similarly productive and only populations simulated at the furthest distance from feeders were unable to maintain their numbers at the simulated carrying capacity. However, if these most distant birds are still reliant on management, even a partial reduction in management intensity could result in destabilising the population and impacting its viability. The specific locations of the two current feeding stations offers a potential route to reducing the cost and effort of the current management programme. Currently, there is one feeding station near the centre of the island and one closer to north-west shore; maintaining this feeding station alone would provide the shortest possible average territory distance for all birds on the island, and almost all birds would be within distance bins 1-5 (Fig 6.2, A) which approximates to within 350m of a feeding station. Maintaining just the field station feeder would leave large parts of the islet at distance 6 or further (Fig 6.2, B). Potentially, therefore, the provision of food to the current population could be reduced to just the central station, reducing expense, disease transmission and staffing time. Further data is required to clarify the use of feeders by the most distant birds, and to minimise the risk of any change in management.

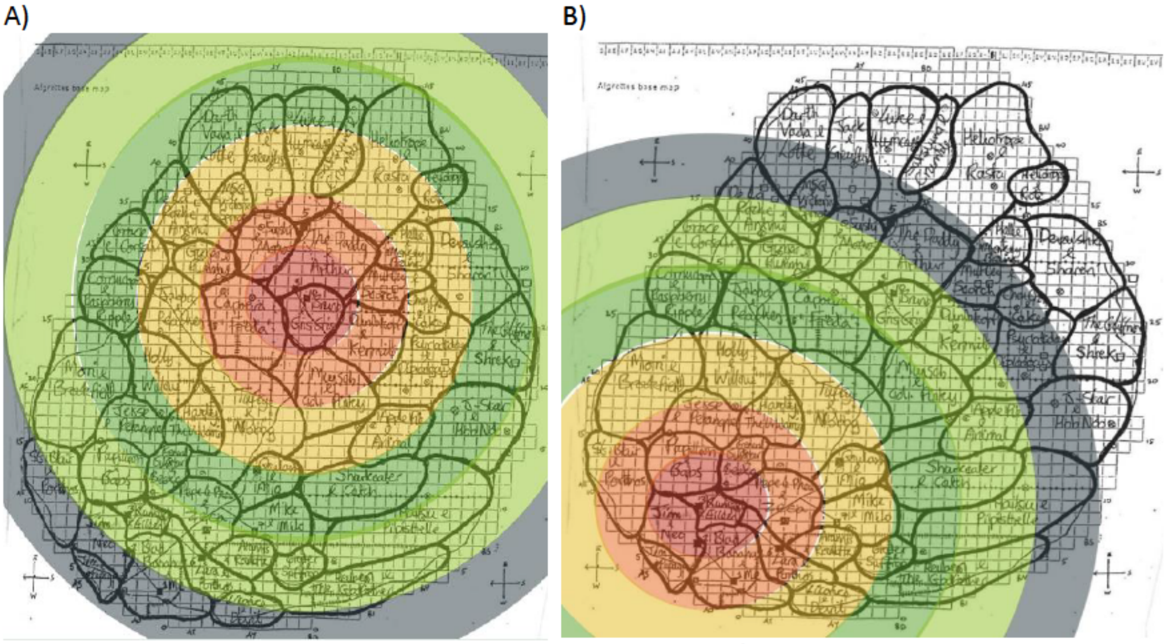

Figure 6.2: Colour bands approximating distance bins 1-6 overlaid on map of Île aux Aigrettes for A) the central feeder and B) the NW shore feeder (note that the map is rotated). If only the central feeder was used, almost all of the island is at <= distance 5; if only the NW shore feeder was used a large part of the S, SE and E areas of the islet are at distance 6 from the feeder and any birds with these territories will be less productive than their peers.

The same population scenarios indicate that when a harvest is performed, or when a new population is being established, intense management is necessary for the original population to recover and for the new to increase rapidly. In the harvest scenarios, the simulated number of individuals to be removed was realistic for the foundation of a new population and approximates the 93 individuals released onto Île aux Aigrettes at the start of the conservation project. With the most intense management in place the population recovers to the estimated carrying capacity of

200 adult birds within around 5 years of the harvest, but populations with reduced intensity management do not recover to the carrying capacity over the timeline of these scenarios.

6.5. Conservation decisions

The outcomes of conservation can sometimes be counter-intuitive; for example supplemental feeding of the Seychelles magpie-robin led to an increase in conflict that reduced the productivity of the highest quality territories (López-Sepulcre et al., 2010); and declaring the Javan Hawk a Precious Animal increased demand for it within the illegal pet trade (Larrosa et al., 2016). Therefore, demonstrating the effectiveness of practical conservation interventions is a key process for managers and will become more vital in the future as anthropogenic pressures on endangered species increase.

Despite this increasing need for conservation as the biodiversity crisis continues and intensifies, budgets available for conservation are not increasing. This means that conservation managers are required to factor finance into their planning, to ensure that measures taken are as cost effective as possible. The provision of supplemental food ad libitum can be highly expensive and could therefore impact negatively on the long-term sustainability of conservation projects (Tollington et al., 2019c). Analyses such as used here can allow managers to determine where and when to focus interventions, and to forecast when management intensity can be reduced with minimal impact on the target species. Evidence-based decisions of this type, which clarify the specific benefits of practical conservation, are vital for any formal conservation planning, whether using Structured Decision Making, adaptive management or the Conservation Standards framework.

In addition, there have been criticisms that the increase in conservation science over recent decades has not been matched by increases in appropriately planned and tested interventions for species of conservation concern (Williams et al., 2020). Decisions around such interventions are frequently made ad-hoc by managers, while being based in a knowledge of the target species; analyses of such decisions are therefore necessarily retrospective and dependent on data quality. A recent review of 554 translocation projects determined that most of these conducted post-release monitoring for a maximum of 4 years; and the projects that failed also failed within the same timescale (Bubac et al., 2019). Unpacking the complex interactions of management and stochastic events as in this study would not be possible with 4 years of data, and this emphasises the calls of Sutherland *et al* (2010) for all conservation studies to include long term monitoring as standard.

6.6. Wider relevance

The need for practical conservation interventions is increasing rapidly and will continue to do so as threats of habitat loss, invasive species and anthropogenic climate change are ongoing. The results illustrated here therefore have a wider applicability with a dual purpose. Firstly, in terms of other species facing similar pressures from invasive species and habitat loss, and secondly in terms of the methods and analyses used to clarify the drivers of reproductive variation and population increase specific to this species.

Supplemental feeding is a very commonly used conservation tool, but managers have faced criticism for implementing it as a default conservation measure with little consideration of potential negative outcomes such as increasing the spread of disease, or of detailed assessment of its positive impacts (Tollington et al., 2019c). Results demonstrate that the provision of supplemental food can play a key role in the establishment and population growth rate of endangered populations, and access to food is vital in maintaining stable numbers. While there is some disease within the Île aux Aigrettes population (largely Trichonomiasis and avian pox (Bambini et al., 2009)), this has not been a major concern in all seasons and does not appear to be a significant limiting factor in the expansion of this population.

The provision of food can interact with other management interventions, by ameliorating the impact of major population perturbations such as the removal of individuals for further translocations, and this evidence of a reduction in risk of such harvests may be useful to managers of other species in similar situations. It seems likely that supplemental feeding would also aid a similar population recovery after significant mortality due to a cyclone or other stochastic event. Cyclones are predicted to increase in occurrence and severity, in the Indian Ocean and globally as a result of anthropogenic climate change (Elsner et al., 2008; Knutson et al., 2019; Thompson et al., 2021), and while the Île aux Aigrettes population has yet to be directly impacted by such an event, understanding the mechanism by which supplemental feeding can boost population productivity after such events is a key part of endangered species management.

Failure to mitigate causes of initial declines are a leading contributor in the failure of a high proportion of reintroduction and translocation projects (Bubac et al., 2019), and results confirm that the establishment of new populations may be more rapid and effective if they are supported by supplemental feeding, especially if the habitat involved has not been fully restored to its full function. Levels of natural food can be greatly reduced in degraded and fragmented habitats, and so the provision of supplemental food acts to enhance habitat quality (Grüebler et al., 2018), enabling individuals to gain body condition for repeat breeding, and provision of chicks and eggs. Given the number of island species worldwide in similar situations to this fody population, confirming the benefit of supplemental food may be useful to managers of other populations.

There have been repeated calls for translocation and reintroduction projects to include long-term monitoring in their planning, to enable the creation of detailed datasets such as used here but which remain rare for species of conservation concern. Ecological data can be highly complex and difficult to analyse, and specific drivers of individual variation which cause some birds to be more successful than others can be masked by concurrent environmental and stochastic variation which also impacts on the same vital rates. In the future, therefore, equivalent methods may be used on similar datasets to unpack such issues for other species. For this reason, in the analyses focused on differences between individuals the productivity metric is centred around the seasonal mean, which removes the impact of seasonal variability and allows assessment of drivers of anomalous productivity which are higher and lower than this seasonal mean. This reveals important impacts of territory proximity to food, and of varied mating systems, which may be relevant to other species but can be difficult to discern in such datasets.

The fody is a highly territorial species (Safford, 1997b) and the specific impacts of supplemental feeding for this population is mediated by territory proximity to feeding stations. The issue of access to feeding stations has been noted in other species (Tollington et al., 2019c), which have also noted that distance from feeding stations determines the access to food and the quantity of food consumed. Results here suggest that a similar process happens within this population, and that birds with territories nearer to either feeder can access more food and increase reproductive effort as a result. In some territorial species, high quality males are able to defend higher quality territories, where the territory quality relates to access to food *(Red-winged blackbird Agelaius Phoeniceus*, Gronstol, 2018; Pribil & Searcy, 2001), or availability of nest sites (White-throated dipper *Cinclus cinclus*, Walseng et al., 2022), and such males are able to attract high quality females or be polygynous as a result.

6.7. Summary

In this thesis results demonstrate the ongoing effectiveness of a conservation intervention, supplemental feeding, in supporting the population growth and persistence of this endangered species. The fody was downlisted from Critically Endangered to Endangered in 2009 because of the rapid increase and establishment of the population on Île aux Aigrettes (Birdlife International, 2019) and results suggests that supplemental feeding has played a key role in this recovery. VORTEX modelling forecasts that this management can continue play this role in the future by reconciling the dual role of this population as a refuge and as a source from which harvests will be taken for further translocations. The success of the Île aux Aigrettes fody population, and the other species supported there, is also a demonstration of the impact offered by ecosystem restoration as well as interventions targeted at individual species.

There is currently a divide within conservation between scientists performing analyses and those working directly with endangered species in a practical capacity. Effective interventions require planning and assessment; and yet conservation science has recently faced criticisms that advances in analysis and quantification of threats to endangered species have not been matched by the translation of knowledge gained into interventions to benefit the species in question. Professor Carl Jones, who has worked in Mauritius conservation since the 1970s, has identified this gulf between analytical scientists and managers as a major issue in conservation today (Jones, 2021). This work contributes to bridging this gap and demonstrates that endangered species will be best served in the future by these two arms of the science becoming more united; by the rapid interventions of managers informed by accurate and appropriate analysis of threats and their mitigation from analysts.

The need for formally assessed conservation outcomes as provided by Structured Decision Making or Conservation Standards may assist with this unification and would make sharing of expertise and methods across projects considerably easier. However, any such system must be informed by accurate data and appropriate analyses, such as those used here. All conservation programmes should include individual-level monitoring as an integral part of their planning, to enable ongoing monitoring both the impact of threats and of population growth and recovery. This study demonstrates how such data and analyses can clarify key drivers of population growth and persistence, and how management can be informed by such analyses. These results may also be informative to managers of species in similar circumstances and facing similar threats, and methods used here have a much wider applicability across conservation in the light of ongoing anthropogenic threats and the global biodiversity crisis.

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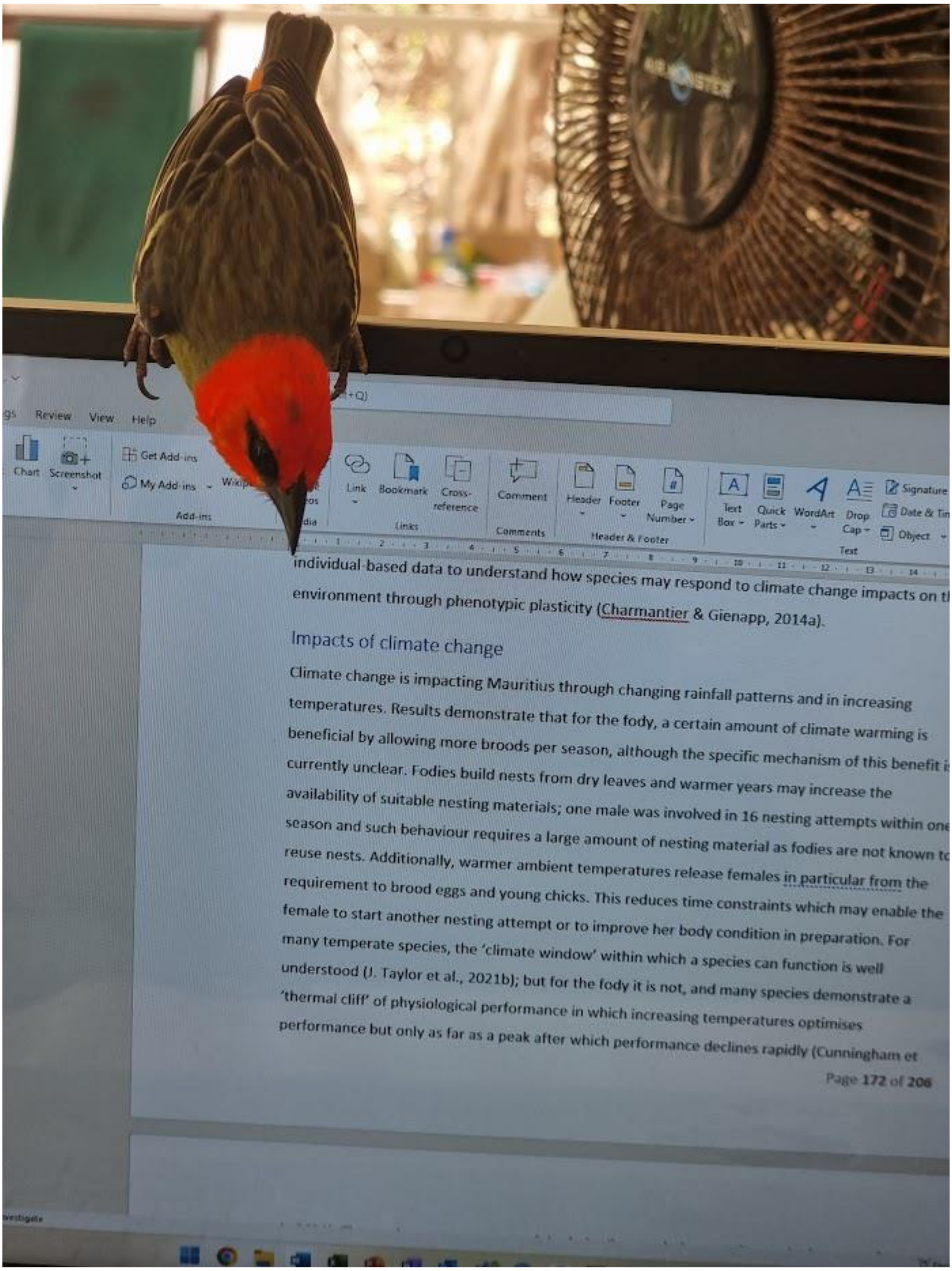

individual-based data to understand how species may respond to climate change impacts on t environment through phenotypic plasticity (Charmantier & Gienapp, 2014a).

Impacts of climate change

Climate change is impacting Mauritius through changing rainfall patterns and in increasing temperatures. Results demonstrate that for the fody, a certain amount of climate warming is beneficial by allowing more broods per season, although the specific mechanism of this benefit i currently unclear. Fodies build nests from dry leaves and warmer years may increase the availability of suitable nesting materials; one male was involved in 16 nesting attempts within one season and such behaviour requires a large amount of nesting material as fodies are not known t reuse nests. Additionally, warmer ambient temperatures release females in particular from the requirement to brood eggs and young chicks. This reduces time constraints which may enable the female to start another nesting attempt or to improve her body condition in preparation. For many temperate species, the 'climate window' within which a species can function is well understood (J. Taylor et al., 2021b); but for the fody it is not, and many species demonstrate a 'thermal cliff' of physiological performance in which increasing temperatures optimises performance but only as far as a peak after which performance declines rapidly (Cunningham et

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Fody 'Eleanor' signs off on this thesis. Île aux Aigrettes, 8th December 2022.