Conservation Management of the Endangered Mauritius Parakeet *Psittacula echo*

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Declaration

I, Helen Claire Gath confirm that the work presented in this thesis is my own. The research was supported by funding from the National Environment Research Council (NERC) as part of a CASE studentship awarded to K. Norris.

All chapter of this thesis were written by H. Gath with guidance and comments from K. Norris, M. Nicoll and B. Collen.

Annual breeding records and individual studbook records were collected by the Mauritius Wildlife Foundation as part of a long-term conservation monitoring programme, with an initial data set provided by C. Raisin and S. Tollington. Information regarding the use of supplementary food by breeding pairs was provided by S. Tollington. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Helen Claire Gath, 26th September 2017

Abstract

Effectively managing wild populations requires drawing upon a range of skills from multiple scientific disciplines. Given the current biodiversity crisis the world now faces, developing these skills is a high priority in conservation science. Improving the success of species recovery programmes and sustaining them requires adopting the correct monitoring regime and implementing suitable restorative tools. To then evaluate their effectiveness and adjust methods accordingly is fundamental to ensuring continued success. The principal aim of this study has been to explore key approaches to conservation practice and their suitability for the management of the Mauritius (echo) parakeet, once considered the rarest parrot in the world. Nearly 25 years after intensive recovery efforts were initiated, their conservation is entering a new phase that looks toward a long-term strategy of minimal management. Achieving this requires a basic knowledge of the population's demography and an assessment of the demographic response to management actions and infectious disease, knowledge which to date, has remained limited

Accurately estimating demographic rates is a cornerstone to assessing the impact of management strategies or environmental conditions. Capture-mark-recapture (CMR) data plays an important role in this, but the accuracy of multistate models used to interpret such data is well debated when a species' life history includes unobservable states. My analysis explored such potential inaccuracies and found that for the echo parakeets at least, unobservable multistate models led to biased estimates of vital rates and excluded important information regarding transitions between states. Combining the extensive CMR data with detailed breeding records, I explored the demographic impact of supplementary feeding (SF), a widely employed conservation tool but one often reporting varied responses from target populations. This study quantified the positive impact that SF has had on fecundity rates, which no doubt played a key role in the population's growth. However, further work as part of this study also revealed that SF exacerbated the negative impact of an outbreak of psittacine beak and feather disease. I explore the extent of the outbreak and its demographic

impact during and after its emergence in the echo population, and discuss the value of my findings in the context of the growing global threat of emerging infectious disease.

The findings from my research provide a basis of vital information that could support evidence-based adaptations to the current management programme. Understanding the influence of management strategies will lead management toward better targeting and more efficient use of resources that will ultimately help to ensure the long term survival of the echo parakeet.

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Chapter 1

General Introduction

1.1 Population regulation

Understanding the factors and mechanistic processes responsible for shaping populations is a central theme in ecology and represents a very large and thriving research field (Lack 1954; Newton 1998; Saether and Bakke 2000; Jones and Coulson 2006; Horswill *et al.* 2014). A population's dynamics ultimately represent the summed life histories of all individuals within a population. The combined effect of these individuals will shape patterns at the population level, patterns which ultimately determine population size and rates of growth or decline (Butler *et al.* 2009). Multiple factors and mechanistic processes drive population regulation and these may operate independently or interact to create change at a range of spatial and temporal scales (Post and Stenseth 1998; Stenseth *et al.* 1999; Ottersen *et al.* 2001; Altwegg *et al.* 2006). Examining these complex processes is not always simple, but exploring the mechanisms governing population stability and regulation provides a fundamental framework for wildlife management.

Population growth is predominantly driven by changes in key demographic parameters: fecundity, survival, recruitment and dispersal (Lack 1954; Newton 1998; Sibly and Hone 2003; Frederiksen *et al.* 2014). Factors influencing demographic rates can largely be categorised into intrinsic (density regulated) and extrinsic (environmental) factors, with interactions occurring between these drivers (Reid *et al.* 2004; Coulson *et al.* 2006). Food availability has long been recognised as a key mechanism underlying demographic processes (Lack 1954) either shaping populations slowly over time, or via a stochastic event such as a drought. Some of the pioneering work on population regulation comes from studying the dynamics between the Canadian lynx (*Lynx canadensis*) and snow-shoe hares (*Lepus americanus*) (Stenseth *et al.* 1997; Krebs *et al.* 1995), and more recently, the cyclical regulation between grey wolves (*Canis lupus*) and elk (*Cervus elaphus*) in Yellowstone National Park (Ripple and Beschta 2012). This research demonstrates that a population can never continue to grow at an exponential rate but is limited upon reaching a certain point, often defined as the carrying capacity for that environment, which is generally when the intrinsic qualities become regulated by population density. At such a point, population size will remain stable or fluctuate around equilibria, constantly being shaped by various mechanisms that work to promote or inhibit growth.

Different species will be limited by different factors in different areas and over different scales (Newton 2003). Various demographic parameters, such as survival or fecundity, will contribute differently to average population growth, and this will vary between species (Clutton-Brock 1988; Newton 1998; Gaillard *et al.* 2000; Coulson *et al.* 2006) and can be closely related to a species' lifespan (Saether and Bakke 2000). Variation in demographic rates does not always affect population growth in an equal manner (Norris and Mcculloch 2003; Reid *et al.* 2004); a small change in breeding success may have a greater effect than an equivalent change in survival (Sæther *et al.* 2013; Dahlgren *et al.* 2016). The scale of their contribution is not static and may vary according to population composition and/or density (Albon *et al.* 2000), or over short time periods; survival rates during the non-breeding season may be more influential than those during the breeding season (Calvert *et al.* 2009), introducing yet more complexity to the understanding of population regulation.

Regulatory processes clearly do not operate in isolation, and there may be interactive and additive effects between them that shape population patterns (Kendall and Nichols 2002; Newton 2003). It is also widely recognised that both density dependent and independent processes can occur together to affect population dynamics (Frederiksen and Bregnballe 2000; Nicoll *et al.* 2003; Pascual *et al.* 1997). This has been documented in range of species for various vital rates and a wealth of understanding has been derived from some iconic, long-term studies including those on great tits (*Parsus major*; Bouwhuis *et al.* 2010), Gunnison sage grouse (*Centrocercus minimus*; Davis *et al.* 2014), Soay sheep (*Ovis aries*; Coulson *et al.* 2006) and many large herbivores (Sæther 1997; Albon *et al.* 2000). These have been pivotal to answering questions about population dynamics and regulatory processes, facilitating the important development of statistical models to make this a more predictable theme in ecology.

1.2 Population regulation for wildlife management

For wildlife managers, quantifying the relative importance of the factors and mechanistic processes regulating a population is pertinent to guiding management decisions, whether for commercial purposes or conservation. For commercial exploitation, such as regulating fish stocks (e.g. Pollock, 1991) it is often necessary to monitor the health of the population (Williams *et al.* 2002) and ensure management practices such as harvesting remain sustainable (Cameron and Benton 2004). Other practices may require the control of unwanted or 'over-abundant' species (Grarock *et al.* 2013; Sanders and Dooley 2014), which will be most effective if based on a good demographic understanding of the population under manipulation.

Given the huge biodiversity crisis in which we currently find ourselves (Jetz *et al.* 2014) managing threatened populations for conservation is of global importance (Sandercock 2006; Frederiksen *et al.* 2014; Roberts *et al.* 2016). Overexploitation, habitat loss and degradation in parallel with introduced species are the main threats responsible for the 58% decline in global biodiversity over the past four decades (WWF 2016), with anthropogenic climate change placing further pressure on the viability of many populations. Island species have experienced the greatest historical declines so far, with 90% of island species accounting for documented extinctions since A.D. 1600 (Derrickson, Beissinger and Snyder, 1998). Today they continue to be the most vulnerable, with over one-third of all the terrestrial species facing extinction occurring on Islands (Courchamp *et al.* 2014).

Understanding what drives the population dynamics of a threatened species can generate valuable insight into the factors responsible for population decline and provide evidence to inform conservation actions (Ewen *et al.* 2012; Horswill *et al.* 2014; Saunders *et al.* 2014;). The common aim of many conservation programmes is to prevent further declines (Jones 2004) and ultimately establish a population that will be self-supporting in the long-term, or at least require minimal intervention (Armstrong and Seddon 2008; Ewen *et al.* 2012). The process of monitoring populations to collect demographic data can help managers learn about the system and provide a basis against which the threats can be identified, along with the underlying mechanism(s) causing decline, as proven in recovery of the endangered Seychelles magpie robin (*Copsychus sechellarum*; Norris and Mcculloch 2003), and the endangered lesser-kestrel (*Falco naumanni*) in Spain (Hiraldo *et al.* 1996). A variety of methods can be employed to achieve this, but the key principle of combining management decisions with demographic knowledge is a springboard for greater success.

Conversely, misdiagnosing the threats faced by a popualtions can lead to ineffective management, as seen in early of efforts to conserve the California Condor (*Gymnogyps californianus*; Snyder and Snyder, 2000). If correctly achieved, diagnosing threats can help managers to determine where conservation efforts should be implemented and identify the most effective 'places' to intervene, whether these be locations, life history phases etc. Intervention measures include: habitat protection or restoration, such as designating marine protected areas (Lascelles *et al.* 2012); legal protection of a species (Martin *et al.* 2014); providing conservation protection of a specific life history stage (Reid *et al.* 2004); provision of supplementary feed (e.g. Hilgartner, Stahl and Zinner, 2014); predator control or removal (Maggs *et al.* 2015); disease management (McCallum and Dobson 1995). In many cases, reversing population declines will require controlling an introduced species (Blackburn *et al.* 2004); species eradications are now a widely used conservation tool within species restoration programmes (Jones and Merton, 2012) but for these to be successful, an understanding of the species population dynamics is also essential (Grarock *et al.* 2013).

Upon implementing any conservation actions, monitoring the response of the managed population can facilitate an assessment of the effectiveness of a management programmes and its methods, (Hiraldo *et al.* 1996; Norris and Mcculloch 2003; Bottrill *et al.* 2008) and subsequently inform any adjustment to ensure ongoing success (Schaub *et al.* 2004; Ewen *et al.* 2015; Canessa *et al.* 2016). An excellent example is the use of species re-introductions in conservation (Armstrong and Seddon 2008) which can involve harvesting from a source, as employed for the recovery of the Mauritius kestrel (*Falco punctatus;* Nicoll, Jones and Norris, 2006) and the New Zealand North Island

Robin (*Petroica longipes*; Dimond and Armstrong, 2007). Conservation practitioners need to consider how harvesting may affect the persistence of the source population, as changes in population structure can affect population growth through changes in competition levels for resources and future life history investments, such as breeding (Butler *et al.* 2009; Seddon *et al.* 2007; Ewen *et al.* 2012). Success of the re-introduced population should also be monitored to determine whether management objectives are met, and decipher which practices may need adjusting.

1.3 The importance of long-term monitoring

Applying good conservation techniques requires a detailed evaluation of the threats limiting populations and the short and long term consequences of adopting any management practice. This can be achieved by integrating population management with science (Beissinger and Bucher, 1992; Jones and Merton 2012), particularly thorugh evaluating the demographic response of a population to a management action. However, typically this requires detailed long-term individual based data, and such data sets for threatened species are not widely available or easy to maintain (Heppell *et al.* 2000). Monitoring of a threatened species is often only established once the population is in decline. Although monitoring may be successfully implemented along-side conservation actions it may target only certain members of the population or key parameters, whilst limited funding may lead to inconsistent monitoring (Bottrill *et al.* 2008). None the less, long-term monitoring with regular evaluation is feasible and integral to achieving real conservation gains. The benefits of this are well illustrated in New Zealand; research on Tiritiri Matangi Island encompasses a wide range of species, including over twenty years of monitoring on the North Island robin *(Petroica longipes)*, the hihi *(Notiomystis cincta)* translocated in 1995, and the South Island takahe *(Porphyrio hochstetteri)* present since 1991 (Armstrong and Ewen 2013). In addition, eight additional bird species have been translocated to the Island and established breeding populations, as well as three reptile species (Graham *et al.* 2013). Consistent monitoring has allowed management to improve their understanding of the dynamics of these populations, identify the qualities that are important to threatened species recovery programmes and assess how conservation actions have driven change. The tools employed to preserve the species on Tiritiri are of global relevance, as predator control, supplementary feeding, translocations and disease control are the essence of many programmes mitigating population declines. With such data and critical reviews of their methods regularly being produced, managers of Tiritiri Island have been able to develop long-term models predicting future population trajectories, detecting subtle changes that would not be possible without such extensive data.

On a similar scale, the Island of Mauritius has seen remarkable endemic species recoveries from near extinction, including the pink pigeon (*Nesoena mayeris*), the Mauritius fody (*Foudia rubra*), the Mauritius olive white eye (*Zosterops chloronothos*) and the Mauritius kestrel (*Falco punctatus*) (Jones and Merton 2012). A clear theme to their recovery has been the result of intensive and dedicated conservation actions coupled with the integration of long-term, individual-based monitoring.

1.4 Parrots - a conservation crisis

Psittaciformes are among the most endangered family of birds in the world (Beissinger and Snyder 1992; Bennett and Owens 1997; Ortiz-Catedral *et al.* 2013; Marsden and Royle 2015) with 42% of all species listed as ‘Threatened’ or ‘Near Threatened’ (BirdLife International 2017a), most of which are endemics. A variety of ecological and anthropogenic factors have resulted in rapid and widespread declines, including: habitat loss and modification (Saunders *et al.* 2007); the introduction of predators and competitors (Moorhouse *et al.* 2003; Ortiz-Catedral *et al.* 2013); novel diseases (Peters *et al.* 2014); and perhaps the most damaging, harvesting for illegal and legal trade (Valle *et al.* 2017). Despite their huge popularity in aviculture (Low, 1984), wild populations of parrots have rarely been the focus of ecological studies resulting in a data deficiency on basic demographic and biological data (Beissinger and Snyder 1992; White *et al.* 2012; Robinet and Salas 1999), their distributions and habitat requirements (Evans, Ashley and Marsden, 2005; Lee and Marsden, 2012; Marsden and Royle, 2015).

Multiple concerns have been raised for the conservation of Psittacines, but restorative actions are still in their infancy (Martin *et al.* 2014). While considerable effort has been made to reduce harvesting for trade (White *et al.* 2012), current in-situ efforts have focused on improving the availability of key resources such as food and nest sites in order to promote survival rates and increase productivity (Clout *et al.* 2002; Brightsmith *et al.* 2005; Ruffino *et al.* 2014). Re-introductions and supplementing wild populations have been attempted with varying degrees of success (e.g. Brightsmith *et al.*, 2005; White, Collazo and Vilella, 2005; Ortiz-Catedral, Hauber and Brunton, 2013). These are reviewed by White *et al*. (2012).

1.5 Conservation management of the echo parakeet

In Mauritius, the Endangered echo parakeet (*Psittacula eques*) provides a remarkable story of psittacine recovery against a backdrop of biodiversity loss. Historically this parakeet was found throughout the island but by the late 1980s, following extensive habitat loss and the introduction of exotic competitors and predators, it was reduced to less than 20 wild birds in 1992, restricted to the remote black river gorges in the South-west of Mauritius. In 1993 a successful species recovery programme was implemented and parakeet numbers have increased to >600 (Jones and Duffy 1993; Henshaw *et al.* 2014). The recovery programme included the management of the remnant wild population (supplemental feeding and the provision and protection of nest sites), captive breeding and re-introductions. In 2005 the re-introduction programme stopped in response to an outbreak of Psittacine beak and feather disease (PBFD) and management is now focused on minimising disease transmission, the provision of supplemental feed and artificial nest sites.

Currently, the population shows continuing signs of growth, yet as with many long-running management programmes, the objectives immediately set out by the monitoring programme may no longer be appropriate, or logistically feasible to maintain. For the echo parakeet, this is becoming increasingly apparent. The rapid growth of the population means that the practices established to support the remnant population in the 1990s are no longer suitable or efficient for managing the larger population which exists today. A wealth of uninterrupted, detailed demographic data has been collected as part of the species recovery but as yet, it has not been utilised to (i) explore key demographic parameters and (ii) examine how these have responded to changes in management practices over the course of their recovery. Valuable research has been conducted on the echo parakeet, but this has focused on their population genetics (Raisin 2010; Raisin *et al.* 2012; Groombridge *et al*. 2004; Tollington *et al*. 2013; Tollington *et al*. 2015), the evolution and ecology of the circovirus responsible for PBFD, and echo parakeet immunity to the virus (Tollington 2012). Hence there remains a very large knowledge gap in the population's basic demography.

1.6 Chapter overview and aims

The recovery programme implemented practices that aimed to encourage population growth by influencing key demographic parameters, but how these practices have met their objectives and contributed to population recovery has yet to be explored. Such information is pivotal towards allowing the recovery programme to progress and ensure a viable and persistent population. An understanding of the demographic impact of the PBFD outbreak is yet to be ascertained; the disease continues to be present in the population today and despite efforts to manage the disease, these decisions are based on limited knowledge. Therefore, this thesis seeks to understand the population's demographic response to management and disease, providing fundamental information that will benefit the future conservation of the echo parakeet.

Chapter Two: Introduction to the echo parakeet, *Psittacula echo*

An introduction to the ecology of the echo parakeet, the history of its decline and the management actions implemented to restore the population. Detailed demographic records collected in parallel with the population's recovery provided the data for this thesis, and methods of its collection are described here.

Chapter Three: Challenging the assumptions of unobservable multi-state models: a case study of *Psittacula echo*

Multistate models using capture-mark-recapture data are often employed to generate survival estimates in different life history phases and the transition rates between them. However, certain species become ‘unobservable’ during key life history stages and parameter estimates during these phases cannot be reliably achieved. Various extensions of multistate models try and account for these periods and estimate associated demographic parameters, but how reliable are the models in doing given that several assumptions must be made in order for them to work? This chapter utilises a unique data set to test the underlying assumptions of multistate models employing unobservable states, quantifies their potential biases and discusses the implications.

Chapter Four: The impact of supplementary feeding on the reproductive success and survival of echo parakeets

This chapter demonstrates the advantages of providing supplementary food to a threatened population, a widely popular yet controversial tool employed in species management. Here, I quantitatively describe the impact of supplementary feeding on two key demographic parameters, breeding success and survival, and the important role it has played in the population’s recovery. These findings are an important step towards reviewing the supplementary feeding regime, and I discuss how new findings could be applied to future management. Through the research of this chapter, the first accurate measures of echo parakeet survival and breeding parameters were also generated, which has previously not been accomplished.

Chapter Five: Exploring the potential demographic impact of a disease outbreak in a small, recovering population

Host-pathogen dynamics are highly varied and the demographic impact of an emerging infectious disease may easily vary between different members of a population and over the course of it emergence. In order to understand how to manage Psittacine beak and feather disease (PBFD) within the echo parakeet population, consideration for the disease’s dynamics and an understanding its demographic impact is essential. To explore the extent of the disease’s impact, this chapter compared changes in key demographic parameters between a time period when PBFD was not documented in the population and following a major outbreak, when cases of PBFD were common. I explored whether its impact was ubiquitous across the population, with a particular focus on the role of supplementary feeding in disease mediation, and go on to discuss the immediate and long-term influence of the disease on population trajectory.

Chapter Six: General discussion

This chapter reviews the findings of the analytical chapters and how an improved understanding of echo population demography has provided valuable insight into the role of management and disease. I discuss certain key aspects of the echo parakeet programme which have contributed to their recovery, and how these findings may be applied in the wider realm of wildlife management. I present ideas on how the current monitoring regime may transition to a more reduced phase of management, and suggest directions for future research.

Chapter 2

Introduction to the Echo Parakeet

Psittacula echo

The World Parrot Trust
is dedicated to saving rare and
endangered Parrots. Our immediate
concern is for the Echo Parakeet
from Mauritius.
Only Twelve
still exist!

Please
Help us
to save him
-leave a donation

Student contribution and impact

Chapter Two introduces the focus species of this PhD thesis, the echo parakeet, describing its key ecological traits, the history of the species' range and the factors which contributed to their near extinction. I summarise the various management actions employed in an effort to mitigate further decline and go on to describe the demographic data which has been collected in parallel as part of the species' recovery programme. Collating this demographic information provided the foundation for this research thesis, and almost one year of my time was invested in compiling the most detailed, demographic data set for the echo parakeet population available to date. Achieving this will prove to be of on-going value both the Echo Parakeet Management Programme in Mauritius and related research projects in the future.

2.1 General background and ecology of the species

2.1.1 Ecology of the echo parakeet

The Mauritius (or echo) parakeet is the only extant parrot remaining of at least six endemic species of *Psittacine* which once existed in the Mascarenes (Cheke 1987; Jones 2004; Samit Kundu *et al.* 2012). Strictly arboreal, the birds occupy lowland, intermediate and scrub forests, foraging widely either alone or in small groups to target different plant species at different times of the year. Their varied diet consists of fruits, flowers, leaves, buds and the bark of a wide range of species (Jones and Owadally 1988). Outside of the breeding season they will travel several kilometres to feed, with travel significantly reduced during breeding (Duffy 1994). It was once thought that echo parakeets would only eat native vegetation on the Island (Jones 1987b), which has rapidly been disappearing in the last century. However, observations of individuals feeding on exotic plant species have increased in frequency in recent years. Such dietary adaptation is likely to be a consequence of the dramatic habitat changes (Henshaw *et al.* 2014).

Echoes are a medium size parakeet, weighing between 130 to 210g, with a dark, rich green, plumage. Males and females are sexually dimorphic; the male has a bright red bill and two incomplete neck collars (one black, one pink) which fail to meet at the hind neck, accentuated with an occiput tinged powder blue. Females have a dark bill, a very subtle black neck collar and are generally a darker green overall (Jones and Duffy 1993) (Figure 2.1). As fledglings, males and females are both identical, only developing their sexual characteristics over the following two to three years of maturation.

At the age of two to three years, echo parakeets become sexually mature and form monogamous pairs for multiple breeding seasons, though divorce can occur and new bonds can form should a partner be lost (Jones and Duffy 1993). Their austral breeding season spans two calendar years and are referred to using those two years e.g. 2012/2013. Nests are formed in cavities of emergent endemic trees, with clutches of one to four eggs laid from September to December. Eggs are laid at one to two day intervals with incubation starting after the first or second egg is laid and lasting around 25 days in total. Only the female is responsible for incubation and is therefore fed by the male at least four to five times a day. Upon hatching, the female remains with the brood until they reach around two weeks of age, after which she will begin to leave the nest for short periods of time to feed independently and assist with provisioning the nestlings (Young 1987; Duffy 1994). Between 53 to 69 days after hatching, at a weight between 130 to 160g (Thorsen *et al.* 1997), chicks fledge from the nest and accompany their parents for at least two to three months, though it is possible for this to continue until they form their own breeding pair (Young 1987). A second clutch can be laid if the first one fails but to date there is no record of a second clutch after already successfully fledging one brood. It is not entirely certain how long echo parakeets can live for, though it likely to be similar to the 25 years observed in Indian rose-ringed parakeets (*Psittacula krameri*), here on referred to as IRRP. This is highly probably given the oldest breeding echo parakeet to date is 20 years old, and many successful breeding pairs are aged between 15 and 20 years.

Figure 2. 1 A male (left) and female (right) echo parakeet, and their very obvious, sexually dimorphic traits.

2.1.2 Historical population decline

Mauritius was first discovered in the 16th Century and it is thought that even long after its colonisation, the echo parakeet reportedly remained “quite common” across the island (Jones 1987; Jones & Duffy 1993). By the late 1900s, rates of human settlement escalated and widespread forest clearance began, leaving less than 2% of the original native vegetation by the 1980s (Vaughan & Wiehe 1937; Duffy 1994; Safford 1997; and see Figure 2.2 taken from Maggs 2016). Between 1973 and 1981 an area ~30km^2, that was believed to be an important component of the echo parakeet’s range, was cleared for agricultural and commercial forestry (Jones 1987b).

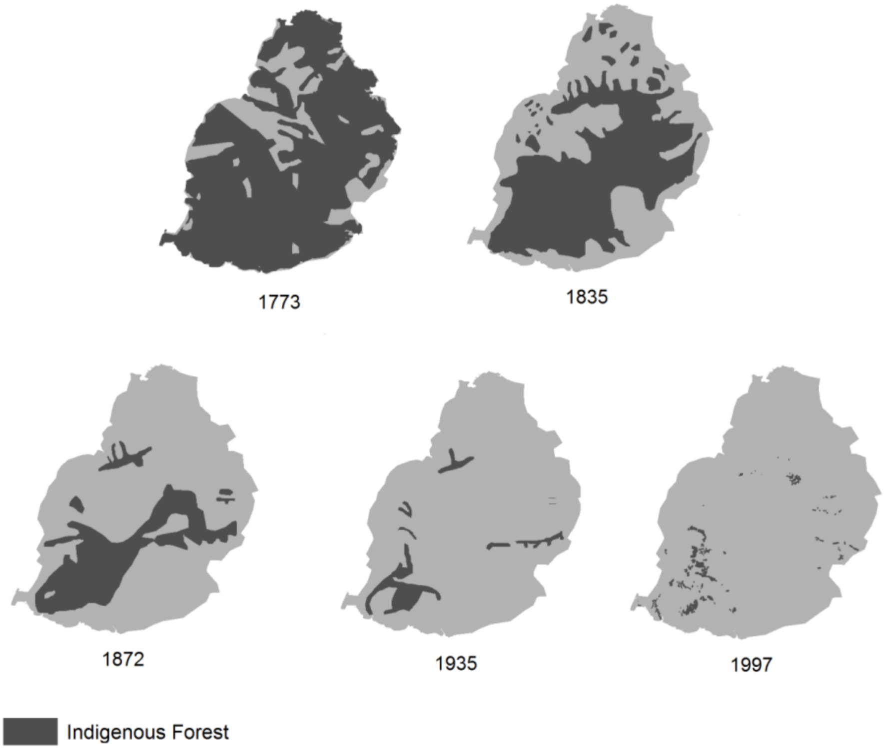


Figure 2. 2 An illustration of the mass deforestation of indigenous forest across mainland Mauritius from the 17th century to the present day (Illustration taken from Maggs 2016, Figure 1.1).

Little interest was paid to the echo parakeet prior to late 1960s as it was regarded as the same race of the invasive IRRP (Jones & Duffy 1993; but see Forshaw & Cooper 1989). Upon recognition of it being an endemic with a growing risk of extinction, conservation efforts began in conjunction with other endemic species recovery programmes in Mauritius in 1973, but efforts were too limited to prevent the population's continuing decline. By 1986, a relict population of less than 20 birds was limited to 40km^2 of indigenous forest, and in continuation with the multi-species conservation programmes, this area was designated as a National Park in 1993 (BRGNP; Figure 2.3) (Jones and Duffy 1993). The BRGNP is composed of highly degraded forest and dominated by a range of exotic flora such guava (*Psidium cattleianum*), privet (*Ligustrum robustum*) and jamrosa (*Syzygium jambos*) (Thorsen *et al*. 1997; Florens 2013). Poor habitat quality and a loss of native trees equated to a loss of high quality food and natural cavities for nesting (Young 1987), but these were not the only factors contributing to the echo parakeet's rapid bottleneck (Tollington *et al.* 2013). Nest predation by the introduced

Ship rats (*Rattus rattus)* and Crab-eating macaques (*Macaca fascicularis),* along with competition for nest sites with the Indian mynah (*Acridotheres tristis)* and white-tailed tropic bird (*Phaethon lepturus),* all contributed to the echo's decline. In addition the echo parakeet is in direct competition with the introduced IRRP for food resources and nest sites (Jones 1987). Extinction of the Critically Endangered echo parakeet seemed imminent by the early 1990s, and was considered the rarest parrot in the world (IUCN 2010; BirdLife International 2017b).

2.2 Population recovery and management

Conservation efforts in the 1970s aimed to mitigate the looming extinction of echo parakeets (Cheke 1987; Jones 1987; Jones & Duffy 1993; Raisin 2010). Limited knowledge of the parakeet's ecology combined with minimal resources meant that establishing sufficient monitoring was of upmost importance; evaluating the species' distribution, ecology and main threats was therefore essential to determining its most immediate conservation needs (Jones and Merton 2012). In 1993, an official species recovery programme commenced, co-ordinated by the Mauritian Wildlife Foundation (MWF). This focused the work and implemented more systematic monitoring and restorative techniques, and in doing so, a breeding group was discovered in the south of the park, referred to as 'Bel Ombre'. It was thought the only remaining echo parakeets were those occupying the northern region of the BRGNP, often referred to as the Grand Gorges population (Figure 2.3), and the Bel Ombre sub-population - separated from Grand Gorges by a plateau of agricultural land and degraded habitat - gave additional hope to the species recovery programme. Several years of 'hands on' management addressed a range of threats limiting the population. These initial efforts - detailed by Jones and Duffy (1993) - applied very broad conservation techniques, all of which worked to promote opportunities to breed, maximise the success of breeding attempts and to improve the fitness and subsequent survival of individuals, thus ultimately promoting population growth. Four main approaches could be considered as key drivers of the echo parakeet's population recovery; nest manipulations, nest site management, supplementary feeding and a release programme to supplement the wild population.

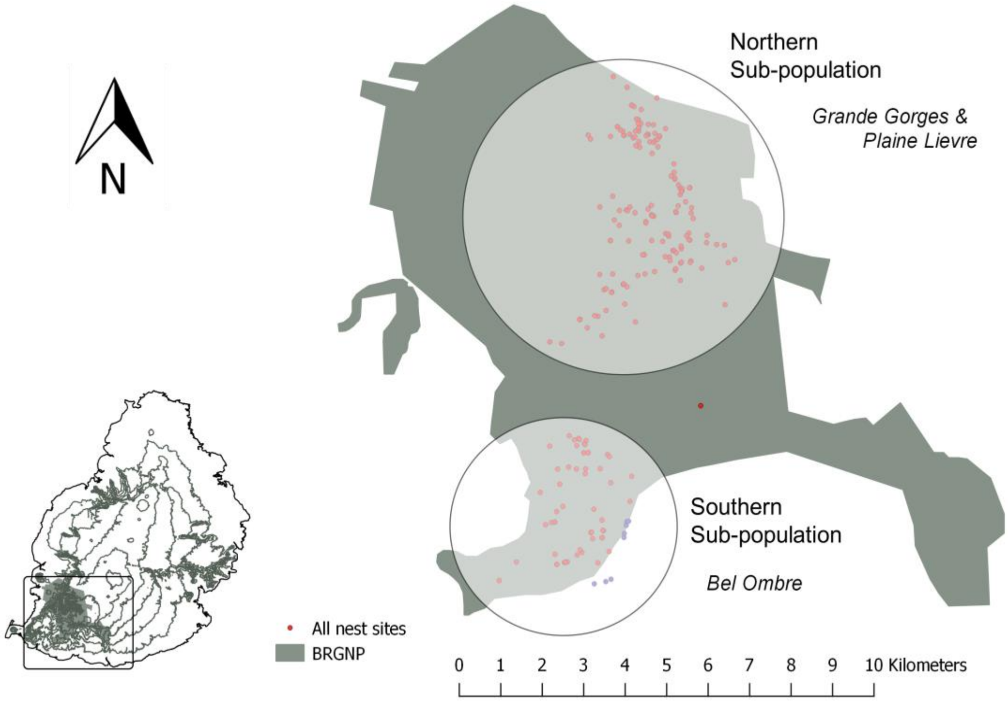


Figure 2. 3 Locations of the two sub-populations surviving in the 67km^2 Black River Gorges National Park (BRGNP).The location of all known echo parakeet nest sites recorded for each region since 1991 are indicated as with red dots, which has risen from <10 nest sites in 1991 to 160 in 2013.

Nest Manipulations

To maximise the success of each breeding attempt, extensive surveys conducted at the early stages of the season located wild nests for subsequent daily monitoring. Chicks were weighed almost daily to monitor their growth, health and the attentiveness of parents. Any chick showing poor development (defined as 20% slower than average; Malham *et al*. 2006) were either given direct medical or nutritional assistance in the nest, or rescued into captivity for hand rearing or rearing under captive foster pairs (commonly the IRRP). Harvesting into captivity was the key approach during early years of management, made possible by a breeding facility on Mauritius (Gerald Durrell Endangered Wildlife Sanctuary, GDEWS). Other methods of clutch manipulation included fostering of similar aged eggs and nestlings between nests, both from wild into captive nests, wild to wild, and captive individuals into wild nests (Lovegrove *et al.* 1995). Downsizing of broods relieved pressure from young, inexperienced females, whilst upsizing the broods of experienced females ensured better survival probabilities of young, who often had their first clutches removed at egg stage to encourage a second clutch and maximise productivity. These intense management techniques began in 1993 and continued until 2005, when an outbreak of PBFD (see section 2.5) prompted the start of reduced management strategy. Since 2005, nest manipulations were avoided unless absolutely necessary (chicks not developing at the expected rate, or death seemed apparent without medical assistance) and the frequency of nest visits within a breeding season reduced. Nonetheless, a sufficient level of monitoring has been maintained to facilitate the collection of individual, detailed life history data.

Nest site management

Echo parakeets typically nest in cavities formed by old, endemic trees, but few nest sites were available in the late 80s, early 90s due to the widespread deforestation. To maximize nest site availability and ‘attractiveness’ of sites to echo parakeets, all existing and new found cavities were, and continue to be modified to ensure they are a safe from predators and competitors but remain accessible to the echos and monitoring staff. This involved cavity deepening to exclude monkeys; narrowing of main entrances to deter tropic birds; access hatches cut in the side to enable access by staff to clutches/broods; weather proofing peaks over the entrances; isolating the crowns of trees to stop rats accessing from adjacent trees; attaching a collar of black PVC sheeting around the tree trunk to prevent small rodents climbing up. When cavities were deemed unsafe and risked the success of a nest attempt, they were closed off by staff and an artificial nest box provided in the vicinity as an alternative. Although new cavities continue to be found today, they are incredibly rare and in the 2013/14 breeding season only 28 were known to exist within the National Park, with only 16 used in breeding attempts. To alleviate the shortage of natural nest cavities artificial nest boxes were provided (Figure 2.4). It took several years and multiple designs before a breeding attempt was recorded in an artificial box in the 2000/01, by a released captive bred bird. By 2013, 132 artificial nest boxes were available throughout the forest for use by wild-bred and captive released birds. Nest boxes continue to be erected on an annual basis, replacing old boxes or cavities which have become unsafe, or to encourage breeding in areas where echo parakeets have been sighted. Currently, this is restricted to the BRGNP, but recent permission by the owner of chasse land has seen the erection of eight nest boxes in a region just bordering the Park (Figure 2.6).

Figure 2. 4 *Left*: Accessing a natural cavity via a modified access hatch. *Top right*: Original entrance to a natural cavity (photograph by Donal Smith©). *Bottom right*: A PVC artificial nest box.

2.3 Supplementary feeding

Another major limiting factor for the population in the 1990's was a shortage of natural food (Jones and Duffy 1993). Since 1979, attempts to compensate for this with supplementary food (SF) were relatively unsuccessful and involved raising small platforms up into the canopy, upon which fruit and vegetables were provided (Jones and Duffy 1993). A revised SF programme was implemented in 1997 as part of the 'soft' release programme and involved the provision of artificial food pellets (Kaytee® Exact®) and permanent feeding stations known as 'hoppers' (Figure 2.5). Wild-bred echoes subsequently 'learnt' to use the artificial food source by copying released birds. Since 2000, four sites with artificial feeding stations have been established in the National Park (Figure 2.6); three stations in the Grand Gorges area (Plaine Lievre, Mare longue and Brise Fer) and one in

Bel-Ombre. During the breeding season, the Plaine Lievre feeding stations are subsidized by two small, additional hoppers at ‘Le Marsh’, a small clearing less than 200 metres away. SF is provided year-round and the specific design of the hoppers excludes access by other species. Raised on poles approximately 1.5 metres above the ground, hoppers are easily accessed by staff and reflect the more arboreal foraging behaviour of the parakeets. Individual consumption rates of SF vary between birds, but 82% of the population is currently known to include it in their diet. Previous research has begun to explore the demographic differences of birds which include SF in their diet (Tollington *et al.* 2015), but with the data available, there is potential to extend this for a more comprehensive review.

Figure 2. 5 Echo parakeets accessing the artificial feeding stations - ‘hoppers’ - filled with artifical food pellets. Their design successfully excludes use by other species.

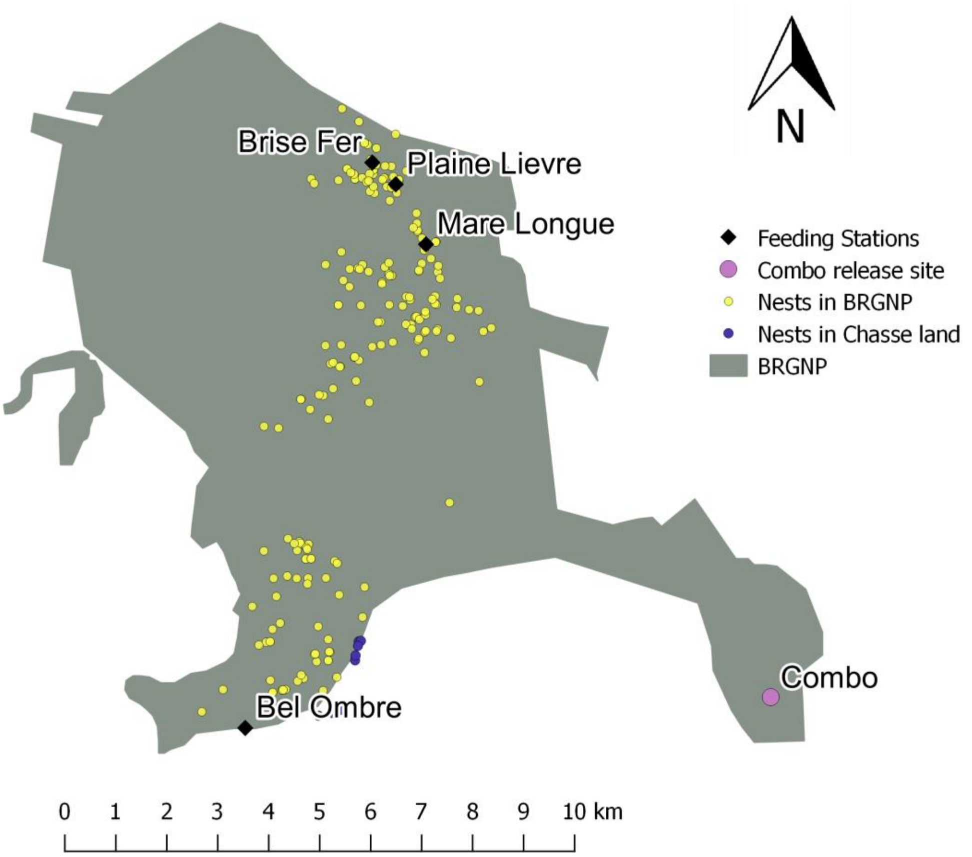


Figure 2. 6 Locations of the four artificial feeding stations maintained throughout the year: Brise Fer, Plaine Lievre, Mare Longue and Bel Ombre. 160 functional nest sites were available in 2013/12 within the BRGNP (yellow dots), including 8 nest sites erected in chasse land in Bel Ombre (blue dots). The combo release site is also indicated (see section 2.4 for details).

2.4 Population supplementation through releases

A release programme was initiated in 1997 to augment the developing wild population. Released birds were captive-bred (foster reared under IRRP or hand reared), wild harvested chicks or chicks rescued form failing wild nests. Following a successful trial in 1997, a total of 50 captive reared echo parakeets were soft-released at Plaine Lievre between 1997 and 2001, with a further 49 released at Bel Ombre between 2002 and 2004 (Table 2.1). An attempt was made to establish a third sub population in the south east of the BRGNP (Combo region, Figure 2.6) in 2004, with the release of 36 echo parakeets. However, this failed due to an outbreak of psittacine beak and feather disease and marked the last year of wild releases.

Table 2. 1 A summary of the number of birds released between 1997 and 2005, at each of the three release sites. *In 2001 a release was originally planned for Bel Ombre, but due to several problems, this was relocated to Plaine Lievre.

	Release Breeding Season								
Release Site	1997 / 98	1998 / 99	1999 / 00	2000 / 01	2001 / 02	2002 / 03	2003 / 04	2004 / 05	**Total**
Plaine Lievre	14	8		7	21				**50**
Bel Ombre					*	19	30		**49**
Combo				4				36	**40**
									139

Genetic homogenisation of sub-populations

The two ‘sub-populations’ occupying Bel Ombre and Grandes Gorges were confirmed to have once been genetically separated. Following intervention by conservation management actions, intensive management involved moving individuals between the two sub-populations, which have consequently become genetically homogenised (Raisin *et al.* 2012). These actions helped to retain overall high genetic diversity, a trait which may also be owing to the great speed at which the population declined (Jones and Duffy 1993; Tollington *et al.* 2013). Genetic homogenization may in fact be considered as a benefit to the health of the population by having reduced the risk of inbreeding effects, a cost often associated with rapid bottlenecks.

Ranges of the two sub-populations have expanded in accordance with the growing population size; today, a narrow corridor of native vegetation connects Bel Ombre and Grandes Gorges, leaving little more than 2km distance separating them. Natural movement between the two geographically separated populations is, however, incredibly rare (Henshaw *et al*. 2014). Whilst the two sub-populations now differ very little in genetic structure, subtle variations have been suggested in demographic patterns such as timing of breeding (Henshaw *et al.* 2014) which could be a result of the variation in landscape characteristics. Variable landscapes create multiple micro-climates across the Island of Mauritius, and even over a few kilometres, environmental conditions can differ quite substantially (Staub *et* *al.* 2014). The southern region of the BRGNP is a slightly different forest type and experiences a slightly warmer, wetter climate comparative to the central and northern coverage of the park.

Nest sites in the southern region of the park are more dispersed and many are only recently established, contrary to the Grande Gorges region where the majority of nest sites are located and the most intense management has been applied. Grande Gorges represents the larger of the two sub-populations, with 76 breeding attempts in the 2013/14 breeding season, but only 28 in Bel Ombre. Owing to previous references to echo parakeet sub-populations, both anecdotally and in published literature (Raisin *et al.* 2012; Tollington *et al*. 2013), I initially explored the extent to which the two sub-populations may differ in key demographics (Table 2.2) but found only minimal differences; both sub-populations showed annual variation in timing of breeding (Figure 2.7), yet within any given season the timing of breeding was nearly identical, with clutches predominantly laid in mid-October (Figure 2.8). Feeding or behavioural differences have not been observed over the years either. In light of this, and the knowledge that both populations have been subject to identical management practices, all analysis throughout this thesis was conducted on the population as a whole. Combining data from both sub-populations was also important as the breeding population in Bel Ombre is almost half that of occupying Grandes Gorges (owing to the historically smaller population) and therefore contributes a reduced amount of demographic data; answering certain research questions in this thesis would have strained the accuracy of results if the Bel Ombre and Grandes Gorges were analysed independently. The classification of sub-population was taken into account where necessary in certain statistical analysis, but essentially this thesis does not distinguish between Grande Gorges and Bel Ombre.

Table 2.2 A table comparing key demographic qualities of the two putative sub-populations of echo parakeet, Bel Ombre and Grande Gorges.

	Bel Ombre	**Grandes Gorges**
Number of breeding females in 2013/14	28	76
Number of fledglings in 2013/14	27	64
Mean clutch first egg date (1993 - 2013)	8th October	11th October
Mean clutch size (1993 - 2013)	2.6 *SE ± 0.05*	2.7 *SE ± 0.03*
Mean brood size (1993 - 2013)	1.97 *SD ± 1.03, SE ± 0.08*	1.83 *SD ± 1.0 , SE ± 0.05*
Mean fledglings per clutch (1993 - 2013)	1.55 *SD ± 1.05, SE ± 0.08*	1.46 *SD ± 1.16, SE ± 0.05*
Mean age of first breeding attempt:		
Female	3.15 *SD ± 1.8, SE ± 0.31*	3.17 *SD ± 1.33, SE ± 0.14*
Male	4.6 *SD ± 2.25, SE ± 0.4*	3.3 *SD ± 1.2, SE ± 0.15*
Sex ratio, Female: Male	1 : 1.3	1 : 1.2

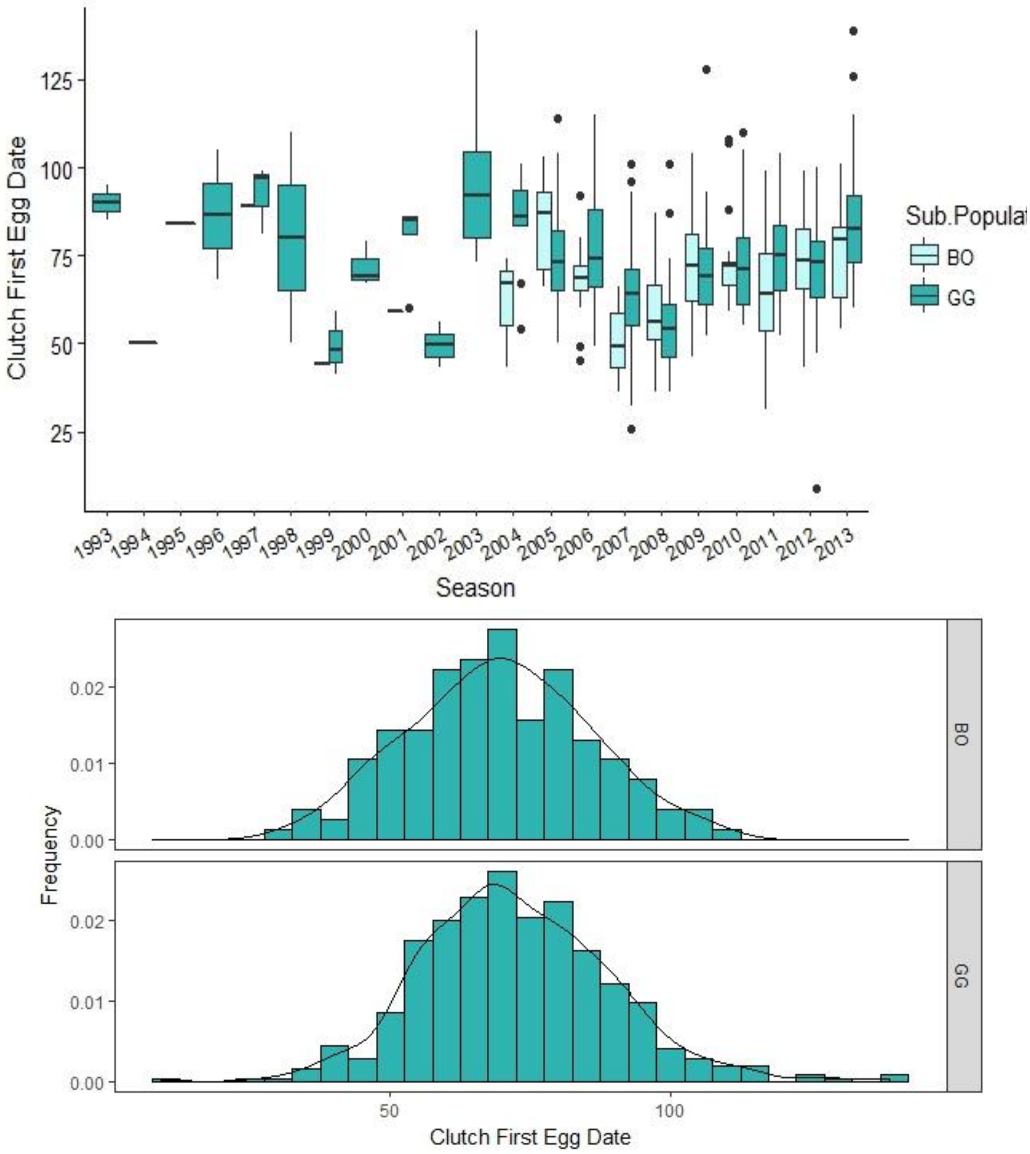


Figure 2. 7 *Top*: Annual variation in the timing of breeding for the Bel Ombre (BO) and Grandes Gorges (GG) sub-populations, reported as the number of days after August 1st when the first egg of a clutch was laid (‘Clutch First Egg Date’). *Bottom*: A histogram reporting the range of first egg lay dates for clutches in BO and GG, which start as early as mid-August and continues until mid-December.

2.5 Psittacine beak and feather disease

Psittacine beak and feather disease (PBFD), a viral infection caused by the Beak and Feather Disease Virus (BFDV), can result in feather dystrophy and immuno-suppression in birds which commonly results in death from secondary infections (Ritchie *et al.* 1989; Regnard *et al.* 2015). At the start of the echo parakeet management programme there was no indication that the disease was present in the population, but routine blood samples of nestlings and opportunistic samples from adults were taken during each breeding season for cautionary purposes, and to acquire information that would help establish a genetic pedigree. Between 1999 to 2002 blood sampling was discontinue due to limited finances, skilled personnel, and no obvious presence of the disease (Greenwood 1996), though there had been one unconfirmed case in 1995/96. BFDV was certainly present within Mauritius, as wild Indian Ring-necked parakeets in the BRGNP had been sighted with clinical signs of PBFD (i.e. missing and broken feathers) as early as 1985, and captive Lesser Vasa Parrots (*Coracopsis nigra*) had been observed with PBFD like lesions (Malham *et al.* 2006). In 2002/03, two echo parakeet chicks were confirmed as PBFD positive and in 2004, nine individuals from the 2003/04 Bel Ombre release cohort became severely ill with a range of infections (Raisin 2010), probably a result of the immunosuppression caused by the virus. A cohort of 36 juveniles (between 60 and 90 days old) was released in the combo region in 2004/05, but by April 2005, many began to show clinical signs of the disease. 90% of the 2004 cohort did not survive to two years old (Tollington *et al.* 2015); ten were euthanised due to such poor health, six were known to have died shortly after released, and at least three individuals dispersed to Bel Ombre and Plaine Lievre (Malham *et al.* 2006). The remainder were never seen again. To contain the impact of the disease, management of the echo parakeet was significantly reduced and strict disease protocols were implemented, focusing largely on minimising the spread of the virus between birds and nest sites. Nests were no longer accessed weekly but limited to key times in the breeding cycle. DuPont^{TM} Tyvek® Chemical suits were worn every time nests were accessed or birds handled, with a different suit for each occasion or bird. Immediately after their use, suits were sealed in bags and later soaked in Virkon®virucide or Virex® - a powerful disinfectant - for 24 hours, along with any other equipment exposed to the risk of contamination. Between breeding seasons, nest sites were disinfected using Virex® to minimise the accumulation of infected material. Feeding hoppers were cleaned on a weekly basis with Virkon®.

Following the outbreak in 2005, PBFD has remained prevalent within the population and juveniles are often still seen with clinical signs. It is possible to overcome the infection and survive into adulthood and the population grows annually, yet very little is fully understood about the epidemiology of this lethal virus. Research is underway to explore how disease transmission is shaped by social dynamics of the populations, and the how management actions may be related to the virus' prevalence (Fogell *et al.* 2016), but this is only the start of understanding a very complex host-pathogen dynamic, as discussed in Chapter 5 of this thesis.

2.6 Monitoring protocols and data

The recovering echo population has been the subject of an intensive monitoring programme since 1991 that was made official in 1993. Almost all individuals are individually identifiable via leg rings and their individual breeding activity documented throughout their lifetime, resulting in a comprehensive, individual-based data set, which forms the basis of this thesis.

Stud book

Co-ordinated by MWF, monitoring of the echo parakeet population was conducted each breeding season from 1993/94 to 2013/14, with minimal management conducted during the non-breeding season (e.g. the provision of SF). At the start of the breeding season all known breeding sites were visited and additional surveys conducted to locate new breeding sites, with all breeding pairs identified by their unique leg rings. One or two closed and numbered aluminium rings with a unique colour combination were attached to one or both tarsus when chicks were 12 to 15 days old, whilst older chicks, fledglings or adults (captured in nest sites or aviaries) were ringed with a thicker, number and colour specific "Hess" ring (Figure 2.8). These colour rings allow identification in the field without capture, whilst the number printed on the ring provides a permanent means of identification. Currently, >95% of the population are ringed.

Figure 2. 8 A selection of colour aluminium leg rings *(left*) attached to one tarsus of the bird or both (*right)* providing a unique identity visible in the field and linked with records in the stud book (Photo by Tommy Durcan ©)

Nest attempts were followed for the entirety of the breeding season, from clutch initiation through to fledging. In this study, I define an active breeding pair as having laid a clutch of at least one egg. Throughout the breeding season data were collected on first egg lay date, clutch size, hatching order and date, and the number of fledglings.

Information from each breeding attempt was collated into a stud book that began in 1991, described to the level of individual eggs and linked with as much life history data as possible. Each egg was issued a unique ID and assigned to annual cohorts defined by the year in which they were produced as eggs. Spanning 23 breeding seasons (1991/1992 to 2013/2014), the stud book encompasses 2323 eggs (from 881 clutches, from 168 different breeding females) recorded in the wild. A further 59 birds were ringed out of the nest as juveniles or adults and for most of these individuals their pedigree is largely unknown. As part of this thesis, I spent up to 9 months developing an existing basic database to create a substantially more detailed, individual-based data set extending 23 years. In doing so, the data set now includes additional information on clutch and brood manipulations, nest box types, release events and re-sightings of non-breeding individuals and has been cross-checked multiple times to improve its accuracy. I have therefore compiled the most comprehensive data set on the echo parakeet, to date, information that will facilitate a much greater scope of research than was previously possible. Already, this dataset is being used as the foundation for PhD research being conducted by another student at the University of Reading. Seven months of my PhD were spent in Mauritius working as a volunteer on the echo monitoring team. This allowed me to follow the entire work process behind monitoring the 2014/15 breeding season, from preliminary surveys to final fledge check. Such time provided valuable insight into the structure of the management programme, the ecology of the species, and valuable anecdotal data. Demographic data from this season (2014/15) was not, however, included in this thesis due to time delays in data availability.

Supplementary feeding and hopper watches

In order to ascertain which members of the population use supplemental feed, ‘hopper watches’ were conducted four days a week. These watches began at dawn and extended one hour following, during which all birds sighted at the hoppers were identified. In addition, the monitoring enabled observational health checks and with aviaries near-by, the opportunity to catch birds if necessary, whether for medical purposes or ringing. Monitoring effort of the hoppers could differ throughout the breeding season and between sites; the Plaine Lievre feeders were monitored most consistently, with additional watches conducted at Brise Fer and Mare Longue when possible. Watches at Bel Ombre varied depending on staffing at the field station, but once a month a full day of watch was conducted to account for this variation.

Incidental field observations

Population monitoring has focused on the breeding segment, but incidental observations of non-breeding birds were made throughout the breeding season. These may be fledglings, young birds reaching sexual maturity or non-breeding adults. On occasion, older birds in a phase of senescence were sighted, though this was rare. All observations were formally recorded with as much auxiliary data as possible (bird ID, time, data, location etc.).

2.7 Current population status

Despite ongoing challenges such as PBFD, limited native forest and the continued presence of direct competitors (Smith *et al.* 2012) the population has avoided what seemed inescapable extinction (Jones 1980). Having recovered from a critically low level, the species was down-listed from Critically Endangered to Endangered in 2007 (IUCN 2010) and by the

2013/14 breeding season, at least 102 females were recorded to attempt breeding in the wild (Henshaw *et al.* 2014). Since management inputs were reduced in 2005 (Figure 2.9), 54 chicks successfully fledged the nest with little intervention by management in that season and by 2013, this had tripled to 167 fledglings. Management intervention continues at a modest level, with a particular focus on minimising disease transmission, continued provision of supplemental feed and artificial nest sites, and the detailed collection of life history data.

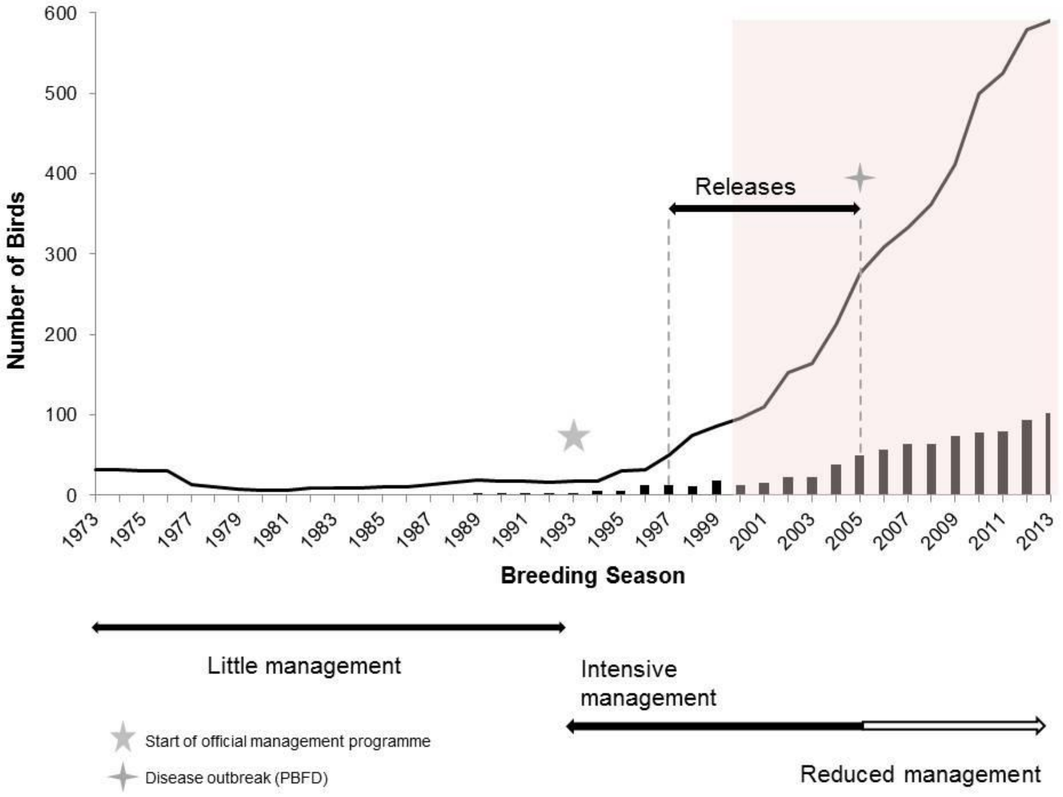


Figure 2.9 An overview of the recovery of the echo parakeet population with an increase in both estimated number of individuals (solid black line) and the number of breeding pairs (vertical bars). Different phases of management throughout the recovery are illustrated, including an eight years release programme (halted by a disease outbreak of psittacine beak and feather disease, PBFD) and the successful provision and use of supplementary feeding and artificial nest boxes for wild birds (region shaded pink). This diagram is adapted from Figure 1, Raisin *et al* 2012).

Chapter 3

Challenging the assumptions of unobservable multistate models: a case study of *Psittacula echo*

“To be forced to assume a priori that parameters are
equal over time or group is unsatisfactory. In fact, testing
that hypothesis might be of interest.”
(Kendall, 2004)

Student contribution and impact

For this study I created the first capture-mark-recapture (CMR) files for echo parakeets by compiling re-sighting data that spanned 20 years. Prior to the work of this thesis Chapter, never before has such CMR information been collated and examined in a way that accurately reports age-structured, annual survival rates for echo parakeets.

Findings from this study make a valuable and very novel contribution to the growing world of CMR studies, addressing the growing discussions regarding the assumptions behind certain CMR models, and their impact on model accuracy. Here, I focus on multistate models with unobservable states. Testing the validity of these models with real ecological data has thus far been impossible; ‘unobservable’ states cannot be observed. The unique echo parakeet system allowed me to test some of the more common, underlying assumptions of unobservable multistate models and confirmed the error that is consequently introduced to key demographic rates estimated. This is particularly critical given that survival estimates often contribute to predictive population models, such as PVAs, or population trajectories.

3.1 Abstract

Accurately estimating vital rates is the cornerstone to understanding population growth and persistence, and for assessing the impact of conservation management actions. Capture-mark-recapture (CMR) models based on marked individuals in wild populations play an important role in this respect, often relying on recapture histories of breeding individuals. This approach can be problematic for long-lived animals in which vital rates change with age. Breeding is often delayed as individuals become sexually mature, or individuals may skip breeding entirely. In both cases, individuals enter a non-breeding state for several years and are effectively unobservable.

In such cases, multistate models have been used to estimate survival rates by treating non-breeding individuals as an unobservable state. Unobservable multistate models (UMS models) assume that the survival probabilities of

non-breeding and breeding individuals are equivalent, and that the transition from non-breeding to breeding states is one-way and irreversible. It is typically impossible to critically examine these assumptions and their consequences due to the lack of data; however, this study makes use of a unique, long-term dataset on a tropical bird population.

The Mauritius (or echo) parakeet (*Psittacula echo*), and hereon referred to as the echo parakeet, is endemic to the island of Mauritius. Individual birds have been marked and re-sighted over 20 breeding seasons as part of a species recovery programme, providing re-sightings of breeding (56% of re-sightings) and non-breeding individuals (44% of re-sightings). Such comprehensive encounter histories provide a unique opportunity to test the underlying assumptions of UMS models in a long-lived species with delayed breeding. A series of multistate models were created ranging from a version that replicated the assumptions of UMS models, through to a version allowing parameters to be estimated independently of these assumptions. The results showed significant differences in age-specific survival probabilities between breeding and non-breeding birds, and significant transition probabilities between breeding and non-breeding states in both directions. These results suggest that older birds skip breeding in some years before returning to the breeding population.

The analyses suggest that vital rates estimated using UMS models produced biased estimates for this species, particularly those in which older birds occasionally skip breeding. It is therefore important to improve understanding of the ecology of non-breeding individuals, for instance by integrating new tracking technologies with more conventional mark re-sighting systems. In the meantime, it is important to explore the consequences of potential biases in vital rates estimated using unobservable state models for population growth and persistence.

3.2 Introduction

3.2.1 Single state models and survival

Demographic information is fundamental to monitoring population patterns: modelling key parameters can deliver powerful information about population processes (Mccaffery and Lukacs 2016). The models have important applications across a range of disciplines, including commercial harvesting (Pascual *et al.* 1997), species-environment interactions (Fay *et al.* 2015), population restoration and translocation programmes (Low and Pärt 2009), and even modelling population trajectories (Pollock 2000). Drivers of population declines can often be identified through the monitoring of demographic parameters, providing information against which to implement appropriate management procedures (Nur and Sydeman 1999; Ewen et al. 2012; VanderWerf et al. 2014; Mccaffery and Lukacs 2016).

A powerful tool for exploring a key demographic parameter, survival, is through capture-mark-recapture (CMR) models, which have accelerated in development over the past century. CMR studies derive information from encounter histories, which are constructed from observations of individuals marked from a known age or a common start point (Seber 1986; Pradel *et al.* 1997). A fundamental CMR model is the Cormack-Jolly-Seber (CJS) model (Cormack 1964), which utilises recapture data from individuals in the same state (such as a breeding state) to estimate apparent survival (φ) and re-sighting probabilities (P) (Figure 3.1); between the re-sighting periods, individuals ether die or survive, and having accounted for differences in re-sighting probability, apparent survival can be estimated. In order for CMR models to work, some inherent assumptions must be adhered. These assumptions are:

1. Every marked animal present in the population at sampling period i has the same probability of being captured or re-sighted.
2. Every marked animal present in the population at sampling period i has the same probability of survival until sampling period i+1.
3. Marks are neither lost nor overlooked and are recorded correctly.

4. Sampling periods are instantaneous (in reality they are very short periods) and recaptured animals are released immediately.
5. All emigration from the sampled area is permanent.
6. The fate of each animal with respect to capture and survival probability is independent of the fate of any other animal.

The CJS framework is relatively simple and thus offers minimal parameter redundancy, meaning it is widely employed to examine survival in breeding individuals, Offering some flexibility, CJS models allow for the incorporation of age structure and time dependence, building models which account for certain ecological traits of the study species by constraining certain parameters appropriately, an example being that of 1 year old individuals never being sighted, thus fixing their recapture to 0. Often this involves relaxing assumptions number one and two.

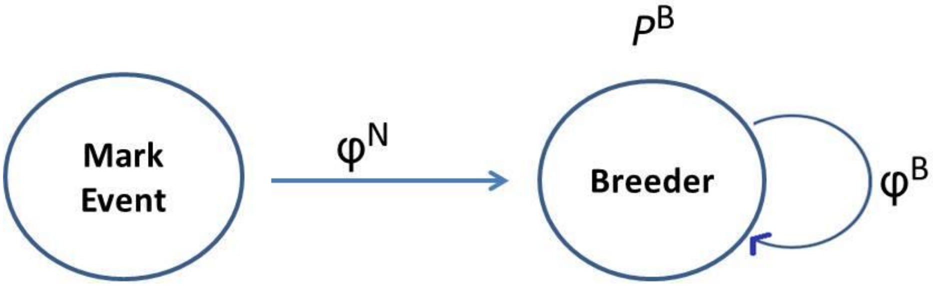


Figure 3.1 Diagrammatic simplification of a CJS model where an individual may only be re-sighted in one state, in this case, as a breeder (B). The model has two estimable parameters, survival (φ) and re-sighting probability (*p*). Compiling encounter histories from multiple individuals, probabilities for φ and *p* may be estimated. An individual may occupy a state prior to B, e.g. non-breeder (N), but in a CJS framework, parameters here are estimated indirectly. Figure is author's own.

The extent of flexibility of the CJS is, however, very limited, and the model framework lacks the ability to reflect the complexities of many natural systems and generally underestimates true survival (Cole 2012). Developments of the CJS model have therefore helped to explore the effects of age and sex on survival in a range of species (e.g Loison *et al.* 1999; Bradshaw *et al.* 2003; Chaloupka and Limpus 2005), and begin to examine additional population rates of interest, such as recruitment or movement. A significant portion of population survival studies have focused on bird populations, given the abundance of longitudinal data sets available (Newton 1998).

3.2.2 Multistate models

For species with short life spans and a quick accession to breeding, CJS models are ideal (Spendelow *et al.* 2002). However, the life histories of long-lived species can be far more complex. Accession to breeding can be slow and even once sexually mature it is not guaranteed an individual will consistently breed. The dynamic nature of a population means individuals may move through several different physical or geographical states, such as sexually immature to mature, or movement between islands. Quantifying the transition probabilities between states can help measure recruitment rates or the demographic differences which occur as a result of experiencing different environmental and physical constraints. Yet these transitions cannot be accurately explored with the classical CJS model, as its structure defines the probability of an individual being seen according to two parameters: the probability that the animal survived and remained in the sample area (φ), and the probability that the animal was encountered (*P*), conditional on being alive and in the sample area.

In response to the need to describe complex systems, the development of multistate models has provided a rich class of models applicable to a great range of scenarios. Multistate models are essentially an extension of the normal CJS, but consider a third parameter – a 'movement' parameter (ψ) – meaning an individual may pass through more than one state (Figure 3.2) (Lebreton *et al.* 2009). This provides a framework to consider a whole range of geographical and/or physical states with which to explore processes such as dispersal (e.g VanderWerf 2008; Fernández-Chacón *et al*. 2013), rates of accession to breeding (e.g. Saunders *et al*. 2014; Fay *et al*. 2015), or the trade-off between states (e.g. Rotella 2009; Souchay *et al.* 2014). Furthermore, understanding the sources of variation in state survival has proven invaluable to the conservation management of a great range of species, even providing insight into the effects of social dynamics on survival (e.g. Khan and Walters 2002) and the importance of individual life-histories in shaping population level dynamics (Sæther *et al.* 2013). Sources of heterogeneity can be individually examined in a multistate model, whereas in a CJS model such traits would be pooled.

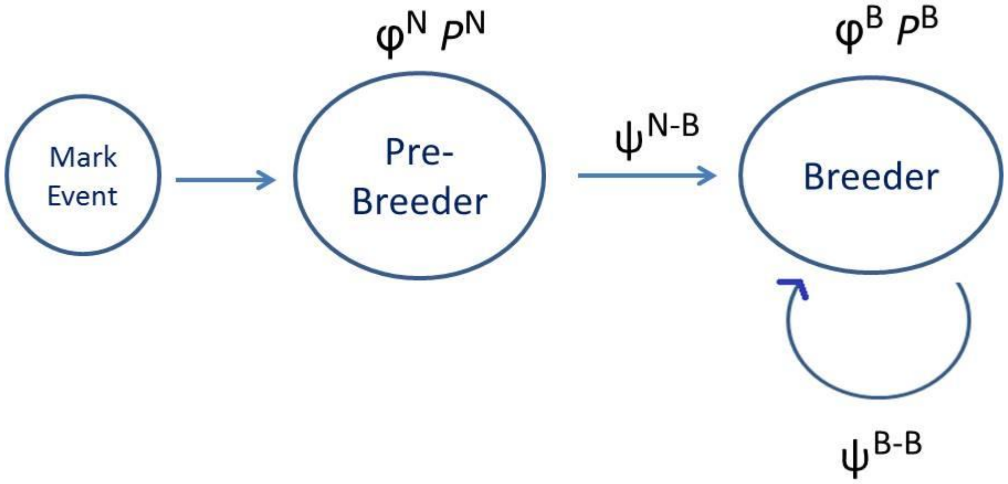


Figure 3.2 Principles of a multistate model where a third parameter, transition (ψ), is estimable. Transition from pre-breeder to breeder ($\psi^{N\text{-}B}$) occurs in one direction, and probabilities of remaining a breeder ($\psi^{B\text{-}B}$) can be estimated. Note that this diagram is based on the default assumption that individuals survive then move. To separately estimate the parameters see Cooch and White (2011). Figure is author's own.

3.2.3 Unobservable states

It is common for many species to move into states which are not logistically possible to observe, a typical example being a non-breeding individual. Non-breeders are often elusive or absent from the breeding area during sampling periods, particularly with territorial species, and thus become unobservable. Non-breeding states may arise due to delayed sexual maturity, skipping a breeding season, or perhaps existing in a state of torpor (Kendall and Nichols 2002; Schaub *et al.* 2004). The extent of this unobservable period depends on the life history and ecology of the study species. Whilst not so problematic for colonial bird species - where non-breeders regularly occupy breeding areas - the monitoring of territorial species has proportionately focused on the relatively easily observed breeders and the areas they occupy (Katzner *et al.* 2011). Consequently, non-breeding members of a population are more frequently overlooked in population studies and populations are only partly monitored (Fay *et al.* 2015; Sanz-Aguilar *et al.* 2016). This is commonly seen in long-lived bird species which are well known for passing through an unobservable state as they become sexually mature, after which they return to breeding sites and become observable (Votier *et al.* 2008; Horswill *et al.* 2014). However, without explicitly re-sighting individuals during these immature years it is impossible to estimate survival for each age class. Often these unobservable periods are of biological interest, and these periods are not just restricted to pre-breeders; even adults can become unobservable, challenging how we estimate their survival as their frequency of re-sighting remains sparse (Souchay *et al.* 2014).

3.2.4 Valuing unobservable states

Breeding individuals have long been considered as key drivers of population dynamics (Newton 1998) yet the survival of juveniles and pre-breeders will critically affect recruitment probability, and ultimately, population growth (Nur and Sydeman 1999; Dybala and Gardali 2013; Fay *et al.* 2015). Survival until first reproduction can also be a major source of information about individual lifetime variation in productivity (Monrós *et al.* 2002), but accurately identifying the links between the two is challenging. Such early-life stages are often unobservable due to methodological limits, and so understanding their contribution to population dynamics has remained limited. For example, re-sighting non-breeders in colonial seabird populations is almost impossible , yet these non-breeder can represent more than 50% of the population (Votier *et al.* 2008). If survival prior to breeding and age of first breeding are indeed of great importance to population dynamics (Lebreton and Clobert 1991; Saunders *et al.* 2014), their exclusion is mis-informative of the entire population dynamics. Demographic models often play an integral role in choosing how to manage populations (Converse *et al.* 2009; Katzner *et al.* 2011), therefore population biologists would benefit from improving current approaches for estimating non-breeder vital rates.

3.2.5 Approaches to modelling unobservable states

The source of these known unknowns lies largely in the ability to physically monitor a whole population, if not representatives from each segment.

Camera traps, genetic sampling, radio telemetry and GPS tracking are just a few recent technological advances which have helped illuminate the more hidden elements of population ecology. However, for logistical and financial reasons, these methods are not easily implemented at a population level. A number of statistical and analytical solutions have been proposed to overcome the methodological challenges of modelling unobservable states and explore survival in more populations with more complex life histories. Unobservable periods have long been dealt with in a similar way to temporary emigration (e.g. Seber 1986; Kendall *et al*. 1997) by applying a similar format to estimate transition probabilities between observable and unobservable states. Pollock's (1982) robust design is one method extension of a CJS offering an insightful approach dealing with unobservable states; the design requires field studies to be conducted in a way that gathers repeated observations from within a sampling period, yet it still fails to accurately measure their vital rates. With real temporary emigration, an individual is not physically within the study area (e.g. a migratory species), whilst an unobservable state is somewhat different; there is potential to observe an individual and they may continue to contribute to the community dynamics, even if not re-sighted. Even then, the general assumption of equal survival between observable and unobservable animals must be observed (Kendall and Nichols 2002).

Another approach to reducing the limitations of CJS and multistate models (Pradel and Lebreton 1999; Kendall 2004) is to include an unobservable state in the Arnason multistate model framework (Arnason 1973; Schwarz *et al.* 1993; Clobert *et al.* 1994). This specifically assigns non-breeders to an unobservable state where re-capture probability is fixed at zero due to zero re-sightings, but permits an estimate of survival to be made (Fujiwara and Caswell 2002; Kendall and Nichols 2002). In a typical multistate framework, should an animal not be observed the model accounts for the probability that it exists in one of the other specified states. If the animal transitions outside any one of these states, it is considered as a permanent transition and ultimately affects estimated mortality rates. Since not all states can be observed, and not all transitions into unobservable states are permanent, UMS models try to estimate demographic differences between breeders and non-breeders, observed and unobserved, and quantify transition probabilities (Schaub *et al.* 2004)

If additional re-sighting information cannot be supplied, such as that provided by employing Pollock's robust design, the following classes of model constraints may be imposed (Kendall and Nichols 2002) in a multistate framework:

1) Relaxing the order of Markovian transition probabilities, thus allowing transitions to be dependent on the previous state (also known as 'memory models').
2) Imposing a degree of determinism on transition probabilities.
3) Removing state specificity of survival probabilities
4) Imposing temporal constancy of parameters

Constraints two and three can be problematic as they prevent important transitions from being detected, and the survival probability of individuals in unobservable states are assumed equal to those estimated for observable states (Kendall and Nichols 2002). Based on an ecological understanding of many species, such assumptions are known to be flawed and introduce bias to parameter estimates. Yet without data being explicitly collected from unobserved states, testing the suitability of these models is limited to using synthetic data analysis.

How the model is structured will vary according to the species' ecological traits, the data available and the questions of interest. Whilst these individual traits will differentially affect the sources of bias in the model, I will briefly highlight the commonplace the underlying assumptions that are of common concern:

- **It is assumed that all mortality takes place before movement:** Mortality is dependent on the state an individual occupies. An animal cannot move to a new state where a different survival probability applies and then die. Therefore if it dies it must do so as a function of its current state. However, it is highly probable that an individual may not be seen for several occasions before death, therefore modelling senescence becomes biased. Without sufficient recapture histories in the post breeder state, transition here cannot be modelled and most models will assume death occurs almost immediately after their final encounter (Lebreton *et al.* 2009). Modelling transition out of the breeding state, and survival outside of the breeder state, is therefore not possible, even though ignoring this process is not always biologically reasonable. If we cannot model movement into this unobservable state then certain ideas on transition probabilities are flawed.

- **State clarity:** It is not always clear what state an individual is in - this can be even when the individual has been seen and *state mis-classification* can occur (Kendall 2009; Lebreton *et al.* 2009; Lebreton and Pradel 2002). More commonly, an individual may not be encountered in a given year and it therefore cannot be assigned to a state with great accuracy. The individual may have bred and not been seen, or not bred and not been seen. There is no way to differentiate, but corresponding terms are automatically built into the model as the model state likelihood takes account of the possible animals that are missed (Lebreton *et al.* 1999). Regardless of how the modle tries to deal with such uncertainty, an additional assumption is forced to be made; **birds not seen in-between breeding seasons are assumed to have an equal survival probability to those confirmed to be in the breeding states**.
- **Recruitment:** The challenge of many ecological scenarios means 100% recapture probability can be almost impossible and observing all states can be even harder, particularly pre-recruits. Estimating recruitment is based largely on the probability of the movement from a non-breeder to breeder. This relies on the survival of pre-recruits being equal to breeders, but having a different transition rate. However, this will mean biased estimates of transition if transition and survival cannot be separated, therefore pre-breeder and breeder survival are assumed equivalent. Another key assumption is that all pre-breeders start breeding by age "*m*" if they are still alive at age "*m*" (Clobert *et al.* 1994; Spendelow *et al.* 2002) This assumption is forced to be made because recapture information is not available on pre-

breeders over a certain age, meaning the model is logically constrained and could be another source of biased estimates. Furthermore, age is often not considered to be relevant once an individual is breeding.

- **Constant breeder probability:** it is assumed that after age *k*, breeding probability is 1, or at least at a high level calculated for adults. However, this could result in very inaccurate estimates; ‘skipping’ is a common behaviour seen in some species (Converse *et al.* 2009). For one, possibly two seasons, an individual may transition out of the breeding population and become a non-breeder, then transition back to breeder state. This means a varied breeding probability both with time and age, and could be very revealing of the conditions which promote or hinder breeding conditions. By not accounting for this year of absence we assume that survival in this period is equal to the breeding population, again resulting in a poor reflection of the population’s dynamics. Secondly, the assumption that all individuals must begin breeding by a certain age or not breed at all excludes any understanding of how the non-breeding members of the population may contribute to population dynamics. It also makes presumptions about individuals which have not been seen, or those which are older than *k* but still under *m*. Finally, it is assumed that survival probability is constant once birds exceed *k*, whether they have begun breeding or not. In most circumstances this is the only suitable means of modelling the data, and it may indeed be a fair representation. Yet it may poorly reflect the rate of acquisition into the breeding population, affecting our insight into the behaviour of non-breeders and their influence on population dynamics. Without age specific recapture histories and encounters in the non-breeder state, a multistate model has few other choices than to make several risky assumptions.
- **Equal survival:** An additional assumption is that all individuals released at age 0 in sampling period *i* have the same probability of survival until sampling period *i* + k. However, to understand population functioning we would ideally like to model this survival as age specific

and with time. In species with a 2-3 year maturation period this may not be so essential, but in longer lived species with delayed sexual maturity, acknowledging key demograophics in these phases is increasingly important.

One of the first attempts to study pre-breeder survival with a UMS model was a case study based on roseate terns (*Sterna dougallii*; Spendelow *et al.* 2002). These birds experienced delayed sexual maturity and occasionally skipped breeding seasons, during which they became unobservable. Defining these periods as a separate state accounted for the transition between different life history stages, times when individuals were known to be alive but could not be sampled. In the case of the roseate terns, this helped to model important state-specific survival in relation to environmental conditions, and inspired a rapid increase in similar studies (Reed *et al*. 2003).

3.2.6 Summarising the constraints of the unobservable multistate models

Since Spendelow's study, a growing number of attempts have been made to incorporate unobservable states into multistate models, trying to more accurately reflect biological systems by drawing more information from CMR data (e.g. Kendall 2004; Saunders *et al.* 2014; Sanz-Aguilar *et al.* 2016). The increased complexity of these models incurs the cost of increased parameters and potentially greater parameter redundancy; the strengths and limitations of these methods have been extensively reviewed (Rotella 2009; Cole 2012; Bregnballe *et al.* 2009; Schaub *et al.* 2004). Of great concern is that the assumptions made when constructing these models (as discussed in 3.2.5) introduces substantial inaccuracies in the parameter estimates generated; for CMR models to work, certain fundamental assumptions are inherent, whether using a CJS or a multistate framework. In the case of multistate models, a range of additional assumptions, many of which are specific to the ecology and biology of the study system, must also be made. For example, pre-breeders may never be seen after their initial mark-capture event, and thus re-sighting probability prior to breeding is set to zero. A very common, yet highly restrictive assumption is that of equal survival probabilities between observed and unobserved states - predominantly that of pre-breeders and breeders (Spendelow *et al.* 2002; Reid *et al.* 2004). This assumption ignores the demographic differences between two very different states, ultimately making model reliability questionable (Pradel *et al.* 2005).

In light of the many underlying constraints, concerns have been raised about the suitability of UMS models (Bailey *et al.* 2010; Kidd *et al.* 2015; Sanz-Aguilar *et al.* 2016; Lee *et al*. 2017). As pointed out by Spendelow (2002) and several other authors employing multistate models (Reed et al. 2003; Converse *et al.* 2009; Jenouvrier *et al.* 2008; Szostek *et al.* 2014; Lee *et al*. 2017 to name a few) the inherent assumptions of CMR models could magnify errors when accounting for unobservable states and therefore poorly reflect the dynamics of the study system (Calvert *et al.* 2009). To what extent do these assumptions affect model accuracy and the ability to describe both unobservable and observable states? Building a model deficient of certain observational data may bias estimates of survival, re-sighting probability and transition rates, but due to the rarity of information it has not been possible to test their reliability beyond theoretical studies. The risk of miscalculating demographic rates could have profound effects for the accuracy of projecting population growth (Lee *et al.* 2017). Population viability analyses are highly valuable in conservation biology, but they rely on accurate estimates of demographic parameters, and an inappropriate survival model could lead to biased population predictions and misinform management (Sanz-Aguilar *et al.* 2016). Comparisons have been made between the performance of CJS and UMS models, estimating the degree of associated bias and the flaw in their assumptions. To the best of my knowledge however, these questions have only been explored through the use of hypothetical data, as re-sightings in unobservable states have not been available.

A demographic analysis of 20 years of long term CMR data on a territorial bird species provided the unique opportunity to establish the suitability of UMS models and test their underlying assumptions. The echo parakeet (*Psittacula echo*) takes two years to reach sexual maturity, with most individuals entering the breeding the population at four or five years old. During this period of maturation, typically an unobservable time period for territorial species, an extensive number of observations have been collected. Whilst the monitoring programme established to recover the once Critically Endangered population has predominantly focused on re-sightings of breeders. In addition, observations were frequently made of pre-breeders and of adult non-breeders seemingly ‘skipping’ breeding seasons or entering senescence.

This study developed a series of models in a multistate framework that range from explicitly including two types of unobservable states which allowed the assumptions of a UMS model to be relaxed, to models with only one distinctly observable state and two unobservable. This allows the performance of typical UMS models to be tested, and the validity of the assumptions imposed. The bias caused by including unobservable states without explicit re-sighting data is then quantified, and the effect of the entire exclusion of temporary emigration in a CJS model on estimates of demographic rates is considered. This aims to establish whether the use of UMS models can be reliably used when considering non-breeders in a population and their contribution to demographic variation.

3.3 Methods

3.3.1 Study system and data collection

In this chapter, only details relevant to the chapter are presented, but further information has been reported in Chapter 2.

There are two key aspects of the echo programme which were fundamental to this study: firstly, that almost the entire population had been ringed at chick stage with individual field-readable rings, and secondly, their intense monitoring has provided regular re-sightings of these birds across their life-time. Information regarding the initial marking of a bird and its subsequent re-sightings was combined to build a comprehensive CMR data set for this analysis. Such information which was collated from the stud book and field observations of non-breeding birds established as part of this thesis.

Echo parakeet stud book and breeding observations

A stud book, managed as part of the echo parakeet monitoring programme, documents the origin of each bird, its key life-history data and its life-time of annual breeding activities (see Chapter 2 for further information). From this file alone, one can track a bird from point of fledging through every breeding attempt in the following years. This stud book begins in the 1991/1992 austral breeding season and continues to 2014/2015.

Non-breeder field observations

The stud book alone provided sufficient detail to produce single-state encounter histories. Unique to this study are observations of non-breeding birds during the breeding season. I sourced these re-sightings from nest records which describe additional birds seen in the field and at active nests, comments in annual reports and publications, feeding observations collected for phylogeny studies, and general field notes. The ID of a bird could then be cross-referenced with the stud book to identify its origin and age, and document the years it was re-sighted in a non-breeding state.

3.3.2 Encounter history files

Re-sightings of breeding and non-breeding birds, with information regarding origin extrapolated from the stud book, were compiled to produce two slightly different forms of recapture file: one suitable for a single state CJS framework and one for a multistate framework.

Single-State CJS Data File

This was developed to produce an encounter history file suitable for a CJS framework, where survival probabilities (φ) and re-sighting probabilities (*P*) could be explored. Data were derived only from the stud book and its associated breeding records. To ensure all birds had a common starting point, I removed individuals which were never ringed, never successfully fledged, or were first marked as adults. In some cases, juveniles were ringed as a fledgling, and these were included if their parentage was known and ringing occurred before the end of the breeding season (end of February).

Such exclusions permitted an accurate age structure to be incorporated in the models.

After a bird's first marking event (i.e. when it was ringed) their subsequent re-sightings were acquired from the breeding records in the stud book, as almost every nest attempt has a confirmed parent ID. Breeders (B) were therefore defined as individuals recruited into the breeding population and known to be breeding. A breeding attempt was defined as at least one fertile egg being laid, and a breeding partner identified.

Re-sightings in the breeding state were coded as ones and zeros: 1 = first capture and mark event, and subsequent observations of the individual in the breeding state; 0 = not re-sighted that season. Therefore, in the format outlined by White and Burnham (1999), an example history may be 100110 which equates to; first mark event, not seen, not seen, seen breeding, seen breeding, not seen. Each number is equivalent to one sampling period, in the case of the echo parrot, the six month breeding season which extends late August to end of February.

Records were available from the 1991/92 breeding season to the 2013/14 season. However, the first chicks to be ringed in the nest and fledge successfully did so in 1994, and so represent the first cohort in this data file. Cohorts of 2012 and 2013 were excluded as they would not become sexually mature (and therefore seen in the breeding state) until 2014/15. A disease outbreak in 2005 resulted in several birds being brought into captivity and euthanised. These birds were retained in the encounter history file, as their deaths were considered inevitable, regardless of human intervention, and formed an important aspect of the survival analysis. Recapture histories of euthanised birds were marked with 'zero return' from 2005 onward within the encounter history file. The model then estimates mortality using patterns and probabilities estimated from the rest of the population. The final dataset spanned 20 consecutive sampling occasions, or seasons, and comprised 1008 individuals from 18 cohorts.

Multistate Data File

To explore state-specific survival (φ) and transition (ψ) rates, a second data file of encounter histories was created that included both breeder re-sightings and non-breeder-sightings. As with the single-state file, the stud book provided information of an individual’s point of first marking and subsequent re-sightings in the breeding state. For this multistate file, re-sightings in two non-breeding states were included; pre-breeder (N) and post-breeder (PO). N defined young birds having fledged the nest but which had not yet attempted to breed. PO defined individuals re-sighted as non-breeders that have bred at least once before. An example encounter history may therefore follow N-N-0-B-B-PO, which is described as; first mark event, re-sighted pre-breeder, not re-sighted, breeding, breeding, re-sighted but not breeding.

In accordance with the assumptions of both CJS and multistate models, only re-sightings during the breeding season were used to allow time to transition between states and age group. Unlike the single state file, birds from the 2012 cohort could be re-sighted in a pre-breeder state in 2013 and were therefore included. The 2013 cohort was still excluded as this study did not include re-sighting data from 2014 onwards. With the first cohort in 1994, the final data file included 20 consecutive sampling occasions with 19 cohorts, a total of 1164 individual encounter histories.

3.3.3 Analytical framework

In order to test the underlying assumptions of a UMS model, this study built a set of models which specifically reflected the classic assumptions of UMS models. The performances of these models were then compared with an additional set of UMS models that were similarly built but relaxed the underlying model assumptions. Analysis of model performance followed the principle of parsimony - based on Aikaike’s information criterion (AIC_c; Burnham and Anderson 2002) - and allowed me to assess how independently estimating observable states contributed to model fit. I then evaluated how the different models impacted the parameter estimates for state-specific survival and transition probability.

3.3.3.1 Single state CJS models

The first step was to model breeder (B) survival in a single state CJS framework using the Single-State Data File. Identifying an appropriate age structure was essential to accurately describe any age specific changes in survival and *P* in a long-lived species; the oldest birds known to date are 19 years old (MWF 2013). This age structure would provide the starting model for the multistate models.

CJS model structure

The focus of the CJS model set was to identify the most parsimonious model describing age and time specific variation in survival and *P* across the echo data. This was explored by manipulating the age structure in survival, and both age and time structure in re-sighting probability. Based on *a priori* knowledge, re-sighting probability was explored with and without time dependence, but survival was built with time dependence in every model: the structure and size of the population has varied dramatically over the 20 years and experienced a severe disease outbreak that affected survival. Preliminary CJS models provided compelling evidence for variation in survival over time. Including time dependence would therefore account for as much variation in the data, and permit an appropriate age structure could be accurately identified. Time dependence in re-sighting probability was also explored in this model set as it was previously unknown whether or not re-sighting probability varied significantly. A consistent monitoring protocol employed for the echo parakeets suggested this not to be the case but testing this parameter was necessary.

Based on an understanding of the biology of the parakeets and population structure, the study began with a general model of ten fully time dependent (t) age classes in survival and re-sighting probability (Model 17, Table 3.1):

$$[\ \varphi(1{=}2,\ 3{:}9,\ 10{+})t\ .\ P(1{=}0,\ 2{:}9,\ 10{+})t\ ]$$

‘1=2’ indicates that first and second year birds were combined to estimate two year old survival, as re-sightings of two year old breeders were rare and it is not possible to re-sight a one year old as a breeder. The second point was enforced forced by fixing first year re-sighting probability at 0.

Subsequent models were built by gradually truncating the oldest age class in both survival and re-sighting until a structure with three age classes (1:2, 3+) was reached (Models 2, 5, 9, 12, 13, 15, 16, Table 3.1).

These eight models were repeated with time independence (.) in re-sighting probability (Models 1, 3, 4, 7, 8, 10, 11, 14, Table 3.1).

3.3.3.2 Multistate models

The CJS models helped explore the principle variation in survival for each age class of breeding echo parakeets, and the most parsimonious age structure was applied in a multistate framework. Using the Multistate Data File, a set of comparative models was built both with and without observable states. Three different states were defined in the UMS model: 'pre-breeders' (N), 'breeders' (B) and 'post-breeders' (PO). Three parameter types were then estimable: survival, re-sighting, and a new parameter type, transition probability (ψ).

3.3.3.3 A model set to test UMS model assumptions

An appropriate general multistate model (MS-1) was primarily built in order to test the data for over dispersion (see section 3.3.6 for details). The next step tested the underlying assumptions of multistate models which included an unobservable state. This unique study system included three observable states, whose survival parameters were manipulated to compare model performance when the UMS assumptions were upheld (N and PO φ assumed equivalent to B) and when they were 'relaxed' (N and PO might be unequal to B). Only survival varied between models, re-sighting and transition probabilities retained a constant structure that was state and age-dependent to provide flexibility in the models and examine the effects of model assumptions on transition estimates.

Breeder Survival Only - MS-2

1 Observable State, 2 Unobservable States

MS-2 was built with the model assumptions upheld, with pre-breeder and post-breeder states made temporarily unobservable and assumed to experience survival equivalent to breeder. This reflected the typical structure of a UMS model, where known unobservable states are accounted for but without explicit re-sightings recorded (Figure 3.3a).

Pre-breeder and Breeder Survival - MS-3

2 Observable States, 1 Unobservable State

MS-3 was an adjusted version of MS-2 which assumed the survival probabilities of pre-breeders and breeders might be unequal, but assumed equivalent between breeder and post-breeder (N≠B=PO; Figure 3.3b). Survival for pre-breeders was therefore separately estimable to breeders. Recognising the states may differ in survival also permitted probabilities of transition to be estimated independently, rather than making potentially inaccurate assumptions about their values.

Breeder and Post-Breeder Survival - MS-4

2 Observable States, 1 Unobservable State

This modelled survival in the opposite way to MS-3. The assumptions of birds in a post-breeder state were relaxed, allowing survival in this state to be unequal to breeder. Those in a pre-breeder state were modelled as an unobservable state, and therefore assumed to have survival equal to breeder (Figure 3.3c).

Pre-breeder, Breeder and Post-Breeder States - MS-5

3 Observable States

MS-5 entirely relaxed the traditional model assumptions, allowing survival for all three states to be separately estimated (Figure 3.3d). Due to increased model complexity, the number of parameters increases. Typically, high parameterisation incurs a cost in AIC_c, but if model fit is improved significantly by these additional parameters - an expectation in this study - then the model’s performance would be expected to surpass that of Models MS-2, 3 and 4.

Fig. 3.3a

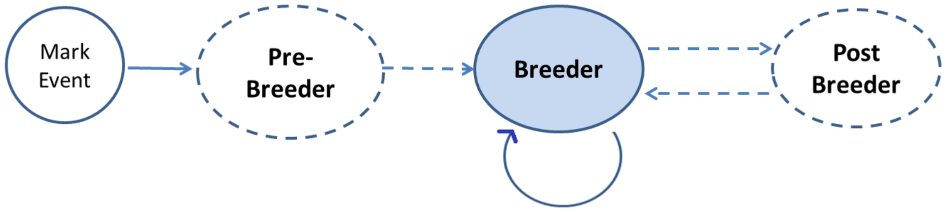


Fig. 3.3b

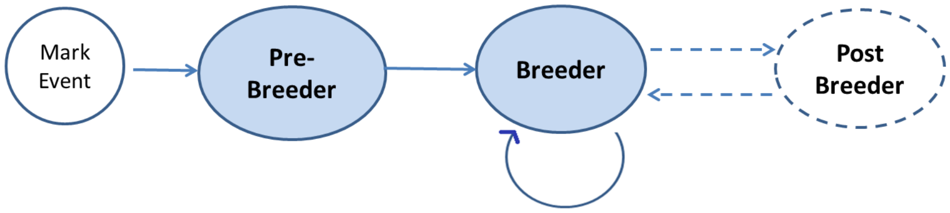


Fig. 3.3c

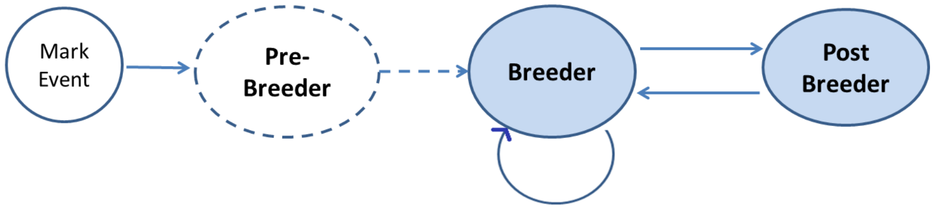


Fig. 3.3d

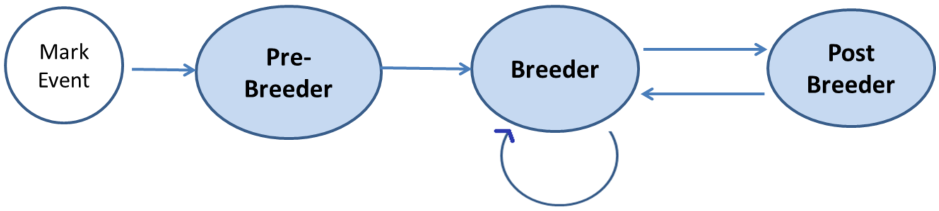


Fig. 3.3e

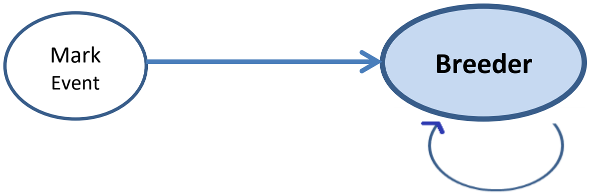


Figure 3.3 a - b. A comparison of the various model structures built depending on whether states were modelled as observable (blue with solid outline) or unobservable (white with dashed outline). 3.3a. The simplest model reflecting CMR studies with only re-sightings in state B, and survival in states N and PO are assumed equal to B and consequently subject to much bias. 3.3b. φ N ≠ B = PO. Advancing from MS-2, this diagram emphasises the separately estimable parameters for N and B, with φ estimates for PO inferred from breeder estimates by assuming equivalence. 3.3c. φ N = B ≠ PO. MS-3 allowed PO φ to be unequal to B, whilst those in state N were considered equal to B φ. Transition estimates from B to PO and PO to B increase in accuracy, but recruitment rates remain biased. 3.3d. φ N = B ≠ PO. MS-4 represented a unique model where re-sightings in the three separate states allowed φ to be independently estimated in addition to ψ. 3.3e. Reference to a CJS single state structure, using only the encounter histories with state B re-sightings and thus far fewer estimable parameters.

3.3.4 Comparison of the UMS models

Model Fit

Models were compared using AIC_c (corrected for small sample size) and were considered a better fit if change in AIC_c was greater than 2 (Burnham and Anderson 2002). If the assumptions of UMS models were accurate, one would expect little difference between the model performances, regardless of whether a model relaxed or upheld the underlying assumptions.

Survival

Survival estimates generated by the models were compared to determine the degree of bias introduced when assumptions are made about state survival. Studies regularly report an expected bias in parameter estimates for unobservable states when re-sighting data is not available, but the extent of this error has not yet been measurable.

Transition Probabilities

Allowing the models to estimate survival probabilities separately for each state gave the advantage of independently estimating transition probabilities rather than making potentially inaccurate assumptions about their values. Estimates generated by the model with relaxed assumptions (MS-5) were examined: did transitions out of the breeder state prove irreversible? Did certain transitions experience particularly high or low probabilities and were these specific to certain age classes? The transition estimates were compared with MS-2 - which upheld the model assumptions - to identify if model assumptions also bias transition estimates.

3.3.5 Comparison of CJS models with UMS models

The UMS models provided a framework in which their fit was comparable by AIC_c and associated model weight, and therefore compared how well each model was able to explain the data. A second concern associated with unobservable states is the bias introduced to parameter estimates if they are not accounted for at all, as is the case in a CJS framework. I therefore compared the parameter estimates generated by MS-5, which relaxed all UMS model assumptions, with those generated from the CJS model (four age classes, constant φ and *P*), where unobservable states may be known to exist but were not accounted for in the model structure. A similar assumption of equivalent survival among states is therefore frequently made.

3.3.6 Modelling details

Goodness of fit - Single-State

All of the models discussed so far make very specific assumptions concerning model fit and these assumptions must be tested when using programme MARK in order to ensure an appropriate model structure is developed. This is achieved through a goodness of fit test (GOF), which provides a diagnostic procedure for testing the assumptions underlying the models we are trying to fit to the data. By following this testing procedure, GOF tests further help to determine if the most general model adequately fits the data; comparing the relative fit of a general model with a reduced parameter model will only provide good inference if the more general model is suitable. Should a ‘lack of fit’ occur, then the expectations determined by the assumptions underlying the models have not been met, and the model is not suitably structured for describing variation in the data.

A severe lack of fit would indicate that the general model violates these assumptions and poorly describes the study system. For example, there may be insufficient age structure in the model and the model structure would need to be re-considered. On a smaller scale, there may simply be extra ‘binomial noise’ (variation), as is often the case with non-experimental studies. Deriving the scale of this over-dispersion can be achieved through estimating the variance inflation factor, median c-hat (ĉ). The median ĉ provides a measure of the lack of fit between the general and saturated models; as ĉ becomes >1, the lack model of fit increases. With typical CMR data, the distribution of the model deviance is often not x^2 distributed. Therefore, the median ĉ approach generates the distribution of model deviances, given the data, and compares the observed value against the generated distribution and thus measures how well (or poorly) the model fits the data.

Prior understanding of the echo study system provided insight into natural heterogeneity in the data, and therefore how best to account for this in the structure of the general model; for the echo parakeet system, variation in the data was accounted for through the model's complexity (10 age classes, multiple states and complete time dependence). With this is mind, and following on from the approach of similar studies (e.g. Converse *et al.* 2009; Cooch and White 2011; Horswill *et al.* 2014), the median ĉ procedure available in programme MARK (White and Burnham 1999) was used to test the most general single state model [φ(age(1=2, 3:9, 10+)t) .*P*(age(1=0, 2:9, 10+)t)]. This was calculated with a lower bound of 1.0, upper bound of 2.7 and 1000 replicates. A score greater than 3 was taken to represent lack of fit and over-dispersion (Lebreton and Colbert 1991). The lower bound value of the simulations was set to 1, as this indicates perfect fit. An upper bound of 2.7 was set as it is generally accepted that anything over 3 indicates fundamental problems with the model. The median ĉ approach provides the observed model deviance as a proportion of the deviance of degrees of freedom - thus for all of the simulations run, the median ĉ value summarises the extent to which the values generated by simulated models differed from the observed model deviance. After 500 simulations, the degree of over dispersion was calculated and could be applied to the data within programme MARK. This results in Quasi AICc values and adjusts the weight of the models.

Goodness of Fit - Multistate

Several methods have been proposed to test GOF in multistate models (e.g. Pradel et al. 2003; Choquet et al. 2009; Abadi et al. 2013) but their suitability is still questionable given that they are often specific to a given model (Cam *et al.* 2004). GOF tests serve to identify heterogeneity in the data, any structural failure and over dispersion and can determine whether the assumptions of the models are violated. Yet the models in this study were built specifically to account for this heterogeneity by modelling age and time specific transitions across the three states, states that were entirely observable and group classifications known. Considering the purpose of this study was to test the validity of certain assumptions, it was only necessary to test for over dispersion, thus the median-ĉ approach was deemed sufficient for the multistate modls as well. This was calculated using the global MS model (MS-1): [φ(age (1:3, 4+)t) *P*(age(1:3, 4+).) ψ(age(1:3, 4+)t)]. One multistate data file was used for the MS and UMS models.

Model Constraints

Across all of the models, certain parameter constraints were applied to reduce parameter redundancy.

In the CJS:

- Survival in age classes 1 and 2 were combined (denoted as 1=2) since re-sighting a breeder at age 1 is not possible, and re-sightings at age 2 were sparse.

In both the CJS and UMS models:

- Breeder re-sighting probability was fixed at 0 for age 1 (denoted 1=0) as echo parakeets cannot enter this state before age 2.
- Breeder re-sighting from age 2 upwards was fixed at 1 as almost every nest attempt is found and breeders identified.

In the UMS models:

- A bird cannot enter the breeding state until 2 years old at the earliest, therefore survival and re-sighting of age 1 breeders were both fixed to 0. The transition of pre-breeder to breeder was consequently fixed at 0 for age 1.
- A bird cannot exist in the post-breeder state until 3 years old at the youngest, therefore survival and re-sighting probability at age 1 and 2 were fixed at 0. Breeder to post-breeder transition was also not possible until age 3 and fixed accordingly.
- Post-breeder to breeder transitions can only happen by 4 years old at the earliest, and a bird must have passed through the breeding state prior to this.
- Breeders to pre-breeder, post-breeder to pre-breeder and pre-breeder to post-breeder were all invalid transitions and fixed to 0.

All models were run with logit link function, and all survival data were analysed using Programme MARK, version 8.1 (White and Burnham 1999).

3.4 Results

3.4.1 Single state CJS models

Calculation of median-ĉ showed a reasonable fit of the general model (ĉ = 1.2). Applying this variance inflation factor, model comparison by quasi-likelihood AIC_c ($QAIC_c$; (Burnham and Anderson 2002) showed that the most parsimonious survival model from the CJS model set (Model 1, Table 3.1) to be:

$$\varphi_{\text{age(1:3, 4+)t}}\ P_{\text{age(1:3, 4+)}}.$$

Model selection for four age classes suggested that variability in survival stabilised progressively with age, fluctuating very little from four years upwards. *P* was best described as constant but age specific.

3.4.2 Multistate models

Age Structure and Goodness of Fit

The four age class structure supported in the CJS model was brought through to the UMS models. Testing the general multistate model (MS-1, Table 3.2) indicated slight over-dispersion and a modest correction factor of 1.4 was applied to the data, meaning all further multistate models to be comparable by quasi-binomial AIC_c ($QAIC_{c)}$.

Whilst there was compelling evidence of age specific, time dependence in survival in the CJS model, for the UMS models, time was only included in the general model to test model fit. To include time in all UMS models would have explained more variation in the data, but due to the extensive change in population size and age structure over the course of its recovery, there was a sparsity of data in certain age and state specific classes. As the purpose of this study was to test model assumptions, the optimum ‘population model’ per say was not required. Furthermore, if a state was truly unobservable, it would not be possible to explore time effects due to lack of observational data, and this analysis aimed to remain in line with the classical UMS structure.

3.4.3 Comparison of UMS models

Model Fit

The multistate model set was built by systematically relaxing the assumptions of UMS models and examining any effects these changes made to explaining variation in the data. In relaxing the model assumptions and allowing state specific survival to differ, the fit of the model varied significantly: MS-5 was a substantially better fit to the data than MS-2, the model which upheld typical UMS model assumptions, with a difference of 59.22 $QAIC_c$ between them (Table 3.2). Model MS-5 explained the most variation in the data comparative to all other models in Table 3.2, scoring highest by model weight and with the lowest $QAIC_c$. Ultimately this indicates that it is invalid to assume survival is equal among states, but there is in fact great variation between breeder and non-breeders which cannot be explained under the typical UMS model assumptions.

Table 3.1 Set of CJS models testing both the suitability of age structure and the influence of time dependence (t) and time independence (.) on survival (φ) and re-sighting probability (*P*) of breeders. Age classes are denoted numerically, ranging from three classes (1:2, 3+) to 10 (1:9, 10+). Model parsimony increases with decreasing QAIC_c. All models were run with logit-link function.

M	Model	QAIC_c	Δ QAIC_c	AIC_c Wts	ML	No. p	Q Dev.
1	$\varphi_{\text{age}(1:3,\ 4+)t}\ P_{\text{age}(1:3,\ 4+).}$	2611.15	0.00	0.99	1	54	1037.2
2	$\varphi_{\text{age}(1:2,\ 3+)t}\ P_{\text{age}\ (1:2,\ 3+)t}$	2620.37	9.22	0.01	0.01	68	1016.5
3	$\varphi_{\text{age}(1:2,\ 3+)t}\ P_{\text{age}\ (1:2,\ 3+).}$	2623.85	12.70	0.00	0.01	37	1086
4	$\varphi_{\text{age}(1:4,\ 5+)t}\ P_{\text{age}(1:4,\ 5+).}$	2625.82	14.67	0.00	0	70	1017.6
5	$\varphi_{\text{age}(1:4,\ 5+)t}\ P_{\text{age}\ (1:4,\ 5+)t}$	2636.08	24.93	0.00	0	99	964.2
6	$\varphi_{\text{age}(1-3,\ 4+).}\ P_{\text{age}(1:3,\ 4+).}$	2645.19	34.04	0.00	0	6	1144.3
7	$\varphi_{\text{age}(1:5,\ 6+)t}\ P_{\text{age}(1:5,\ 6+).}$	2645.76	34.61	0.00	0	85	1005.0
8	$\varphi_{\text{age}(1:6,\ 7+)t}\ P_{\text{age}\ (1:6,\ 7+).}$	2669.15	58.00	0.00	0	99	997.6
9	$\varphi_{\text{age}(1:4,\ 5+)t}\ P_{\text{age}(1:4,\ 5+)t}$	2670.74	59.59	0.00	0	128	933.5
10	$\varphi_{\text{age}(1:7,\ 8+)t}\ P_{\text{age}\ (1:7,\ 8+).}$	2690.70	79.55	0.00	0	112	990.1
11	$\varphi_{\text{age}(1:8,\ 9+)t}\ P_{\text{age}(1:8,\ 9+).}$	2710.47	99.31	0.00	0	124	982.8
12	$\varphi_{\text{age}(1-5,\ 6+)t}\ P_{\text{age}(1:5,\ 6+)t}$	2716.25	105.10	0.00	0	155	916.4
13	$\varphi_{\text{age}(1:6,\ 7+)t}\ P_{\text{age}(1:6,\ 7+)t}$	2761.92	150.77	0.00	0	180	902.6
14	$\varphi_{\text{age}(1:9,\ 10+)t}\ P_{\text{age}(1:9,\ 10+).}$	2762.55	151.40	0.00	0	135	1010.1
15	$\varphi_{\text{age}(1:7,\ 8+)t}\ P_{\text{age}(1:7,\ 8+)t}$	2801.67	190.52	0.00	0	203	886.1
16	$\varphi_{\text{age}(1:8,\ 9+)t}\ P_{\text{age}(1:8,\ 9+)t}$	2840.59	229.44	0.00	0	224	872.5
17	$\varphi_{\text{age}(1:9,10+)t}\ P_{\text{age}(1:9,10+)t}$	2864.02	252.87	0.00	0	243	847.2
18	$\varphi_{(t)}\ P_{(t)}$	4000.88	1389.7	0.00	0	37	2477.3
19	$\varphi_{(t)}\ P_{(.)}$	4162.94	1551.8	0.00	0	20	2676.38

M = Model number. QAIC_c = quasi-likelihood AIC_c. ML = Maximum likelihood. No.P = number of parameter. φ for ages 1 and 2 were always grouped (1=2) but for brevity this is not stated. Models without time in φ are not reported to maintain the focus on examining variation in φ over time.

Survival

Comparing parameter estimates from the different UMS models confirmed that a significant degree of bias is introduced when models try to describe unobservable states, leading to an inaccurate description of demographic rates. An underlying assumption of UMS models is that non-breeder survival is considered equivalent to breeder survival, but this was found to be untrue. The full model (MS-5) estimated very different survival for each of the three states (Figure 3.4). Survival for pre-breeders for age 4+ was estimated at 0.78 (95% confidence intervals [CI] = -0.719 / +0.833,) whilst breeder survival was 19% higher at 0.97 (CI = -0.937 / +0.986) and post-breeder survival was 0.67 (CI = -0.539 / +0.782). With further evaluation, it is apparent that the estimates for an *observed* state were in fact compromised when an unobservable state was included. Whilst MS-2 and MS-5 generated the same survival probabilities for pre-breeders, ages 1 and 2, their estimates for breeders differed; MS-2 estimated breeder survival age 4+ at 0.90 (CI = -0.880 / +0.921), whilst MS-5 has reported a probability of 0.97 (CI = -0.937 / +0.986). Differences are illustrated in Figure 3.4 (for original estimates, see Appendix 3.1).

The model comparisons and their estimates indicate that UMS models underestimate breeder survival and inflate non-breeder survival, and that for this study system at least, non-breeders and breeders experience very different survival probabilities.

Table 3.2 Set of multistate models comparing a general model (MS-1) with four additional models which independently estimated φ for either one, two or all three states, N, B and PO (indicated in the column ‘Model Explained’). ‘≠’ indicates a non-breeding state φ was allowed be unequal to state B and therefore independently estimable. ‘=’ indicates a non-breeding state’s φ was built to assume equal survival with B. Only φ was manipulated in the models, *P* and Ψ retained the same structure across all models, which were age and state specific. A four age class structure was applied in all of the models and each of the three parameter types, φ, P and ψ. Models are ordered by their Quasi Akaike Information Criterion(QAIC$_c$) No.P = Number of parameters. Q Dev = Q Deviance.

Model Name	**φ**	***P***	**ψ**	**No. P**	**Q Dev.**	**QAIC$_c$**	**Δ QAIC$_c$**	**Model Explained**
MS 5	$\varphi^{state}_{1:4+.}$	$P^{state}_{1:4+.}$	$\psi^{state}_{1:4+.}$	21	1840.12	4791.6	0	N≠B≠PO
MS 3	$\varphi^{N,B}_{1:4+.}$	$P^{state}_{1:4+.}$	$\psi^{state}_{1:4+.}$	19	1876.93	4824.35	32.8	N≠B=PO
MS 4	$\varphi^{B,PO}_{1:4+.}$	$P^{state}_{1:4+.}$	$\psi^{state}_{1:4+.}$	18	1891.64	4837.04	45.4	N=B≠PO
MS 2	$\varphi^{B}_{1:4+.}$	$P^{state}_{1:4+.}$	$\psi^{state}_{1:4+.}$	16	1909.47	4850.82	59.2	N=B=PO
MS 1	$\varphi^{state}_{1:4+t}$	$P^{state}_{1:4+ t}$	$\psi^{state}_{1:4+.}$	263	1421.42	4906.35	114.8	N≠B≠PO

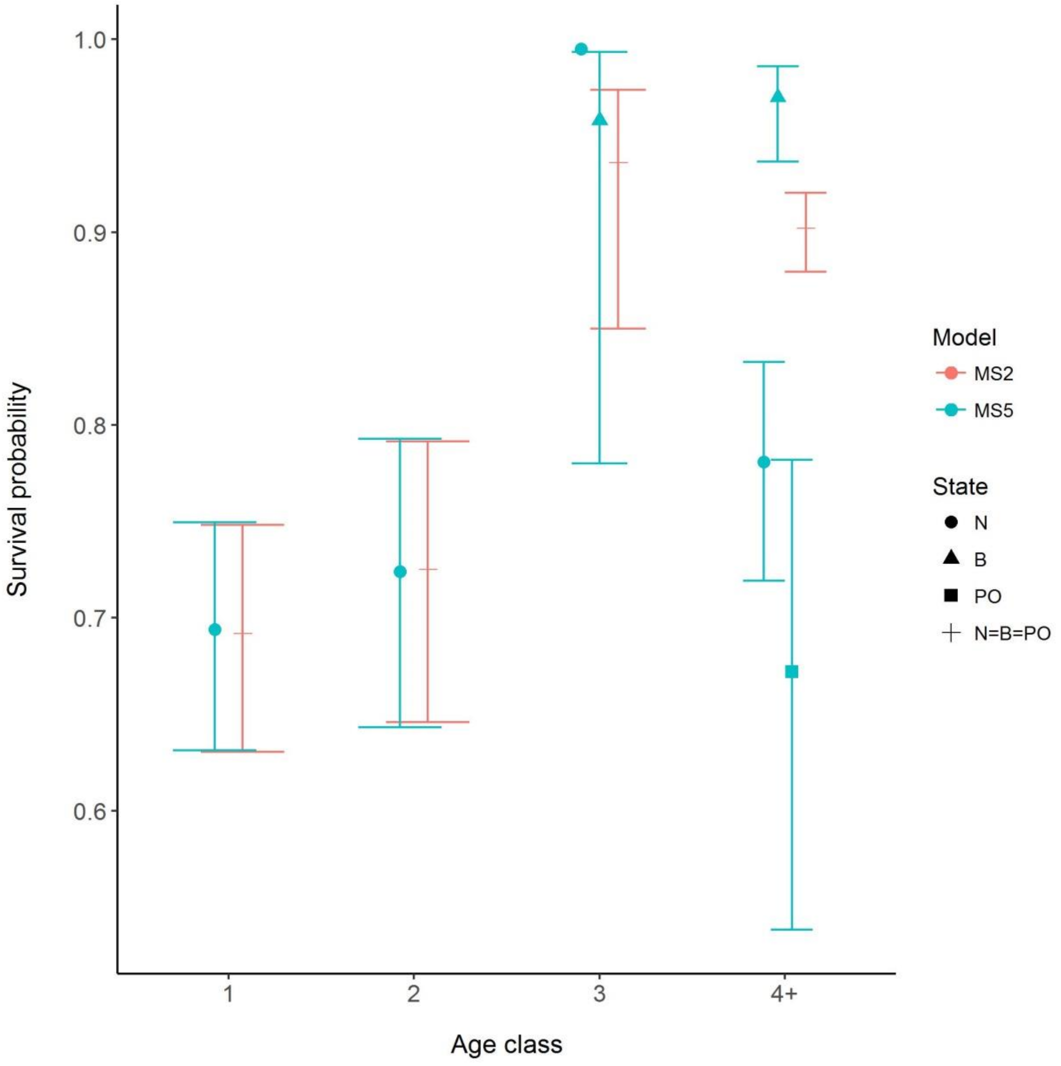


Figure 3.4 Comparison of the φ estimates produced by MS-5 (blue) and MS-2 (red). State specific estimates are differentiated by the shapes of the points. MS-5 independently estimated φ for states N, B and PO in the relevant age classes. MS-2 assumed equivalent φ across the 3 states (N=B=PO). In MS-2, age 1 may only represent birds in states N, age 2 is an estimate for birds in N and B, and ages 3 and 4+ represent an estimate for N, B and PO due to assumed equivalence. Note that the y-axis does not start at 0. Vertical bars represent 95% confidence intervals, though 95% CI for age 3 N, in model MS-5, are excluded due their large range (CI = 0 / 1), a result of data deficiency.

3.4.4 Comparison of CJS and UMS model estimates

The explanatory power of a model was undisputedly better when integrating at least one unobservable state, revealing that the assumptions of UMS models were flawed. The final step was to explore the extent to which estimates were biased under such typical limitations. The parameter estimates generated by the four age class CJS model, with time independence in survival and re-sighting probabilities, were therefore compared with the estimates of MS-5 (Table 3.3).

Table 3.3 Comparison estimates of φ produced for each age class in the single state CJS and multistate framework (MS-5 specifically). Estimates for age 3 N φ, age 2 B φ, and ages 2 and 3 PO φ from MS-5 were excluded as data deficiency produced unreliable results here. SE = standard error. CI-/CI+ = 95% confidence intervals.

CJS-1 Model Estimates

Age Class	State	φ	SE	CI-	CI+
1 = 2	B	0.580	0.019	0.542	0.618
3	B	0.924	0.040	0.798	0.973
4+	B	0.943	0.008	0.924	0.957

MS-5 Model estimates

Age Class	State	φ	SE	CI-	CI+
1	N	0.694	0.030	0.631	0.749
2	N	0.724	0.038	0.643	0.793
4+	N	0.781	0.029	0.719	0.833
3	B	0.958	0.038	0.780	0.993
4+	B	0.970	0.012	0.937	0.986
4+	PO	0.672	0.063	0.538	0.782

Breeder Survival

In the CJS model, survival estimates in the breeding state had tight confidence intervals (Figure 3.5 and Table 3.4), but these estimates were biased low compared to those of MS-5, with a difference of 4% by age 4+.

Non-Breeder Survival

Estimates from MS-5 for post breeder survival were low (0.672, CI = -0.538/+0.782) (Table 3.4 and Figure 3.5) and over-estimated by the single state models. By ignoring observations of adult non-breeders, a CJS model would assume their survival probability mirrors those in the breeding state at 94%. Integrating unobservable states appears to affect the estimation of both non-breeder and breeder survival. A full model output of the MS-5 model is reported in Appendix 3.2, which includes re-capture probabilities and again indicates the fixed parameters,

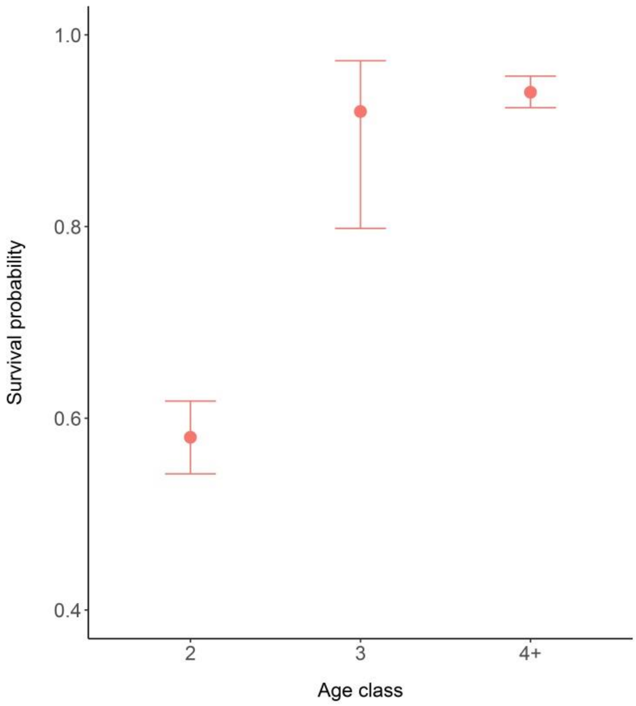
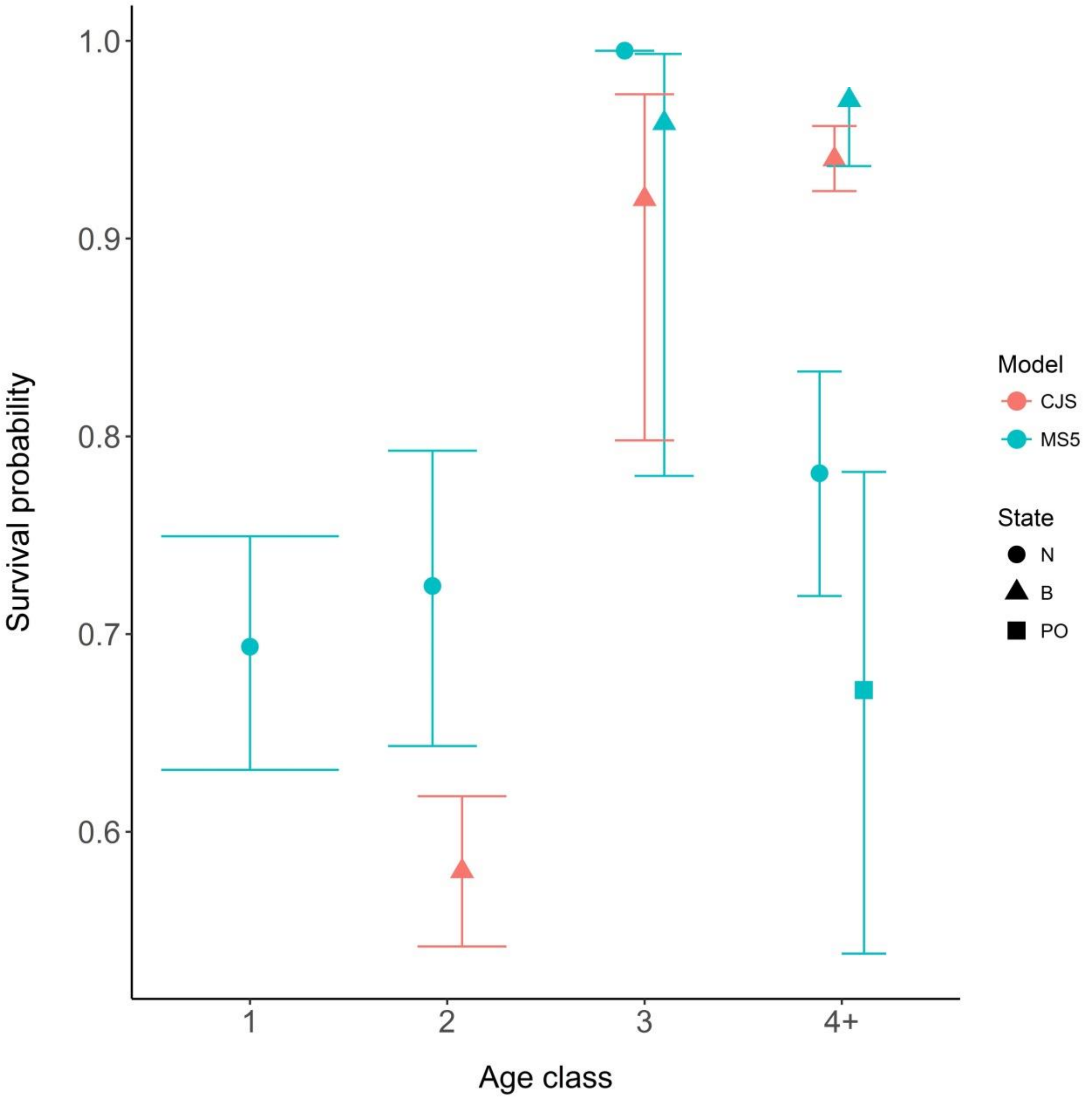


Figure 3.5 *Left*: Age-specific φ estimates generated by the single state CJS model for state B only. *Below:* Direct comparison of estimates from the CJS model with the UMS model, MS-5, which included three states (N, B & PO) with independently estimable φ. The comparison indicates a bias incurred in CJS models if unobservable states are not accounted for, under-estimating B φ, and inflating φ estimates of non-breeders (N & PO). Vertical bars represent 95% confidence intervals Y-axis does not start at zero in either of the plots.



3.4.5 Transition probabilities in the UMS framework

If an individual was not observed on a sampling occasion, a typical UMS model framework cannot differentiate whether they transitioned into an unobservable state, or if they remained in an observable state but were not seen. If a bird is never re-sighted again it may be presumed dead, and it is therefore unknown at what time, point and state in which they died is therefore unknown. Alternatively, an animal may recruit and breed permanently in an unobservable area or state. This potentially important transition rate is assumed as death and becomes confounded with mortality, with estimated model parameters referring only to monitored animals. A CJS model is not capable of estimating transitions at all, and whilst UMS models attempt to account for these important differences, it comes at the cost of biased results, the extent of which cannot be measured. The results of this study, however, indicate the importance of accurately accounting for state differences. Including observations for all states, as modelled in MS-5, allowed survival to be estimated with greater precision partly as a result of these accurate transitions, and confirmed that different states experience different survival. The addition of pre-breeder observations permitted precise recruitment rates, a crucial component of population growth, but more unusual was the estimation of movement back and forth between states: in the case of the echo parakeets, this described a skipping behaviour in breeding efforts, as birds transitioned forwards and backwards between breeder and post-breeder.

Table 3.4 Transition probabilities estimated by MS-5 for the feasible movements pre-breeder (N) to breeder (B), breeder to post-breeder (PO), post breeder to breeder. Certain transitions for particular age classes were redundant and therefore fixed at zero. SE = standard error. CI-/CI+ = 95% confidence intervals.

Transition	Age Class	ψ	SE	CI-	CI+
N - B	2	0.153	0.019	0.119	0.195
N - B	3	0.255	0.030	0.201	0.317
N - B	4+	0.202	0.026	0.157	0.257
B - PO	3	0.131	0.052	0.058	0.271
B - PO	4+	0.109	0.015	0.083	0.142
PO - B	4+	0.581	0.072	0.437	0.712

3.5 Discussion

3.5.1 Key findings

This study demonstrated that UMS models which relaxed underlying assumptions and independently estimated state specific parameters, fitted the data profoundly better than models which made assumptions about unobservable states. As a result, the suitability of UMS models is questionable for this species at least. Consequently it may also be unsuitable for species with long-life histories and unobservable states similar to those of echo parakeets. This is based upon findings that (i) age-specific survival probabilities differ significantly between breeding and non-breeding birds, particularly in older individuals and (ii) transitions between non-breeding and breeding states can occur in both directions - in the case of the echo parakeet, adults of breeding age may return to the breeder state after skipping a breeding season. Although not statistically tested, examining the raw data suggests this extends only one to two breeding season. Excluding unobservable states from a model causes marked bias in survival and transition estimates for both observed and unobserved states, but trying to account for them incurs a new set of costs. This implies the use of unobservable multistate models require further refinement if demographic rates are to be estimated accurately.

3.5.2 Method suitability

Employing multistate models, whether including unobservable states or not, necessitates certain assumptions. In this study the aim was to test the validity of one particular assumption; equal survival between non-breeder and breeders. This does not, however, rule out the importance of recognising potential sources of bias within this study to ensure confidence in the results. The breeding population has remained the primary focus of the monitoring programme, with sightings and identification of non-breeders being comparatively infrequent. Field monitoring actively searches and checks breeding sites, whilst non-breeder sightings are much more incidental and thus collected opportunistically. Whilst monitoring efforts for each state varied (i.e. breeders were specifically monitored .vs. opportunistic sightings of non-breeders) this bias had remained consistent as the monitoring design has remained unchanged.

The power of multistate modelling is only informative if individuals are accurately assigned to their state (Lebreton and Pradel 2002; Kendall 2009). It is possible that some breeding attempts were missed entirely, or early clutches which failed might have gone unrecorded. In such cases, a breeder may either escape detection entirely or be classified as a non-breeder. Alternatively, a non-breeding bird seen as a floater at a nest site might be recorded as the resident breeder. Floaters are often adult non-breeders ‘hanging-around’ at active nest sites, or curious, young pre-breeders. When the population was very small during early years of management, nest helpers of breeding attempts had been recorded, probably a result of more potential breeders than available nest sites as echo parakeets are not recognised for their social breeding strategies (Thorsen *et al.* 1997). However, the echo monitoring programme began to survey the forest and check nests sites prior to the start of the breeding season, therefore any early nests should have been identified, in addition to new nest sites. Breeding pairs are highly monogamous and show high nest site fidelity, which, combined with repeated visits to nest sites during the season, ensures the correct breeding pair is identified. For these reasons, all models were run with perfect recapture in the breeding state, as the monitoring programme has an exceptionally high success rate of finding all nest attempts and ringing chicks before fledging. This perfect recapture is exemplified by the fact that only 13 birds have been found as fledglings outside of the nest without an ID ring. In some cases were these nest were not unknown, but chicks had fledged before they were ringed.

The frequency of successful, unrecorded breeding attempts would be too low to significantly influence the models, but to cross check the effects of this possibility, the models were repeated with imperfect recapture in the breeding state. This widened the confidence intervals around certain estimates, but did not affect the rank of model performance by $QAIC_c$.

Skipping Behaviour or Senescence?

In this study, post-breeder states could in fact relate to one of two possible events: a bird skipping a breeding season or a bird having permanently entered senescence. The first option is more likely to occur at younger ages, whilst the latter is indicative of old age. To account for these differences a four state model could differentiate between birds skipping a breeding season and those assumed to have entered senescence. This would, however, require a strong confidence in state assignment. Given that such a small number of the individuals in the study entered a post-breeder state and never 'left' - indicating senescence - the power of the model would likely decline with an increase in parameter numbers and decrease in re-sightings per state. One final option to help differentiate between skipping and senescence could be to advance the study to use multi-event model (Sanz-Aguilar *et al.* 2016). This approach is often used for partially monitored populations. With this, only a specific state can be associated with additional probability of being in a different state and accounts for incorrect state assignment. This would be an interesting path of analysis to explore, but given that the focus of this study is to test the assumptions of a multistate model, this would have to be an extension of the current work.

Choosing Model Age structure

The age structure implemented in the multistate framework was based on the most parsimonious model identified in the CJS model set, which considered breeders only. It could be argued that age structure should have been similarly explored in the multistate, rather than retaining the same four age class structure for all UMS models. To assume that age specific survival followed an identical pattern across states might be inaccurate due to a difference in sensitivity between states and changes in the factors regulating individual survival. Not accounting for this may have limited the explanatory power of the models. For example, a five age classes structure might have been more suitable for describing pre-breeder survival, particularly those which survive but never go on to breed. Conversely, the post-breeder state becomes more relevant in older age classes, and a different age structure may have been necessary to account for this. Alternative age structures were explored in the multistate framework, generally differing by the grouping of age classes, for example 1=2, 3=4. Although this was not an exhaustive exploration, there was no indication of an improvement on the current structure. Further modification may be important if models were directly used to guide the management of echo parakeets. In long-lived species, survival rates of the oldest age class or most populated state often have the highest elasticity value (Saether and Bakke 2000). This implies that management actions focused here will have the greatest effect and future research on the echo parakeet could examine this further. Regardless of this potential refinement, changing the age structure would be unlikely to affect the fundamental differences between the UMS models, and the conclusions regarding their assumptions.

Time Dependent Survival

During the single-state model selection procedure, it was found that that time dependence in survival improved model fit, but for the multistate analysis all parameters remained independent of time. The population of echo parakeets has experienced a skewed distribution over the course of its recovery. In 1994 there were five breeding females and two fledglings, but by 2013 there were 97 breeding females and 170 fledglings. Therefore the age structure of the population has changed dramatically, as have the number of birds existing in any one state. For the purpose of this analysis, biologically meaningful estimates were not necessary; therefore excluding time dependence still provided an adequate model structure and removed the complications of a changing population structure.

3.5.3 Assessing the suitability of UMS models for long-lived species with delayed breeding

Developing UMS models has helped reduce certain limitations of classic survival analyses, enabling models to consider complex life-histories and become increasingly realistic (Cole 2012). The profound difference in UMS model performances in this study emphasised the importance of acknowledging these complexities. The inherent assumptions behind the models appear to be unrealistic, as employing a UMS model poorly reflects unobservable states and even compromises estimates for observable states, as seen in the echo parakeet and other studies (e.g. Bailey *et al*. 2010; Sanz-Aguilar *et al.* 2016; Lee *et al*. 2017). The extent and effect of bias in parameter estimates has been explored under a variety of model approaches, such as CJS, robust designs and integrated models, when unobservable states are known to occur (Converse *et al.* 2009; Kendall and Nichols 2002; Bailey *et al.* 2010; Cole 2012). Until now, many evaluations have remained limited to analytical and numerical approaches (e.g. Fujiwara and Caswell 2002; Szostek *et al.* 2014) and real data has not been available to accurately test the extent of bias, which this study has found to be quite profound. How to deal with these biases now poses a new set of challenges, particularly as the ecological interpretation of ‘unobservable’ varies across contexts.

3.5.4 Implications for population models

State variables are dynamic over time, so an understanding of the association between states and their differences in demographic vital rates helps describe life-history qualities and contribute to stage-based modelling (Caswell, 2001). Specific parameter estimates generated from various survival models are often integrated into population models to measure the growth and persistence of a population (Armstrong and Ewen 2002; Maggs *et al.* 2015; Mccaffery and Lukacs 2016). This is widely used for commercial purposes such as harvesting, species translocation and relocation programmes, as well as conservation purposes such as small population management. As with many statistical models a certain degree of uncertainty is accepted (Converse *et al*. 2009; Bailey *et al.* 2010), but the use of inaccurate demographic data could result in the wrong identification of key life-history traits which could mislead projections for population growth and lead to inappropriate management recommendations (Pascual *et al.* 1997; Nichols and Armstrong 2012; Kidd *et al.* 2015)(Nichols and Armstrong 2012). This is highly relevant for the echo parakeet population, which continues to be managed and will be for the foreseeable future. Describing the historical changes during the population's recovery contributes to identifying the regulatory mechanisms of vital rates such as survival and breeding effort. Under the assumptions of a typical multi-state model, breeding effort would have been considered consistent and the skipping behaviour would not have been identified. Its identification could influence how the population is managed, pushing focusing onto increasing breeding rates by reducing skipping. Finally, demographic values integrated into population growth models will affect estimated trajectories. Pre-breeder survival rates drive population growth and the quality of the data underpinning a model will determine prediction of population trajectory, information which often influences decisions regarding population management.

3.5.5 Valuing non-breeders

Traditionally, monitoring programmes of many species use the breeding segment to assess population dynamics (Newton 1998). Instead, we should see a change in monitoring, reflecting the growing awareness of the importance of monitoring unobservable states, such as non-breeders, and describing the effects of a population's heterogeneity on its growth (Abadi *et al.* 2013). A recent publication by Lee *et al.* (2017), demonstrated non-breeders and breeders differentially affect population growth rates (λ), with growth rates being most sensitive to changes in the non-breeder parameters. This highlights the considerable influence of commonly ignored non-breeders on population dynamics, and demonstrates the degree of bias brought about by considering only breeders.

Recognising the differences in non-breeders and breeders highlights the need to better understand their ecological differences, including behavioural aspects, and the consequences of interactions between states. For example, non-breeders may promote or negate breeding success, either through helping behaviour (Khan and Walters 2002; Paquet *et al.* 2015), competition (Carrete *et al.* 2006) or aggression (Cubaynes *et al.* 2014). Whether negative or positive, the effects of non-breeders on whole population dynamics are proving equally important.

Acquiring accurate, precise estimates are a high priority for species of conservation concern, and research is increasingly invested by others to improve monitoring methods themselves (Erb *et al.* 2015; Brown *et al.* 2017) as well as the statistical approach for their analysis (e.g Lee *et al.* 2017). Rapid advances in monitoring technology help to illuminate the more hidden elements of populations via camera traps, genetic sampling, radio telemetry and GPS tracking. Monitoring methods and statistical analysis have not, however, developed alongside one another, and data is often not amenable with the analytical methods and their inherent requirements (Brown *et al.* 2017). Combining more conventional mark re-sighting systems with advanced data collection methods could help observe the currently unobservable, but for this to succeed, more time must be invested in the planning phase to improve the effectiveness of the entire study - from data collection through to analysis.

3.6 Conclusions

The implications of my findings are that is incorrect to assume that the survival rates of breeders and non-breeders are equivalent. Assuming equivalence leads to inappropriate inferences from survival models when unobservable states are included, but re-sightings are not explicitly available. Clear flaws in the assumptions of UMS models therefore lead us to question their overall suitability when modelling population demographics. If unobservable states are known to exist, there is no clear approach to accounting for them. Excluding them entirely in a CJS framework incurs biased parameter estimates, yet to try and account for them in a UMS model also generates biased results. Further work is necessary to explore the consequences of producing biased vital rates estimated by UMS models and their impact on in population growth models. Combining new tracking technologies with traditional CMR studies could help to monitor non-breeder states, whilst exploring multi-event models, robust designs and even integrated modelling approaches may provide additional solutions if non-breeders are to remain unobservable.

Chapter 4

Determining the impact of supplementary feeding on the reproductive success and survival of echo parakeets

Student contribution and impact

Developing the methods of Chapter Three, Chapter Four provides the first ever accurate measures of certain key demographic parameters for the wild population of echo parakeets; breeding success, age and state specific survival rates, and transition (predominantly recruitment). Breeding success has been previously examined in relation to the use of supplementary food (Tollington *et al.* 2015), but this chapter extends this work both in depth and time by utilising the extensive data set established as part of this PhD. Current understanding of echo parakeet ecology and demography has been considerably advanced through this research chapter, which considers the impact of supplementary food on breeding success in parallel with age and state specific survival. Both are essential demographic parameters to understand within population dynamics, but rarely are the two examined in unison, meaning an important correlation between them may be overlooked. In light of the widespread use of supplementary feeding in wildlife management, this chapter makes a valuable contribution to species conservation programmes already employing this tool, or considering its use, by more explicitly examining the potential costs and benefits.

4.1 Abstract

As the world faces a biodiversity crisis, many small populations are declining at unprecedented rates. In particular isolated species such as island endemics, or those with small range and slow life histories. Focused research which aims to aid management strategies that support such populations and promote population growth is therefore of immeasurable value. The provision of supplementary food (SF) has become a well-established tool in wildlife management. Implemented with relative ease for small populations, it can directly affect target populations or relieve the constraints of other environmental pressures. Despite the widespread use of SF, rarely are the effects of such a major intervention critically evaluated, nor the ecological and logistical implications considered in long-term management. While SF has appeared to play a crucial role in the recovery of certain populations, success across sites, populations and species is variable. In the case of the Mauritian (echo) parakeet, the provision of SF has played an integral role in the population’s recovery from near extinction. 80% of the breeding population now rely on supplementary food, yet the relative impact of SF on key demographic parameters has not been explored until now.

Using 20 years of field monitoring data, this study aims to describe the simultaneous impact of SF on three key demographic parameters: breeding success, survival and recruitment. Breeding success was improved by the use of SF and the effects continued into later life, as individuals originating from supplementary fed nests were twice as likely to recruit into the breeding population, and were less likely to skip a breeding season. Conversely, SF had no apparent effect on an individual’s survival. Overall, SF has introduced positive demographic changes to the population, and findings from this study provide information relevant to optimising future management efforts, both for echo parakeets and the wider application of SF as a conservation tool. These results demonstrate the potential benefits of further work exploring the role of SF in behaviour, disease ecology and its interaction with environmental conditions.

4.2 Introduction

4.2.1 The role of food supply in population dynamics

Productivity, survival and mortality are recognised as three pivotal demographic parameters which ultimately regulate population dynamics (Newton 1998). The complexity of individuals and their environment mean multiple factors interact to shape these parameters, and one crucial determinant is that of food supply. Food availability has long been recognised as a key mechanism underlying demographic processes (Lack 1954), identified from correlations between naturally occurring spatial and temporal fluctuations in food supply, and observed changes in a population (Frederiksen *et al.* 2014).

Studies on bird populations widely report food as a determinant of the timing and span of the breeding season (Reed *et al.* 2009; Breton and Diamond

2014). Examples include mass seed dispersal events triggering reproduction in birds (Curran *et al.* 2000) and the emergence of invertebrate prey governing when birds begin to breed (Hinks *et al.* 2015). Phenology shifts such as this can directly and indirectly affect breeding success, though rarely has a variation in timing of breeding led to population growth (Dunn and Møller 2014; Morrison *et al.* 2015).

More regularly associated with population growth are specific measures of breeding success. A meta-analysis by Robb *et al*. (2008) identified the important role of food supply in egg and clutch size, hatch rates, chick growth and fledgling success in a range of species. These changes may be driven by the greater food availability improving individual fitness, reducing competition and aggression events at feeding grounds, improving chick provisioning, or decreasing the risk of nest abandonment (Vafidis *et al.* 2016). The diversity of responses to food supply highlight its complex role as a regulatory mechanism with the potential to limit population growth (Armstrong and Perrott 2000)

4.2.2 Supplementary feeding regimes

The growing understanding that food availability can limit populations (Newton 1998; Armstrong and Perrott 2000) underpins the established use of artificial food in commercial wildlife management such as game harvesting. Ring-necked pheasants *(Phasianus colchicus),* are an excellent example, as the birds are traditionally provided with supplemental grain during the shooting season to maintain good physical condition, increase survival and therefore maintain the populations for future hunting (Draycott *et al*. 2005). Enhanced survival and reproduction through supplementary feeding (Elliott *et al*. 2001; González *et al*. 2006; Maggs 2016) has encouraged its use as a popular conservation tool to assist threatened populations (Ewen *et al.* 2015) and the global scale of its use is expanding. Accelerated rates of habitat loss and degradation, combined with the introduction of direct competitors, have been linked to numerous population declines (BirdLife International 2013) as they often lead to sub-optimal conditions and reduced food availability. Small populations are far more sensitive to environmental conditions, and coinciding changes in food supply can significantly contribute to regulating population dynamics.

In response to these challenges, providing supplementary food aims to mitigate, and ideally reverse, population declines (Ewen *et al.* 2015) by improving individual fitness and survival, even if food supply is not directly limiting. Accessible, nutrient rich resources can buffer against unpredictable environments that may limit the survival or breeding probabilities of vulnerable populations (Rodriguez-Hidalgo *et al.* 2010; Correia *et al*. 2015). Unlike many other management strategies, supplementary feeding can be implemented relatively quickly and initiate a rapid response, enhancing productivity to restore a viable, self-sustaining population (Jones and Merton 2012). Successful examples include the pink pigeon (*Nesoenas mayeri*) in Mauritius (Concannon 2014), the kakapo (*Strigops habroptilus*) in New Zealand (Elliott *et al*. 2001), White storks (*Ciconia ciconia*) in Western Europe (Hilgartner *et al.* 2014), the scrub-Jay (*Aphelocoma coerulescens*) in Florida (Schoech *et al*. 2008), and the Magpie robin (*Copsychus sechallarum*) in the Seychelles (Komdeur 1996). Predominantly employed for small population conservation, benefits have encouraged its application in translocation and re-introduction programmes as a means of support and post-release monitoring (e.g. hihi *Notiomystis cincta* - Castro *et al*. 2003; brown teal *Anas chlorotis* - Rickett *et al.* 2013) or to compensate for sub-optimal habitat conditions (e.g. takahe *Porphyrio hochstetteri* - Hegg *et al.* 2012).

4.2.3 Understanding the impact of supplementary feeding

Relatively easy to implement, the effects of SF can often be immediate and address a selection of threats to populations. Despite the scale of its use and highly intrusive nature, the decision to provide SF is increasingly implemented without any real comprehension of the theory of population limitation (Ewen *et al.* 2015), or the wider repercussions of its practice. It has been suggested that SF is becoming a part of a dogmatic approach to conservation (Ewen *et al.* 2015) employed as part of a suite of conservation measures and continued in its provision as long as there are no obvious drawbacks. It is easily assumed SF will generate the desired, positive response, yet a crucial part of providing SF is to critically assess its utility as a conservation tool and its ability to fulfil specific conservation goals (Elliot, Merton & Jansen, 2001; González *et al*. 2006; Schoech *et al*. 2008). Longer term effectiveness remains largely unexplored and hypothetical (Selva *et al.* 2014; Oro *et al.* 2008), with particular risks that SF may develop a high level of dependence on a costly resource, lack a feasible exit strategy or significantly alter the naturally complex dynamics of food supply.

Despite reports of positive responses from some studies, others report no obvious benefit (Meek *et al.* 2003; O'Leary and Jones 2006) or negative consequences (Robb et al. 2008; Harrison et al. 2010; Blanco et al. 2011; Selva *et al*. 2014 to name but a few). For example, Carrete et al. (2006) found that supplementary feeding of Bearded vultures (*Gypaetus barbatus*) led to territory compression which ultimately decreased productivity, whilst Adelman et al. (2015) found that a higher use of supplementary feeding stations directly increased disease transmission in house finches. SF may even provoke mixed effects as seen with the kakapo (*Strigops habroptilus*) in New Zealand, where SF improved recruitment rates, but supplementary fed pairs produced male-biased offspring (Clout *et al.* 2002). Responses of the kakapo were also inconsistent, varying from negative, to neutral to positive, depending on the Island to which they were re-introduced (Elliott *et al.* 2001). In small or endangered populations there is little room for error and the mixed responses highlight the need for on-going assessments of SF's impact. A lack of understanding of its impact could lead to its improper use, unwanted responses from the target population, and indirect effects for non-target populations and the local environment.

Employing SF regimes in conservation management largely focuses on promoting survival and reproductive success in order to stabilise, if not enhance, population size (Robb *et al.* 2008; Ruffino *et al*. 2014). Measuring the consequences of this regime on demographic parameters has seen a bias toward the individual and short term impacts and identifying the corresponding changes in reproductive parameters. Considering the population level effects is fundamental to ensuring long-term success, particularly as these key parameters will determine population trajectory.

Increasing the frequency of breeding and the success rate of each breeding attempt will of course contribute to population growth (Newton 1998), but populations are regulated by more than offspring production. The probability of juveniles surviving to recruit into the breeding population can also determine population size and structure, with population patterns further shaped by adult survival probabilities. Important work has been done by many of the long term studies on multiple species of vultures and report great benefits from SF (Houston *et al.* 2005). The endangered bearded vulture (*Gypaetus barbatus*) experienced no change in adult survival with SF, yet pre-adult survival markedly improved with SF (Oro *et al.* 2008). For the hihi in New Zealand (*Notiomystsis cincta*), their long term monitoring was able to generate estimates of several breeding parameters (such as lay date, clutch size) alongside the provision of SF and its demographic impact beyond the nest; so beneficial has the provisioning been that fledge rates and recruitment nearly doubled when SF was available (Castro *et al.* 2003). Eight years of monitoring this passerine was pivotal to such findings and emphasises the importance of long term monitoring when assessing the impact of SF on population demographic parameters. For this population, it became clear that SF may be crucial to the population's persistence. The capacity to monitor both breeding and survival parameters better guides the identification of how this conservation tool affects a population, justifies its use and improves its implementation, lessons which in the case of the hihi, went on to benefit similar programmes within New Zealand (Armstrong *et al.* 2007).

Monitoring the effects of SF over an individual's life-time will further help to identify the less immediate impact of its use. Resource availability can directly affect adult survival, but it may also have delayed effects; there is growing evidence indicating long-term consequences or carry-over effects from earlier life-history phases (Morrison *et al.* 2015) such as food supply experienced at a younger age. As an example: the nutritional conditions experienced during key stages of development have been identified as an important determinant of an organism's subsequent life-history traits, including their breeding strategy (Becker and Bradley 2007; Cartwright *et al.*

2014). Poor nutrition during early development can permanently affect an individual’s fitness, regardless of the conditions as an adult (Metcalfe and Monaghan 2001; Vincenzi *et al.* 2013). These medium to long-term trade-offs may therefore be of equal importance to regulating population dynamics as the immediate implications of food supply, and illuminate the poorly understood interaction between young and adult environments (Vincenzi *et al.* 2013).

It is now not uncommon for studies to consider the differential impacts of SF over multiple key demographic parameters and its variable influence in the short and medium term, whether experimentally (Vincenzi *et al.* 2013) or in a conservation context (Piper *et al*. 1999; Schoech *et al*. 2008). Once a supplementary feeding regime is well established, there is potential to manipulate management actions and explore how they may be improved (Meretsky and Mannan 1999; Armstrong *et al.* 2007; Ewen *et al.* 2015; Canessa *et al*. 2016; Maggs 2016). Monitoring the outcomes of management actions should be encouraged, as they will become crucial to the long-term viability of both a management programme and its focus species. Without a good knowledge of the study system, however, even hypothesising improvements to current strategies is not possible; ground work information is required on the basic demographic functioning of the population and the main impact resulting from a conservation actions. Evaluating the possibility that food supply may have a different impact on different members of a population, and differ across key life-history stages, would provide a novel insight into the role of food in population regulation. Such information is insightful to practitioners wishing to manage populations through controlling food supplies, whether for commercial or conservation purposes. For a species of conservation concern, the more information that can be made available regarding management options, the more informed their decision making process will be regarding if and how to implement such a strategy. Recognising and understanding the demographic consequences of supplementary feeding creates a pathway for successfully modifying and improving this tool, work which provides a springboard for greater conservation success.

4.2.4 Case study

A deficiency in the quantity and quality of natural food was considered a key factor behind the rapid population decline in the once critically endangered echo parakeet, constraining survival and breeding output as a result of malnutrition (Jones and Duffy 1993). As one of several efforts to recover the population from near extinction, SF has been provided *ad libitum* for nearly 16 years, with the goal of improving nutritional status and so improving both survival and reproductive performance. The additional food coincides (alongside other management activities, including nest box provision and population supplementation) with the general population growth of echo parakeets to a current estimate of 500-600 individuals (Henshaw *et al.* 2014) or 101 breeding pairs in 2013/14 season (Figure. 4.1). Increased productivity as a result of SF may have contributed to the population’s recovery (Tollington *et al.* 2015), but productivity is not the only vital rate mediated by food availability and the wider extent of SF’s role in driving population change remains unexplored. It is necessary to identify which demographic parameters in echo parakeets have been affected by SF, the magnitude of its impact and the potential for SF to continue driving population growth.

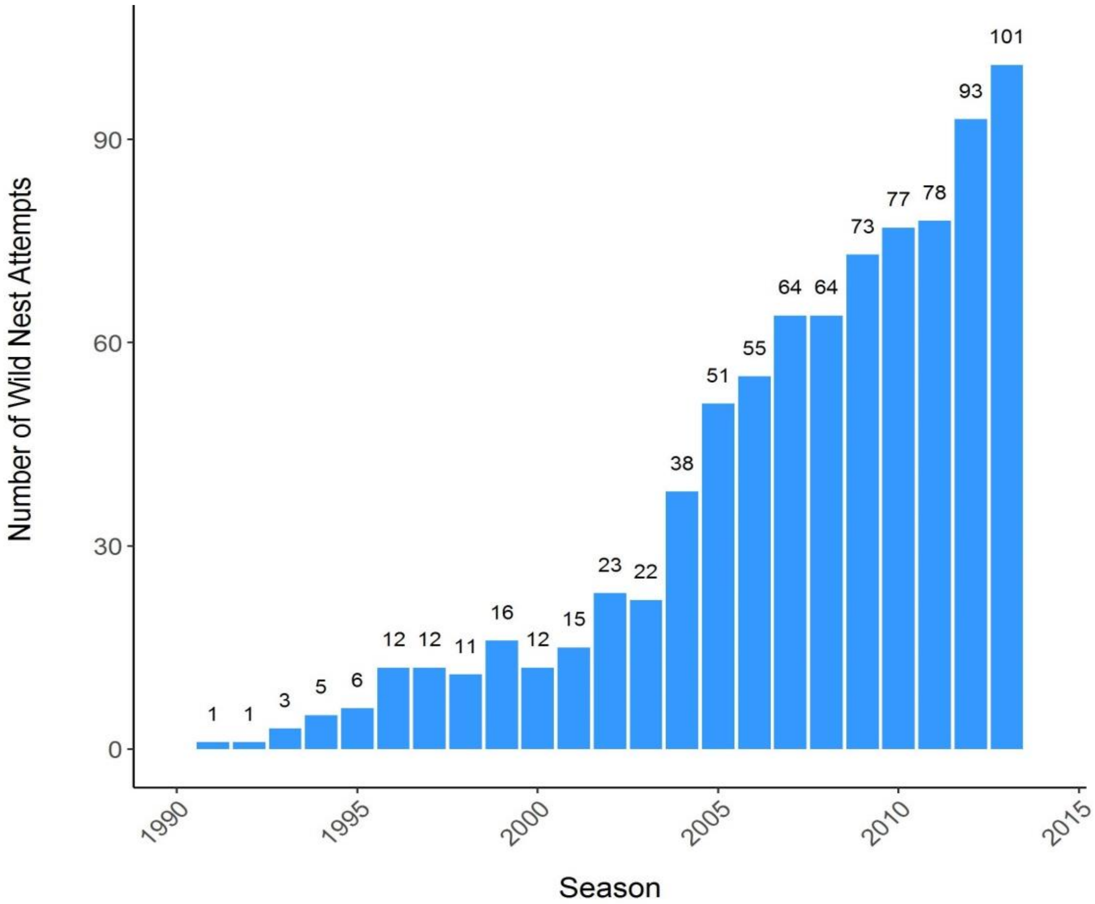


Figure 4.1 Annual record of wild nest attempts from 1991/92 season to 2013/14, illustrating the population's rapid recovery. Numbers report first clutches only.

Using detailed life-history data, this chapter aims to determine the short and medium-term impact of SF by comparing the breeding success, recruitment and survival rates of birds reared in the nest with supplementary food, and those reared without. The unique ability to simultaneously consider three key demographic parameters in a closed population over an extended time period will provide a broader understanding of this management practice at multiple scales and its capacity to influence population dynamics. With growing recognition of the importance of evaluating conservation actions, this study will review the effectiveness of this management strategy and could help guide future management decisions regarding the continued use of SF.

4.3 Methods

4.3.1 Study system and monitoring

The study species, the echo parakeet, and its longitudinal monitoring programme are detailed in Chapter 2 of this thesis. To avoid repetition, only details of relevance to the current chapter are provided here.

4.3.1.1 Supplementary feeding programme

Supplementary feeding began in 1979 (Jones 1987) but was relatively un-used by wild echo parakeets. Between 1997 and 2005, the wild population was augmented with birds raised in captivity, trained to use artificial feeding stations to access SF. Over time, wild bred birds have learnt to access food from the 'hoppers' (artificial feeding stations) by observing the behaviours of released birds.

SF was provided in the form of a commercial pellet (Kaytee® Exact®) at four main hopper sites throughout the species' range (Figure 4.2). The use of SF has become well established in the population with both wild bred and released birds utilising this resource, which is monitored via 60 minute observations at feeding hoppers each morning at sunrise, four days a week throughout the breeding season. The IDs of birds were recorded in a central database, with *ad hoc* sightings or unusual observations also recorded.

4.3.1.2 Distinguishing fed and unfed birds

This study did not follow a controlled, experimental framework but is based on a wild population from which information has been formally collected. The aim of the study was to analyse this longitudinal data set to compare the demography of birds with and without access to supplementary food. It was therefore essential to primarily define how to distinguish birds (breeding pairs) that use or do not use SF. Monitoring of the hoppers provided the information to define 'Pair SF', whether or not a breeding pair used SF in a given breeding season and subsequently reared their nest on SF. If one or both members of the breeding pair were seen using the hoppers in that breeding season, their nest attempt was classified as "SF1". Conversely, if neither member of a breeding pair was sighted at a feeding station that breeding season they were considered not to be supplementary feeders (here-on referred to as “SF0”).

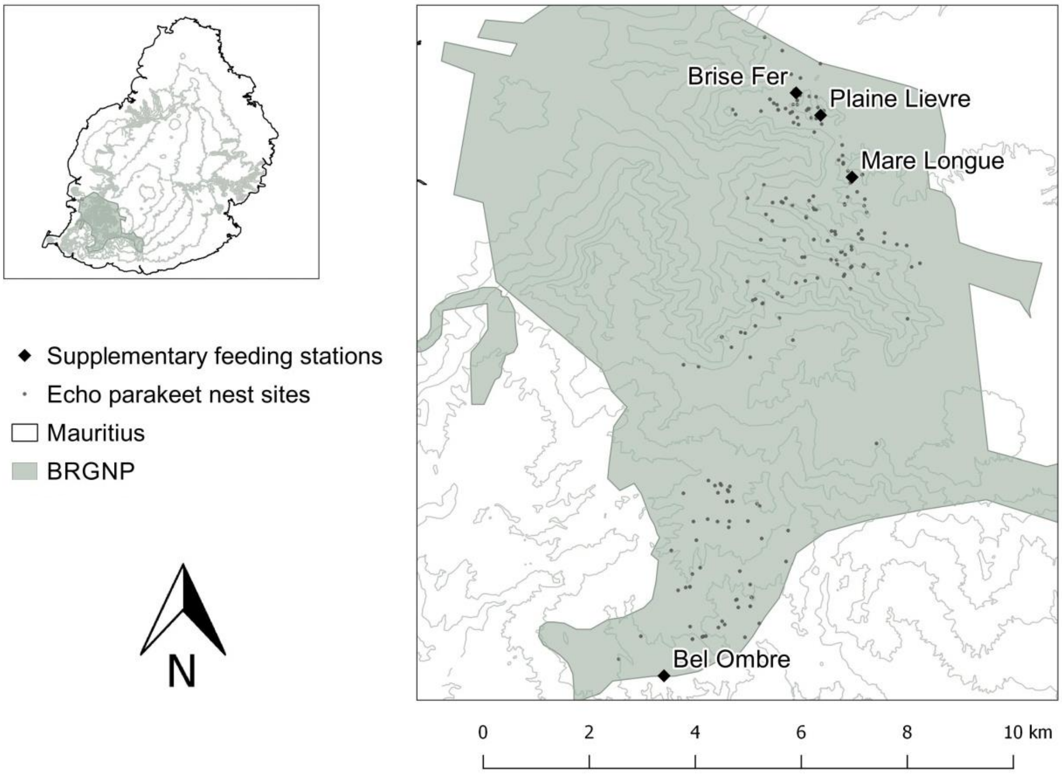


Figure 4.2 Four permanent feeding stations located throughout the National Park (BRGNP). The largest station at Plaine Lievre was subsidised with a smaller station (not indicated on the map) <100m from Plaine Lievre. A further two were located at Brise Fer and Mare Longue, stationed in Conservation Management Areas (CMAs). A final station was based at Bel-Ombre and served this sub-population alone.

Although information on the individual use of SF is available, the only information digitised to date is to the level of the breeding pair. In light of this and in the absence of a pre-experimental design, I first explored any other measures of feeder use to be certain the most appropriate predictor variable was used in analysis. It was hypothesised that feeder use by breeding pairs might be related to the proximity of nests to feeding stations; during breeding, foraging decisions are based upon a compromise between the energetic cost of flight time to a known resource, and how much food can be returned to the nest (Andersson 1981). Distances between each nest and the nearest feeding stations were calculated in kilometres using the open source software QGIS (QGIS Development Team, 2015). The probability of a pair using supplementary food was then modelled as a function of distance in a univariate GLMM, with distance as a predictor of the dependent, binary, variable, PairSF. Built with binomial error family and logit link function, I found a highly significant result for the probability of feeder use declining as distance increased (*P* = < 0.001). Predictions from the model output revealed that this decline was not gradual, but experienced a sharp drop at 2km, taking the probability of using SF from 98% to <5% at a distance of 3km (Figure 4.3).

A multi-variate GLMM then tested whether the effect persisted when accounting for potential variation. This included individual and environmental qualities which may have had confounding effects on the impact of supplementary feeding, or may have worked to falsely report an apparent relationship between distance and supplementary feeders. These included: season, female age, origin of the male and female parent (wild or released), sub population, lay date of first egg in the clutch. Male age was excluded as it was highly correlated with several other variables (correlation co-efficients >0.3). Even after accounting for such variation, distance to the nearest hopper remained a significant predictor of PairSF (*P* = <0.001) (Appendix 4.1).

Whilst distance could be relevant when considering breeding success on a spatial scale, using the original classification of PairSF was considered a more direct measure of the role of SF in breeding attempts. As the use of SF was a sharp decline and not that of a gradual one, using distance as a predictor would not reveal more subtle, underlying effects. Therefore, the binary measure of PairSF formed the predictor variable in all subsequent analysis.

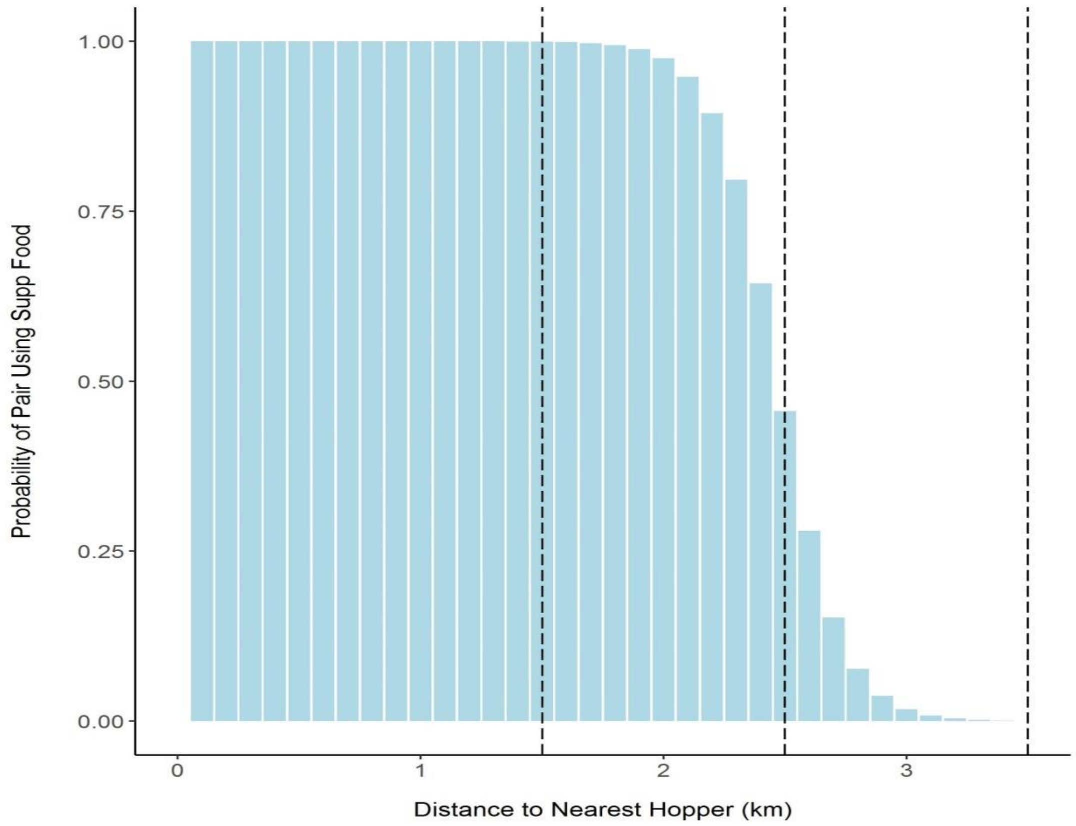


Figure 4.3 A probability curve produced from the output of the model testing the likelihood of a breeding pair using artificial feeding stations in response to the distance from nest to stations (kilometres). 50% probability point lies at 2.4 km, with a rapid decline in probability after this point.

4.3.1.3 Breeding data

Since the inception of an official management programme in 1993, the recovering population of echo parakeets has been closely monitored with a focus on the annual breeding season which extends from late August to March. Echo parakeets typically form monogamous pair bonds and show high nest site fidelity, with all known nests spatially referenced. At the start of each breeding season and throughout, all nest sites are checked and closely followed to determine parent ID. Breeding attempts are monitored from egg laying to fledging, with as much life history data as possible collected in parallel. Typically only one clutch is laid, but a second clutch is possible should the first entirely fail at an early stage. Chicks are individually ringed with a unique combination of colour rings (anodised aluminium, one ring on each tarsus) within the nest, prior to fledging. It is rare for nest inaccessibility or nests being found too late to prevent ringing, resulting in the ringing of >95% of the population (Henshaw *et al.* 2014). All breeding records are annually added to the echo parakeet stud book managed by the Mauritian Wildlife Foundation. As the echo parakeet is only found in the Black River Gorges National Park, it is, in effect, a closed population, and whilst the broad management approach initially adopted has reduced in intensity over time, the core information has been collected with a consistent level of accuracy.

4.3.1.4 Field re-sightings

Monitoring of the breeding population has established a framework for a longitudinal capture-mark-recapture study. The majority of re-sightings were of breeding birds and extracted from the breeding records. In addition, birds were, on occasion, observed during the breeding season as non-breeding individuals.

4.3.2 Analytical framework

The objective of this study was to examine whether the use of SF affects three key demographic parameters of the echo parakeet population: breeding success, survival and recruitment. Breeding success was examined using productivity data from the stud book, whilst survival and recruitment were determined by compiling re-sighting data into individual encounter histories.

4.3.3 Supplementary food and breeding success

The hypothesis that pairs of birds using SF had higher breeding success than those that did not was tested by analysing five reproductive parameters of the echo parakeet. The main measure of breeding success was by number of fledglings per clutch per pair, over the total of 13 seasons, as this best represented per capita fecundity, and therefore a key vital rate that might affect population growth. To understand the processes leading to the final result of successful fledglings, I then examined key stages of the breeding cycle: clutch size, hatch success, brood survival (the probability of a chick surviving through to successfully fledge the nest), and egg to fledge survival (the probability of an egg surviving its entire development through to fledging).

Initially I compared the mean number of fledglings per clutch between SF0 and SF1 pairs in a simple Generalised Linear Mixed Model (GLMM) with PairSF as the only explanatory variable. A global model was created which contained a set of biologically-reasonable background variables (defined in Table 4.1). Additional variables might have affected the number of fledglings and therefore masked or confounded the effects of SF if not accounted. These included intrinsic factors such as parental effects (female age, origin etc.), natural environmental variation across seasons, and within season variation in timing of breeding.. A check of any correlation between the predictor variables was also completed to ensure all models were appropriately built and would not compromise model outcomes (Table 4.2).

Table 4.1 Definitions of possible intrinsic and environmental candidate variables considered in GLMMs to describe the role of SF in breeding success.
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Variable Name	Variable Type	Definition
Pair SF	Categorical	A 2 level factor describing whether the parents of a clutch were considered as supplementary feeders (1), or not (0)
Season	Categorical	A 14 level factor representing the 14 breeding seasons.
Clutch Size	Continuous	Numeric integer. Minimum of 1 egg, maximum of 4.
Brood Size	Continuous	Numeric integer. Minimum of 0 chicks, maximum of 4 chicks.
Number of Fledglings	Continuous	Numeric integer. Minimum of 0 chicks, maximum of 4 chicks.
First Egg Date	Continuous	A numeric integer, this is the number of days after August 1st of that breeding season on which the first egg of the clutch was laid.
Female Age	Continuous	Age of breeding female in years (integer). Fitted as a quadratic term to account for natural change with age.
Female Origin	Categorical	2 Level factor; R = Female was either released as part of captive rearing programme. W = raised and fledged in the wild.
Male Origin	Categorical	As with female origin.
Sub Population	Categorical	2 level factor to represent sub-populations: BO = Bel Ombre; GG = Grande Gorges.

Differences in the number of fledglings between SF1 and SF0 pairs could arise for several reasons. SF1 pairs may lay more eggs than SF0 pairs, egg survival to fledging may be higher for fed pairs, or both processes may occur. Therefore, in addition to comparing the number of fledglings per clutch in response to Pair SF, a number of models were also fitted to the data to explore the effects of SF on different measures of breeding success (listed above). In each case the same analytical procedure was followed as previously, initially building a simple GLMM with one response and one predictor variable (Pair SF), followed by complex, multivariate models that accounted for potentially confounding effects. Explanatory variables included in each global model differed slightly according to response variable being explored. Only biologically-reasonable and relevant background variables were included in the global model, and consideration taken for any highly correlated variable, for example, clutch size was highly correlated with the number of fledglings and was thus excluded as a predictor variable.

The global model was progressively simplified by the backwards step-wise deletion of non-significant terms using sequential ANOVA, with only significant (*P*-value< 0.05) retained. If PairSF, the predictor variable, was significant in the final model, then this indicated an independent effect of SF on the response variable. Whilst this procedure provided insight into the additional factors affecting the different stages of breeding success, this study was conducted to most accurately understand the influence of SF on breeding success, not to describe the influence of a complex environment on breeding success, particularly as weather data was not available for inclusion. Additional influential variables were therefore acknowledged but were not explored to any greater extent.

Table 4. 2 Correlation co-efficients describing the extent of correlation between all possible predictor and response variables that were to be considered when examining the impact of SF on breeding success. Co-efficients of ≥0.3 were considered highly correlated and were not used in the same GLMM unless it was deemed suitable based on *a priori* understanding of the system.

Variable	**Season**	**Pair SF**	**Female Origin**	**Female Age**	**Male Age**	**Male Origin**	**Sub Population**	**Nearest Hopper**	**Clutch Size**	**Brood size**	**Number Fledglings**
Season											
PairSF	0.15										
Female Origin	0.23	0.28									
Female Age	**0.41**	0.23	0.17								
Male Age	0.24	**0.3**	**0.3**	**0.65**							
Male Origin	0.11	0.17	0.18	0.18	0						
Sub Population	0	0	0.13	0	0.14	0.27					
Nearest Hopper	0	**0.5**	0	0	0.19	0	0				
Clutch Size	**0.47**	0.19	0	0.21	0.15	0	0.11	0.19			
Brood size	0.23	0.2	0	0.17	0.08	0	0	0.13	0.47		
Number Fledglings	0.19	0.28	0	0.11	0.08	0	0	0.19	**0.37**	**0.79**	
Clutch FED	0.13	0.22	0.15	0	0.05	0.18	0	0.18	0.29	0.25	0.22

4.3.3.1 Modelling details

All models were run using programme R version 3.3.1 (R Development Core Team 2016). Models were fitted to the data assuming a poisson error distribution when the response variable was count or categorical data (clutch size, number of fledglings per clutch), and binomial error structure assumed with proportional data (hatchability, brood survival, egg to fledge survival). Following a method recommended by Thomas *et al* (2015) the GLMMs were tested for over-dispersion. On reviewing the ratio of the estimated sum of squared Pearson residuals and the residual degrees of freedom (SSQ residuals/rdf = 0.7) the data was slightly under-dispersed, for which no action can be taken. To account for repeated observations of individual breeding females in the dataset, female identity was included in the GLMMs as a random effect. Female age was fitted as a quadratic term to reflect the age-associated improvement and decline in measures of breeding performance.

4.3.3.2 Data

All data were taken from the echo stud book which began in 1991 and continues today. SF was used by wild birds from the 2000/01 season onwards, which was also the first season any birds originating from the release programme began to breed, and therefore the first occasion that wild nests were reared by breeding pairs using SF. From this point onwards observational monitoring of the hoppers began and use of SF by birds systematically recorded, enabling breeding pairs (and therefore nests) to be classified as SF0 or SF1. This study spanned from the 2000/01 breeding season to 2013/14. In addition, the following nest attempts were excluded from this analysis: second clutches, nests with an unidentified breeding pair, nests which had been directly provisioned with supplementary food either within the nest or <5m from the nest (relevant just in the early years of the management programme) and any clutches experiencing management interventions such as harvesting or fostering (see Chapter 2). The resulting data set consisted of 678 clutches from 151 females.

4.3.4 Supplementary food, survival and recruitment

This analysis compared age-specific survival and transition rates between the non-breeding and breeding population for birds that originated from SF1 and SF0 nests. The analytical approach was based on a multi-state modelling framework using programme MARK (White and Burnham 1999) which estimates survival rate (φ), re-sighting probability (*P),* and transition rates between states (ψ). Birds were marked in the nest prior to fledging and could be re-sighted in one of three defined states, as described in Chapter 3: pre-breeders (N), breeders (B) and post-breeders (PO).

The classification of a breeding pair as SF0 or SF1 was an accurate reflection of how SF directly affects breeding success. For the survival analysis however, this classification became an indirect measure of SF use as it defined the natal environment of a bird. When considering the influence of SF on life-time survival and transition rates, this study focused on the long term impact of a parakeet’s natal environment in relation to food.

In order to identify any effect of SF on survival and recruitment, a two-step approach was adopted. The first step identified a model which adequately described the influence of time, age and state survival, re-sighting and transition probabilities. This model would then provide a framework upon which the influence of SF on survival and transition could be explored.

An initial multistate model adopted an appropriate age structure from previous analyses completed in Chapter 3. This recognised four age classes: 1 year old bird, 2 years old birds, 3 year old, and all birds aged 4 years and above (denoted ‘4+’). These four ages classes were applied in survival, transition and re-sighting probabilities, with three possible state transitions: pre-breeder to breeder from age 2 upwards, denoted “N-B”; breeder to post-breeder, denoted “B-PO”; post-breeder back to breeder, denoted “PO-B”. This provided the structure for the baseline model (Model 1; Table 4.3), and therefore the primary reference for model comparisons in the first step of analysis:

Model 1:

φ ((N| 1:4+**.**)(B| 2:4+**.**)(PO| 3:4+**.**)) ***.P*** ((N| 1:4+**.**)(B| 2:4+**.**)(PO| 3:4+**.**))
.ψ ((N-B| 2:4+**.**)(B-PO| 3:4+**.**)(PO-B| 4+**.**))

4.3.4.1 Step 1: describing population survival

Step 1 involved three stages in order to identify the most suitable model describing any time dependence (*t*) in age and state-specific survival across the population.

Stage 1 began with Model 1, retaining the entire model structure except for sequentially introducing time-dependence in survival to age classes 1 to 4+ in pre-breeder state, and then in combinations of age classes when time dependence indicated an effect. Returning to Model 1, the process was repeated for state B. Time dependence was not explored in post-breeders due to limited re-sightings in this state. The best models for pre-breeders and breeders were merged (Model 4) and compared within the set of candidate models (Table 4.3) to identify the most parsimonious model considering age and state specific time dependence in survival probability.

Analysis from Chapter 3 did not indicate any influence of time dependence in re-sighting probability (*P*). As such, this parameter was built without time dependence but included age and state specific. This maintained throughout all modelling procedures.

Stage 2 followed a similar process to Stage 1, but examined transition for time dependence. First considering N-B, each plausible age-specific state transition was examined for time dependence and then explored in each possible combination of age specific transition where evidence of time dependence was identified. The same process was repeated for breeder to post-breeder transition, but not post-breeder to breeder, as data was too sparse, as previously stated. The most parsimonious models explaining time dependence in each age and state specific transition for N-B were merged and compared in the candidate set of models (Table 4.4).

For the third stage of Step 1, the most parsimonious model structures for survival and transition were combined into one model (Model 13, Table 4.4) and compared in the final model set. Comparing the fit of the models I was able to identify the most appropriate model describing time, age and state-specific survival and transition across the population of wild bred echo parakeets. Within this final set of models, Model 2 remained the most parsimonious (Table 4.4) and provided a new baseline model upon which the effects of supplementary food use could be examined in Step 2.

Model 2:

φ ((N| 1:2t, 3**.**, 4+t)(B| 2:4+**.**)(PO| 3:4+**.**)) ***.P*** ((N| 1:4+**.**)(B| 2:4+**.**)(PO| 3:4+**.**))
.**ψ** ((N-B| 2:4+**.**)(B-PO| 3:4+**.**)(PO-B| 4+**.**))

4.3.4.2 Step 2: exploring the effect of SF on survival and recruitment

Having identified Model 2 as the most appropriate model for describing age and state specific survival, Step 2 adopted a similar approach to Step 1 in order to explore SF as group effect. Encounter histories were classified into one or two groups, SF0 or SF1, based on whether or not the nest from which they fledged was considered as supplementary fed or not. 249 individuals were raised by breeding pairs classified as SF0, and 771 individuals originated from SF1 nests.

Stage 1 explored the effect of SF on age specific survival in pre-breeders and breeders with the same approach taken in Step 1. A set of candidate models were built where SF was specified independently in one age class at a time, then for each possible combination of age classes where evidence of an effect was identified (Table 4.5). Due to the limited number of re-sightings of three year old birds in a pre-breeder state it was not possible to critically examine a group effect in this parameter. Final models were compared (Table 4.5) to identify the most suitable model describing any effect of SF in survival.

Stage 2 returned to Model 2 to explore SF in transition, separately introducing the group effect to each age class for the following transitions: pre-breeder to breeder, breeder to post-breeder and post-breeder to breeder. The most parsimonious models for each of the three state specific transitions were then merged (Model 38) and compared within the model set (Table 4.6).

No compelling evidence had been found for a group effect in survival. Therefore, the final model set (Table 4.6) compared the best model structure describing survival (Model 2) with models exploring SF in transition (models 33 to 41). The most parsimonious model was selected for describing time, age and state specific effects of SF in wild bred echo parakeets on survival and transition. Owing to each age class in a state being observable in this study system, transition rates of pre-breeder to breeder were a direct estimate of recruitment, whilst transitions between breeder and post-breeder report measures of breeding propensity.

4.3.4.3 Modelling details

Data: constructing encounter histories

Encounter histories for 1020 individuals were constructed based on the re-sighting histories of individuals made over the course of each breeding season from 1994/95 to 2013/14. Birds which formed part of the release programme (n=144) were excluded as the focus was to explore the impact of being reared on SF on an individual's survival. This could only be meaningfully tested using birds with a common origin. Therefore, released birds were excluded as they were raised in different conditions, being taken into captivity as an egg or chick and then raised on supplementary food. The 2013 cohort was excluded as it could not include any subsequent re-sightings.

Fixed parameters

Based on the biology of the echo parakeet, certain implausible transitions were fixed at zero in all models:

1. A bird cannot enter the breeding state (B) until 2 years old at the earliest, therefore survival (φ) and re-sighting probability (*P*) for breeders at age 1 was fixed to 0. Transition of pre-breeder to breeder ($\psi^{N\text{-}B}$) was fixed at 0 for age 1.
2. Re-sighting probabilities for both SF0 and SF1 birds were assumed to be equal, as the whole population is monitored with equal effort. Age and state were, however, still retained in the model structure.
3. Breeder re-sighting probability from age 2 upwards was fixed at 1 as almost every nest attempt is found and breeders identified.
4. A bird cannot exist in the post-breeder state (PO) until 3 years at the youngest; therefore survival and re-sighting at age 1 and 2 were fixed at

0. Transition of breeder to post-breeder (Ψ^{B-PO}) was not possible until age 3 and fixed accordingly at zero.

5. Transition from post-breeder to breeder ($\psi^{PO-}B$) may only occur by 4 years old at the earliest, and a bird must have passed through breeder prior to this.

Transitions breeder to pre-breeder (ψ^{B-N}), post-breeder to pre-breeder (ψ^{PO-N}) and pre-breeder to post-breeder (ψ^{N-PO}) are not possible. A goodness of fit test was conducted using the median-ĉ method in programme MARK.

Model Selection

Correcting for any over-dispersion, Quasi-likelihood Akaike's information criteria (QAIC$_c$; (Burnham and Anderson 2002)) was used to select the most parsimonious model from a set of candidate models. For one model to be considered a better fit to the data, it is recommended that the difference (Δ) in AIC$_c$ should exceed 2 (Burnham and Anderson 2002). The logit link function was used throughout the modelling procedure which was completed entirely in Programme MARK, Version 8.1

4.4 Results

4.4.1 Supplementary food and breeding success

Over the 14 breeding seasons, a greater number of clutches were classified as SF1 (n=495) than SF0 (n=183) (Figure 4.4) and breeding pairs using SF experienced better breeding success. The primary measure of breeding success, the number of fledglings per clutch, was significantly positively affected by SF. This effect was true in both the univariate GLMM (*P* = <0.001; Appendix A4.1.1) and in the multivariate GLMM (*P* = <0.005; Table 4.2). This equated to an estimate of SF1 breeding pairs fledging 1.7 chicks per clutch, and SF0 pairs fledging 1 chick per clutch (Figure 4.5).

The overall probability of an egg surviving all the way through to fledging was significantly and positively affected by SF (univariate model *P*-value = 0.001; multivariate model *P*-value = <0.001), which equated to eggs from SF1 nests experiencing a survival probability of 0.63 (± 0.04), whilst for SF0 nests this was only 0.39 (± 0.03)(Figure 4.6). Exploring which stages of the breeding cycle contributed to this overall higher productivity from SF1 nests, SF did not affect clutch size, both when tested in the univariate and multivariate GLMMs. Timing of breeding did indicate a negative relationship with clutch size (*P*-value = 0.216) and potentially female age (*P*-value = 0.06). Whilst hatch success was affected by several variables, a significant relationship with SF remained (*P*-value = 0.05), which is further illustrated in the estimates generated from the null models in Figure 4.6. Brood success was positively and significantly affected by SF (univariate model *P*-value = 0.002; multi-variate *P*-value = 0.002), with survival from chick to fledging to being 20% greater in SF1 nests (Figure 4.6). Full model outputs from all univariate and multivariate models are available in Appendix 4.2 to 4.11.

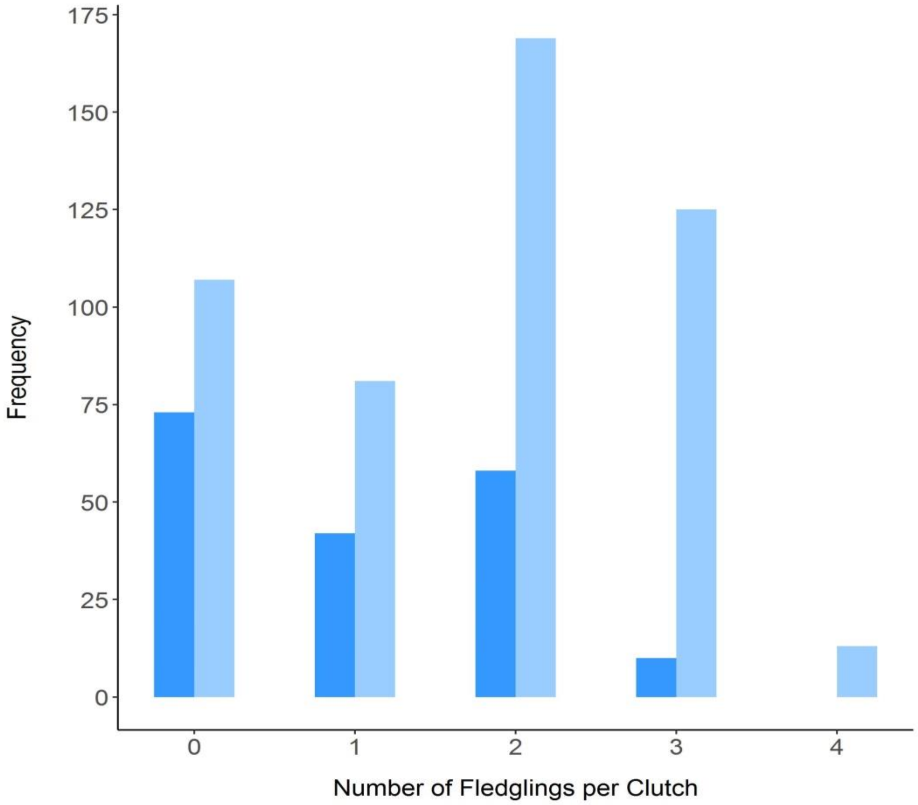


Figure 4.4 Frequency of the number of nests fledging 0, 1, 2, 3 or 4 chicks per clutch over the 14 breeding seasons. Dark blue bars illustrate SF0 nests, light blue illustrate SF1 nests.

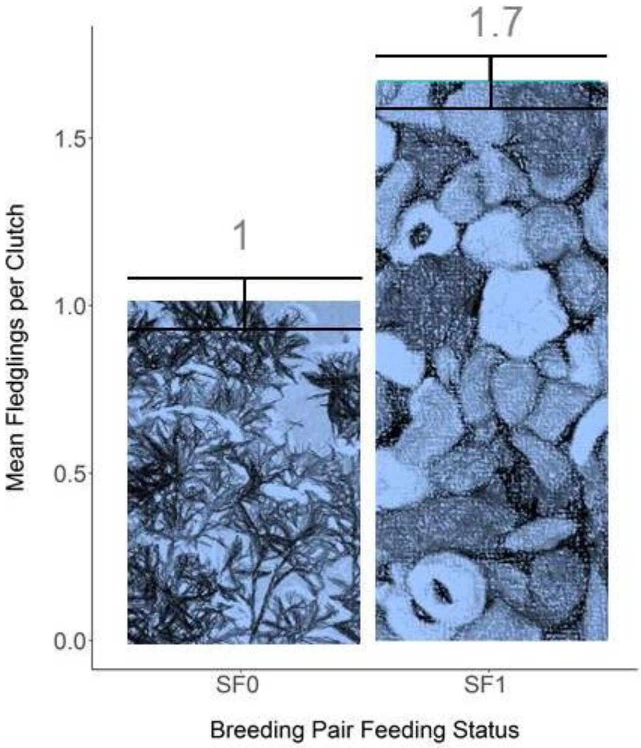


Figure 4.5 Mean number of fledglings per clutch for SF0 and SF nests estimated from the null model output. Vertical bars represent standard error around the mean.

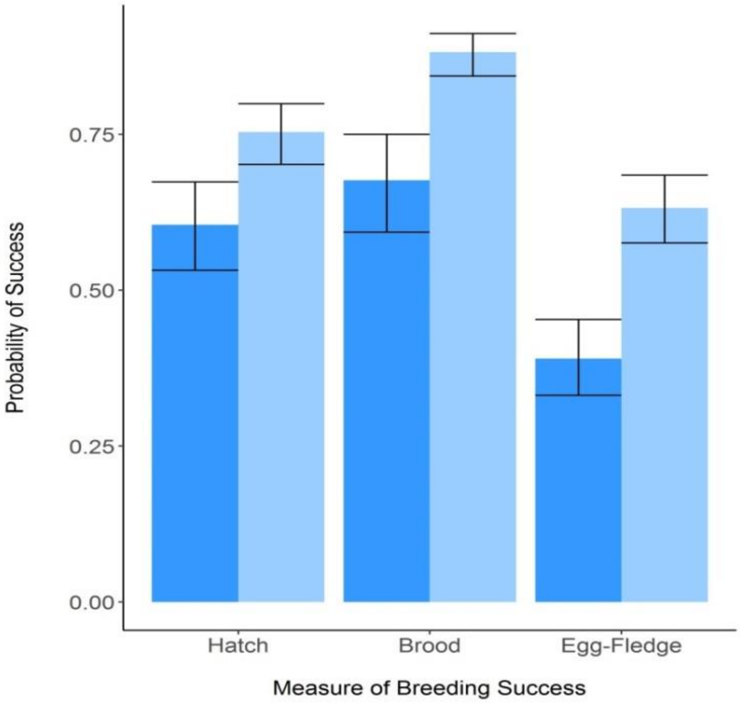


Figure 4.6 Comparing three measures of breeding success for SF0 (dark blue) and SF1 pairs (light blue. *Hatch;* probability of egg hatching. *Brood*; probability of a chick surviving from hatch to fledge. *Egg-Fledge*; probability of surviving from egg to fledge. Probabilities were generated from null estimates. Vertical bars represent standard errors around the mean.

Table 4.3 Generalised linear mixed effects model (GLMM) outputs examining the effect size of supplementary food (SF) on four measures of breeding success: total number of fledglings, probability of hatching (hatch success), brood success, and egg to fledge success. All GLMMS began as a global model, including all predictor variables, and through step-wise deletion, models were reduced to their key components, which are reported in the table. Clutch size was not affected by any of the predictor variables explored in this analysis, including PairSF, and is therefore not reported. All models included Female ID as a random effect. Model error structures differed according to whether the response was proportional or count data. The data examined 678 clutches spanning 14 breeding seasons (2000/01 to 2013/14). S.E. = standard error; Fem.Age^2 = quadratic term for Female Age. Definitions of predictor variables are found in Table 4.1.

	RESPONSE VARIABLE							
PREDICTOR VARIABLE	**Number of Fledglings**		**Hatch Success**		**Brood Success**		**Egg to Fledge Success**	
	P-value	S.E	*P*-value	S.E	*P*-value	S.E	*P*-value	S.E
Season	0.002	0.217	<0.001	0.026			<0.001	0.025
Female Age	0.055	0.053						
Female (Age^2)	0.142	0.004						
Female Origin								
Male Origin								
Sub. Population			0.01	0.23				
Clutch FED	<0.001	0.037	<0.001	0.079			<0.001	0.073
Pair SF	**<0.001**	0.101	**0.053**	0.23	**<0.001**	0.296	**<0.001**	0.227

4.4.2 Supplementary food, survival and recruitment

Goodness of fit

Over-dispersion was estimated to be relatively low ($\hat{c} = 1.25$), and this correction factor was applied prior to model selection procedures. All models were subsequently compared by quasi-binomial AIC ($QAIC_c$).

4.4.2.1 Step 1: describing population survival

Model 2 (Table 4.3) was identified as the most parsimonious for the data set when examining the effects of time on survival, with compelling evidence of time-dependence on survival in age classes 1, 2 and 4+ of pre-breeders (N). No evidence of time-dependence in transition (Table 4.4) placed Model 2 as most suitable for describing time, age and state-specific survival.

4.4.2.2 Step 2: exploring the effect of SF on survival and recruitment

Introducing SF as a group effect in Models 24 to 32 (Table 4.5) provided no compelling evidence of an effect on survival, therefore Model 2 remained the best structure for describing the effect of SF on survival (or ultimately, the lack of effect).

In contrast, transition rates were positively affected by SF and the most parsimonious model within the final set (Model 33) indicated an effect of SF in transition from pre-breeder to breeder in ages 2 and 4+, and transition from breeder to post-breeder for age 4+ birds (Figure 4.7). There was no evidence of an SF effect on transition from post-breeder back to breeder, yet this could be an artefact of limited re-sighting data.

Final SF Model, Model 33:

φ ((N| 1:2t, 3., 4+t)(B| 2:4+.)(P|3:4+.)) .*P* ((N| 1:4+.)(B| 2:4+.)(P| 3:4+.))
ψ ((N-B| 2.**g**, 3., 4+**g**.)(B-PO| 3., 4+.**g**)(PO-B| 4+.))

Individuals originating from SF1 nests experienced much higher recruitment rates than those originating from SF0 nests; at age 2 an individual had 0.09 (CI = -0.04 / +0.16) probability of becoming a breeder if raised without SF, but if raised on SF this increased to 0.219 (CI = -0.16 / +0.28). The same pattern persisted at age 4+, with a recruitment probability of 0.17 (CI = -0.12 / +0.24) with SF0 vs 0.41 (CI = -0.29 / +0.54) with SF1. The effect of SF continued as an adult, positively affecting the probability of remaining a breeder (Figure 4.6). Once breeding, birds originating from an SF0 nest were more likely to skip a breeding season and move to a post-breeder state (0.14 [CI= -0.10 /+0.19] vs.0.07 [CI=-0.04/+0.12]), respectively).

The key findings from the model are that of SF affecting transition rates. This final model is also the most accurate model yet to describe age, state and time dependent survival in the wild population of echo parakeets. The full output of the model and its associated parameter estimates are reported in Appendix 4.12, 4.13 and 4.14, with estimates of key demographics listed below:

- Pre-breeders of ages 1, 2 and 4+ years showed strong evidence of time dependent annual survival rates, ranging from as low as 0.35 (CI = -0.29/ +0.39) to as high as 1 in certain years.
- Annual breeder survival showed no evidence of time dependence but was stable and high; 0.95 (CI = -0.78/+0.99) at age 3 and 0.98 (CI = -0.94/+0.99) for 4+ years.
- Post-breeder survival was considerably lower (0.72 [CI = -0.57/ +0.83]), also showing no evidence of variation in time or influence by SF.
- The probability of re-sighting a pre-breeder ranged with age from 0.4 (CI = -0.31/+0.50) to 0.62 (CI = -0.55/+0.69). This did not vary with time.
- Post-breeder re-sighting probability was estimated 0.5 (CI = -0.39/ +0.65) for age 4+ years. No evidence of time dependence.
- *(NOTE: re-sighting probabilities of breeders had been fixed at 1 in the model structure).*

Table 4.3 Model set testing the influence of time on state specific survival (φ) with a four age class structure. States include pre-breeders (N), breeders (B) and post-breeders (PO). Numbers refer to the age classes within each state. All model structures are based upon the baseline model, Model 1. For brevity, models are denoted according to how they differ from Model 1; ~ denotes model structure identical to Model 1; t denotes full time specific variation; **.** denotes constancy among years; ML refers to Maximum likelihood; No.P refers to number of parameters. Models are ordered according to QAIC$_c$. Model parsimony increases with decreasing QAIC$_c$. All models were run with logit-link function. Full model structure for baseline Model 1:
φ ((N| 1:4+.)(B| 2:4+.)(P| 3:4+.)) . ***P*** ((N|1:4+.)(B|2:4+.)(P|3:4+.)) . **ψ** ((N-B| 2:4+.)(B-PO| 3:4+.)(PO-B| 4+.))**.**

	Survival (φ)								
Model No.	**N**	**B**	**P**	**QAIC$_c$**	**Delta QAIC$_c$**	**AIC$_c$ Weight**	**ML**	**No. P**	**Q Deviance**
2	1:2t, 4+t	~	~	4273.78	0.00	0.50	1.00	71	1610.11
3	1:4t	~	~	4282.35	8.58	0.01	0.01	87	1584.56
4	1:2t, 4+t	4+t	~	4292.87	19.10	0.00	0.00	86	1597.23
5	1:2t	~	~	4293.96	20.19	0.00	0.00	56	1661.89
6	1:3t	~	~	4301.23	27.45	0.00	0.00	72	1635.44
7	1t	~	~	4331.09	57.31	0.00	0.00	39	1734.35
1	**1:4+.**	**2:4+.**	**3:4+.**	**4391.55**	**117.77**	**0.00**	**0.00**	**21**	**1831.71**
8	~	4t	~	4409.37	135.59	0.00	0.00	36	1818.82
9	~	3t	~	4418.08	144.30	0.00	0.00	37	1825.47
10	~	2t	~	4426.38	152.60	0.00	0.00	38	1831.71
11	~	3-4+ t	~	4436.16	162.39	0.00	0.00	52	1812.45

Table 4.4 Model set testing the influence of time on state specific transitions (ψ) with a four age class structure. Transitions include pre-breeder to breeder (N-B), breeder to post-breeder (B-PO) and post-breeder to breeder (PO-B). Models are ordered according to QAIC$_c$. Model parsimony increases with decreasing QAIC$_c$. All model structures are based upon Model 1. For brevity, models are denoted according to how they differ from Model 1; ~ denotes model structure identical to Model 1; t denotes full time specific variation; **.** denotes constancy among years; ML refers to Maximum likelihood; No.P refers to number of parameters.

	Survival (φ)			**Transition probability (ψ)**								
Model No.	**N**	**B**	**P**	**N-B**	**B-PO**	**PO-B**	**QAIC$_c$**	**Delta QAIC$_c$**	**AIC$_c$ Weights**	**ML**	**No. P**	**Q Deviance**
2	1:2t, 3**.**, 4+t	~	~	~	~	~	4273.78	0	0.999	1	71	1610.11
12	1:2t, 3**.**, 4+t	~	~	4+t	4+t	~	4287.18	13.41	0.001	0.001	101	1559.16
13	1:2t, 3**.**, 4+t	~	~	2t	4+t	~	4291.39	17.62	0	0.	103	1559.02
14	~	~	~	2t	~	~	4389.05	115.27	0	0	38	1794.37
15	~	~	~	2t, 4t	~	~	4390.70	116.92	0	0	53	1764.89
1	**1:4+.**	**2:4+.**	**3:4+.**	**2:4+.**	**3:4+.**	**4+.**	**4391.55**	**117.77**	**0**	**0**	**21**	**1831.71**
16	~	~	~	4+t	~	~	4392.62	118.84	0	0	36	1802.06
17	~	~	~	2t	4+t	~	4400.10	127.22	0	0	53	1775.19
18	~	~	~	2:3t	~	~	4401.75	127.97	0	0	54	1773.86
19	~	~	~	~	4+t	~	4403.08	129.30	0	0	36	1812.52
20	~	~	~	2:4+t	~	~	4404.27	130.49	0	0	69	1744.84
21	~	~	~	3:4+t	~	~	4405.69	131.91	0	0	52	1781.98
22	~	~	~	~	3t	~	4411.66	137.88	0	0	37	1819.04
23	~	~	~	~	3:4+t	~	4423.49	149.71	0	0	52	1799.77

Table 4.5 Models tested show the influence of supplementary food (g) on age specific survival (φ) in pre-breeders (N) and breeders (B), where a four age class structure is used. All model structures are based upon the baseline Model 2. For brevity, models are denoted according to how they differ from Model 2; ~ denotes model structure identical to Model 2; t denotes full time specific variation; **.** denotes constancy among years; Models are ordered according to QAIC_c. Model parsimony increases with decreasing QAIC_c. The logit-link function was used for all models. Full model structure of model 2: **φ** ((N| 1:2t, 3., 4+t)(B| 2:4+.)(P|3:4+.)) ***.P*** ((N| 1:4+.)(B| 2:4+.)(P| 3:4+.)) **.ψ** ((N-B| 2:4+.)(B-PO| 3:4+.)(PO-B| 4+.))

	Survival (φ)			**Transition probability (ψ)**								
Model No.	**N**	**B**	**P**	**N-B**	**B-PO**	**PO-B**	**QAIC_c**	**Delta QAIC_c**	**AIC_c Weight**	**ML**	**No. P**	**Q Deviance**
2	**1:2t, 3., 4+t**	**2:4+.**	**3:4+.**	**2:4+.**	**3:4+.**	**4+.**	**4273.78**	**0**	**0.444**	**1**	**71**	**1610.11**
24	~	4+**.**g	~	~	~	~	4275.83	2.05	0.159	0.36	72	1610.04
25	~	3**.**g	~	~	~	~	4275.87	2.10	0.156	0.36	72	1610.08
26	~	2**.**g	~	~	~	~	4275.90	2.12	0.154	0.35	72	1610.11
27	~	2-3**.**g	~	~	~	~	4277.99	4.21	0.054	0.12	73	1610.08
28	~	2:4+**.**g	~	~	~	~	4280.04	6.26	0.019	0.04	74	1610.01
29	1tg	~	~	~	~	~	4280.77	6.99	0.013	0.03	84	1589.41
30	4+tg	~	~	~	~	~	4286.90	13.12	0	0.00	81	1601.96
31	2tg	~	~	~	~	~	4290.26	16.48	0	0.00	83	1601.04
32	1:2tg	~	~	~	~	~	4298.56	24.78	0	0.00	96	1581.37

Table 4.6 Models tested show the influence of supplementary food (g) on age and state specific transition probabilities (ψ) for pre-breeder to breeder (N-B), breeder to post-breeder (B-PO) and post-breeder to breeder (PO-B). All model structures are identical to baseline Model 2 where ~ denoted such repetition. Models are therefore denoted according to how they differ from Model 2; t denotes full time specific variation; **.** denotes constancy among years; N denotes pre-breeder φ; B denotes breeder φ; PO denotes post-breeder φ. Models are ordered according to QAIC$_c$. Model parsimony increases with decreasing QAIC$_c$. The logit-link function was used for all models.

	Survival (φ)			**Transition probability (ψ)**								
Model No.	**N**	**B**	**P**	**N-B**	**B-PO**	**PO-B**	**QAIC$_c$**	**Delta QAIC$_c$**	**AIC$_c$ Weights**	**ML**	**No. P**	**Q Deviance**
33	~	~	~	**2.g, 4+.g**	**4+g**	**~**	**4253.19**	**0.00**	**0.46**	**1.00**	**74**	**1583.16**
34	~	~	~	2.g, 4+.g	~	~	4256.81	3.61	0.08	0.16	73	1588.90
35	~	~	~	4+.g	~	~	4263.33	10.13	0.00	0.01	72	1597.54
36	~	~	~	2.g	~	~	4267.38	14.18	0.00	0.00	72	1601.59
37	~	~	~	~	4+.g	~	4270.16	16.97	0.00	0.00	72	1604.38
38	~	~	~	~	3:4+.g	~	4270.28	17.08	0.00	0.00	73	1602.37
2	**1:2t, 3., 4+t**	**2:4+.**	**3:4+.**	**2:4+.**	**3:4+.**	**4+.**	**4273.78**	**20.58**	**0.00**	**0.00**	**71**	**1610.11**
39	~	~	~	~	3.g	~	4273.90	20.70	0.00	0.00	72	1608.11
40	~	~	~	3.g	~	~	4275.10	21.91	0.00	0.00	72	1609.32
41	~	~	~	~	~	4+.g	4275.12	21.93	0.00	0.00	72	1609.34

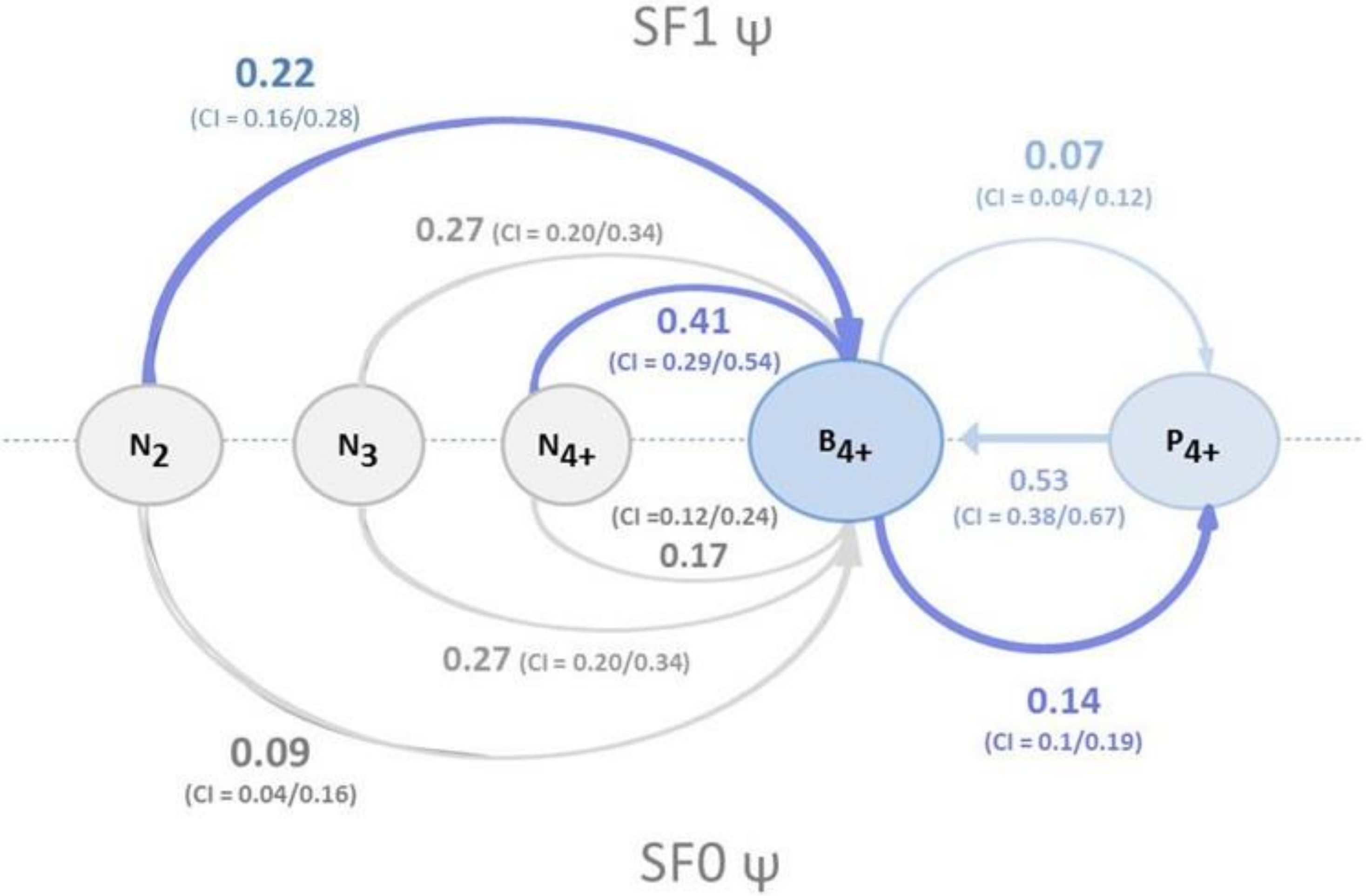


Figure 4.7 Age and state-specific transition probabilities (ψ) for individuals not reared on supplementary food, SF0 (below dashed line), and those raised in a nest classified as supplementary fed, SF1 (above dashed line). Probabilities were generated by Model 38 (Table 4.6). Non-breeders may transition to a breeder at age 2, 3 and 4 + years (denoted N_2, N_3, N_{4+}). Only the breeder (B) transition to post-breeder (PO) for ages 4+ (denoted B_{4+}) exhibited an effect from SF, thus for brevity, transition at 3 years is not included. Post-breeder transition (PO_{4+} to B_{4+}) did not reveal a group effect, largely a consequence of minimal data. 95% confidence intervals are indicated in the brackets below survival estimate. Image is authors own.

4.5 Discussion

4.5.1 Key findings

By combining longitudinal productivity and CMR data collected alongside the provision of SF, this study demonstrates a simultaneous analysis of the immediate and medium-term effects of SF on three key demographic parameters: breeding success, recruitment and survival. Although SF had no significant effect on the survival of wild echo parakeets, there was compelling evidence for improved recruitment rates, propensity to breed and total reproductive output. These results suggest that providing SF has potentially played a pivotal role in the population's recovery and may be crucial to its long-term persistence and continued growth.

4.5.2 Supplementary food and breeding success

In this study, food supply was found to have a strong, positive effect on breeding success of echo parakeets, confirming earlier findings of Tollington *et al.* (2015). Eggs experienced a 20% greater chance of surviving to fledge (0.68 *vs* 0.88) if parents were known to use SF. Nests with SF pairs ultimately fledged more chicks per clutch. A similar positive effect on fledge rates has been reported in several species of birds provided with SF (Soler and Soler 1996; Wiehn and Korpimäki 1997; Castro *et al.* 2003; González *et al.* 2006; Hilgartner *et al.* 2014), and in common with such studies, the effects of SF varied across the stages of the breeding cycle. As an immediate conservation tool it may be sufficient to simply recognise a positive measurable effect, but as a long-term management approach, there may be great benefit, both for population outcomes and conservation resource use efficiency, in understanding the finer details of when SF is most influential. Identifying time periods or life history stages when the need for SF is greatest could allow its provision to be adjusted accordingly, which may in turn reduce the level of intervention by management as well as reducing costs. An experiment by Armstrong *et al.* (2007) found that SF did not need to be provided year-round, but outside of the breeding system this management could be relaxed. For echo parakeets, a reliable food supply may be more important during brood rearing, when food demands might logically be at their highest, a theory supported by the results of this study. Malnutrition was seen as one of the key reasons for nest failures in the early 1990s (pers comm, Prof. Carl Jones), and accessible, nutrient rich SF may increase the fitness of chicks. Irrespective of such finer details, providing SF has clearly contributed to the programme’s goals of maximising nest success to increase the population size (Jones and Duffy 1993; MWF 2013).

4.5.3 Supplementary food, survival and recruitment

Being raised in a nest with supplementary food had no effect on the survival of an individual, either in early life as a pre-breeder, or in older age classes and different states. Other studies have found that SF increases survival in avian species, including the Cape Griffon vultures (*Gyps coprotheres*) (Piper, Boshoff and Scott, 1999) and the hihi (*Notiomystis cincta* - Castro *et al.* 2003). Studies predominantly explore the impact of SF on the survival of juveniles or first year birds, and often with regards to their use alongside translocations or re-introductions (Houston *et al.* 2005; Meek *et al.* 2003). Whilst it is surprising to see no real difference in echo parakeet survival, mixed effects (e.g. Oro *et al.* 2008) or an absence of impact on survival is also widely reported in programmes employing supplementary food (Armstrong *et al.* 2007; Rickett *et al.* 2013). As yet, there is no clear explanation for the equivalent survival rate in fed and unfed parakeets, but it suggests natural food availability in the National Park is sufficient for maintaining a reasonable level of fitness to ensure survival and SF is not an essential subsidy. Contrary to this, recruitment into the breeding population requires an individual to meet greater physical demands associated with a breeding attempt, and continue to meet those demands as long as they wish to breed (Martin 1987). The positive impact of supplementary food on recruitment has been reported in the hihi (Castro *et al.* 2003). Echo parakeets raised on SF were inclined to start breeding from a younger age and this probability of breeding remained high in every age class. SF may enable individuals to maintain a certain level of fitness which facilitates higher breeding propensity, or potentially through buffering natural variation in resource availability. Individuals not using SF may be more vulnerable to environmental fluctuations, and the decision to breed may be affected by resource availability. The energetic costs of breeding may also explain the skipping behaviour of SF0 birds, as nutritional intake will affect their recovery time (Martin 1987).

4.5.4 Suitability of the study

This study was not a controlled experiment but used data collected as part of the on-going management and monitoring of the echo parakeet population. The programme has experienced a high change-over of staff since 1993, which could have introduced inconsistencies in the data collection. However, several measures have been established by the Mauritian Wildlife Foundation to minimise such risk. Specific monitoring protocols maintain consistency, and regular staff training has been provided to ensure these standards were met and error minimised. Repeated visits to nest sites ensured that all breeding pairs were correctly identified. Ringing efforts began when the population fell short of 20 wild birds and in parallel with the population's growth. It has been possible to maintain a population of which >95% is identifiable by a unique colour ID leg ring (Raisin 2010). High nest site fidelity of breeding pairs, low divorce rates and widespread field surveys minimise the chance of missed breeding attempts. If unrecorded nests had been successfully fledging chicks, there would have been a high re-sighting rate of un-ringed birds, which was not observed.

The analytical methods used should also be assessed for their capacity to accurately examine the effects of SF. Environmental factors over a range of scales are known to influence breeding success, survival and recruitment, both as a result of natural climatic variation on an annual basis, and due to stochastic events (Lack 1966). In addition, natural food availability is tightly regulated by environmental conditions (Ruffino *et al.* 2014) and could mask the importance of SF. Timing of breeding varies annually in many species according to seasonal conditions, which may ultimately be linked with breeding success (Monrós *et al.* 2002; Robb *et al.* 2008; Hinks *et al.* 2015). Such variability is true of the echo parakeets, with supplementary fed pairs generally breeding earlier than unfed nests (Appendix 4.15). If ignored, environmental factors might have confounded any effect of SF in this study. Due to the retrospective nature of the research, the corresponding environmental data sets were not available. Instead, season was included in all multivariate GLMMs to account for such annual variation. Exploring the influence of environmental conditions, could, however, be a valuable aspect of future research.

A key detail of the study was the classification of SF use, primarily based on systematic observations by field staff of birds using the feeding stations. It is possible that certain birds using the feeding stations were not re-sighted, but with monitoring occurring four days of the week and over the course of six months, it is unlikely an individual would be unobserved and misclassified as SF0 or SF1. Another factor to consider is the change in use of SF over the breeding season and the importance of the male in providing for the nest. In the ~25 day period from egg-laying through to the hatching, the female rarely leaves the nest, relying on the male to return with food. When chicks exceed at least seven days old the food demands increase and the female begins to leave the nest for short periods. These time periods lengthen as the brood matures, fledging at around 60 days old (Young 1987). Whilst the female still contributes to the diet of the chicks, the role of food supply at the early stages of a breeding attempt is therefore biased towards the male's foraging abilities. Understanding the role of SF at an individual level should not be overlooked; efficient foraging by the male may permit increased female attendance at the nest and consequently improve nest success, as found with reed warblers (Eikenaar *et al.* 2003). Further work could explore the influence of the male's feeding strategy on productivity. Although such information is available, it is not currently digitised and was not possible within the scope of this study.

The spatial ecology of food supply has also been known to influence foraging efficiency and the decision to use SF (Houston *et al.* 2005). Hilgartner *et al.* (2014) found that White Storks breeding closer to supplementary feeding sites experienced better reproductive success. Of course each species will experience regulatory pressures differently, and the role of SF will no doubt vary in time and space, and should be considered case by case (Robb *et al.*

2008; Ewen *et al.* 2015). Choosing where to position artificial nest sites and feeding stations could become an important aspect of future management decisions for the echo parakeet programme. Rarely is supplementary feeding provided to reflect the spatial and temporal abundance of natural food supplies or foraging strategies. Testing different methods of food provisioning would allow managers to refine current practices to ensure maximum gain for the focus species (Armstrong *et al.* 2007), in addition to eliminating associated risks such as increased aggression, habituation to one site with decreased dispersal, or nutritional imbalances (Meretsky and Mannan 1999).

4.5.5 Valuing detailed, longitudinal data collection

The results of this study have generated the first, accurate measures of key demographic parameters for echo parakeets and the role which SF plays in shaping them. Such information could help refine current management strategies and guide similar conservation programmes employing SF. By exploring the simultaneous impact of SF on multiple key demographic parameters, this study was able to develop a more holistic understanding of the wider effects of SF, information which is essential for driving effective species management. Increased fledge rates can promote population recovery, but such a gain is negated if the number of breeding attempts per season and recruitment rates are too low. To recognise this requires monitoring more than one demographic parameter, and other study systems should be encouraged to establish long-term monitoring systems that will accurately assess the extent of SF's impact and not just the key parameters being targeted. This would help to develop a feedback loop of information between management actions and the response of the target species, following changes through time (Magurran *et al.* 2010) and across life-history stages in response to a range of management actions. Predictive models (e.g. Maggs 2016) may be an important aspect of future management decisions regarding SF, helping to develop a feasible exit strategy should this be a long-term goal.

Conservation programmes have certainly improved in their assessment of providing supplementary food and species support tools in general, but there is still a great tendency to state the findings and believe that ‘knowing more’ automatically improves their practice. For a managed population, a detailed understanding of the study system is half the battle, and of course a crucial foundation for further work and refinement. Driving this knowledge forward and applying these findings to management is the next challenge. Findings must be evaluated where relevant, integrated into future management policies and regularly reviewed in terms of the objectives of a particular method such as supplementary feeding (Armstrong *et al.* 2007; Ewen *et al.* 2015; Canessa, Guillera-Arroita, *et al.* 2016; Canessa, Genta, *et al.* 2016). Reviewing these in line with the wider goals of a management programme will support the long-term success of the echo parakeet. Adopting more structured decision making processes to improve current supplementary feeding regimes has been employed by several conservation programmes (e.g. Meretsky and Mannan, 1999; Ewen *et al.* 2015; Maggs, 2016) but this approach has not yet been initiated in the echo parakeet management programme. Whilst decision making frameworks can offer guidance to managers there remains a great fear of change in conservation (Meek et al. 2015), even with support available. In the case of supplementary feeding this may involve not knowing what change would involve, how it could be achieved, or how to predict the expected and unexpected consequences of such. Wildlife managers should be encouraged to be pro-active both in improving supplementary feeding regimes and across a much wider range of management strategies. For the echo parakeet, this study has provided essential ground work to help inform future decisions regarding the supplementary feeding regime which now require further exploration.

4.6 Conclusions

The results of this study demonstrate that for the echo parakeet, employing supplementary feeding as a conservation tool has a positive effect on the population and its recovery. Although SF had no apparent effect on survival, it has an immediate effect on breeding success. The effects continued into later life, as individuals originating from supplementary fed nests were twice as likely to recruit into the breeding population, and were less likely to skip a breeding season. The findings are important for other programmes managing small populations with SF. Although negative responses to SF were not identified in this study period, further work should explore its potential underlying effects, such as reduced dispersal, behavioural changes or disease risk.

Chapter 5

Exploring the potential demographic impact of a disease outbreak in a small, recovering population

"……infectious diseases have undoubtedly been the main agents of morbidity and mortality in human populations for the past 10,000 years….it is folly to think that wild birds and other wildlife are less susceptible to the influences of disease than humans and domestic animals…."

Haldane, 1949

Student contribution and impact

Understanding if and how to control disease in managed populations requires knowledge of how the disease functions at an individual level, alongside knowledge of its effects at the population level. Answering this question is currently a high priority for the management of the echo parakeet, where an outbreak of Psittacine beak and feather disease occurred in 2005. Through collating a detailed demographic data set focused on breeding data and re-sighting information, this chapter is novel in its ability to simultaneously consider the impact of the disease on two key demographic parameters, breeding success and survival. Researching and cataloguing the history of PBFD in Mauritius, and combining this with my data, facilitated an opportunity in this Chapter to ask in greater detail, precisely when the virus began to affect key population demographics. This has consequently shed new light on the outbreak period of the disease and improved current understanding of disease functioning in the echo population. Never before has the impact of PBFD been explored on echo parakeet survival, and to current knowledge, this have not been described in any other parrot species. My work makes a valuable contribution to the currently sparse understanding of PBFD, both in Mauritius and globally.

5.1 Abstract

Emerging infectious diseases (EIDs) are now considered one of the top five drivers of widespread population declines and extinctions. Ameliorating the threat of an EID requires linking epidemiological and ecological research, enabling conservation practitioners to better understand the dynamics of a host-pathogen relationship and how the impact at an individual level carries through to the population level. Identifying how a disease may threaten a population's persistence can guide the implementation of appropriate in situ strategies, which may strengthen the resilience and stability of a population.

This chapter aims to examine the extent to which an outbreak of Psittacine beak and feather disease (PBFD) impacted key demographic parameters in an endangered population of parakeet, *Psittacula echo.* Using 20 years of

demographic data, changes in breeding success, survival and recruitment were examined prior to, during and after a documented outbreak. Guided by field observations of the disease and serological tests for prevalence, analysis explored (i) the extent of the disease period and by extension whether different demographic parameters were affected over a different time scale during the disease emergence, and (ii) whether the impact was ubiquitous across the population.

Results revealed that breeding success was negatively affected during the emergence of the disease and outbreak, and impacts were more pronounced in breeding attempts associated with the use of supplementary food. Non-supplementary fed nests experienced only a reduction in hatching success. Remarkably, the effects of this often fatal disease were short lived across the population and breeding success quickly returned to pre-disease period levels. In contrast, there was no evidence to suggest that survival or recruitment in the wild population was affected prior to or during the outbreak. However, survival in all age classes of pre-breeders was lower in the post-outbreak phase.

This study illustrates the potential negative impacts of EIDs on key demographics at a population level during both pathogen emergence and outbreak, and identifies conservation management actions that may exacerbate its expansion and/or persistence. Longitudinal data sets which consider both the host and the pathogen provide vital information that may guide disease management, bridging the gap between research and conservation.

5.2 Introduction

5.2.1 Emerging infectious diseases - a new challenge for conservation

Management of small and/or threatened populations present challenges for conservation practitioners. In recent years, emerging infectious diseases have become a very serious threat to wildlife and epidemiology now plays a major role in conservation biology (McCallum and Dobson 1995; Fisher *et al.* 2012; Hyatt *et al.* 2015; Tompkins *et al.* 2015). Given the right conditions

EIDs have the potential to shrink the geographic ranges of their host (McCallum and Dobson 1995; Smith *et al.* 2006), extirpate local populations (Cunningham and Daszak 1998; Daszak *et al.* 2000) and alter whole communities and ecosystem functioning (Whiles *et al.* 2013; Gerber *et al.* 2017). EIDs are caused by pathogens that (i) have increased in incidence, geography or host range, (ii) have changed pathogenesis; (iii) have newly evolved, or (iv) have been discovered or newly recognised (Lederberg *et al.* 1992; Daszak *et al.* 2000). It was traditionally thought that an infectious disease could not be key a driver of a local extinction, as they are dependent upon the survival of their host populations (McCallum and Dobson 1995). There is, however, increasing work modelling pathogens with multiple hosts, small populations and pathogen reservoirs (both biotic and abiotic) which has shown that infectious disease may be attributed to far more extinctions than previously recognised (McCallum and Dobson 1995; Tompkins *et al.* 2015; Cunningham *et al.* 2017).

Multiple factors contribute to the current epidemiological crisis. However, the majority of these factors result from the human-mediated activities such as global development, urbanisation and sprawl, increased rate in human travel and global trade (e.g. Daszak *et al.* 2000; Smith *et al.* 2009; Tompkins *et al.* 2015). Certain actions have increased interaction rates between domestic animals and wildlife, which has also been attributed to the increase in EIDs (Bar-David *et al.* 2006; Tompkins *et al.* 2015; Cunningham *et al.* 2017). Taken together, these factors and mechanisms provide movement corridors for pathogens, allowing for pathogen introductions and range expansions, be it by host range (including reservoir hosts) or geographically. Disease prevalence has consequently increased in a range of species and locations, becoming a threat so substantial that EIDs are now considered one of the top five drivers of species extinctions (Smith *et al.* 2006; Smith *et al.* 2009).

EIDs have been implicated in the widespread population decline of species as taxonomically diverse as soft corals (Aeby *et al.* 2016), amphibians (Martel *et al.* 2014; Price *et al.* 2014), marine mammals (Wilson *et al.* 2014) and numerous land mammals. From the rapid decline of bats in North America (Lorch *et al.* 2016), Eurasian squirrels in the United Kingdom

(Macpherson *et al.* 2016; Rushton *et al.* 2006) to African canids (Goldman *et al.* 1996; Kruchenkova *et al.* 2009), EIDs present a diverse, global threat from the scale of individual species to human and whole ecosystem health (Hoberg and Brooks 2015; Cunningham *et al.* 2017). Across these taxa, endangered populations or island species are under a greater threat as their small population sizes and small geographic range exacerbates their vulnerability, elevating their extinction risk. Notable examples include the numerous extinctions of endemic Hawaiian birds (Smith *et al.* 2006; Liao *et al.* 2017) and rainforest frogs in Australia (Laurance *et al.* 1996) and Central America (Berger *et al.* 1998). While exposure does not always culminate in extinction, EIDs can seriously jeopardise the persistence of small or threatened populations. This has proven detrimental to several iconic species restoration programmes such as the re-introduction of the black footed ferret (*Mustela nigripes*; Thorne and Williams 1988), the Caspian seal (*Pusa caspica;* Wilson *et al. 2014)*, conservation management of the endangered pink pigeon (*Nesoemas mayeri*; Swinnerton *et al*. 2005), and more recently the Ethiopian wolf (*Canis simensis*; Gordon *et al.* 2015). Whether a primary or secondary cause of population decline, EIDs are challenging conservation programmes more than ever before. Investigating the pathways for novel disease emergence, and understanding how they threaten host ecology at an individual and population scale, represents a crucial area for current and future research.

5.2.2 Understanding how to manage EIDs

The practical tools currently available for mitigating the impact of a disease are limited and can be difficult to implement in free-living populations. Possibilities include: preventative quarantine procedures (Langwig *et al.* 2015); culling (Woodroffe *et al.* 2006); separating infected individuals from the naïve population (Mbaiwa and Mbaiwa 2006), treatment or vaccination (Stice and Briggs 2010; Chauvenet *et al.* 2011); or selective breeding of individuals with greater disease resilience (Ragone Calvo *et al.* 2003). In the most extreme circumstances, entire pathogen eradication from the environment may be possible, such as the successful eradication of *Batrachochytrium dendrobatidis* from five permanent ponds in Spain (Bosch *et al.* 2015). The suitability of a control measure is context dependent (Langwig *et al.* 2015) and options for disease control are determined by a host of factors, from the availability of management resources, to the stage of pathogen invasion.

For these tools to be effective, it is important to consider three fundamental scales over which disease dynamics operate and determine infection outcomes, often referred to as the ‘disease triangle’ (Scholthof 2007). This triangle recognises that the outcome of an infection arises from the interaction between (i) the ecology and evolutionary history of the host e.g. resistance and tolerance, (ii) the genotype and phenotype of the pathogen e.g. infectivity, and (iii) the surrounding abiotic and biotic environment. Understanding the various disease dynamics at each scale can help to understand how EIDs present a threat, and potentially provide some insight toward their management. For example, in the latter category, reservoir host species or intermediate hosts may contribute to disease transmission, and in some cases it may be more effective to manage disease prevalence in the reservoir population than the threatened host population(s) (Cleaveland *et al.* 2002; Langwig *et al.* 2015). It should not, however, be assumed that human intervention will be successful, particularly as interventions have been correlated with increased disease risk or unintended consequences for other members of the ecosystem (Chauvenet *et al.* 2011). This highlights how disease dynamics operate over multiple scales with interactive effects (Scholthof 2007) and should be considered in any management actions.

Of course, the opportunity to manage disease does not come without its own set of controversial challenges, such as the application of Virkon® S on a large scale in an open environment (Bosch *et al.* 2015), culling badger populations in the UK (Woodroffe *et al.* 2006), or using chlorine and copper sulfate to eliminate the black-striped mussel (*Mytilopsis sallei;* Ferguson 2000). It is far too easy to be seen applying observable steps towards mitigating the impact of an EID, but too often these actions are a haphazard, quick and dirty response and are not evidence based (Woodroffe 1999). To tackle the threat of EIDs, scientists from a range of disciplines and wildlife practitioners must work collaboratively in order to correctly understand how diseases may drive a population decline and how this can be managed.

5.2.3 Recognising the stages of disease emergence for effective management

Whilst there is a growing body of literature reporting both novel epidemics and dynamics within wild populations, the right tools for efficient disease recognition and disease management need to improve concurrently. This requires an understanding of how an infectious disease becomes a threat to a population, to what extent this threat becomes manifested and to whom, and at what point does it compromise population persistence (Daszak *et al.* 2000). These are not determined by a simple number of factors, as host-pathogen factors operate across nested levels of biological organization, which will vary according to the host, the pathogen and the environment (Scholthof 2007); within-host processes underlie amongst-host processes within a population. How an EID enters and expands within a population and the extent of its impact (over time, space, across life histories and between individuals) will thus be shaped by the disease dynamics at each level. Studies looking to gain insight into epidemiological processes driving this need to consider within-host processes up through to population level dynamics.

Part of understanding how a disease becomes a threat is to understand how the disease enters and expands within a population. According to Langwig *et al.* (2015), the invasion process can comprise four distinct stages: pre-arrival, invasion front, epidemic and established. Illuminating the pathways through which an EID can enter a population, and considering the importance of each development stage, may provide valuable information regarding the epidemiology of infections, the dynamics of host-pathogen relationships and the qualities or conditions that increase disease risk. As these stages vary, disease management can become context-dependent (Langwig *et al.* 2015), allowing it to be more appropriately targeted. For example, identifying the species' immunological or behavioural traits that facilitate disease emergence has been put forward as a focus for preventing invasion (Lachish *et al.* 2011;

McDonald *et al.* 2017), whilst identifying signals of the disease will further help in its prevention or control. This could allow wildlife managers to act proactively i.e. an intervention being implemented pre-pathogen arrival or at point of invasion, instead of reactively i.e. during the epidemic or when the pathogen has established. The earlier control strategies can be implemented, the more effective the intervention should prove (Lachish *et al.* 2011; Langwig *et al.* 2015; Tompkins *et al.* 2015). Acquiring such knowledge requires sufficiently detailed data on both the host and the pathogen, documenting its stages of development prior to, during and after an outbreak

Documentation of a novel disease emerging in an endangered species is not unheard of (e.g. Salmonella in the hihi (*Notiomystis cincta*); Ewen *et al.*, 2007; White-Nose Syndrome, a fungal disease in North American bats, Blehert *et al.*, 2009; ranaviruses in a range of amphibian species, Price *et al.*, 2014; chytrid fungus, *Batrachochytrium salamandrivorans,* in Western Palearctic salamanders, Martel *et al.* 2014) but suitable population ecology data collected over key time periods is incredibly rare. Combining epidemiology and wildlife management require much improvement, but recognising the growing threat of EIDs has begun to encourage pre-disease monitoring, along with the development of advanced diagnostic tools, protocols for prevention or treatment, and advanced predictive models which look to inform effective management strategies (McCallum *et al.* 2001; Rohani and King 2010; Gerber *et al.* 2017; Russell *et al.* 2017). The ability to take action whilst the disease is emerging could make a crucial difference to the survival of a population. Developing predictive models to forecast disease outbreaks and predict their potential effects has been suggested as a means of aiding management decisions for mitigating or controlling the impact of an EID at critical stages (Russell *et al.* 2017), but the reliability of such predictive models would be much improved with real-life examples.

5.2.4 The demographic consequences of EIDs

Disease is a very natural part of the environment, playing an important role in population regulation and natural selection. Whether transient within the population or a geographic range, or present at a low level - be it prevalence or intensity of infection - a disease can be considered non-threatening to the overall stability of the population (Cassirer *et al.* 2017). Novel diseases as well as existing ones become a threat and increase extinction risk when they negatively and substantially change key demographic parameters regulating population growth (Woodroffe 1999; Peters *et al.* 2014). Attributing changes in demographic traits to disease is not easy and to definitively prove that the decline or extinction of a species was a direct consequence of a novel disease is almost impossible. This could partly explain why the potential for disease to significantly alter population trends was overlooked for so many years (Robinson *et al.* 2010). The first definitive report was of the Polynesian tree snail, *Partula turgida*, (Cunningham and Daszak 1998), with a more recent example including global extinction in amphibians (Rosa *et al.* 2017). Establishing the connection required the documentation of both disease prevalence and the evidence of an impact on demographic rates, reinstating the importance of detailed demographic data on the host and the pathogen.

A novel pathogen ultimately makes a population vulnerable to extinction by influencing either mortality or fecundity, or both (Lachish *et al.* 2011). The ability to identify who is affected within the population and how, is central to understanding the dynamics of the disease. The impact of disease on mortality rates may be specific to certain members of the population, with susceptibility varying according to life history stages or groups (e.g. social class or sex). Determining links between population structure and pathogen persistence can help to determine practical steps toward control, prevention or treatment (Lyles and Dobson 1993; Lachish *et al.* 2011; VanderWaal and Ezenwa 2016). Recovery efforts of the Arctic fox (*Otodectes cynotis*) focused on treating cubs with anti-parasitic drugs, for example, because parasite induced cub mortality was the key driver of population decline (Goltsman *et al.* 1996). Individuals with high-risk traits may prove a target for management interventions, as did the treatment of male yellow-necked mice (*Apodemus flavicollis*) to reduce the population-level prevalence of gastro-intestinal helminths (Ferrari 2003). Targeting specific type of individuals in a population is particularly important if there are super-spreaders or a super-excretors of a virus, as their movement patterns will contribute to determining the scale of disease impact at a population level over time and space (VanderWaal and Ezenwa 2016; McDonald *et al.* 2017). Disease may also impact fecundity in the short term and target specific stages of the breeding cycle, as with the reduced hatching success of Pied flycatchers (*Ficedula hypoleuca)* driven by disease (Sanz *et al.* 2001)*.* Alternatively, effects of disease may be delayed and become manifested in an individual's life history traits (Descamps *et al.* 2009). A long-term study on great reed warblers (*Acrocephalus arundinaceus*) found that chronic infection with avian malaria reduced lifetime reproductive success and offspring quality (Asghar *et al.* 2015). Understanding the various scales over which an EID acts within a population will subsequently determine its demographic impact on the processes leading to population decline.

The challenge for endangered species management is to develop effective strategies to abate the threat of EIDs, limit transmission and promote population resilience (Cassirer *et al.* 2017). Conservation measures may differ according to whether the EID was an endemic or novel pathogen (Rachowicz *et al.* 2005), but for either circumstance, detailed demographic data that spans the pre, during and post emergence stages of an EID can facilitate improved disease management. Unfortunately, there is a severe deficiency in such data during the first stage of emergence, a phase termed as 'pre-invasion' and 'invasion front' by Langwig *et al.* (2015). Diseases can appear with no indication of their arrival, but act immediately with devastating effects, forcing a 'crisis management' scenario to be adopted (Woodroffe 1999). Monitoring is then only implemented in the later stages of an outbreak when it is often too late and monitoring is rarely maintained. Consequently, little information of use can be harnessed regarding an important stage in disease dynamics, the stage of emergence in a population. disease emergence. Increasing recognition for the importance of individual heterogeneity in disease ecology, i.e. employing multiple observations of individuals across years, and how this scales to population level consequences, has encouraged the integration of pathological and epidemiological studies into wildlife monitoring (Cunningham *et al.* 2017). However, this needs to become a more standardized process. Opportunities to use long-term individual based data-sets will improve our mechanistic understanding of the epidemiological process behind EIDs (Rohani and King 2010), identifying links between disease and demographic process that will ultimately guide strategies for disease management.

5.2.5 Case study

5.2.5.1 Disease in the echo parakeet

The recovery of the echo parakeet (*Psittacula echo)* in Mauritius presents a rare opportunity to observe the emergence, pathology and population-level impact of an EID. Long-term monitoring of this endangered species was established as part of an on-going recovery programme, recording individual based demographic data throughout the population's recovery which included an outbreak of Psittacine beak and feather disease (PBFD) in 2005. In the space of one year, clinical signs were commonplace in the population and 41% of birds sampled between 2005 and 2006 tested positive for PBFD (Kundu *et al.* 2012). This outbreak of PBFD prompted the end of a successful release programme and initiated a new phase of reduced management. Despite the sudden expansion of the virus, the population continued to grow seemingly unaffected (Figure 5.1). Presently, PBFD remains prevalent in the population though symptoms are generally restricted to fledglings within their first one or two years (Henshaw *et al.* 2014).

Previous and on-going research focuses on the evolutionary history and genotype of the strain of BFDV within the echo parakeet population (Kundu *et al.* 2012), susceptibility of individual echos (D. J. Fogell, *pers comms*) and the complex host-virus dynamics which includes the introduced population of *Psittacula krameri* (Tollington 2012; Kundu *et al.* 2012). The range of research conducted needs to consider the multiple levels at which disease dynamics vary, as there is a current lack of knowledge in this area. This includes the factors driving within-host disease processes, where most research has previously focused, and how changes in the host develop to affect population-level dynamics.

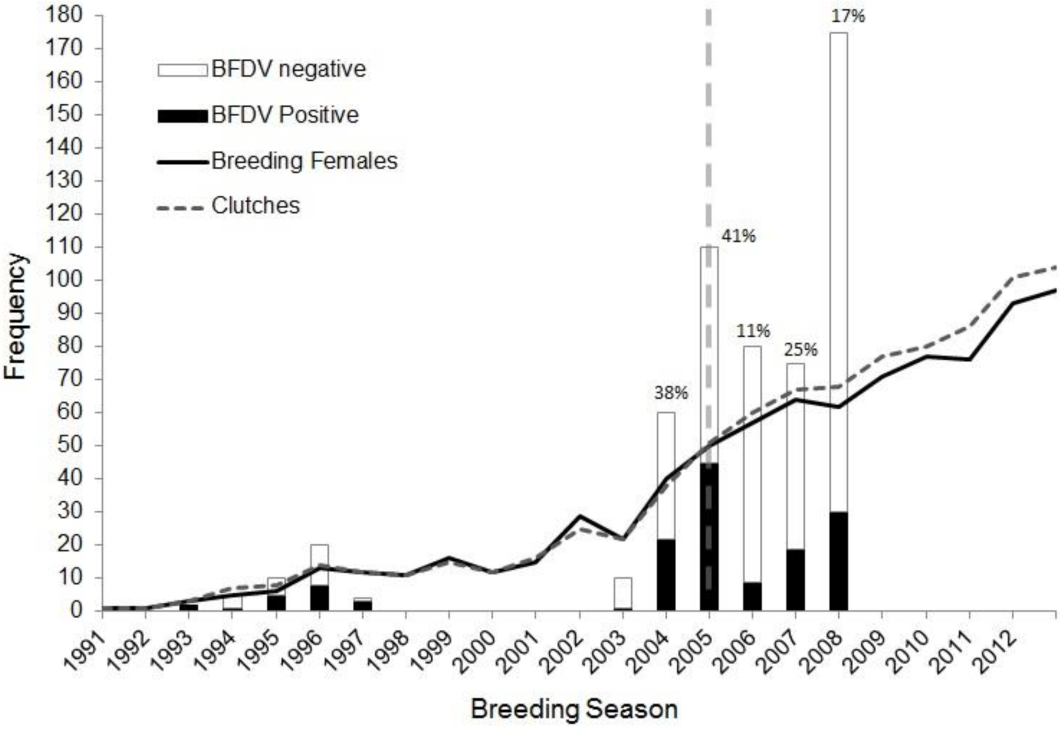


Figure 5.1 The continued growth in the annual number of breeding females and clutches of echo parakeets throughout the study period. Stacked bars utilise data adapted from Kundu *et al*. (2012) representing the number of infected and uninfected parakeets for breeding seasons between 1993 and 1998, and between 2003 and 2009. Blood samples were not collected from 1998 to 2002, and samples from 2009 onward were not yet published, hence an absence of bars. Estimated prevalence of BFDV per season is indicated as a percentage. Breeding seasons are indicated by the calendar year in which they began (e.g. 2005 refers to the 2005/06 season).

5.2.5.2 Psittacine beak and feather disease

PBFD is a highly infectious viral disease among Psittaciformes, an order of birds already experiencing alarming declines on a global scale (Marsden and Royle 2015; BirdLife International 2017a). The smallest member of the circovirus family, infection with beak and feather disease virus (BFDV) can lead to chronic, debilitating secondary infections that are mostly fatal. The diversity of the BFDV virus means genetically adapted strains can be species specific (De Kloet and De Kloet 2004; Khalesi *et al.* 2005) and even these strains are known to regularly evolve (Varsani *et al.* 2010; Kundu *et al.* 2012; Regnard *et al.* 2015). Originating in Australia, BFDV has been detected in both wild and captive bred parrot populations since the 1970s (Ritchie *et al.* 1989) and is now the most prevalent viral disease in parrots (Heath *et al.* 2004; Regnard *et al.* 2015a; Hakimuddin *et al.* 2016). Cases have been confirmed in a total of 78 wild species (Fogell *et al.* 2016), of which more than a quarter are classified as threatened, such as the endangered Cape Parrot *(Poicepahlus robustus*; Regnard *et al.* 2015a) and the extant population of the Australian Orange-Bellied Parrot (*Neophema chrysogaster;* Peters *et al.* 2014).

The virus can be vertically transmitted through the embryo (Rahaus *et al.* 2008), or horizontally through ingestion or inhalation of crop secretions, fresh or dried excrement, and feather or skin particles (Woods *et al.* 1993; Todd 2004). The latter enables further transmission between ecologically disconnected species (Regnard *et al.* 2015), particularly as it is extremely stable in the environment and can remain in nest hollows for years (Varsani *et al.* 2010). As parrots frequently re-use their own nests sites and those of conspecifics, re-infection is highly likely. The only effective means of removal is with a strong disinfectant that inactivates the virus, such as 1% Virkon® S (DuPont Inc) or Virex® virucide (DuPont Inc). Most knowledge of PBFD is based on cases from captivity (Fogell *et al.* 2016), and as the spread of BFDV into wild populations has increased, it is becoming increasingly apparent that little is understood about the patterns of the disease dynamics in wild populations and how it functions.

5.2.5.3 Pathology of the virus, BFDV

The time over which the disease develops varies, largely depending on the age and fitness of an individual and the mode of exposure. Juveniles (under 3 years) are generally more susceptible (Todd 2004). Clinical signs of PBFD include weight loss and diarrhoea, with chronic PBFD causing feather dystrophy, discolouration (Figure 5.2) and loss, beak abnormalities, and fragile skin vulnerable to infection (Todd 2000; Rahaus *et al.* 2008). These symptoms can develop at different rates over various life history stages. The degree of pathogenicity is highly variable and so is common for individuals to be acting as carriers while showing apparent immunity (De Kloet and De Kloet 2004).

Figure 5.2 An echo parakeet with yellow feather discoloration, typical clinical signs of PBFD infection. Photo by Sam Watson ©

Disease screening of blood samples to test for the presence of BFDV offers one means of diagnosis (Regnard *et al.* 2015) and two commonly available methods exist: Polymerase Chain Reaction (PCR) and an Enzyme Linked ImmunoSorbent Assay (ELISA). However, these are not entirely reliable, as subclinical infections are difficult to detect, and false positives are often recorded from blood samples (Rahaus and Wolff 2003; Tollington 2012; Ledwoń *et al.* 2014). In addition, there have even been cases of birds showing clinical signs of the disease but consistently testing negative for current BFDV infection (Raisin 2010). A correlation between viral load, infection status and clinical symptoms has gained increasing support through recent studies (e.g. Regnard *et al.* 2015; D.J Fogell, University of Kent, *pers comm*), and current research indicates that many Psittacines are carriers of the virus, maintaining a sub-clinical infection with viral load varying over time. Full development into PBFD becomes possible if their immunity is challenged, or viral load becomes particularly high. As such, the prevalence of PBFD in a population is not always clear and often only noted when clinical signs are evident (Hakimuddin *et al.* 2016). Although no extinctions of Psittacine species have been documented due to PBFD, its increasing threat is driving a worldwide effort to screen for BFDV and identify its prevalence amongst other parrot species. This will enhance current understanding of the virus' movement and genetic evolution (Heath *et al.* 2004; Ortiz-Catedral *et al.* 2009; Varsani *et al.* 2010; Harkins *et al.* 2014; Fogell *et al.* 2016).

5.2.5.4 Study focus: exploring the extent of the disease's demographic impact

Understanding the ecology of PBFD is crucial for its management, both for the echo parakeet and Psittaciformes in general. It is known that the hatching success of echo parakeets was reduced in 2005 due to PBFD (Tollington *et al.* 2015), but it has not yet been explored whether the extent of the disease impact extended earlier than this, as blood samples and field observations would suggest. Using 20 years of detailed demographic data that coincided with the PBFD outbreak, this chapter examines (i) the extent of the disease period and the possibility that key demographic parameters were affected over a different time scale during the disease emergence and main outbreak, and (ii) whether or not the impact was ubiquitous across the population. Three key demographic parameters, breeding success, survival and recruitment, are known to be affected by disease in birds (Norris and Evans 2000). In this study, these three parameters were explored in relation to the known presence of the disease in the population, the timing of the PBFD outbreak and whether a management tool - supplementary feeding - may have exacerbated the effects of disease.

5.3 Methods

5.3.1 Study system and monitoring

The echo parakeet population and recovery programme are described in detail in Chapter 2. Consequently, only details of relevance to this study are reported here. Between 1993 and 2013, intensive conservation efforts have restored the population from less than 20 wild birds in 1986 (Jones and Duffy 1993) to a current estimate exceeding 500 (Henshaw *et al.* 2014). This recovery is the result of a combination of brood manipulations (such as rescuing of underdeveloped chicks to captivity, and upsizing and downsizing between wild nests), provision of artificial nest boxes, supplementary feeding, and a release programme which augmented the wild population. Across this entire period, intensive monitoring protocols have collected detailed, individual based life-history data and established a population of which more than 95% is uniquely identifiable.

5.3.1.1 Breeding data

Management has focused on monitoring the annual breeding season, following all breeding activity of echo parakeets throughout the Black River Gorges National Park (BRGNP), a 70km^2 protected area in which the only population of wild echo parakeets remains (Figure 5.3). Methods of data collection follow that described in Chapter 4, with full details provided in Chapter 2.

5.3.1.2 Re-sighting data

All the re-sighting information was compiled to produce individual encounter histories for almost every member of the population. Methods follow those described in detail in Chapter 3 and 4.

5.3.1.3 The history of PBFD in echo parakeets

The timing of the introduction of BFDV to Mauritius is not specifically known, particularly as at least 56 species of exotic birds have been introduced to Mauritius since the 17th Century (Cheke and Hume 2008), but the most likely host is the Indian rose-ringed parakeet (here on referred to as IRRP for brevity) which arrived in 1886 (Cheke and Hume 2008). Although a behavioural and ecological separation between the two species is described in field reports and literature (Groombridge *et al.* 2004), the persistence of the virus in the environment can enable indirect transmission, which may explain the related ancestry of the viral strains carried by *P. echo* and *P. krameri* (Kundu *et al.* 2012). Although rare, sightings of echo parakeets socialising with IRRP are not unheard of, and IRRPs are frequently evicted from echo nest sites.

Interpreting the prevalence of BFDV within the echo population continues to be a challenge and most information regarding the virus' emergence has been acquired through retrospective analysis (Raisin 2010; Kundu *et al.* 2012; Tollington *et al.* 2015). Combining this with observational data collated from field reports, it has been possible to develop a timeline of key events leading up to the major outbreak in 2005 (Figure 5.3 and 5.4). At the start of the official echo parakeet management programme, blood samples were routinely taken from chicks and, opportunistically from adults, to test for BFDV. Despite one suspected but unconfirmed case in 1995, negative results and lack of clinical signs in the population gave the impression of a population seemingly free of the disease. In 1998, blood sampling was discontinued. However, in 2002/03, a case of PBFD was presented in the population and blood sampling resumed. Cases of PBFD slowly increased, particularly in intensely managed nests, and the number of reported illnesses in *P. echo* concurrently increased so much that by the start of the 2005 breeding season, clinical signs were rife across the whole population (which just exceeded 300 birds (Malham *et al.* 2006). Due to the high mortality and clinical signs, the 2005/06 season has been regarded as the year of the major outbreak, here-on referred to as the Pre-Defined Outbreak period. Further releases were halted, all cross-fostering, rescuing and hand rearing ceased, and the frequency of nest site visits reduced. Monitoring protocols were refined (Appendix 5.1) in order to minimise any disease transmission that had potentially been facilitated mediated by management actions.

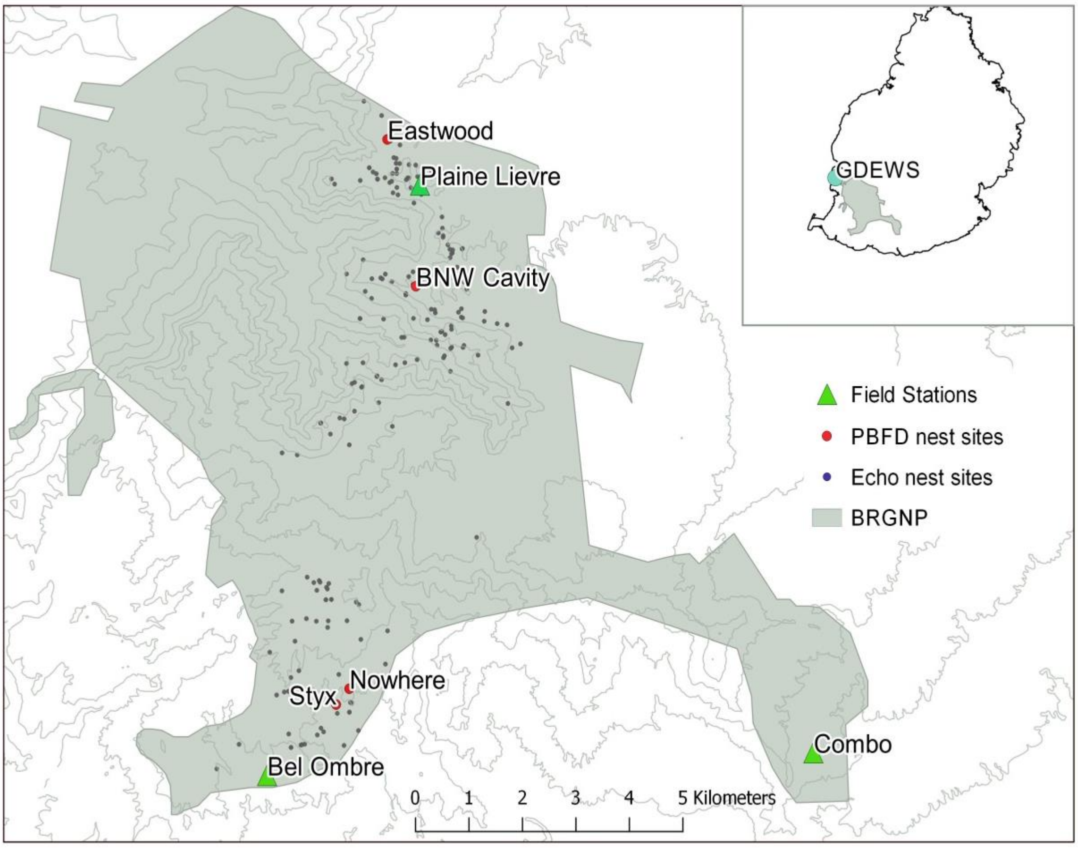


Figure 5.3 A supporting map and key which contextualises the information provided in Figure 5.4.

PL - Plaine Lievre: location of the main field station supporting the northern sub-population referred to as 'Grandes Gorges'

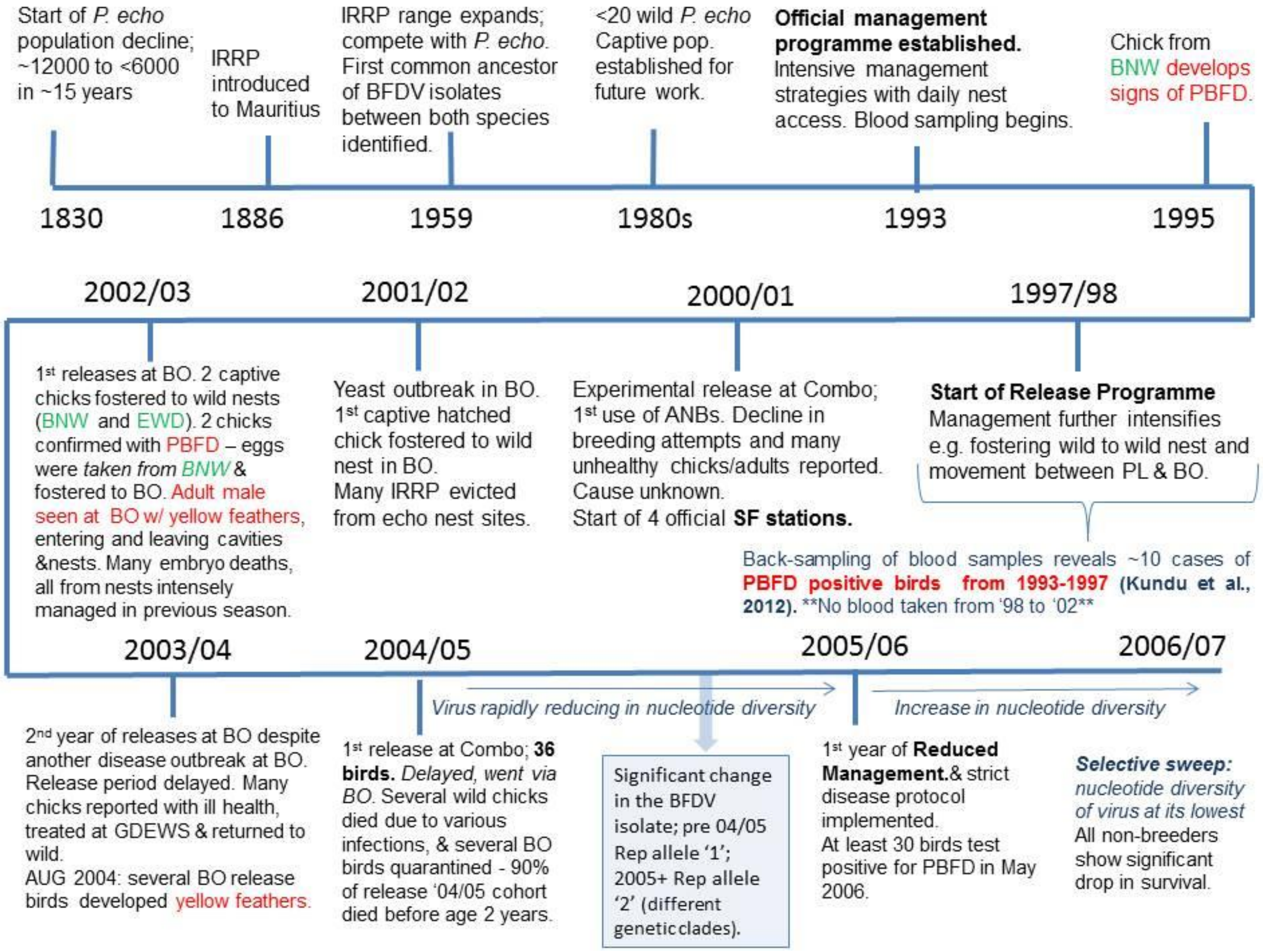
BO - Bel Ombre represents the southern sub-population of echo parakeets. Contains a field station built to support releases in this area.

Combo - Release site and field station. No natural, wild echo nest sites identified, but this was the site for releases in 2004/05.

BNW - **'**Brave New World', nest site producing PBFD positive chicks

EWD - **'**Eastwood' and 'Styx**'** - two nest sites frequently visited by a male indicating clinical signs of PBFD in 2002/03

GDEWS - Captive rearing facility, Gerald Durrell Endemic Wildlife Sanctuary



1830

Start of *P. echo* population decline; ~12000 to <6000 in ~15 years

1886

IRRP introduced to Mauritius

1959

IRRP range expands; compete with *P. echo*. First common ancestor of BFDV isolates between both species identified.

1980s

<20 wild *P. echo* Captive pop. established for future work.

1993

Official management programme established. Intensive management strategies with daily nest access. Blood sampling begins.

1995

Chick from BNW develops signs of PBFD.

1997/98

Start of Release Programme Management further intensifies e.g. fostering wild to wild nest and movement between PL & BO.

Back-sampling of blood samples reveals ~10 cases of **PBFD positive birds from 1993-1997 (Kundu et al., 2012).** **No blood taken from '98 to '02**

2000/01

Experimental release at Combo; 1st use of ANBs. Decline in breeding attempts and many unhealthy chicks/adults reported. Cause unknown. Start of 4 official **SF stations.**

2001/02

Yeast outbreak in BO. 1st captive hatched chick fostered to wild nest in BO. Many IRRP evicted from echo nest sites.

2002/03

1st releases at BO. 2 captive chicks fostered to wild nests (BNW and EWD). 2 chicks confirmed with PBFD – eggs were *taken from BNW* & fostered to BO. Adult male seen at BO w/ yellow feathers, entering and leaving cavities &nests. Many embryo deaths, all from nests intensely managed in previous season.

2003/04

2nd year of releases at BO despite another disease outbreak at BO. Release period delayed. Many chicks reported with ill health, treated at GDEWS & returned to wild.
AUG 2004: several BO release birds developed yellow feathers.

2004/05

1st release at Combo; **36 birds.** *Delayed, went via BO.* Several wild chicks died due to various infections, & several BO birds quarantined - 90% of release '04/05 cohort died before age 2 years.

Virus rapidly reducing in nucleotide diversity

Significant change in the BFDV isolate; pre 04/05 Rep allele '1'; 2005+ Rep allele '2' (different genetic clades).

2005/06

1st year of **Reduced Management.** & strict disease protocol implemented.
At least 30 birds test positive for PBFD in May 2006.

Increase in nucleotide diversity

2006/07

Selective sweep: *nucleotide diversity of virus at its lowest*
All non-breeders show significant drop in survival.

Figure 5.4 Time line of the key events leading up to the Pre-Defined disease outbreak of PBFD in the 2005/06 breeding season. Information has been compiled from records collected at the time and from retrospective information revealed from recent research. See Figure 5.3 for supporting map and key.

IRRP - Indian rose-ringed parakeets, *P. krameri*

ANB - Artificial nest boxes

SF stations - Supplementary feeding sites, located at all three field stations.

Captive pop. - Captive populations

5.3.2 Analytical Framework

5.3.2.1 Defining the disease period

The aim of this study is to explore how the emergence of the disease and subsequent outbreak impacted key demographic parameters in the echo parakeet population. Previous work by Tollington *et al.* (2012) had identified reduced breeding success in the main outbreak year (2005), but with increased demographic data, field reports and retrospective blood samples, there evidence to suggest that the disease was present from as early as 2002. If so, then the outbreak's impact may extend prior to 2005. In order to determine the extent of the disease period, different possible time periods that suitably described the period of disease establishment and outbreak were first identified. Based on prior knowledge of the study system and past research, six 'disease periods', D, were created, grouping breeding seasons together that would extend the Pre-defined Outbreak period (i.e. 2005 only) to describe the emergence of PBFD in the population (Table 5.1). D1 to D4 recognised a Pre-outbreak, Outbreak and Post-outbreak period. D5 and D6 included an 'Early' outbreak period that would account for a potential establishment phase of the disease when it was expanding and increasing in prevalence. Except for one unconfirmed case, PBFD was not evident in the population prior to 2002, hence seasons prior to this were not considered as part of the Outbreak or Early outbreak periods.

Table 5. 1 Six possible Disease Periods identified according to grouping of breeding seasons to describe the impact of disease on breeding success and survival over time. D1 corresponds with the originally Pre-defined Outbreak Period.

Disease Definition	Pre-Outbreak	Outbreak	Post-Outbreak	
D1	1993/94 - 04/05	2005/06	2006/07 - 13/14	
D2	1993/94 - 03/04	2004/05 - 05/06	2006/07 - 13/14	
D3	1993/94 - 02/03	2003/04 - 05/06	2006/07 - 13/14	
D4	1993/94 - 01/02	2002/03 - 05/06	2006/07 - 13/14	
	Pre-Outbreak	**Early Outbreak**	**Outbreak**	**Post-Outbreak**
D5	1993/94 - 03/04	2004/05	2005/06	2006/07 - 13/14
D6	1993/94 - 02/03	2003/04 - 04/05	2005/06	2006/07 - 13/14

5.3.2.2 Defining supplementary fed nests

Previous work from within this thesis (Chapter 4) identified significant differences in breeding success between supplementary and non-supplementary fed nests. Published literature on the echo parakeet has previously indicated a negative effect of disease with supplementary food (SF) during the Pre-defined outbreak (Tollington *et al.* 2015). In light of these facts, the possibility that SF may have interactive effect with disease was considered within this study. As defined in Chapter 4, breeding attempts were classified as supplementary fed (SF1) or non-supplementary fed nests (SF0). Fledglings were subsequently classified as SF1 or SF0 according to the type of nest in which they were reared. Feeding stations were located both at Bel Ombre and Plaine Lievre to support the two sub-populations (Figure 5.3).

5.3.3 Disease and breeding success

5.3.3.1 Model process

The number of fledglings per clutch was considered the primary measure of breeding success and examined first to investigate which disease period would most suitably describe the impact of PBFD. Supplementary food (SF) was included within the model set (Table 5.2) to identify any interactive effect with the disease that may help to explain changes in breeding success.

To understand the impact of PBFD on the different stages of breeding, the modelling procedure was repeated for 1) hatchability and 2) the overall probability of an egg surviving through to fledge. In this study, it was not possible to model brood survival due to insufficient data. In total, three measures of breeding success were therefore examined for the impact of the disease prior to the outbreak: (i) the number of fledglings per clutch, (ii) egg hatching probability, and (iii) the probability of an egg surviving the clutch and brood stages and successfully fledging the nest.

5.3.3.2 Modelling details

A Generalised Linear Mixed Model (GLMM) in package ‘lme4’ (Bates *et al.* 2015) fitted models to the data which assumed a poisson error distribution with the number of fledglings per clutch, and assumed binomial error structure with the proportional data (hatchability and egg to fledge survival). To account for repeated observations of individual breeding females in the dataset, female identity was included as a random effect. Models were compared by Akaike's information criteria (AIC_c) (Burnham and Anderson 2002) in order to identify the most parsimonious models from the set of candidate models. All models were run using programme R Version 3.3.1 (R Development Core Team 2016). A minor degree of under-dispersion was estimated across the models (ratio 0.7), but this is an acceptable measure (Thomas and Guidebook Development Team 2015) and no further action was taken.

Table 5. 2 Summary of the model combinations examining the impact of the disease on three measures of breeding success prior to the outbreak, according to how the Disease Period was defined (D). Models also considered the interactive effect with supplementary food (SF).

Model	Predictor Variable
Model 1	Null
Model 2	SF
Model 3	D 1
Model 4	D 1 * SF
Model 5	D 2
Model 6	D 2 * SF
Model 7	D 3
Model 8	D 3 * SF
Model 9	D 4
Model 10	D 4 * SF
Model 11	D 5
Model 12	D 5 * SF
Model 13	D 6
Model 14	D 6 * SF

5.3.3.3 Data

This study utilised productivity data collected from 1993 to 2013. Certain data were excluded; second clutches, clutches with unidentified parents, or where the clutch size was unknown. During the period of intense management (1993 to 2004, inclusive) many nests were manipulated in order to maximise productivity and to include them for analysis would have biased productivity estimates. However, their exclusion meant a significant reduction in the data set. Therefore, to minimise the loss of data and maximise sample size, two data sets were created. Data Set 1 excluded any nest manipulated at chick stage but not at egg stage, which maximised the data available to analyse hatchability. Data Set 2 excluded all nests manipulated at any stage (egg or chick) to allow an unbiased analysis of egg to fledge survival and fledgling production. A summary of the two data sets is provided in Table 5.3 and expanded in Appendix 5.2 and A 5.3.

Table 5. 3 Summary of the two data sets used to examine breeding success in response to various Disease Periods. Breeding attempts were grouped according to whether breeding pairs were known to include supplementary food in their diet during a given breeding season (SF1) or did not (SF0).

	Total No. Clutches	**Total No. Eggs**	**Total Hatched**	**Total Fledged**
	Data Set 1			
SF0 Nests	246	638	426	*N.A*
SF1 Nests	525	1439	1059	*N.A*
	Data Set 2			
SF0 Nests	198	510	310	199
SF1 Nests	500	1372	999	853

5.3.4 Disease and survival

5.3.4.1 Model process

A capture-mark-recapture data set was studied in a multistate modelling framework to explore the potential impact of PBFD on survival (φ) and transition rates (ψ), including recruitment, in the wild population of echo parakeets. While PBFD negatively impacted survival in the 2004/05 release cohort, the impact on survival in the wild population was unclear. Monitoring effort remained constant across the study period and as previous work provided no evidence of time dependence in re-sighting probability (*P)* this parameter was not explored in relation to disease. The model process consisted of two steps and adopted a similar approach to that employed for examining disease impacts on breeding success:

Step 1 - A set of models was built to identify the most appropriate Disease Period (D) for explaining variation in survival and transition probabilities over time. Disease Periods were identical to those previously employed (Table 5.1).

Step 2 - Supplementary food (SF) was introduced as a group effect into the most parsimonious model(s) from Step 1 to systematically explore whether disease and SF had an interactive effect on survival or transition.

Step 1

A multi-state model structure provided the framework for this initial step in which re-sighted birds could be assigned to one of three possible states: pre-breeder (N), breeder (B) and post-breeder (PO). Four separate age classes were recognised within each state (age 1, 2, 3, and 4+ years), and each built without time dependence (i.e. constant, '**.**').

Basic Model Structure:

φ ((N| 1:4+**.**)(B| 2:4+**.**)(PO| 3:4+**.**)) **.*P*** ((N| 1:4+**.**)(B| 2:4+**.**)(PO| 3:4+**.**))
.**ψ** ((N-B| 2:4+**.**)(B-PO| 3:4+**.**)(PO-B| 4+**.**))

Retaining this basic structure, parts of the model were manipulated to independently introduce D1 to D6 in three separate ways:

1) Disease periods applied in pre-breeder survival only
2) Disease periods applied in pre-breeder to breeder and breeder to post-breeder transitions only
3) Simultaneously applied Disease periods in pre-breeder survival and pre-breeder to breeder and breeder to post-breeder transitions

Only survival in pre-breeders was explored on the basis that time dependence had not been evident in any other states *a priori.* Time dependence had also not been previously identified in transition, but because SF had proven to be significant in transition in previous work, it was an important element to consider in this analysis.

A total of 18 models were built, with two further models included for comparison (Table 5.7): the most parsimonious model describing age and state specific survival identified in Chapter 4 (Model 1), and the most parsimonious model previously identified for describing the age and state-specific effect of SF (Model 2).

Step 2

Step 2 took the most parsimonious (set of) model(s) from Step 1 to explore whether:

i) Disease was important in survival and/or transition rates

ii) Whether SF (denoted ‘g’ in the model nomenclature) had an interactive effect with Disease and whether this was in transition rates only or also survival.

This was achieved by building the following set of models (Table 5.8):

1) Disease in survival and SF in transition probabilities
2) SF in survival and Disease in transition
3) SF and Disease both in survival and transition
4) SF and Disease in survival, and only SF in transition
5) SF in survival, but SF and Disease in transition

A group-only effect model was built as a comparison (Model 36), and the best survival and best SF models were retained for comparison, as were the best models from Step 1 (Models 8, 11 and 14).

5.3.4.2 Modelling details

Data: constructing encounter histories

For this analysis, 1020 recapture histories from individuals of known origin were used, their common start point being a successfully fledged and ringed pre-breeder. Each individual was classed as either SF0 or SF1 according to the supplementary feeding status of their parents. Their histories were constructed based on re-sightings of individuals made over the course of each breeding season, the first cohort being of 1994/95 breeding season and continuing annually until 2013. The 2013 cohort was excluded, as re-sightings after marking were not available. Released birds were also excluded from the study as they experienced a very different set of natal conditions to those of wild fledged birds, including hand-rearing and time in captivity.

Based on the known biology of the echo parakeet, certain implausible transitions were fixed in all models (see Appendix 5.4).

Model Selection

All multi-state models were run in Programme MARK Version 8.1 (White and Burnham 1999). As certain parameters were fixed, all models were run with the logit link function. Following the justifications outlined in the methods section of Chapter 3, goodness of fit was tested using the median-ĉ approach within MARK. An estimated correction factor of 1.25 was applied to all models, which were subsequently compared by Quasi-likelihood Akaike's information criteria ($QAIC_c$; Burnham and Anderson 2002).

5.4 Results

5.4.1 Disease and breeding success

Results from this study indicate that the disease impact on breeding success spanned multiple years rather than 2005 only. There is compelling evidence that all three measures of breeding success were reduced during the period of disease establishment (i.e. prior to 2005), though this effect was not ubiquitous across the population. An interaction between disease and SF meant that the effects of PBFD were most prevalent in SF1 nests, where-as SF0 nests only saw a temporary reduction in hatchability and no other breeding parameter.

Exploring the most suitable time period to best describe the impact of disease on the number of fledglings per clutch, two models within the set of GLMMs were closely tied as the most parsimonious (Models 4 and 12, Table 5.4). This indicated that the disease impact on this breeding parameter was predominantly occurred in the main Outbreak years of 2005/06, but some negative impact was experienced as early as 2004/05. Transforming the parameter estimates generated by the most parsimonious model of this set (Model 12) provided real values to quantify the changes in the number of fledglings. Values are illustrated in Figure 5.5. This indicates the lack of disease impact on SF0 nests during the disease emergence period, but the contrastingly severe reduction in fledglings from SF1 nests.

Table 5. 4 Generalised linear mixed models examining the suitability of different Disease Periods (D1-6) to describe the extent of PBFD's impact on the number of fledglings per clutch and the potential interaction effect of SF. Descriptions of D are described in Table 5.1. df.resid = residual degrees of freedom.

Number of fledglings per clutch					
Model No.	**Model Description**	**AIC**	**Log Lik**	**Deviance**	**df. resid**
12	D 5 * SF	2044.4	-1013.2	2026.4	683
4	D 1 * SF	2046.1	-1016.1	2032.1	685
14	D 6 * SF	2046.8	-1014.4	2028.8	683
6	D 2 * SF	2047.4	-1013.7	2033.4	685
8	D 3 * SF	2049	-1017.5	2035	685
10	D 4 * SF	2051.3	-1018.7	2037.3	685
2	SF	2062.7	-1028.3	2056.7	689
3	D 1	2066.5	-1029.2	2058.5	688
11	D 5	2066.7	-1028.4	2056.7	687
13	D 6	2067.8	-1028.9	2057.8	687
5	D 2	2070.7	-1031.4	2062.7	688
7	D 3	2070.8	-1031.4	2062.8	688
9	D 4	2071.6	-1031.8	2063.6	688
1	Null	2092.8	-1044.4	2088.8	690

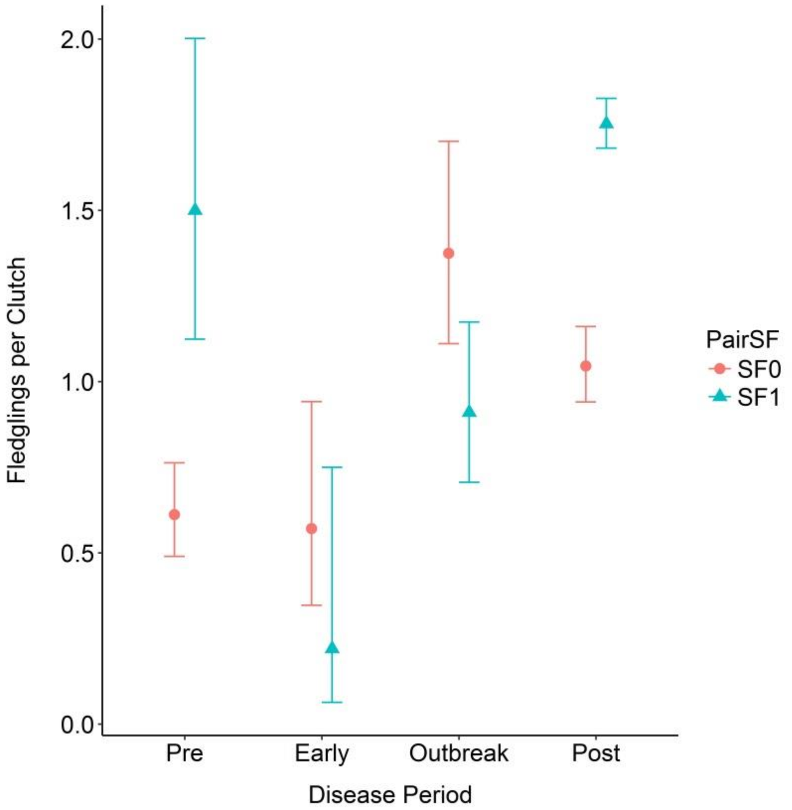


Figure 5.5 Number of fledglings per clutch for SF0 and SF1 nests over four disease periods. *Pre:* 1993/94 - 2003/04. *Early*: 2004/05. *During*: 2005/06. *Post*: 2006/07 - 2013/14. Estimates derived from Model 12, Table 5.4. Vertical bars represent standard errors.

In exploring the probability of an egg surviving through to fledging, compelling evidence was revealed that the disease impact extended beyond 2005 only, with Models 12, 14 and 6 all scoring within 2 AIC_c of one another (Table 5.5). The negative impacts of the disease during its emergence began to affect the population prior to 2005, potentially as early as 2003/04 (Model 14), but as Figure 5.6 illustrates, this was impact was see only in SF1 nests.

In exploring the most suitable time period over which to describe changes in hatching success in association with PBFD, there was compelling evidence that the disease impact was greatest on this breeding parameter. Model comparisons provided compelling evidence that hatchability was reduced from as early as the 2002/03 breeding season, and the extent of its impact was ubiquitous across the population, with both SF0 and SF1 negatively affected. Despite reduced hatching success from 2002 up to and including 2005, the reduction was short-lived and during the post-outbreak period, hatching success improved, though not quite to same level as seen prior to outbreak (Figure 5.7). This model recognised three different periods, (pre, outbreak, post-outbreak), unlike the models identified in other analyses, which best described the number of fledglings and egg to fledge survival probability using Disease Period Definitions 5. Model 12 of Table 5.6 was therefore plotted (Figure 5.8) for illustrative purposes, as it recognised the same four disease periods as those in Figure 5.4 and 5.5 (pre, early, outbreak and post-outbreak).

Table 5. 5 Generalised linear mixed models examining the suitability of different Disease Periods (D1-6) to describe the extent of PBFD's impact on the probability of an egg surviving through to fledge and the potential interaction effect of SF. Descriptions of D are described in Table 5.1. df.resid = residual degrees of freedom.

Egg to fledge survival probability					
Model No.	**Model Description**	**AIC**	**Log Lik**	**Deviance**	**df. resid**
12	D 5 * SF	1758	-870	1740	683
14	D 6 * SF	1758.5	-870.3	1740.5	683
6	D 2 * SF	1759.2	-872.6	1745.2	685
8	D 3 * SF	1760	-873	1746	685
4	D 1 * SF	1760.8	-873.4	1746.8	685
10	D 4 * SF	1764.1	-875	1750.1	685
2	SF	1775.9	-884.9	1769.9	689
3	D 1	1787.7	-889.9	1779.7	688
11	D 5	1788.8	-889.4	1778.8	687
13	D 6	1789.6	-889.8	1779.6	687
7	D 3	1789.8	-890.9	1781.8	688
5	D 2	1790	-891	1782	688
9	D 4	1790.4	-891.2	1782.4	688
1	Null	1801.9	-898.9	1797.9	690

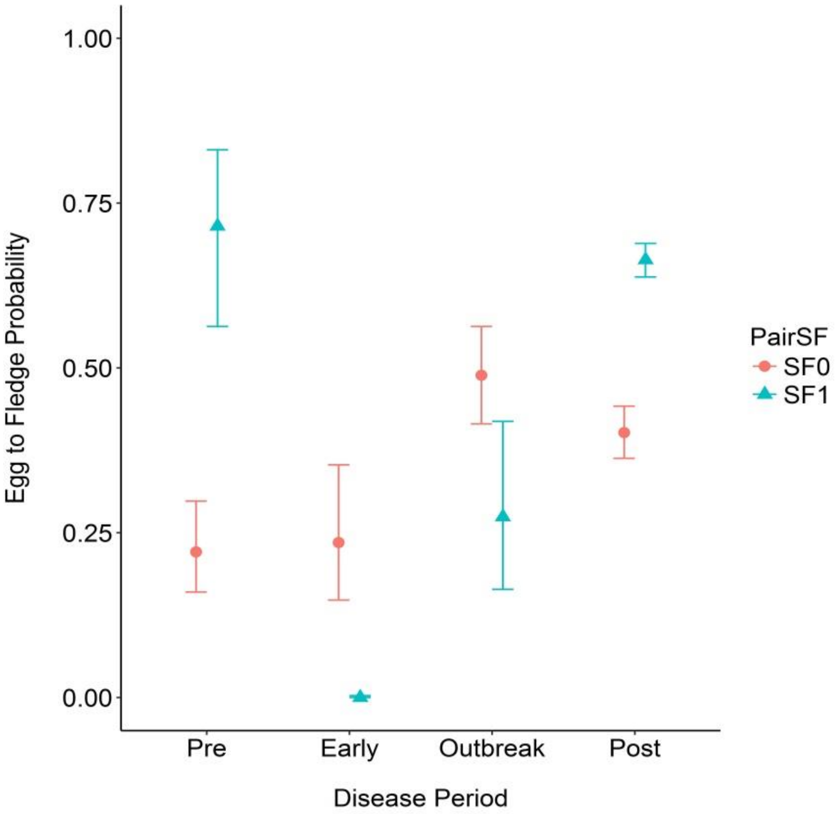


Figure 5.6 Egg to fledge survival probability for SF0 and SF1 nests over four disease periods. *Pre:* 1993/94 - 2003/04. *Early*: 2004/05. *During*: 2005/06. *Post*: 2006/07 onwards. Estimates derived from Model 12, Table 5.4. Vertical bars represent standard errors.

Table 5. 6 Generalised linear mixed models examining the suitability of different Disease Periods (D1-6) to describe the extent of PBFD's impact on egg hatching probability and the potential interaction effect of SF. Descriptions of D are described in Table 5.1. df.resid = residual degrees of freedom.

Hatching probability					
Model No.	**Model Description**	**AIC**	**Log Lik**	**Deviance**	**df. resid**
10	D 4 * SF	1749.8	-867.9	1735.8	759
14	D 6 * SF	1755.4	-868.7	1737.4	757
12	D 5 * SF	1756.2	-869.1	1738.2	757
9	D 4	1757	-874.5	1749	762
6	D 2 * SF	1759.8	-872.9	1745.8	759
8	D 3 * SF	1765	-875.5	1751	759
4	D 1 * SF	1766.7	-876.4	1752.7	759
5	D 2	1772.3	-882.2	1764.3	762
7	D 3	1773.8	-882.9	1765.8	762
11	D 5	1774.3	-882.2	1764.3	761
13	D 6	1775.2	-882.6	1765.2	761
3	D 1	1784.2	-888.1	1776.2	762
2	SF	1790.9	-892.5	1784.9	763
1	Null	1791.4	-893.7	1787.4	764

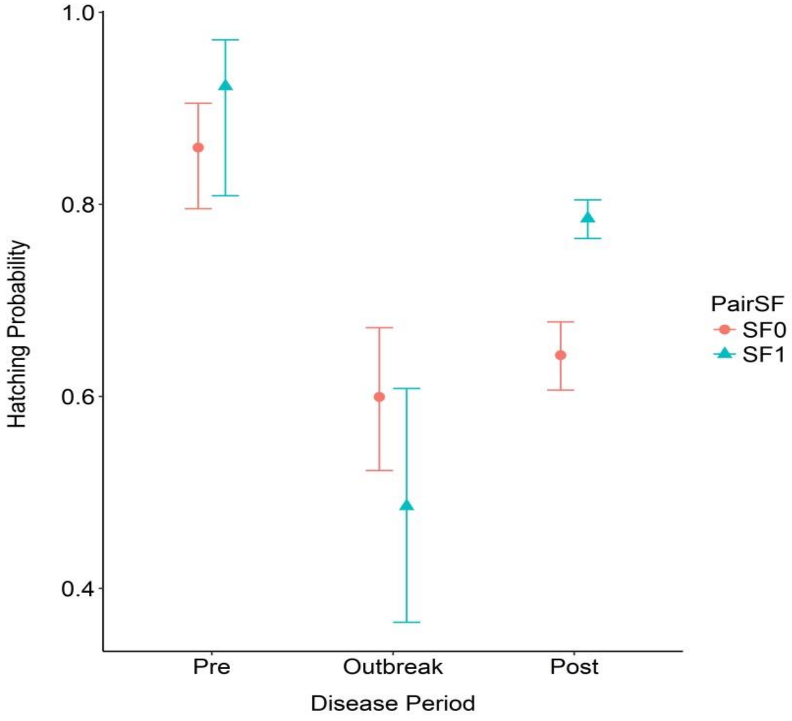


Figure 5.7 Hatching probability of eggs from SF0 and SF1 nests over three disease periods. *Pre:* 1993/94-2003/04. *During*: 2002/03 -2005/06. *Post*: 2006/07 onwards. Estimates derived from Model 10, Table 5.4. Vertical bars = standard errors. Note that the y-axis does not begin at zero.

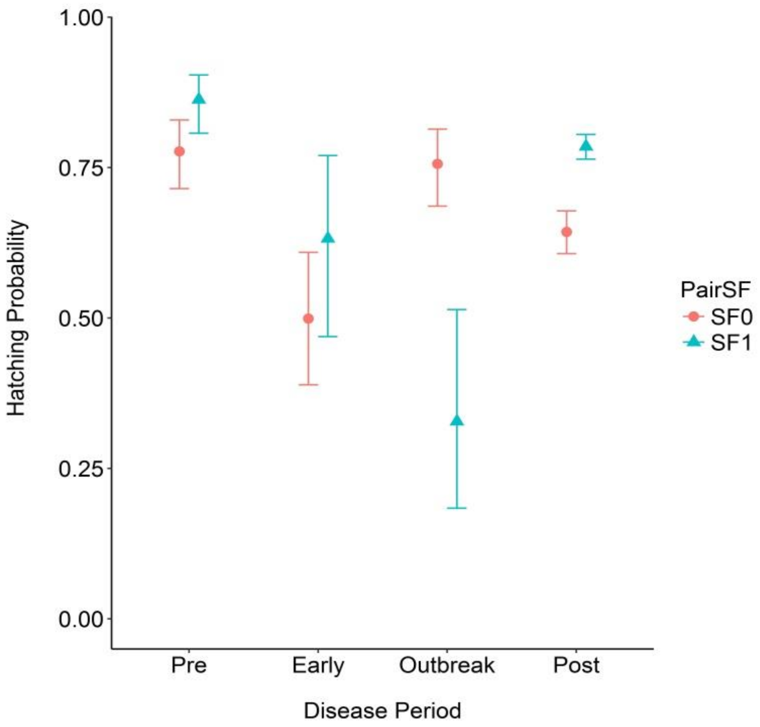


Figure 5. 8 Hatching probability of eggs from SF0 and SF1 nests over four disease periods. *Pre:* 1993/94-2003/04. *Early*: 2004/05. *During*: 2005/06. *Post*: 2006/07 onwards. Estimates derived from Model12, Table 5.4. Vertical bars = standard errors.

5.4.2 Disease and survival

Comparison of the model set in Step 1 (Table 5.7) reported that models built with D2, D3 and D4 in survival and transition were a better fit to the data than the best SF model (Model 2) which included full time dependence in pre-breeder survival, ages 1, 2 and 4+. No single parsimonious model was evident, and the top three models which were tied (Models 8, 14 and 11) were brought forward into Step 2 of the analysis.

Introducing SF (‘g’) in Step 2 indicated a strong influence on transition but this was not associated with disease periods, as models including an interaction effect between D and SF scored poorly relative to those with g in transition only (Table 5.8). Assessing the final $QAIC_c$ scores in this final model set, there was indication that pre-breeder survival varied between the different disease periods, with the most parsimonious model (Model 23, Table 5.8) including D4 in pre-breeder survival only. However, examining parameter estimates from the most parsimonious model (Model 23, Table

5.8) revealed no apparent change in pre-breeder survival between the Pre-outbreak and Outbreak periods in any age class (Figure 5.8). Whilst first year pre-breeders indicated a slight increase in survival from pre-outbreak to outbreak, this is likely to be attributed to the increasing number of fledglings as the population grew. However, there was compelling evidence that post-outbreak, survival in all age classes of pre-breeder were typically lower than those estimated by the model prior to 2005 (Figure 5.8).

Table 5. 7 The use of age-structured multi-state models to examine the different Disease Periods (1-6) and their suitability for explaining variation in φ and recruitment of echo parakeets, and thus the extent of PBFD impact. Models are ordered by QAIC$_c$ values. Model nomenclature is as follows: D = Disease Period e.g. D4; N = pre-breeders; N-B = transition of pre-breeder to breeder; B-PO = denotes transition of breeder to post-breeder. Each states recognised 4 age classes (1:4+) with implausible classes per state fixed accordingly. Models highlighted in bold indicate the best model describing survival in the population (Model 1) and best supplemental feed and time dependent model (Model 2). Only manipulated parameters are reported, with the following structure otherwise retained: φ ((N| 1:4+.)(B| 2:4+.)(PO| 3:4+.)) .P ((N| 1:4+.)(B| 2:4+=1) (PO| 3:4+.)) .ψ ((N-B| 2:4+.)(B-PO| 3:4+.)(PO-B| 4+.)). Model No.= model number; ML = maximum likelihood; No. P = number of parameters.

		Survival (φ)	**Transition (ψ)**							
Model No.	**Disease Definition**	**N**	**N-B**	**B-PO**	**QAIC$_c$**	**Delta QAIC$_c$**	**AIC$_c$ Weights**	**ML**	**No. P**	**Q Deviance**
8	D2	1:4+ D2	2:4+ D2	3:4+ D2	4248.75	0.00	0.36	1.00	39.00	1652.01
14	D4	1:4+ D4	2:4+ D4	3:4+ D4	4249.14	0.39	0.30	0.82	39.00	1652.40
11	D3	1:4+ D3	2:4+ D3	3:4+ D3	4249.74	1.00	0.22	0.61	39.00	1653.01
12	D4	1:4+ D4	~	~	4252.38	3.64	0.06	0.16	29.00	1676.21
2	**Best SF**	**1:2t, 3., 4+t**	**2.g, 3., 4+.g**	**3., 4+.g**	4253.19	4.45	0.04	0.11	74.00	1583.16
9	D3	1:4+ D3	~	~	4255.64	6.90	0.01	0.03	29.00	1679.47
5	D1	1:4+ D1	2:4+ D1	3:4+ D1	4255.78	7.03	0.01	0.03	39.00	1659.04
6	D2	1:4+ D2	~	~	4257.47	8.73	0.00	0.01	29.00	1681.30
3	D1	1:4+ D1	~	~	4258.72	9.97	0.00	0.01	29.00	1682.55
20	D6	1:4+ D6	2:4+ D6	3:4+ D6	4262.13	13.39	0.00	0.00	48.00	1646.75
18	D6	1:4+ D6	~	~	4263.04	14.29	0.00	0.00	33.00	1678.66
17	D5	1:4+ D5	2:4+ D5	3:4+ D5	4264.05	15.31	0.00	0.00	48.00	1648.67
15	D5	1:4+ D5	~	~	4266.62	17.88	0.00	0.00	33.00	1682.24
1	**Best φ**	**1:2t, 3., 4+t**	**2:4+.**	**3:4+.**	4273.78	25.03	0.00	0.00	71.00	1610.11
7	D2	~	2:4+ D2	3:4+ D2	4383.60	134.85	0.00	0.00	31.00	1803.32
10	D3	~	2:4+ D3	3:4+ D3	4386.46	137.72	0.00	0.00	31.00	1806.19
13	D4	~	2:4+ D4	3:4+ D4	4389.58	140.84	0.00	0.00	31.00	1809.31
4	D1	~	2:4+ D1	3:4+ D1	4389.79	141.04	0.00	0.00	31.00	1809.51
19	D6	~	2:4+ D6	3:4+ D6	4391.28	142.53	0.00	0.00	36.00	1800.72
16	D5	~	2:4+ D5	3:4+ D5	4391.42	142.68	0.00	0.00	36.00	1800.87

Table 5. 8 Examination of the influence of disease period and supplemental feed on the φ and ψ recruitment of echo parakeets using age-structured multi-state models. Models are ordered by QAIC$_c$ values and for brevity, only models scoring higher than Model 2 are reported. Model nomenclature is as follows: D indicates Disease Period e.g. D4; g indicates a supplemental feed effect; N denotes pre-breeder; N-B denotes transition from pre-breeder to breeder; B-PO denotes transition from breeder to post-breeder. Each states recognised four age classes (1:4+) with implausible classes per state fixed accordingly. Models highlighted in bold indicate the best model describing survival in the population (Model 1) and best supplemental and time dependent model (Model 2). These provided a basis for initial model comparison. Only manipulated parameters are reported, with the following structure otherwise retained: φ ((N| 1:4+.)(B| 2:4+.)(PO| 3:4+.)) .P ((N| 1:4+.)(B| 2:4+=1) (PO| 3:4+.)) .ψ ((N-B| 2:4+.)(B-PO| 3:4+.)(PO-B| 4+.)). Model No.= model number; ML = maximum likelihood; No. P = number of parameters.

Model Structure				**Survival (φ)**	**Transition (ψ)**							
φ	**ψ**	**Model No.**	**Disease Definition**	**N**	**N-B**	**B-PO**	**QAIC$_c$**	**Delta QAIC$_c$**	**AIC$_c$ Weights**	**ML**	**No. P**	**Q Deviance**
D	g	23	D4	1:4+ D4	2:4+. g	3:4+. g	4230.75	0.00	0.79	1.00	34.00	1644.32
D	g	22	D3	1:4+ D3	2:4+. g	3:4+. g	4234.10	3.35	0.15	0.19	34.00	1647.66
D	g	21	D2	1:4+ D2	2:4+. g	3:4+. g	4235.85	5.10	0.06	0.08	34.00	1649.41
gD	g	30	D2	1:4+ D2 g	2:4+. g	3:4+. g	4247.98	17.23	0.00	0.00	46.00	1636.75
gD	g	32	D4	1:4+ D4 g	2:4+. g	3:4+. g	4248.01	17.25	0.00	0.00	46.00	1636.78
gD	g	31	D3	1:4+ D3 g	2:4+. g	3:4+. g	4248.13	17.37	0.00	0.00	46.00	1636.90
D	D	8	D2	1:4+ D2	2:4+ D2	3:4+ D2	4248.75	18.00	0.00	0.00	39.00	1652.01
D	D	14	D4	1:4+ D4	2:4+ D4	3:4+ D4	4249.14	18.39	0.00	0.00	39.00	1652.40
gD	gD	27	D2	1:4+ D2 g	2:4+ D2 g	3:4+ D2 g	4249.73	18.98	0.00	0.00	66.00	1596.64
D	D	11	D3	1:4+ D3	2:4+ D3	3:4+ D3	4249.74	18.99	0.00	0.00	39.00	1653.01
gD	gD	29	D4	1:4+ D4 g	2:4+ D4 g	3:4+ D4 g	4252.19	21.44	0.00	0.00	66.00	1599.10
t	g	**2**	**Best SF**	**1:2t, 3., 4+t**	**2.g, 3., 4+.g**	**3., 4+.g**	4253.19	22.44	0.00	0.00	74.00	1583.16

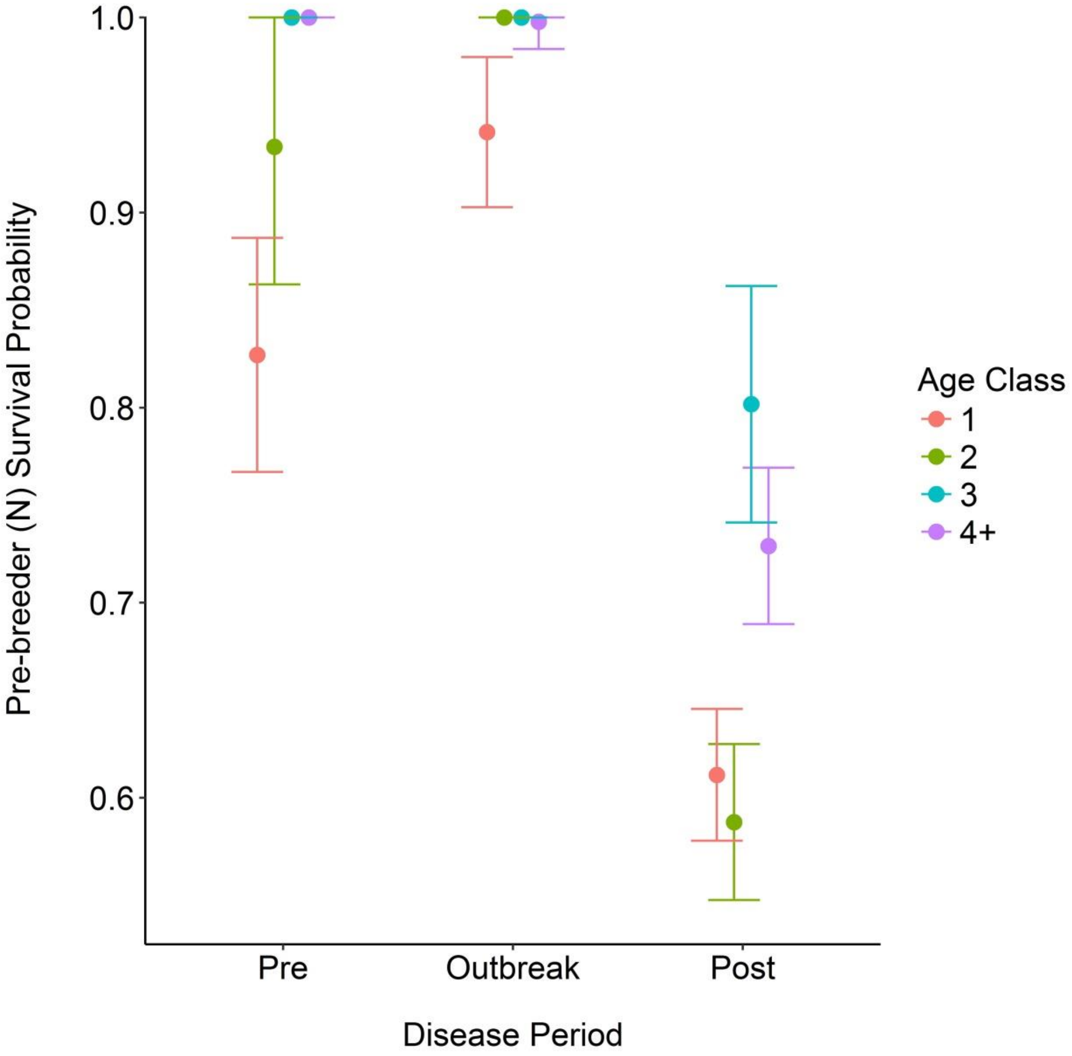


Figure 5.9 Age specific N φ according to periods associated with the outbreak of PBFD in 2005. Estimates were generated from Model 23, which defined periods as follows: *Pre* = 1993/94 - 2001/02; *Outbreak* = 2002/03 - 2005/06; *Post = 2006/07 - 2013/14.* Vertical bars represent 95% confidence intervals.

5.5 Discussion

5.5.1 Key findings

This study provided a unique opportunity to explore (i) the impact of an EID on breeding success, survival and recruitment, prior to, during and after an outbreak of PBFD (ii) the use of supplemental feeding in this process. Findings indicated that breeding success was negatively impacted prior to the documented outbreak in 2005 and that impacts were more pronounced in nest attempts associated with the use of supplementary food. However, post-outbreak breeding success quickly returned to levels equal to those estimated prior to the when disease was evident in the population (i.e. before 2002). There was no compelling evidence that survival rates significantly changed as the disease emerged in the population, even during the reported outbreak of 2005. However, from 2006 onwards, survival rates for all age classes of pre-breeders were typically lower than those reported prior to 2005. Recruitment rates appeared not to vary across the different disease periods.

5.5.2 The impact of disease on breeding success

Findings from this study compliment previous work by Tollington *et al.* (2015) which found hatching success to be significantly reduced in the Pre-defined outbreak period of 2005 and exacerbated by the use of supplementary food. In this chapter, it was possible to extend previous research and explore whether PBFD was beginning to impact breeding success at the population level when the first incidences of PBFD were documented in 2002/03. Findings here confirm that when describing the disease period and its associated impact, it is more appropriate to consider a period of 2002/03 to 2005/06. Therefore, even during the emergence of PBFD in the population, the disease was having a negative impact at the population level. Such a result is crucial for understanding when and to what extent PBFD threatens population persistence even when present at a seemingly low level.

The process of the disease emergence may have been accelerated by several factors, including the rapid growth in the population in the early 2000s, direct management intervention methods at nests sites and a high environmental resilience of the virus (Varsani *et al.* 2010), all of which could provide opportunities for viral transmission (Woods *et al.* 1993; Todd 2004). It would be expected that any initial impact of the disease would have forced birds make a decision regarding life-history investments and their infection status (Norris and Evans 2000); breeding events already incur energetic and reproductive costs, both in the short and long-term (Beauplet *et al.* 2006), and so birds would typically choose not to breed during the disease period, an unfavourable environment. This would suggest fewer birds would have chosen to breed either during the disease period, yet the number of birds breeding during this period was uncompromised (Figure 5.1). Previous work in this thesis has also given little suggestion of a change in breeder survival. This suggests that either, the breeding performance of a pair was compromised by infection, not breeder survival specifically, (Greenwood 1996; Lachish *et al.* 2011; Hõrak and Männiste 2016), or a more sub-lethal effect was directly affecting eggs and chicks. The first explanation is difficult to confirm because individuals can often be *infected* but not *affected* (Lyles and Dobson 1993), and there is growing evidence that the level of viral load is a key determinant of infection status (Regnard *et al.* 2015). The second explanation is more plausible, the capacity for horizontal and vertical virus transmission (Rahaus *et al.* 2008) would allow the virus to quickly reach a substantial number of nests throughout the population.

Transmission pathways were clearly pivotal in the expansion of PBFD in echo parakeets, as a second crucial finding from this study was the underlying negative effect of supplementary food. Negative associations between disease and supplementary food have been previously reported not just in echo parakeets (Tollington *et al*. 2015), but in many conservation and recreational feeding programmes (Robb *et al.* 2008; Robinson *et al.* 2010; Blanco *et al.* 2011; Lawson et al. 2012; Sorensen et al*.* 2014; Adelman *et al.* 2015). High densities of birds at feeding stations can increase contact rates and disease transmission (Donnelly *et al.* 2013), whilst the environmental resilience of the BFDV virus facilitates indirect transmission via feeding stations and surrounding areas (Page 2013; Murray *et al.* 2016) as seen with indirect transmission of avian influenza viruses (Rohani *et al.* 2009). This presents a serious risk to small, threatened populations, as disease transmission is not necessarily density-dependent (Smith *et al.* 2009; McDonald *et al.* 2017) but may be frequency-dependent. Subsequently the pathogen is not subject to population density thresholds and disease prevalence may increase even if population densities are low (Smith *et al.* 2009). Small or fragmented populations are therefore particularly vulnerable.

Chapter 4 of this thesis provided clear evidence that supplementary food significantly improved breeding success, which in the long term will be positive for population growth. However, findings here demonstrate supplementary feeding as a key mechanism encouraging the spread of disease. In the case of the echo parakeet, the continued population growth and recovery of breeding success suggests that the threat level may not be as high as expected, and perhaps a certain level of tolerance is being established. For any management programme wishing to track the emergence of a similar EID, this study illustrates the importance of monitoring the many levels of disease processes including the ecology of the host and its resistance across life history stages, the pathology of the disease and how it may infect and affect its host, and the surrounding abiotic and biotic environment which determines environmental resilience and modes of transmission (Scholthof 2007).

5.5.3 The impact of disease on survival

Throughout the emergence of PBFD in the population, survival rates were consistently high across all age classes of pre-breeders, and little evidence was found of an interactive effect between supplementary food and transition rates in relation to the disease. It should be noted that survival in breeding birds was also stable, as confirmed in previous analysis, but consequently not examined in this study. After the outbreak however, survival in all age classes of pre-breeder was typically lower than that reported prior to and during the outbreak (Figure 5.10).

It is strange that compared to breeding success, survival of wild echo parakeets was unaffected during the emergence of the disease and outbreak. There are two possible explanations for this lack of effect during the disease periods. The first is that the trend could be indicative of density dependent processes driving population changes (Newton 1998). However, the decline is sharply correlated with the 2005/06 PBFD outbreak.

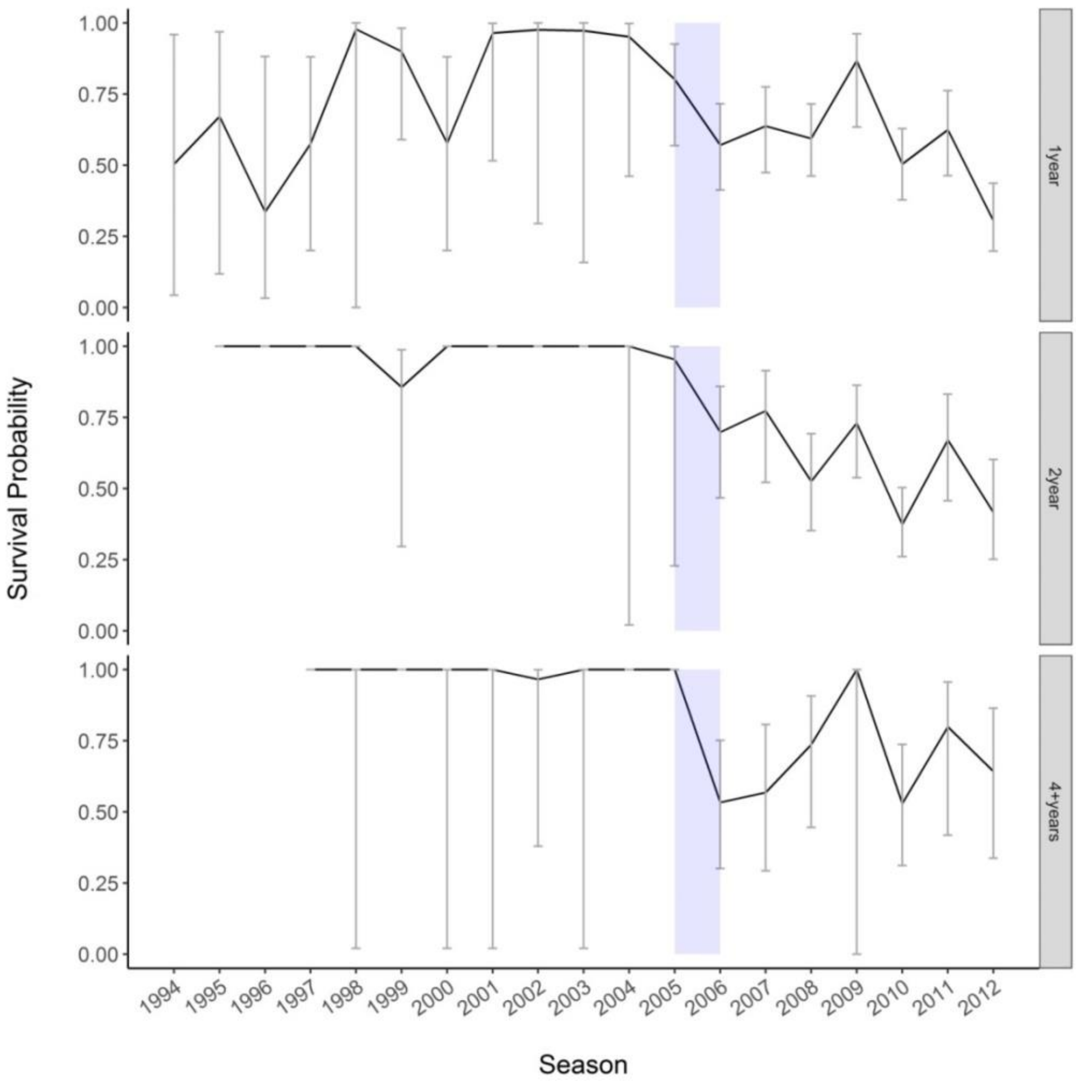


Figure 5.10 Panel plot of the annual N φ for ages 1, 2 and 4+ echo parakeets. Season labels refer to years in which the breeding season began, for example, 1994 refers to the 1994-1995 austral breeding season. Re-sightings of three year old pre-breeders were too sparse to generate meaningful estimates over time, but a constant survival of 0.94 (95% CI = 0.66 / 0.99) was predicted. Parameter estimates were generated from Model 3 (Table 1, Best SF model). Vertical lines represent 95% confidence intervals.

Currently there are no obvious limiting factors that would cause such an effect, as management ensures that food and nest sites are never limited. It is possible that due to the central and unchanging location of supplementary feeding sites, it is in fact dispersal which is being compromised and leading to what appears to be density dependence, but may actually be density dependence and the birds are not limited in any real way by other factors. To account for this effect requires further life-history data, in particular that of individual viral load and its influence on disease susceptibility, information which is currently not available. The second explanation for the apparent change in survival may be due to sub-lethal effects of the virus prior to 2005. The viral strain then changed to a highly virulent strain, with a more lethal impact post 2005.

This theory is supported by evidence that in 2005, the BFDV virus within the wild echo parakeet population underwent a complete selective sweep: prior to 2005, one type of BFDV isolate was present in the majority of echo parakeets, but by early 2005, new isolates began to appear. By February 2006, an entirely different isolate dominated the population (Kundu *et al*. 2012). Host species continually evolve their defence against infection (Van Valen 1973; Medzhitov *et al.* 2012), but short strand viruses like BFDV have high evolutionary rates (Kundu *et al.* 2012), and given sufficient transmission opportunities (e.g. supplementary food) or biotic and abiotic reservoirs, these rates can exceed the adaptive abilities of the host.

5.5.4 Advancements in understanding the threat of EIDs

This study has helped to elucidate timescales of disease emergence, identify the demographic parameters most affected by the virus and the time period over which the demographic effects of the disease extended. In doing so it was possible to recognise that the impact of a disease may not always be ubiquitous across the population, and that vital rates may be substantially affected even during the emergence of the disease and when clinical signs are minimal. For the echo parakeets, describing the demographic consequences of the PBFD outbreak is only the start of understanding if, and how, to manage the disease in the long term. The role of the disease in shaping population dynamics is clearly quite complex, further information is required to understand the underlying mechanisms driving the host-pathogen dynamics, and how individual variation in a host may affect its relationship with the disease and to what extent these create an impact at the population level. This will require further epidemiological studies of the virus itself, correlating viral load with susceptibility (Regnard *et al.* 2015), exploring genetic susceptibility to the virus and identifying other individual traits of echo parakeets that may help to explain disease transmission and risk. For example, identifying virus ‘super-spreaders’ within the population (McDonald *et al.* 2017), which could subsequently assist in targeting efforts to control PBFD. Alongside this detailed research, an adaptive style of management (Armstrong *et al.* 2007) could help test the effectiveness of disease control strategies. This could identify conditions that increase disease risk, whether management mediated or natural in the environment, and even illuminate key pathways of the disease expansion (Hyatt *et al.* 2015; Langwig *et al.* 2015). Efforts to do so have already begun for the echo parakeet, systematically testing the effectiveness of chemical suits in limiting management-mediated disease transmission (Smith *et al.* 2012; Henshaw *et al.* 2014). Of course, the most important outcome of these strategies will be whether the effect is sufficient to create change at a population level, which will only be confirmed through on-going monitoring of the population.

On a wider scale, EIDs are undeniably a major concern to conservation practitioners across the world (McCallum and Dobson 1995; Fisher *et al.* 2012; Hyatt *et al.* 2015; Tompkins *et al.* 2015). There is now a growing body of literature available to help wildlife practitioners understand ecology of the disease in wild Psittacines due to increasing reports of its novel emergence of PBFD, even in non-psittacine species. To the best of my knowledge, however, very few have been able to accurately describe the demographic impact of the disease, or document the multiple stages of disease emergence. As this study shows, detailed, documented monitoring of a host population in parallel with a pathogen or disease outbreak provides fundamental information on host-pathogen relationships and how they vary across many complex levels. Monitoring small populations, ideally in the absence of the disease, should be established to ensure the long term persistence of a population and to monitor any changes. This would allow the disease to be detected as early as possible in its phase of arrival (Langwig *et al.* 2015) and implement control measures appropriately. Small populations are typically under intense management, which is aimed at benefiting the target population. However, there are many cases of management actions leading to unintended negative outcome, such as the increase in disease risk (Woodroffe 1999; Grenfell *et al.* 2002; Chauvenet *et al.* 2011; Tollington *et al.* 2013; Sorensen *et al.* 2014; Rushton *et al.* 2006; Page 2013; Cassirer *et al.*

2017). For conservation practitioners across the world, evaluating the potential risks of management interventions should be incorporated into practice and regularly reviewed.

5.6 Conclusions

EIDS are increasingly recognised as a global threat to many wild populations and yet very little is understood of how they impact the demographics of the host population. This is particularly challenging to decipher, given that the response in a population is subject to a range of factors and complex mechanisms that can change over space and time. PBFD has recently become a severe threat to Psittacines, a family of birds already experiencing widespread and rapid population declines. Very little is known about the potential demographic impact of the disease as previous research has predominantly focused on the ecology of the BFDV virus. The echo parakeet population provided an excellent opportunity to explore changes in vital rates from a time when PBFD was absent in a population through a major outbreak and afterwards. The disease was found to have negatively impacted breeding success for a time period greater than the documented outbreak of 2005. A short-lived impact, breeding success quickly returned to levels seen when PBFD had not been documented in the population, suggesting that a tolerance to the virus was quickly established. However, the impact of the disease on survival rates was less clear. Little difference was noted in survival rates between pre-outbreak and the outbreak periods, but following a complete selective sweep of the BFDV virus in 2005, survival rates of pre-breeders were generally much lower. This demographic change coincides with the genetic change in the virus, but the virus cannot be definitively reported as the main cause of reduced pre-breeder survival; their survival may be confounded by other factors such as density dependence, which were not explored in this chapter. Considering the increase in population trajectory and the short-lived reduction in breeding success, there appears to have been no short term impact on population demographics. This is not to say, however, that the future may not see delayed impacts of the disease. In particular, the consequences of reduced pre-breeder survival may lead to a reduction in the non-breeder pool and it is uncertain what effect this will have on the long-term trajectory of the population.

Chapter 6

General Discussion

6.1 Overview

Intensive management of wild populations is increasingly necessary in order to reduce the continued loss of biodiversity and ameliorate the threats associated with human-altered environments. Reports of conservation successes remain rare in comparison to growing reports of declining populations, and reversing this trend will require understanding what aspects of management promote success, and what can hinder it. If the underlying principles of conservation successes can be identified, they may be applied elsewhere to assist other conservation programmes. Using long-term individual-based data, this thesis has explored the underlying demography of the echo parakeet population, allowing an accurate assessment of the impact made by management actions aimed to encourage population recovery. The emergence and outbreak of an infectious disease (PBFD) during the population’s recovery provided a unique opportunity to explore the extent of the outbreak’s impact, and its effect on key demographics over time. Overall, findings from the thesis show that intense, restorative efforts can significantly improve key demographic parameters promoting population growth. Such actions should be coupled with detailed, consistent monitoring that considers individuals from multiple life-history states and ages. However, the implications of management actions in the short and medium term can be both positive and negative, as was exemplified in this study. In order to minimise risks and promote successes, scientific research should be embedded within the management actions, which themselves should be guided by clear objectives. A willingness of managers to become proactive in their approach toward species management, combined with accurate and on-going evaluations of management strategies, can act as a powerful springboard for improving conservation.

The echo parakeet presents a remarkable story of conservation success, offering both hope and constructive guidance for wildlife practitioners facing similar challenges. In 1992, less than 20 echo parakeets remained in the wild and extinction seemed inescapable (Jones and Duffy 1993). Through intensive management the population has been restored to >600 birds (Henshaw *et al.* 2014), but details have remained unclear regarding how management affected the key population demographics of the population to encourage this growth. Whilst this has been anecdotally reviewed and basic demographic estimates provided in annual reports to the Mauritian Wildlife Foundation (e.g. Smith *et al.* 2012), a comprehensive demographic study that considers the role of management has not been fully addressed. Current practices need refining but this cannot be reliably achieved without evaluating the processes which have led to this point. This limited understanding currently hinders any effective management developments.

Research conducted in Chapter 3 provided an opportunity to test the underlying assumptions of multistate models that include an unobservable state ('UMS' models). Population models such as this are widely employed to guide decisions in wildlife management, but inaccuracies in the models may incorrectly portray population demography and misinform management. Beyond empirical theory, quantifying their bias has remained impossible but observations of echo parakeets in unobservable (non-breeder states) confirmed that for this study system at least, these underlying model assumptions are flawed. This led to biased survival estimates of individuals in unobservable states and even biased the survival estimates for birds in observable states. Accounting for unobservable states without explicit re-sighting data also affected transition rates. This obscured an important finding that echo parakeets may skip breeding seasons and as revealed through further work in Chapter 4, this behaviour that was reduced if birds used supplementary food (SF).

In the case of the echo parakeet, inaccurate population models could have led to an inaccurate interpretation of how management has impacted their key demographics. Employing the reliable population models built in Chapter 3, Chapter 4 examined the demographic impact of a widely used conservation tool, supplementary feeding (SF). Responses to SF are reportedly mixed across many species and populations, but for the echo parakeet, the use of SF has had a positive impact on their breeding success, recruitment rates and breeding propensity. This suggests that whilst the local habitat may provide essential food resources, either its quality or quantity may be insufficient to develop an optimal fitness for breeding, which further compromises breeding propensity. SF may buffer any negative environmental impacts of food supply, but this could not be confirmed in this thesis.

Chapter 5 revealed that despite SF's positive influence on fecundity, it was associated with an underlying negative effect of disease as the demographic impact of PBFD's expansion throughout the population was predominantly worse in breeding pairs associated with the use of SF. Findings compliment previous research by Tollington *et al*. (2015) but through this study, I have increased our understanding of the temporal impact of the disease, which had previously been considered to be restricted to 2005; here I revealed a significant reduction in breeding success as early as 2002, despite minimal clinical signs in the population at this time. Regardless of the fatal nature of the disease, the impact of the outbreak was short-lived, suggesting that PBFD may not present such a threat to the population as a tolerance to the virus can be established. Such findings are of wider relevance to Psittacine populations across the world, where the BFDV virus is being increasingly reported. Unfortunately, there is limited knowledge on how it can impact population demographics and what approaches to its management have been successful. However, there is much more yet to be understood about the long-term implications of the disease, particularly as pre-breeder survival in the echo population has typically declined on an annual basis since 2006

6.2 The importance of quantity and quality in population monitoring

6.2.1 Utilising long-term data sets

What can we learn from our successes and failures, and how can it be applied to future conservation efforts? From what we have learnt, what opportunities have opened up, and what new challenges do they bring? Asking such questions is an important aspect of driving conservation programmes forward, but they are reliant on the establishment of an appropriate monitoring system that collects suitable, relevant data alongside management actions, as seen with the intensive management of the critically endangered takahe (*Porphyrio hochstetteri*; Hegg *et al.* 2012). Longitudinal data sets which encompass several phases of a species' restoration can improve our ability to answer such questions as they provide an opportunity to understand ecological change and evaluate the effectiveness of management actions (Rohani and King 2010; Sutter *et al.* 2015). This can directly benefit ongoing management of the focal species whilst assisting evidence-based management decisions for other conservation programmes (Cook *et al.* 2013; Pullin *et al.* 2004; Sutherland *et al.* 2004). When implementing a recovery programme there is rarely the luxury of time to consider the range of practical options, balanced with financial and logistical limitations. The process can then become further strained by the risks and fears of choosing the 'wrong' approach, delaying the process further (Meek *et al.* 2015). Waiting too long then risks the species' recovery entirely (Snyder and Snyder 2000; Turvey 2010). However, the fear of taking action is increasingly unnecessary given the growing number of tools available to guide conservation practitioners. Structured decision making frameworks have been proposed to offer guidelines for species management and are increasing applied with great success (Jachowski *et al.* 2015; Canessa *et al.* 2016; Robinson *et al.* 2017). This process may help to address broad challenges for species restorations, or for facing problems as specific as disease (Russell *et al.* 2017) or considering employing strategies such as supplementary feeding (Ewen *et al.* 2015).

Decision making frameworks may help in the process of planning management, but advice regarding specific details may require seeking guidance from a similar project with common challenges, one that reflects similar needs on a similar scale (Sutter *et al.* 2015). Findings from this thesis are of great value not only to managing threatened species, but may be of particular importance to the global conservation of Psittacines. Despite being classed as the most endangered family of birds (Ortiz-Catedral *et al.* 2013; Marsden and Royle 2015), their conservation is limited by a lack of basic demographic and biological data. Restorative actions have included trials with nest boxes (Downs 2005) and supplementary feeding (Brightsmith *et al.* 2005) but these practices have been met with mixed success, as has the use of captive-rearing for wild population supplementation (White *et al*. 2012). The availability of literature on the status and ecology of Psittacines is growing (Martin *et al.* 2014; Marsden and Royle 2015), but as with most conservation programmes, the time and skills necessary to publish findings - be they successes or failures - hinders communication of relevant information between conservation programmes (Sutherland *et al.* 2004). This thesis has directly addressed two key threats shared globally by parrots across the world - loss of food resources and PBFD - and examined the effectiveness of practical steps taken to ameliorate these threats. Whilst a clear solution to disease control may not be achievable, it has been possible to improve current understanding of the complex host-pathogen relationship, information that will contribute to the wider discipline of disease research.

6.2.2 Whole population monitoring for quality data sets

Whilst there are clearly gains to be made from ensuring longitudinal data collection (Rohani and King 2010), the quality and breadth of data available for analysis may be equally important as findings from Chapter 3 illustrate. As discussed in this chapter, a long term data set may be of little use if it only considers one segment of the population. Unfortunately this is true of many studies, where emphasis is placed on monitoring individuals in a breeding state. Statistical models may then try to account for the unobserved states, but as proven in Chapter 3, this leads to biased estimates of demographic parameters for all states, observed or not. Biased estimates could incorrectly portray key demographics such as survival and measures of reproductive costs (Kendall *et al.* 1997; Fujiwara and Caswell 2002; Spendelow *et al.* 2002; M Schaub *et al.* 2004). If these fundamental parameters are incorrect, exploring them as part of an evaluation of management could lead to the misinterpretation of management strategies, compromise the accuracy of population projections (Nicoll *et al.* 2003; Norris and Mcculloch 2003). In this study the ability to include re-sighting data from typically unobservable states revealed important trends about supplementary feeding effects (Chapter 4), patterns in annual survival (Chapter 5) and an important movement between breeder and post-breeder states in relation to supplementary food (Chapter 4).

Through chapters 3, 4 and 5, I provide compelling evidence to suggest that exclusive monitoring of the breeding segment limits our understanding of population regulation. My research has focused predominantly on the demographic patterns in pre-breeders, but the process of senescence may also represent an important contribution to population dynamics (Beauplet *et al.* 2006), as reported in the pink pigeon (Concannon 2014). Where possible, other study systems should be encouraged to develop monitoring protocols that encompass these unobservable phases. Even if the focus of a management action is to effect change in the breeding segment, the output from such a study could be biased without monitoring the non-breeders segments. Recognising the value of non-breeders does not, however, resolve the challenge of observing them. As discussed in Chapter 3, there are an increasing number of statistical approaches towards modelling non-breeders, but how valuable are they given the inaccuracies proven here? Developing field monitoring skills or tools in order to acquire observations from unobservable states may prove advantageous over relying on model structures. Given current advances in technology, this is increasingly feasible. One solution is to combine new statistical approaches with field data, which has already proven a benefit; by combining genetic sampling and population models, Katzner *et al.* (2011) were able to include non-breeding imperial eagles (*Aquila heliacal*) into new models. In doing so, they found previous population estimates to be biased. Bayesian methods also offer some distinct advantages, such as improving the use of minimal data; studies are often forced to exclude data altogether as re-sightings of non-breeders may be too sparse (e.g. Votier *et al.* 2008). Exclusion of information is not uncommon but developing Bayesian methods may help maximise this data and could reduce bias from traditional UMS models.

6.3 Developing the conservation management of the echo parakeet

6.3.1 Reduced management

As the echo parakeet population continues to grow, the ability of staff to monitor every breeding attempt and ring all chicks prior to fledging is increasingly strained and will soon become unsustainable. When management first began, three to four field staff monitored a handful of nests.

Now a team of an equivalent size monitors over 100 nest sites in a given breeding season. To accommodate this change the focus on the breeding population could be reduced and a wider approach to monitoring could be adopted. I suggest that future work should determine the 'optimal monitoring' level of the breeding population; what proportion of the population can be monitored each breeding season in order to obtain the same estimate of demographic rates? This entails sub-setting and re-sampling data using monitoring scenarios with a different monitoring effort. A similar approach was employed to review the monitoring of the pink pigeon (*N. mayeri)* population and has proven highly successful (Concannon 2014). For the echo parakeet programme, a small proportion of breeding attempts could be monitored each season. Annually updating and reviewing the population's demography would permit key population trends to be tracked for important changes. Several gains could be made from this change. First is that reduced management would navigate towards establishing a more self-sustaining population. A significant reduction in management was adopted in 2005 and the population did not go back into decline following this; having endured this change it is unlikely a second reduction would prove detrimental. Secondly, reduced visits to nests would further minimize the spread of disease between nest sites via human-mediated transmission as the current protocols only reduce risk, they do not assuredly eliminate risk. Thirdly, there are concerns over the plucking behaviour of several breeding females which regularly results in chick mortalities (Henshaw *et al.* 2014). Although unconfirmed, it is thought that this behaviour may be initiated by a nervous response to nest access by staff. Finally, monitoring fewer breeding attempts would improve the cost-effectiveness of the programme, reducing staffing and equipment costs. Visiting nest sites causes wear and tear to expensive climbing gear and goods consumptions are high (e.g. antiseptic hand gel, wood shavings, ropes and wire used as anchor lines). Although only small, these costs accumulate and are of serious concern to an NGO with limited funds. Identifying the minimal level of monitoring required to meet the objectives of the programme could provide more time to invest in surveys throughout the Black River Gorges National Park and obtain more re-sightings of non-breeders. Alternatively, time could be invested in restoring the native habitat within National Park. This would be of a wider benefit to the many other threatened, endemic flora and fauna of Mauritius, and as discussed by Florens (2013), would shift the focus away from the predominantly species-centric approach that has been widely employed, to a more all-encompassing and thus sustainable ecosystem approach.

A caveat to reduced monitoring of breeding attempts would be that fewer chicks would be ringed prior to fledging. A remarkable feature of the echo parakeet management programme has been the ability to uniquely identify >95% of the wild population, information which has been pivotal to much of the research generated from this thesis and other scientific studies (e.g. Raisin *et al.* 2012; Tollington *et al.* 2013; Tollington *et al.* 2015). If the population continues to grow without simultansoulsy increasing the scale of monitoring effort, regardless, the number of unringed birds will increase. A reduced monitoring approach would, however, need to consider *which* nests should be monitored in order to fairly represent the population in terms of age, classes of feeding habits (use of SF), geographic location, sub-populations etc. Perhaps a change in survey style could first be considered to obtain the most valuable information, as was tested by Brown *et al.* (2017) to improve monitoring of wood turtles (*Glyptemys insculpta*). These questions will require collaboration between the relevant stake-holders and field workers, efforts which refects the needs of many consevrtaiosn prgrammes across the world; bridging the gap between conservation and science, and developing formal links between decision makers and scientific researchers, has been was well discussed by Cook *et al.* (2013) and others (Pullin *et al.* 2004; Sutherland *et al.* 2004; Meek *et al.* 2015; Roux *et al.* 2006).

Consistency and continuity in data collection provides a foundation for advancing the long-term management of a species (Armstrong and Ewen 2013; Sutter *et al.* 2015), and the continuation of the longitudinal echo data set would be incredibly valuable, even if reduced to a lower intensity. An understandable predicament of population management is whether to invest efforts elsewhere rather than focus on one project (Armstrong and Ewen 2013), particularly if the focus species has seemed to stabilise, or major threats have reduced. Yet certain environmental and/or management effects may be delayed and a certain levels of monitoring of the echo parakeet should continue in order to account for this, particularly if the decline in pre-breeder survival (Chapter 5) is to be better understood. Another justification for continued monitoring to some extent is that the demographic rates of a rapidly growing population are inherently different from those of a population at a low carrying capacity (Correia *et al.* 2015). It is not yet clear if the echo parakeet population has reached its carrying capacity, or if the demography of the population may continue to change.

6.3.1 Adaptive Management

With the exception of reduced management since 2005, there have been few major changes to the echo parakeet monitoring programme. Research conducted for this thesis provides an excellent example of the gains to be made from consistent monitoring and illustrates the importance of establishing data collection on key parameters as early as possible in a conservation projects. This is not to say the management programme has not 'tweaked' and 'adjusted' certain practices along the way and the persistent trials of nest box designs and feeding stations has been essential to their success (Tatayah *et al.* 2007). Flexibility in any programme should be encouraged, with regular evaluations established to harness their gains and respond to their faults. Populations change and evolve, their requirements will vary, and though one threat may be ameliorated, a new threat may take its place. Wildlife managers should act to become aware of these ongoing challenges. A move towards more adaptive management could enhance progression within the programme and allow research findings to be applied, not simply reported and set aside. Adaptive management can help in this process, as it enables actions based on a hypothesis to be tested and improved, amending them through several steps of experimental management (Gibbs *et al.* 1999; Lindenmayer and Likens 2009; Black *et al.* 2013; Canessa *et al.* 2016). This process can identify causal relationships which then guide conservation decisions at a larger scale, helping them to deciding which component of a current management regime is most pertinent (Dimond and Armstrong 2007; Gerber *et al.* 2017). This has proven effective in several study systems, such as helping to evaluate the effects of management initiatives for cormorants (Frederiksen and Bregnballe 2000), and for the Mauritius olive white eye (*Zosterops chloronothos)*, where combining small scale field experiments with demographic models has improved on-going management practices (Maggs *et al.* 2015). Thus research in population management can move from being reactive to proactive. For the echo parakeet, short-term experiments could provide better guidance in how to adjust current management, as long as they are well planned and consider the long term goals of management. An experimental and adaptive management approach has already begun in relation to the control of PBFD. Trials of not wearing chemical suits during visit to nests site are underway to determine their effectiveness in reducing disease transmission and environmental accumulation of the BFDV virus. How this translates into viral prevalence in new offspring will then be assessed (D. J. Fogell, *pers comms*). Understandably there is a fear of changing aspects of programme which has seen continued success since it began, but adaptive approach allows only small, measured risks to be taken and the most appropriate change to be determined. Baseline demographic data has been produced through this thesis, providing the groundwork for more pro-active management.

6.4 Future research Questions

6.4.1 Supplementary Feeding

This thesis has considered the impact of management and disease predominantly in the context of population demography. However, habitat use models and behaviour based complexes should also be considered in order to understand parakeet demographics. Whilst all three may be inherently linked, they provide a focus for long-term management and gives structure to future research questions (Norris 2004). For example, there may be unforeseen genetic consequences of providing SF, as birds using SF become over-represented in the population due to their higher fecundity rates. How external factors, such as weather, influence the role of SF and natural food supplies will also need to be understood to appropriately adapt the current regime. Although I explored food as a regulatory factor, the role of weather was not included. The appropriate climatic data was not available to include in this thesis, yet it may further explain additional underlying factors and mechanistic processes driving population regulation. Current work by PhD student Jo Taylor at the University of Reading aims to explore the role of weather conditions in echo parakeet demographics. SF may contribute to buffering the negative effects of adverse weather, or unpredictable years of low food abundance in natural resources. If this were the case, one may expect less variation in the demographics rates of birds using SF and greater sensitivity to weather patterns in nests not associated with SF.

I began to explore the geographic influence of SF in Chapter 4 as part of preliminary analysis for the study and confirmed a significant relationship between the use of SF and distance to travel. At 2km there was definitive reduction in the probability of a breeding pair using SF. When released birds were excluded from the analysis, the probability of using SF extended to a greater distance, suggesting wild bred birds were less likely to travel greater distances to use the feeding stations. Illustrating these estimates onto a map of the National Park helps to interpret the spatial influence of SF (Figure 6.1). It remains unclear whether individuals breeding closer to feeding stations occupy these better sites because they are in fact fitter individuals capable of maintaining ‘better’ territories, forcing weaker - and consequently poorer breeders - to occupy sites further away. If non-supplementary fed breeding pairs have lower fecundity rates, as revealed in Chapter 4, then erecting nest boxes in more remote areas of the park may require additional feeding stations to be established. It is therefore necessary to continue exploring ecological and behavioural factors influencing the demand for supplementary food and the consequences. Behavioural observations at the feeding stations indicate certain individuals spend a proportionally small amount of time at the feeder, whilst others (generally those nesting in close proximity) are seen daily at the feeders. Accurately quantifying SF consumption rates would be valuable future research, and the practicalities of doing so see ongoing disucssion. As stated in Chapter 4, there is clearly further work to be achieved in terms of further describing the current crude definition of either using or not using supplementary food, and further still, how diet in the non-breeding season affects individual fitness, which has been known to contribute to population in other long-lived species (Sæther 1997). Already, unpublished work from the University of Kent has employed stable isotope analysis to explore this question, finding that the diets of birds breeding closer to feeding stations included very little natural vegetation and were disproportionately high in artificial food (Dr. S. Tollington, *pers. comm*).

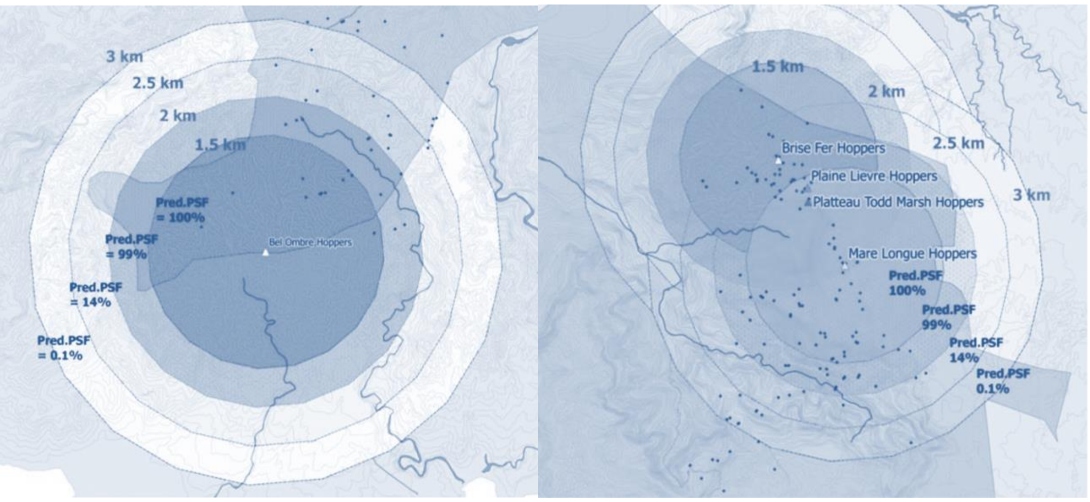


Figure 6.1 Echo parakeet nest sites (black dots) in relation to AFS (marked triangles with site names). 'Zones' of distance from AFS are marked from1.5 to 3km. At each distance the probability of a pair using SF (PredPSF) is indicated as a percentage. *Left:* Bel Ombre sub-population supported by one AFS. *Right*: the Grande Gorges sub-population, with 5 AFS. 'Zones' drawn around the most northern and southern AFS (Brise Fer and Mare Longue).

6.4.2 Exploring PBFD

Previous research has focused on the genetic evolution and ecology of the BFDV virus and the immunity of echo parakeets, and current work is exploring viral load in relation to susceptibility. Through this thesis, it has now been possible to describe the individual and population level demographic impact of the disease. Whether PBFD continues to threaten population persistence of the echo parakeet is uncertain. Given the findings of this study, the population would have likely re-entered into decline if breeding rates had not recovered. If the selective sweep of the virus exaggerated the impact of the disease, then given the prevalence of the disease in the population today, there will always be a risk in the future of another major change in viral strain. Should the population size be large enough at such a time, an associated outbreak may once again be only short lived and minimally impact at the population level. Today, clinical signs are still commonplace within the population. This was not the case prior to the outbreak of PBFD, yet the population has continued to grow unhindered.

Huge knowledge gaps still remain with regard to host-pathogen dynamics, both in the echo parakeet population and generally; poorly understood are the mechanisms driving the on-going persistence and prevalence of a novel pathogen once it has entered the host population (Plowright *et al.* 2017) and the importance of heterogeneity in infectious periods (Woolhouse 2011). The phenomenon of super-spreaders and super-shedders may play an important role in maintaining infections in a population at a low lying level. These become increasingly challenging to test given that pathogen loads can vary enormously over different time periods (Plowright *et al.* 2017). In the echo parakeet study system, garnering information from historical blood samples is of use in answering some questions of the disease, but inferences from such cross-sectional studies cannot explore the aforementioned challenges, potentially misleading control efforts. The repeated sampling required to fully explore the dynamics of the disease requires time, staffing and considerable funds. However, the echo parakeet population does offer an opportunity for a ‘living laboratory’ to test various hypotheses study host-pathogen dynamic in a free-living population. Work by D.J. Fogell from the University of Kent hopes to explore this further, identifying the influence of social networking in disease transmission, and the links between viral load and susceptibility. At present it is crucial that monitoring disease and demographics in the echo population is continued as disease impacts are not always instantaneous and there may be more to understand. Potential carry-over effects of an EID or outbreak (Morrison *et al.* 2015) have yet to be explored; the consequences of exposure to the virus in the nest, or the influence of viral load from a young age, may not yet have transpired.

The additional questions generated from this study emphasise the need for integrating disease into wildlife monitoring and cross-discipline collaboration (Woolhouse 2011; Hyatt *et al.* 2015). There is a clear call for the wider unification of discipline to combine wildlife and disease ecology, evolutionary biology, immunological biology and genetics. Integrative research will help explain the consequences of individual heterogeneity and how these determine population-level pathogen dynamics (McDonald *et al.* 2017). Such a cohesive link between science and conservation management in being increasingly encouraged, promoting the flow of ideas and information in both directions (Cook *et al.* 2013; Meek *et al.* 2015). Given sufficient information and combined knowledge, the complexities of EIDs can slowly be teased apart and practical guidelines developed for conservation practitioners, which will help t ensure actions are implemented rapidly and targeted most effectively (Hyatt *et al.* 2015; Langwig *et al.* 2015; Gerber *et al.* 2017; Russell *et al.* 2017). To be a real benefit however, it is clear that any actions taken need to be part of a long-term research investment.

6.5 Conclusions

This thesis aimed to provide detailed information regarding the population demographics of the echo parakeet population, and improve current understanding for the roles management and disease have contributed in shaping the population that exists today. Findings provide the tools for evidence-based conservation; guiding management decisions based on sound knowledge to reduce future risks, and ensuring actions and responses are correctly interpreted. Equally, the research provides information that helps to better understand the current risks of certain management practices if they do not adapt, and offers suggestions on how current practice could evolve. Ensuring a viable population of parakeets - ideally one which is less intensely managed - will require innovative and flexible research management. The approaches and responses of this population are case specific but provide a framework for researchers and managers for a range of species. Though there is no universal rule for what will and will not work for the management of threatened species, we can at least learn from what has been achieved, whether a success or a failure, and apply this to current decision making processes. From this study it is clear that population management requires so much more than simply preventing a population decline. It takes stages of different types of work, from initial ‘triage’ to developing long-term goals, each of which require different skills, knowledge and action. For conservation programmes to succeed they must be interdisciplinary. They require employing the appropriate statistical models and monitoring frameworks, reliable and skilled field workers and practical ‘hands-on’ techniques. Even organised management behind the scenes is of upmost importance to ensure there is sufficient funding and the clear communication of ideas and findings. Managing threatened populations may take some bravery when little is known about a study system, particularly when identifying and measuring potential threats present challenges of their own. Given the right guidance, an effective, well managed monitoring system, and a willingness to learn and adapt, even in the face of imminent extinction, there is always hope.

Appendix

Appendix 3.1 Comparison of the age and state specific survival estimates generated by MS-2 and MS-5, reported with standard errors (SE) and 95% confidence intervals (CI-/+). MS-5 reports the multistate model with three observable states (N, B and PO), with a four ages class structure. MS-2 used the same data but upheld the assumptions of a typical UMS model by assuming non-breeders (N and PO) experience survival equivalent to breeders (B).

MS-5 - 3 Observable States

Age Class	State	φ	SE	CI-	CI+
1	N	0.694	0.03	0.632	0.750
2	N	0.724	0.038	0.643	0.792
3	N	0.995	0.058	0.000	1.000
4+	N	**0.781**	0.029	0.719	0.833
3	B	0.958	0.038	0.78	0.993
4+	B	**0.97**	0.012	0.937	0.986
4+	PO	**0.672**	0.063	0.539	0.782

MS-2 - 1 Observable State

Age Class	State	φ	SE	CI-	CI+
1	N=B=PO	0.692	0.03	0.630	0.748
2	N=B=PO	0.725	0.037	0.646	0.792
2	N=B=PO	0.936	0.029	0.851	0.974
4 +	N=B=PO	**0.902**	0.01	0.880	0.921

Appendix 3. 2 Parameter estimates of survival (φ), recapture (*P*), probability and transition probability (ψ) generated from the CJS and full multistate model (MS-5), where all model assumptions were relaxed. Three states are indicated: N = pre-breeder; B = breeder; PO = post-breeder. Certain illogical parameters were fixed at zero, whilst breeder recapture was fixed at 1 as all breeding birds are re-sighted.

CJS Model Estimates					
Age Class	**State**	**Parameter Estimate**	**SE**	**CI -**	**CI +**
Survival (φ)					
1 = 2	B	0.58	0.019	0.038	0.038
3	B	0.92	0.04	0.122	0.053
4+	B	0.94	0.008	0.016	0.017

M-5 Model estimates						
Age Class	**State**	**Parameter Estimate**	**SE**	**CI -**	**CI +**	**Fixed Parameter?**
Survival Probability (φ)						
1	N	0.694	0.03	0.063	0.055	
2	N	0.724	0.038	0.081	0.069	
3	N	0.995	0.057	0.995	0.005	
4+	N	0.781	0.029	0.062	0.052	
1	B	0				Yes
2	B	**0.47*				
3	B	0.958	0.038	0.178	0.035	
4+	B	0.97	0.012	0.033	0.016	
1 - 2	PO	0				Yes
3	PO	**0.47*				
4+	PO	0.672	0.063	0.134	0.11	
Recapture Probability (P)						
1	N	0.487	0.028	0.433	0.541	
2	N	0.512	0.034	0.445	0.578	
3	N	0.371	0.043	0.291	0.457	
4+	N	0.365	0.040	0.291	0.446	
1	B	0				Yes
2 - 4+	B	1				Yes
1 & 2	PO	0				Yes
3	PO	0.615	0.228	0.195	0.913	
4+	PO	0.547	0.069	0.412	0.676	
Transition Probability (ψ)						
1	N - B	0				Yes
2	N - B	0.153	0.019	0.119	0.196	
3	N - B	0.255	0.030	0.201	0.317	
4+	N - B	0.202	0.026	0.157	0.257	

1 & 2	B - PO	0				Yes
3	B - PO	0.131	0.052	0.057	0.271	
4+	B - PO	0.109	0.015	0.083	0.142	
1 - 3	PO - B	0				Yes
4+	PO - B	0.581	0.072	0.437	0.712	

*0.47 = this is not a real estimate, but indicates that there were too few re-sightings in this age class and state to generate an accurate estimate.

Appendix 4. 1 Multivariate GLMM testing whether Nearest Hopper remained a significant predictor variable of the response ‘PairSF’ when accounting for additional causes of variation. PairSF is the classification of whether a breeding pair was known to use supplementary food (SF1) or not use SF (SF0).

Predictor Variable	**Estimate**	**Standard Error**	**Z-value**	***P*-value**	
Intercept	21.662	11.415	1.898	0.058	.
Season	0.635	0.221	2.881	<0.001	**
Female Age	-2.401	0.682	-3.520	<0.001	***
Female Origin	-6.006	2.668	-2.252	0.024	*
Male Origin	-6.614	10.749	-0.615	0.538	
Sub Population	-9.314	2.915	-3.195	<0.001	**
First Egg Date	-0.608	0.476	-1.276	0.202	
Nearest Hopper	-7.349	1.615	-4.550	<0.001	***

Appendix 4. 2 Model output from univariate GLMM with only PairSF as the predictor variable for the number of successful fledglings per clutch from 2000/01 breeding season to 2013/14 (total of 682 clutches). Female ID was included as a random effect to account for repeated clutches from females over the course of the study.

Predictor Variable	Estimate	Standard Error	Z-value	*P*-value
Intercept	0.01867	0.08236	0.227	0.821
Pair SF1	0.49797	0.09063	5.494	3.92e-08 ***

Appendix 4. 3 Model output of the global GLMM examining the effect size of supplementary feeding on the number of fledglings per clutch from 2000/01 breeding season to 2013/14 (total of 682 clutches). Female ID was included as a random effect to account for repeated clutches from females over the course of the study. Female age was built as a quadratic term. Definitions of Predictor Variables are in Chapter 4.

Predictor Variable	Estimate	Standard Error	Z-value	*P*-value
Intercept	-0.122681	0.28293	-0.434	0.664571
Season	0.047432	0.017043	2.783	0.005385
Female Age	0.103135	0.054454	1.894	0.058227
I(FemaleAge^2)	-0.005453	0.003653	-1.493	0.135477
Female Origin	-0.024632	0.086914	-0.283	0.776868
Male Origin	-0.008445	0.111355	-0.076	0.939545
Sub Population	-0.034648	0.081854	-0.423	0.672083
First Egg Date	-0.83737	0.224874	-3.724	0.000196
Pair SF1	0.465742	0.112944	4.124	<0.005***

Appendix 4. 4 Model output from the univariate GLMM with only PairSF as the predictor variable for clutch size from the 2000/01 breeding season to 2013/14 (total of 682 clutches). Female ID was included as a random effect to account for repeated clutches from females over the course of the study.

Predictor Variable	Estimate	Standard Error	Z-value	P-value
Intercept	0.95191	0.04751	20.035	<2e-16
Pair SF1	0.06769	0.05475	1.236	0.216

Appendix 4.5 Model output of the global GLMM examining the effect size of supplementary feeding on clutch size from 2000/01 breeding season to 2013/14 (total of 682 clutches). Female age was built as a quadratic term. Parameter definitions in Chapter 4, Table 4.1.

Predictor Variable	Estimate	Standard Error	Z-value	*P*-value
Intercept	0.787449	0.217973	3.613	0.000303
Season	-0.008994	0.012682	-0.709	0.4782
Female Age	0.089967	0.041713	2.157	0.031022
I(FemaleAge^2)	-0.004247	0.002801	-1.516	0.129434
Female Origin	0.092185	0.068077	1.354	0.175697
Male Origin	-0.016404	0.089675	-0.183	0.854858
Sub Population	0.023702	0.064336	0.368	0.712574
First Egg Date	-0.323138	0.170484	-1.895	0.058037
Pair SF1	0.154786	0.079241	1.953	0.050778

Appendix 4.6 Model output from the univariate GLMM with only PairSF as the predictor variable for egg hatchability from the 2000/01 breeding season to 2013/14 (total of 682 clutches). Female ID was included as a random effect to account for repeated clutches from females over the course of the study.

Predictor Variable	Estimate	Standard Error	Z-value	P-value
Intercept	0.469	0.1796	2.612	0.00901
PairSF1	0.6177	0.2127	2.905	0.00367

Appendix 4.7 Model output of the global GLMM examining the effect size of supplementary feeding on egg hatchability from 2000/01 breeding season to 2013/14 (total of 682 clutches). Female ID was included as a random effect to account for repeated clutches from females over the course of the study. Female age was built as a quadratic term.

Predictor Variable	Estimate	Standard Error	Z-value	P-Value
Intercept	0.633205	0.626682	1.01	0.312
Season	0.199141	0.040343	4.936	<0.001
Female Age	0.034818	0.108795	0.32	0.749
I(FemaleAge^2)	-0.004174	0.007276	-0.574	0.566
Female Origin	-0.140912	0.258251	-0.546	0.585
Male Origin	0.075134	0.295245	0.254	0.799
Sub Population	-0.576799	0.241654	-2.387	0.017
First Egg Date	-2.004564	0.484064	-4.141	<0.001
Pair SF1	0.378175	0.26253	1.441	0.15

Appendix 4.8 Model output from the univariate GLMM with only PairSF as the predictor variable of chick to fledge probability. Study period spanned the from the 2000/01 breeding season to 2013/14 (total of 682 clutches). Female ID was included as a random effect to account for repeated clutches from females over the course of the study.

Predictor Variable	Estimate	Standard Error	Z-value	P-value
Intercept	0.7554	0.202	3.739	0.000185
Pair SF1	1.2121	0.2457	4.934	8.06E-07

Appendix 4.9 Model output of the global GLMM examining the effect size of supplementary feeding on chick to fledge survival from the 2000/01 breeding season to 2013/14 (total of 682 clutches). Female ID was included as a random effect to account for repeated clutches from females over the course of the study. Female age was built as a quadratic term. Clutch size was not included as variable as it was too closely correlated with hatch success.

Predictor Variable	Estimate	Standard Error	Z-value	P-value
(Intercept)	0.879391	0.863057	1.019	0.30824
Season	0.03095	0.053548	0.578	0.56327
Female Age	0.103747	0.145464	0.713	0.47572
I(FemaleAge^2)	-0.006583	0.009401	-0.7	0.48377
Female Origin	-0.156174	0.359291	-0.435	0.6638
Male Origin	-0.562468	0.425153	-1.323	0.18584
Sub Population	0.154852	0.297063	0.521	0.60218
First Egg Date	-0.174657	0.645385	-0.271	0.78668
Pair SF1	1.102647	0.352672	3.127	0.002

Appendix 4. 10 Model output from the univariate GLMM with only Pair SF as the predictor variable of egg to fledge probability. Study period spanned from the 2000/01 breeding season to 2013/14. Female ID as a random effect to account for repeated clutches from females over the course of the study.

Predictor Variable	Estimate	Standard Error	Z-value	P-value
Intercept	-0.4948	0.1674	-2.956	0.00312
Pair SF1	1.0227	0.1966	5.203	1.96E-07

Appendix 4.11 Model output of the global GLMM examining the effect size of supplementary feeding egg to fledge probability from the 2000/01 breeding season to 2013/14 (total of 682 clutches). Female ID was included as a random effect to account for repeated clutches from females over the course of the study. Female age was built as a quadratic term. Clutch size was not included as variable as it was too closely correlated with hatch success.

Predictor Variable	Estimate	Standard Error	Z-value	*P*-value
Intercept	-0.451178	0.58738	-0.768	<0.001
Season	0.151158	0.038751	3.901	0.00010
First Egg Date	-1.398391	0.45216	-3.093	0.00198
Female Origin	-0.116696	0.255636	-0.456	0.64804
Male Origin	-0.280323	0.285378	-0.982	0.32596
Female Age	0.092579	0.100326	0.923	0.35612
I(FemaleAge^2)	-0.007302	0.006626	-1.102	0.27045
Sub Population	-0.312812	0.22702	-1.378	0.16823
Pair SF1	0.822722	0.258603	3.181	0.00147

Appendix 4.12 Echo parakeet survival estimates (φ) for pre-breeders (N), breeders (B) and post-breeders (PO), generated by the most parsimonious model describing the impact of SF on age and state-specific survival. No effect of SF was detected on φ,. 'Group' indicates whether parameter is relevant only SF0, SF1 or both (no effect). Season = time dependent survival or not. Param Estimate = annual survival rate. S.E = standard error of the parameter estimate. CI- and CI+ = 95% lower and upper confidence interval around the estimate.

Group	**Param.**	**State**	**Age Class**	**Season**	**Param. Estimate**	**SE**	**CI -**	**CI +**
SF0/1	φ	N	1	1994	0.504	0.399	0.043	0.959
SF0/1	φ	N	1	1995	0.672	0.307	0.118	0.969
SF0/1	φ	N	1	1996	0.336	0.307	0.033	0.882
SF0/1	φ	N	1	1997	0.577	0.211	0.200	0.881
SF0/1	φ	N	1	1998	0.978	0.128	0.000	1.000
SF0/1	φ	N	1	1999	0.900	0.084	0.590	0.982
SF0/1	φ	N	1	2000	0.577	0.211	0.200	0.881
SF0/1	φ	N	1	2001	0.965	0.056	0.515	0.999
SF0/1	φ	N	1	2002	0.977	0.054	0.293	1.000
SF0/1	φ	N	1	2003	0.973	0.071	0.159	1.000
SF0/1	φ	N	1	2004	0.952	0.073	0.461	0.998
SF0/1	φ	N	1	2005	0.802	0.091	0.569	0.926
SF0/1	φ	N	1	2006	0.571	0.080	0.413	0.716
SF0/1	φ	N	1	2007	0.638	0.079	0.474	0.775
SF0/1	φ	N	1	2008	0.594	0.066	0.462	0.715
SF0/1	φ	N	1	2009	0.868	0.078	0.634	0.962
SF0/1	φ	N	1	2010	0.504	0.065	0.378	0.629
SF0/1	φ	N	1	2011	0.625	0.078	0.463	0.762
SF0/1	φ	N	1	2012	0.305	0.062	0.198	0.437
SF0/1	φ	N	2	1995	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	1996	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	1997	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	1998	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	1999	0.856	0.166	0.297	0.988
SF0/1	φ	N	2	2000	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	2001	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	2002	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	2003	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	2004	1.000	0.000	1.000	1.000
SF0/1	φ	N	2	2005	0.954	0.096	0.227	0.999
SF0/1	φ	N	2	2006	0.698	0.104	0.467	0.859

SF0/1	φ	N	2	2007	0.773	0.102	0.522	0.914
SF0/1	φ	N	2	2008	0.525	0.090	0.352	0.693
SF0/1	φ	N	2	2009	0.730	0.085	0.538	0.863
SF0/1	φ	N	2	2010	0.374	0.063	0.261	0.503
SF0/1	φ	N	2	2011	0.671	0.100	0.457	0.832
SF0/1	φ	N	2	2012	0.416	0.093	0.251	0.602
SF0/1	φ	N	3	ALL	0.944	0.058	0.663	0.993
SF0/1	φ	N	4+	1997	1.000	0.000	1.000	1.000
SF0/1	φ	N	4+	1998	1.000	0.000	1.000	1.000
SF0/1	φ	N	4+	1999	1.000	0.000	1.000	1.000
SF0/1	φ	N	4+	2000	1.000	0.000	1.000	1.000
SF0/1	φ	N	4+	2001	1.000	0.000	1.000	1.000
SF0/1	φ	N	4+	2002	0.966	0.064	0.379	0.999
SF0/1	φ	N	4+	2003	1.000	0.000	1.000	1.000
SF0/1	φ	N	4+	2004	1.000	0.000	1.000	1.000
SF0/1	φ	N	4+	2005	1.000	0.000	1.000	1.000
SF0/1	φ	N	4+	2006	0.533	0.124	0.301	0.751
SF0/1	φ	N	4+	2007	0.568	0.145	0.293	0.807
SF0/1	φ	N	4+	2008	0.737	0.124	0.445	0.907
SF0/1	φ	N	4+	2009	1.000	0.003	0.001	1.000
SF0/1	φ	N	4+	2010	0.529	0.116	0.311	0.737
SF0/1	φ	N	4+	2011	0.799	0.140	0.418	0.957
SF0/1	φ	N	4+	2012	0.642	0.148	0.337	0.864
SF0/1	φ	B	1	ALL	0			
SF0/1	φ	B	2	ALL	**0.475*	0.000	0.475	0.475
SF0/1	φ	B	3	ALL	**0.948**	0.041	0.782	0.989
SF0/1	φ	B	4+	ALL	**0.976**	0.012	0.937	0.991
SF0/1	φ	P	1	ALL	0			
SF0/1	φ	P	2	ALL	0			
SF0/1	φ	P	3	ALL	**0.475*	0.000	0.475	0.475
SF0/1	φ	P	4+	ALL	**0.719**	0.066	0.574	0.830

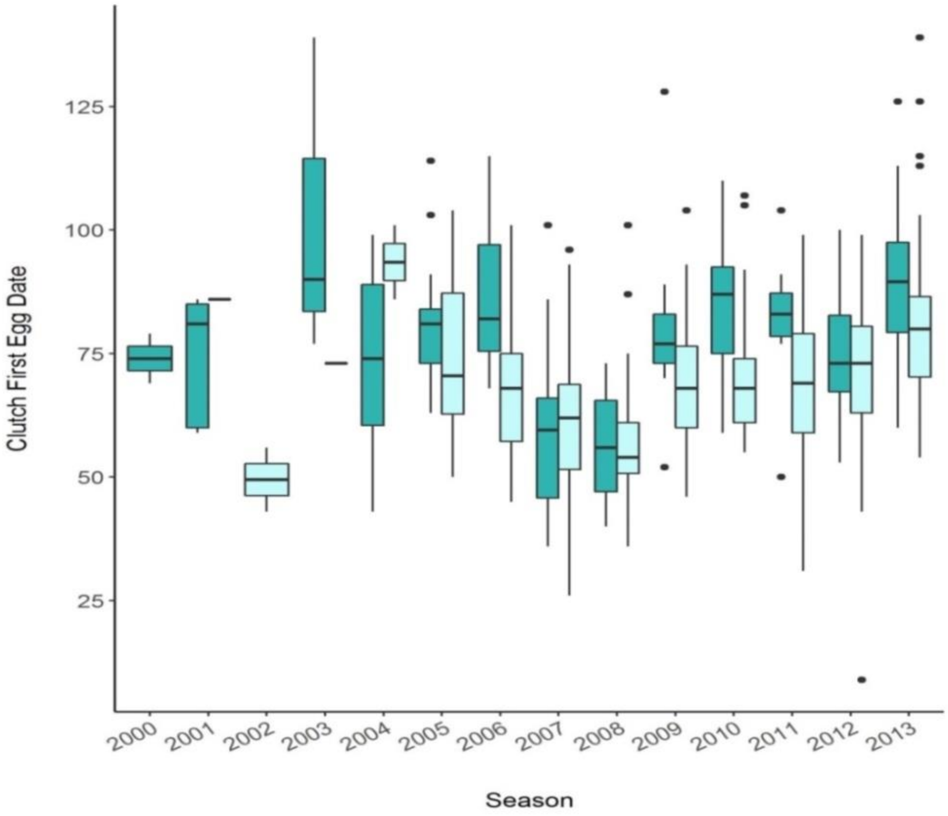
Appendix 4.13 Re-sighting probability (*P*) estimates for echo parakeet pre-breeders (N), breeders (B) and post-breeders (PO), generated by the most parsimonious model describing the impact of SF on age and state-specific survival. No effect of SF was explored in *P*, therefore parameter estimates are applicable to both SF Groups (SF1 and SF0). Param Estimate =probability of re-sighting in any given year. S.E = standard error of the parameter estimate. CI- /CI+ = 95% lower and upper confidence intervals.

Group	Param.	State	Age Class	Season	Param. Estimate	SE	CI -	CI +
SF0/1	*P*	N	1	ALL	**0.568**	0.030	0.510	0.625
SF0/1	*P*	N	2	ALL	**0.620**	0.035	0.548	0.686
SF0/1	*P*	N	3	ALL	**0.404**	0.049	0.313	0.502
SF0/1	*P*	N	4+	ALL	***0.457**	0.043	0.374	0.543
SF0/1	*P*	B	1	ALL	0			
SF0/1	*P*	B	2	ALL	1			
SF0/1	*P*	B	3	ALL	1			
SF0/1	*P*	B	4+	ALL	1			
SF0/1	*P*	P	1	ALL	0			
SF0/1	*P*	P	2	ALL	0			
SF0/1	*P*	P	3	ALL	**0.585**	0.225	0.186	0.896
SF0/1	*P*	P	4+	ALL	**0.507**	0.072	0.369	0.645

Appendix 4.14 Transition estimates (ψ) generated by the most parsimonious model describing the impact of SF on movement from pre-breeder to breeder state (N-B), breeders to post-breeder (B-PO), and post-breeder back to breeder (PO-B) 'Group' indicates whether the estimate is relevant to SF0 or SF1 birds, or both (SF0/1). Param Estimate=probability of transition in any given year. S.E = standard error of the parameter estimate. CI-/CI+ = 95% lower &upper confidence intervals.

Group	Param.	State	Age Class	Season	Param. Estimate	SE	CI -	CI +
SF0/1	ψ	N-B	1	ALL	0			
SF0	ψ	N-B	2	ALL	**0.090**	0.028	0.048	0.161
SF1	ψ	N-B	2	ALL	**0.219**	0.030	0.166	0.283
SF0/1	ψ	N-B	3	ALL	**0.267**	0.033	0.207	0.337
SF0	ψ	N-B	4+	ALL	**0.171**	0.029	0.121	0.236
SF1	ψ	N-B	4+	ALL	**0.407**	0.067	0.286	0.541
SF0/1	ψ	B-P	1 & 2	ALL	0			
SF0/1	ψ	B-P	3	ALL	**0.137**	0.055	0.060	0.282
SF0	ψ	B-P	4+	ALL	**0.140**	0.023	0.102	0.191
SF1	ψ	B-P	4+	ALL	**0.072**	0.020	0.041	0.123
SF0/1	ψ	P-B	1 & 2	ALL	0			
SF0/1	ψ	P-B	4+	ALL	**0.526**	0.078	0.375	0.672

Appendix 4.15 Variation in first egg date of clutches laid by SF0 (dark blue) and SF1 (light blue) breeding pairs between the two groups. First egg date is measured as the number of days after August 1st.



Appendix 5. 1 Disease management protocol

Protocols were developed in 2005/06 to address risks of spreading the virus between individual birds and nest sites, and these have been annually throughout the duration of this study. The protocols focus on strict hygiene with a view to minimising the risk of carrying feather dust (in particular) between all nest sites, our equipment, field stations and the GDEWS. DuPont™ Tyvek®Chemical suits were worn when handling birds or accessing nest sites, with a different suit worn for each bird or occasion. After each occasion the suit was either placed directly in Virex® virucide (if at the field station) or inside sealed bags for the journey back to the field station (where it was placed in Virkon®). Holes were placed in strategic places in the suits so that climbing harnesses could be worn under the fabric. Wood shavings were only removed at the end of the season to minimise the risk of spreading feather dust. Hands were cleaned immediately before and after bird handling with antiseptic hydro alcoholic gel (Manugel85®). For each brood a fresh weighing container or bag was used to reduce the risk of disease transmission between nests. All equipment used at a nest site (e.g. Pesola, ringing pliers) was thoroughly cleaned with alcohol prior tore-use. The containers and bags were disinfected in Virex® virucide before re-use. Nest sites were also disinfected using Virex® between breeding seasons to minimise accumulation of infected material.

The feeding stations are seen as a key area in terms of disease transmission and disinfection practices. All feeding hoppers are removed and disinfected with Virkon® weekly. Hopper poles and perches are cleaned with Virkon® once a week at the Plaine Lievre feeding stations and at the other feeding stations on a regular basis. The aviaries are also scrubbed down with Virkon® as required to try and minimise disease transmission.

The echo parakeet monitoring programme entered a new ‘reduced management’ phase from 2005 onwards. This highlights the challenge of interpreting any post-outbreak measure of breeding success, which experienced a different set of management conditions. Nest sites were accessed a little as possible after 2005; three to four visits over the entire breeding period compared to the almost daily visits attempted pre-outbreak. Reduced disturbance and the reduction in management-mediated disease transmission may have benefits breeding attempts, whilst the stricter disease protocols - particularly the use of chemical suits - would have further reduced environmental accumulation of the virus. Several factors seemed to have combined in a perfect storm leading to the outbreak, and increased transmission of the virus between the two *Psittacula* populations may have begun as far back as the 1950’s when the range of Indian ring necks began expanding into the native forest (Cheke and Hume 2008).

Appendix 5.2 Summary of data set 1 used to analyse hatching probability**.**

Season	No. of Clutches	No. of eggs	No. of hatchlings
1993	2	4	3
1994	1	2	2
1995	4	9	8
1996	7	15	13
1997	7	17	12
1998	9	20	15
1999	13	40	31
2000	7	18	12
2001	9	22	18
2002	15	40	21
2003	10	23	14
2004	24	57	29
2005	49	132	73
2006	55	148	101
2007	64	176	119
2008	61	172	125
2009	69	199	145
2010	74	208	142
2011	74	198	149
2012	93	245	176
2013	96	257	213
Total	**743**	**2002**	**1421**

Appendix 5.3 Summary of data set 2 used to analyse number of fledglings and egg to fledge survival probability.

Season	No. of Clutches	No. of Eggs	No. Hatched eggs	No. of Fledglings
1993	2	4	3	0
1994	1	2	2	0
1995	2	5	4	2
1996	2	5	4	2
1997	4	8	5	2
1998	3	4	1	1
1999	6	20	11	5
2000	5	13	7	4
2001	7	16	11	11
2002	9	24	5	5
2003	7	16	7	6
2004	15	31	7	7
2005	50	135	76	57
2006	54	144	97	64
2007	64	176	119	100
2008	61	172	125	104
2009	69	199	145	130
2010	74	208	142	119
2011	74	198	149	118
2012	93	245	176	151
2013	96	257	213	164
Total	**698**	**1882**	**1309**	**1052**

Appendix 5. 4 List of parameters fixed in survival analysis:

1. A bird cannot enter the breeding state (B) until two years old at the earliest, therefore survival (φ) and re-sighting probability (*P*) for breeders at age one was fixed to zero. Transition of pre-breeder to breeder ($\psi^{N\text{-}B}$) was fixed at zero for age one.
2. Breeder recapture from age two upwards was fixed at 1 as almost every nest attempt is found and breeders identified.
3. A bird cannot exist in the post-breeder state (PO) until three years at the youngest, therefore survival and *P* at age one and two were fixed at zero. $\Psi^{B\text{-}PO}$ was not possible until age three and fixed accordingly.
4. $\psi^{PO\text{-}B}$ may only occur by four years old at the earliest, and a bird must have passed through breeder prior to this.
5. Transitions $\psi^{B\text{-}N}$, $\psi^{PO\text{-}N}$ and $\psi^{N\text{-}PO}$ are not possible.

Appendix 5.5 Parameter estimates generated by the most parsimonious model (model 12, Table 5.4) according to AIC weight, examining the number of fledglings per clutch in response to disease periods. 'No. of Fledglings' is the parameter estimate transformed and compares supplementary fed (SF1) and non-supplementary fed (SF0) nests. *Pre:* 1993/94 - 2003/04. *Early*: 2004/05. *Outbreak*: 2005/06. *Post*: 2006/07- 2013/14. S.E = standard error; LSE = lower standard error; USE = upper standard error.

PairSF	Disease Period	Parameter Estimate	SE	**No. of Fledglings**	LSE	USE
SF1	Pre	0.406	0.289	**1.500**	1.124	2.002
SF1	Early	-1.516	1.228	**0.220**	0.064	0.750
SF1	Outbreak	-0.094	0.255	**0.910**	0.706	1.174
SF1	Post	0.561	0.041	**1.753**	1.682	1.827
SF0	Pre	-0.492	0.221	**0.612**	0.490	0.763
SF0	Early	-0.560	0.500	**0.571**	0.347	0.942
SF0	Outbreak	0.319	0.213	**1.375**	1.111	1.702
SF0	Post	0.044	0.105	**1.046**	0.941	1.161

Appendix 5.6 Parameter estimates generated by the most parsimonious model (model 12, Table 5.5) from the model set examining egg to fledge survival probability per clutch in response to disease. 'Egg to fledge probability' is the parameter estimate transformed and compares supplementary fed (SF1) and non-supplementary fed (SF0) nests. *Pre:* 1993/94 - 2003/04. *Early*: 2004/05. *Outbreak*: 2005/06. *Post*: 2006/07-2013/14. S.E = standard error; LSE = lower standard error; USE = upper standard error.

PairSF	Disease Period	Parameter Estimate	SE	**Egg to fledge probability**	LSE	USE
SF1	Pre	0.922	0.668	**0.715**	0.563	0.831
SF1	Early	-12.228	6.528	**0.000**	0.000	0.003
SF1	Outbreak	-0.977	0.649	**0.274**	0.164	0.419
SF1	Post	0.682	0.114	**0.664**	0.638	0.689
SF0	Pre	-1.259	0.400	**0.221**	0.160	0.298
SF0	Early	-1.179	0.572	**0.235**	0.148	0.353
SF0	Outbreak	-0.044	0.298	**0.489**	0.415	0.563
SF0	Post	-0.397	0.164	**0.402**	0.363	0.442

Appendix 5.7 Parameter estimates generated by the most parsimonious model (model 10, Table 5.6) from the model set examining hatching probability per clutch in response to disease. 'Hatching probability' is the parameter estimate transformed and compares supplementary fed (SF1) and non-supplementary fed (SF0) nests. *Pre:* 1993/94 - 2003/04. *Outbreak*: 2002/03-2005/06. *Post*: 2006/07-2013/14. S.E = standard error; LSE = lower standard error; USE = upper standard error.

Pair SF	Disease Period	Parameter estimate	SE	**Hatching Probability**	LSE	USE
SF1	Pre	2.485	1.041	**0.9231**	0.8091	0.9714
SF1	Outbreak	-0.0573	0.4971	**0.4857**	0.3648	0.6082
SF1	Post	1.2966	0.1197	**0.7853**	0.7644	0.8048
SF0	Pre	1.8083	0.4498	**0.8592**	0.7955	0.9053
SF0	Outbreak	0.4031	0.3118	**0.5994**	0.5228	0.6715
SF0	Post	0.5881	0.1549	**0.6429**	0.6066	0.6777

Appendix 5.8 Parameter estimates generated by the model 12, Table 5.6 from the model set examining hatching probability per clutch in response to disease. ‘Hatching probability’ is the parameter estimate transformed and compares supplementary fed (SF1) and non-supplementary fed (SF0) nests. *Pre:* 1993/94 - 2003/04. *Early*: 2004/05. *Outbreak*: 2005/06. *Post*: 2006/07 -2013/14. S.E = standard error; LSE = lower standard error; USE = upper standard error.

PairSF	Disease Period	Parameter Estimate	SE	**Hatching probability**	LSE	USE
SF1	Pre	1.838	0.407	**0.863**	0.807	0.904
SF1	Early	0.541	0.666	**0.632**	0.469	0.770
SF1	Outbreak	-0.718	0.774	**0.328**	0.184	0.514
SF1	Post	1.297	0.120	**0.785**	0.764	0.805
SF0	Pre	1.249	0.331	**0.777**	0.715	0.829
SF0	Early	-0.004	0.446	**0.499**	0.389	0.609
SF0	Outbreak	1.129	0.347	**0.756**	0.686	0.814
SF0	Post	0.588	0.155	**0.643**	0.607	0.678

Appendix 5.9 Parameter estimates of pre-breeder survival (N) generated from the most parsimonious Disease and Supplementary feeding model 23, Table 5.8.

Disease Period	**Age Class**	**Survival ϕ Estimate**	**Standard Error**	**LCI**	**UCI**
Pre	1	0.827	0.060	0.767	0.887
During	1	0.941	0.038	0.903	0.980
Post	1	0.612	0.034	0.578	0.646
Pre	2	0.934	0.070	0.863	1.000
During	2	1	437E-05	0.999	1.000
Post	2	0.588	0.040	0.548	0.628
Pre	3	1	0	1	1
During	3	1	3E-07	1	1
Post	3	0.8018	0.061	0.741	0.862
Pre	4	1	0	1	1
During	4	0.998	0.014	0.984	1.001
Post	4	0.729	0.040	0.689	0.769

Appendix 5. 10 Table summarising the data contributing to the recapture file used to examine survival in association with disease periods.

	Season																				**Total**
	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	
Total number of Individuals marked (ringed in the nest and successfully fledged)																					
SF1	0	0	0	0	0	0	3	5	10	11	17	35	56	79	96	109	106	112	132	NA	771
SF0	2	3	3	7	11	18	4	15	11	5	14	22	15	22	17	23	18	15	24	NA	249
All	**2**	**3**	**3**	**7**	**11**	**18**	**7**	**20**	**21**	**16**	**31**	**57**	**71**	**101**	**113**	**132**	**124**	**127**	**156**	NA	**1020**
Counts of re-sightings per state (N, B and P) and group (SF0 and SF1)																					
N, SF1	0	0	0	0	0	0	0	1	0	2	6	8	28	32	56	62	99	60	75	52	429
N, SF0	0	0	0	0	2	11	11	18	3	14	14	17	57	29	20	15	29	10	10	9	260
																					689
B, SF1	0	0	0	0	0	0	0	0	0	3	7	13	22	28	33	48	63	72	98	104	491
B, SF0	0	0	0	0	0	2	3	6	15	17	26	30	32	38	38	38	42	38	45	40	410
																					901
P, SF1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	4	2	1	2	4	15
P, SF0	0	0	0	0	0	0	0	0	0	1	0	0	6	0	1	8	10	5	3	7	41
																					56

Appendix 6.1 Methodology employed to examine the relationship between the probability of a breeding pair being classified as supplementary fed (SF1) in relation to the distance to the nearest artificial feeding station (AFS).

Distances between each nest and the nearest feeding stations were calculated in kilometres using the open source software QGIS (QGIS Development Team, 2015). Using programme R version 3.3.1(R Development Core Team 2016) I determined the probability of feeder use by breeding pairs in relation to distance between their nest site and the nearest feeding stations. Using a generalized linear mixed effects model (GLMM) in package 'lme4' (Bates *et al.* 2015), I modelled distance to the nearest feeder as a predictor of PairSF. "PairSF" describes the two-level factor of being SF1 or SF0. Built with binomial error family and logit link function, distance was highly significant as a predictor of PairSF, with the probability of using SF declining as distance increased (*P*=<0.001). Predictions from the model output revealed a definitive change in probability at a distance of 2km, taking the probability of using SF from 98% to <5% at 3km (Fig 4.2).

A multi-variate model tested whether the effect persisted. This included individual and environmental qualities which may have had confounding effects on the impact of SF, or may have worked to falsely report an apparent relationship between distance and use of SF. Distance to the nearest hopper remained a significant predictor of feeder use. Whilst informative at a spatial scale, the two-level classification of PairSF was considered a more direct measure of the role of SF in breeding attempts and thus formed the independent variable in subsequent analysis.

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Thankyou