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Exploring the implications of climate trends and extreme weather events for species conservation in Mauritius

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Declaration

I confirm that the work presented in this thesis is my own, with the following exceptions:

> Chapter 4 is adapted from a manuscript co-authored by Malcolm Nicoll, Emily Black, Caroline Dunning, Carl Jones, Vikash Tatayah, Pier Luigi Vidale and Ken Norris. My own contribution to the analysis and writing is estimated to be 80%.
>
> The analysis of rainy season onset and cessation in Chapter 4 was carried out by Caroline Dunning.
>
> Chapter 5 is adapted from a draft manuscript co-authored by Malcolm Nicoll, Emily Black, Carl Jones, Vikash Tatayah, Pier Luigi Vidale and Ken Norris. My own contribution to the analysis and writing is estimated to be 90%.

The use of all material from other sources has been properly and fully acknowledged.

Joseph Taylor
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This thesis is dedicated to Andy Taylor.
He helped to foster my interest in the natural world, but sadly has not been able to see me achieve all my ambitions relating to ecology and conservation.

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Abstract

Species conservation is expected to become more challenging in a changing climate, and this may be most acute in the speciose tropics, where species are generally adapted to a narrow temperature range from which novel climates are projected to emerge this century. Island endemic species are expected to show particularly low adaptive capacity. Yet, climate change vulnerability assessments are constrained by a shortage of detailed and long-term datasets, uncertainty over the impacts of extreme events, and poor understanding of implications for tropical animal phenology. These knowledge gaps limit our capacity to design management strategies to alleviate the impacts of future climate risks.

This thesis explores these issues for species in Mauritius, where successful recovery programmes have involved the collection of detailed individual-based datasets. Long-term climate trends, including for extremes, were quantified for areas of high conservation importance. Detailed analyses were carried out into climate impacts on the breeding phenology and demography of the Mauritius kestrel (*Falco punctatus*) and echo parakeet (*Psittacula eques*).

Climate trend analyses reveal local-scale variation in long-term trends, with nearby populations of conservation concern under different pressures from changes in rainfall. Detailed analysis for the Mauritius kestrel shows that its breeding phenology is tracking shifts in a seasonal climate window. Individual birds show plasticity in response to temperature increases, despite the effects of a severe population bottleneck. In contrast, echo parakeets show maladaptive adjustments to climate variability, with delayed breeding in drier years increasing exposure to tropical cyclones. Cyclones appear to mediate reproductive senescence, but this risk is reduced through the re-scheduling of breeding by supplementary food provision.

Based on these results, vulnerability assessments and management plans for restricted-range species, such as those endemic to tropical islands, should incorporate local-scale climate trends, meteorological indices for extremes, and analysis of phenology and temporal exposure to climate risks.

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Chapter 1

Introduction

1.1 Biodiversity conservation in a changing climate

Humans are having profound impacts on the Earth's natural systems, including biodiversity loss through habitat destruction and degradation, pollution, the introduction of non-native species and human-induced climate change, such that it has been argued that the current geological epoch should be classed as the Anthropocene (Zalasiewicz *et al.*, 2008; Zalasiewicz *et al.*, 2011). The contemporary rate of global extinctions is estimated to be 100-1000 times higher than background rates without human-caused processes (Pimm *et al.*, 1995), prompting discussion of whether we are entering or in the midst of a sixth mass extinction event (e.g. Barnosky *et al.*, 2011). Global indices estimate that vertebrate populations have halved since 1970 (WWF, 2016), and overall are becoming more threatened with extinction (Hoffmann *et al.*, 2010). The loss of species and ecosystems, and degradation of habitats, threatens important ecosystem services that human society relies upon and values, such as water and climate regulation, nutrient cycling and cultural enrichment (e.g. Costanza *et al.*, 1997; Díaz *et al.*, 2006).

Temperature trends in many regions of the world have already departed from the trend expected from natural influences (forcings) and variability alone (IPCC, 2014). The three warmest years on record have been 2015, 2016 and 2017, with 2017 being the warmest without an El Niño event, and all three years have exceeded a warming of 1°C above pre-industrial (1880-1900) conditions (WMO, 2018). There is compelling evidence that most of the recent warming in the global climate is attributable to anthropogenic interference with the climate system, primarily through greenhouse gas emissions (e.g. IPCC, 2014). In 2016, the average monthly atmospheric carbon dioxide (CO_2) concentration exceeded 400 ppm for the first time in at least 800,000 years (WMO, 2018). Two thirds of the total atmospheric carbon quota consistent with a 2°C rise in temperature has already been emitted (Friedlingstein *et al.*, 2014), meaning that human society has already committed to continued warming.

Current international targets aim for the global mean temperature to be kept below an increase of 2°C relative to pre-industrial levels, with efforts to limit this to an increase of 1.5°C (UNFCCC, 2015). In order to achieve this, it is likely that a global peak in fossil fuel emissions will be needed in c.2020-2030, after which emissions must decline (IPCC, 2014; Rogelj *et al.*, 2016). Emissions targets set by recent international agreements and subnational actors imply that progress is being made; however, this may not be sufficient to limit warming to below 2°C (Rogelj *et al.*, 2016).

The projected rate of climate change, based on plausible emissions scenarios, exceeds natural changes that have occurred in the past 10,000 years (Hurrell and Trenberth, 2010). While the velocity of warming has been most rapid at higher latitudes, particularly in the Northern Hemisphere, tropical regions will be among the first areas to emerge from recent climate variability into relatively novel climate regimes, owing to more limited intra- and interannual variability (Mora *et al.*, 2013; Hawkins *et al.*, 2014a). Novel climates are projected to emerge this century, with tropical and subtropical regions being among the first (Williams *et al.*, 2007). Temperatures are projected to emerge from variability in many tropical countries by the 2030s (Mahlstein *et al.*, 2011). In general, precipitation is projected to increase in the wetter areas of the world and decrease in drier areas (IPCC, 2014), although trends will not necessarily be monotonic (Hawkins *et al.*, 2014b).

Compelling evidence implies that climate change is already having impacts on a broad range of biological systems, including changes in the timing of life-history events (phenology) and shifts in the geographical and elevational ranges of species, as the distributions of suitable climate conditions change (Parmesan and Yohe, 2003; Rosenzweig *et al.*, 2008). There is a growing body of research into the vulnerability of species to climate change and the prediction of climate change impacts on biodiversity. Climate change vulnerability is often based on a framework of exposure, sensitivity and adaptive capacity (Williams *et al.*, 2008; Dawson *et al.*, 2011; Moritz and Agudo, 2013). The methods that have been used to model species vulnerability to climate change can be categorised as 1) spatially correlative, 2) mechanistic uses of detailed impact parameters, and 3) approaches that use species traits (Pacifici *et al.*, 2015).

Increasing numbers of species are projected to become vulnerable to climate change impacts (Foden *et al.*, 2013), and climate change may result in increased extinction rates during the 21st century (Pereira *et al.*, 2010; Urban, 2015), although this will depend on modes of resilience and adaptation (Urban, 2015; Urban *et al.*, 2016). Climate change-caused extinctions may occur through a variety of processes, perhaps most importantly through the disruption of species interactions, including changes in food availability (Cahill *et al.*, 2012). For example, phenological shifts can result in trophic mismatch, in which the timing of a life-history event, such as reproduction, in one species moves out of synchrony with a peak in abundance in an important prey species (reviewed by Miller-Rushing *et al.*, 2010). The implications of climate change for the phenology of temperate animal populations have been well studied; however, much less is known about the implications for animal populations in the tropics (Rosenzweig *et al.*, 2008; Charmantier and Gienapp, 2013; Cohen *et al.*, 2018). Other mechanisms through which climate change could cause extinctions or negatively impact demographic vital rates include direct effects on physiology (Cahill *et al.*, 2012). The magnitude of global warming is expected to influence impacts on biodiversity, and it has been projected that mitigation to limit warming would reduce impacts on species (Warren *et al.*, 2013; Smith *et al.*, 2018; Warren *et al.*, 2018). It is important to recognise that climate change does not affect natural systems in isolation, but does so in concert and synergy with other processes, such as habitat fragmentation and alien species introductions (Parmesan *et al.*, 2000).

Influential global reviews of climate change impacts on species often have geographical and taxonomic biases owing to limitations in data availability, with insufficient coverage of tropical and marine species, plants and ectothermic animals (Feeley *et al.*, 2016). Changes in the tropics are of great concern, given that at least 78% of all species occur at tropical latitudes, including 91% of terrestrial birds species (Barlow *et al.*, 2018). Tropical species may be some of the most vulnerable to climate change, owing to their adaptation to a relatively narrow range of conditions (Deutsch *et al.*, 2008). Among those, tropical island species are expected to be particularly vulnerable to global change (Fordham and Brook, 2010). Globally, islands are particularly rich in biodiversity, but they are acutely vulnerable to human impacts. The global total of over 180,000 islands (up to 786,000 km^2 in land area) harbour more than 20% of all terrestrial plant and vertebrate species within less than 5% of total land extent (Kier *et al.*, 2009; Bellard *et al.*, 2014; Courchamp *et al.*, 2014). Species endemism on islands exceeds that in mainland areas by factors of 8.1 and 9.5 for vertebrates and plants respectively (Kier *et al.*, 2009). However, the longer-term isolation of insular biotas is linked with an increased vulnerability to invasive species (Berglund *et al.* 2009). Limited population size, habitat area and genetic diversity in island species can increase susceptibility to new pressures (Strauss *et al.*, 2006). Furthermore, island species have limited scope for range shifts in response to climate change (Foden *et al.*, 2013). Long-term demographic studies into the impacts of climate change on tropical species and ecosystems are greatly needed as the projection of impacts is constrained by a paucity of such data (Brawn *et al.*, 2017). The need is arguably very acute for island biota, owing to their high vulnerability and the impacts of other threats.

The protection of species and continued recovery of threatened species is expected to become more challenging as pressures from climate change intensify (Dawson *et al.*, 2011). Conservation actions will require new strategies, as protected areas may provide only limited refuge from the impacts of climate change (Monzón *et al.*, 2011). Adaptive management strategies could represent the necessary response for reducing the vulnerability of species (Stein *et al.*, 2013); however, detailed studies are needed to provide baseline data and to quantify climate impacts. Four common challenges, which are usually neglected, have been identified in the planning of conservation actions for species under climate change, including the need to consider sensitivity and adaptive capacity in addition to exposure, the importance of changes in extreme events and not only gradual changes, taking into account current impacts as well as future impacts, and considering the interactions of climate change impacts with other threats (Butt *et al.* 2016). Climate change, in conjunction with other threats, is putting the Earth's natural heritage and important ecosystem services at risk. A better understanding of the ecological impacts of climate change is needed if the majority of species and ecosystems are to be protected.

1.2 Climate change and extreme events

Strong evidence indicates that, as well as changes in global average conditions such as temperature and precipitation, projected climate change is likely to be accompanied by changes in the occurrence of extreme weather events, also termed extreme climate or climatic events and hereafter referred to as 'extreme events'. Changes are projected in their frequency, intensity, extent, duration and timing (e.g. IPCC, 2014). Such changes are frequently cited in discussions of "dangerous anthropogenic interference with the climate system", due to the potential implications for human society and natural systems (IPCC, 2014). Extreme events are typically defined by their rarity and severity, and may include tropical and extra-tropical cyclonic storms, other severe convective storms and heavy rainfall events, droughts and temperature extremes (Stephenson, 2008). Evidence indicates that climate change is already driving changes in extreme events, with much recent evidence coming from the developing area of event attribution (NAS, 2016). Increases in average temperature increase the risk of very hot events, can lead to increases in evaporation that worsen droughts, and increase the moisture content of the atmosphere and thus the risk of very heavy precipitation (NAS, 2016).

Increases in the frequency of extreme heat events have been linked to anthropogenic changes to the climate. For example, King *et al.* (2016) found a significant human contribution to the probability of record-breaking global temperature events as early as the 1930s, with all of the last 16 record-breaking hot years globally since then having an anthropogenic contribution to their probability of occurrence. In the absence of changes to circulation patterns and relative humidity, thermodynamic factors suggest that extreme precipitation intensity should increase with increasing global mean surface temperature, scaling at about 7% per 1°C increase, as expressed by the Clausius-Clapeyron equation, which describes that capacity of the atmosphere to hold moisture. However, some studies report a scaling of extreme precipitation above this rate (reveiwed by Wasko *et al.*, 2016). The intensity of daily precipitation and proportion of rainfall occurring on extreme precipitation days are projected to increase across wide portions of global land area over the course of the 21st century, based on a climate change scenario with high greenhouse gas emissions (Representative Concentration Pathway [RCP] 8.5) (Giorgi *et al.*, 2014). Increases in the probabilities of daily extreme heat and precipitation events are projected to be substantially greater under 2°C of warming compared with 1.5°C (Kharin *et al.*, 2018). Human influences on the probability of particular events can be estimated. For example, anthropogenic climate change is likely to have increased the chances of the extreme rainfall observed in the southern USA that was associated with Hurricane Harvey in 2017 (Risser and Wehner, 2017). The occurrence of extreme precipitation is expected to be influenced by changes in the magnitude and frequency of large-scale dipole events, such as the El Niño-Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) (Cai *et al.*, 2014; Cai *et al.*, 2015; Cai *et al.*, 2018), in which sea surface temperature anomalies shift in distribution in the tropical Pacific and Indian Oceans respectively, influencing regional convection and rainfall patterns.

Climate models project increased aridity in the 21st century, with drying expected over most of Africa, southern Europe, the Middle East, most of the Americas, Australia and South-East Asia (Dai, 2011). Parts of these regions, so-far unaffected by serious droughts, may see a switch to persistent severe droughts in the coming decades (Dai, 2011). The consistency of observed global aridity changes between 1950 and 2010 and model simulations suggest that severe and widespread droughts will occur over many land areas during the next 30-90 years, caused by either reduced precipitation or increased evaporation (Dai, 2013). Trenberth *et al.* (2013) point out that global warming may not function to ‘manufacture’ droughts, but could exacerbate them and expand their coverage in the subtropical dry zone. This would result from increased heat in the climate system causing droughts to be quicker in their onset, more intense, and being more protracted and spatially extensive (Trenberth *et al.* 2013).

It may be too early to reliably infer trends in tropical cyclone characteristics and links to climate change, as satellite data are only available since the early 1960s (Dvorak, 1984), and because of disagreement over how these data are interpreted (Walsh, 2004; Pielke *et al.*, 2005). However, studies continue to produce evidence of trends and links to climate change, including an increase in the peak intensity of the strongest tropical cyclones globally since the early 1980s (Elsner *et al.*, 2008; Kossin *et al.*, 2013). A study by Kishtawal *et al.* (2012) found evidence that, over the period 1986-2010, tropical cyclones in most basins exhibited increases in the speed of intensification. The use of global climate models for projecting future trends is repeatedly indicating that under scenarios of continued greenhouse gas emissions tropical cyclones will become less frequent or show little change in frequency globally, but with an increase in the number of very intense storms and an increase in rainfall rates (Bengtsson, 2007; Knutson *et al.*, 2010; Bell *et al.*, 2013; Walsh *et al.*, 2016; Bacmeister *et al.*, 2018). At least one recent study (Emanuel, 2013) has projected increases in both the frequency and intensity of tropical cyclones globally over the next century under RCP 8.5. In line with predictions for a warming atmosphere, the movement (translation speed) of tropical cyclones appears to have slowed since the mid-20th century, with implications for rainfall totals at landfall (Kossin, 2018).

1.3 The ecological impacts of extreme events

Extreme events are usually omitted from studies that project future climate change impacts on biodiversity. This is largely owing to a lack of understanding about their impacts and what factors make species more or less vulnerable. Indeed, research on the effects of disasters on natural communities remains uncommon owing to the unpredictability of disasters and generally poor baseline data (Johnson and Winker, 2010). Yet, it has been argued that changes in the frequency and intensity of extreme events may pose a greater threat to ecosystem functioning than shifts in global average temperatures and precipitation regimes (Jentsch and Beierkuhnlein, 2008). It is notable that climate and weather played a role in around a quarter of documented mass mortality events in nonhuman animal taxa, particularly birds and mammals, between 1940 and 2010 (Fey *et al.*, 2015). The potential implications of extreme events in negatively impacting the survival and reproductive success of individuals form a recipe for population extinction (Moreno and Møller, 2011).

Climate and weather extremes are difficult to study because such events are rare and their ‘extremeness’ is very context-dependent in terms of the historic climate record and what a given area or location has experienced in the past (Smith, 2011). This has resulted in a lack of consistency in how extremes are defined in ecological studies, ranging from the use of meteorological definitions of rarity and intensity, or biological definitions based on impacts, with proposed hybrid definitions that incorporate both meteorological and biological thresholds (Smith, 2011; Bailey and van de Pol, 2016; van de Pol *et al.*, 2017). However, such hybrid definitions, with two or more thresholds, may actually limit the ability of research to identify all biologically important events. It is argued that more consistency in the terminology and definitions used for extreme events is needed in ecological research (van de Pol *et al.*, 2017).

Research into the impacts of extreme events on natural systems gathered pace with other avenues of ecological research in the late 20th century, but despite this our understanding remains limited. Extreme events have been documented as impacting ecological communities, usually with detrimental consequences. Research has focussed particularly on the impacts of high wind speeds on forests and trees (reviewed by Lugo *et al.*, 2000; Lugo, 2008; Mitchell, 2013). Numerous studies have looked at the impacts of tropical cyclones on birds (e.g. Johnson and Winker, 2010) and corals (e.g. Lugo *et al.*, 2000), with occasional studies on other taxa, such as amphibians (e.g. Luja and Rodriguez-Estrella, 2010), insects (e.g. Grimbacher and Stork, 2009) and arachnids (e.g. Schoener and Spiller, 2006). Research into drought impacts has spanned many taxa, including trees (reviewed by Allen *et al.*, 2010), mammals (e.g. Foley *et al.*, 2008) and birds (e.g. Butler *et al.*, 2014; Selwood *et al.*, 2015). Extreme events have also been linked with the spread of alien invasive species (Bellingham *et al.*, 2005; Hellmann *et al.*, 2008; Bhattarai and Cronin, 2014). It is possible that there is a publication bias towards reporting significant negative impacts. Some positive or ambiguous impacts of extreme events have also been noted, including the role of tropical cyclones in the maintenance of species diversity in tropical forests (Murphy *et al.*, 2014) and positive correlations between regional cyclone activity and age-dependent survival in seabirds (Nicoll *et al.*, 2017).

Much research on the ecological impacts of extreme events has been opportunistic because of the unpredictable nature of such events, and most studies have only provided one or a few 'snapshots' of a study system. Studies that use 'before and after' data are powerful in presenting individual case studies of extreme events; however, it is argued that there is a need for longer-term studies that look at the impacts of multiple events (Bailey and van de Pol, 2016). There have been many calls for more research on the ecological impacts of extreme events, including for species vulnerability studies (Chapman *et al.* 2014) and spatial conservation prioritisation (Jones *et al*. 2016). It is difficult to generalise about the effects of extreme events on populations and ecosystems (van de Pol *et al.*, 2017; Harris *et al.*, 2018; Sergio *et al.*, 2018), and it may be helpful to view the ecological effects of extreme events as 'responses', rather than 'impacts' (Sergio *et al.*, 2018). In a broader sense, extreme events are seen as contributing to a 'press and pulse' dynamic in climate change effects (Harris *et al.*, 2018). In addition, the timing of extreme events is known to influence their impacts on demography (van de Pol *et al.*, 2017; Sergio *et al.*, 2018).

We still have a poor understanding of the selection pressures that result from extreme events and how the species and ecosystems that are cyclically exposed to high intensity natural disturbances respond to such pressures (Luja and Rodriguez-Estrella, 2010). It has been argued that extreme events tend to exert 'truncation selection', where mass mortality occurs in a population on one side of a phenotypic threshold (Moreno and Møller, 2011). It has also been argued that extreme events cause selection at the species or phyla levels, rather than at the individual level (Combes, 2008). Species-level selection due to extreme events has been documented for a desert rodent community in the south-western USA, where flooding caused differential mortality among already competing species and reset the community composition (Thibault and Brown, 2008). However, the view advocated by Combes (2008) somewhat neglects the potential importance of individual variation in physical and behavioural resilience to extreme events. Evidence for an island lizard species suggests that hurricanes can exert rapid phenotypic selection on populations (Donihue *et al.*, 2018).

The contemporary impacts of extreme events on natural systems must be viewed in the context of the pressures exerted by human activities. The modern human-dominated landscape, with its inherent fragmentation, degradation and depletion of populations and habitats, has likely altered the potential for species and ecosystems to exhibit resilience and adaptation to future climate change (Parmesan *et al.*, 2000). Extreme events may also act in synergy with human impacts, as has apparently been the case with the critically endangered Chinese crested tern (*Thalasseus bernsteini*) (Chen *et al.*, 2015). This species is impacted by egg-harvesting and increasingly frequent typhoons, and apparently the interaction of these threats, where egg harvesting results in later re-nesting and increased exposure to typhoons (Chen *et al.*, 2015). Furthermore, the impacts of extreme events on humans can cause increases in the pressures that they exert on ecosystems, as descriptively studied in the Louisiade Archipelago of Papua New Guinea after the occurrence of Cyclone Ita in 2014 (Goulding *et al.*, 2016). While conservation actions aim to tackle threats to species and ecosystems, extreme events may directly threaten the conservation actions themselves and the gains already made through the investment of substantial resources and effort. For example, the eradication of introduced rats (*Rattus* spp.) through baiting on the island of Honuea in the Society Islands of French Polynesia failed when Tropical Cyclone Oli caused the entire island to be flooded in January 2010 (Courchamp *et al.*, 2014).

Discussions about the needs and methods for human adaptation to projected climate change have put increasing weight on ecosystem-based adaptation (e.g. Royal Society, 2014) and the concept of social-ecological systems (e.g. Folke *et al.*, 2005), in which human communities and nature are recognised as tightly coupled, if usually also imbalanced. The ecological impacts of changes in extreme events are therefore increasingly relevant to wider human society, and there remains a need to reconcile the needs of biodiversity and human society when building resilience. Developing a resilience management framework for natural systems requires an understanding of a community's resilience potential and processes, and its response to disturbance (Johnson and Winker, 2010). The resilience of populations to extreme events may be studied through trends in abundance and breeding activity during and after events, as has been applied to drought-impacted birds in Australia (Selwood *et al.*, 2015). However, the resilience of an ecosystem to extreme events may also be defined by the historical range of variation (HRV) of some of its attributes and how long it takes to return to the HRV after an event (Seidl *et al.*, 2016).

1.4 Biodiversity and climate change in Mauritius

Mauritius is an icon of both species extinction and species conservation. It is one of the few countries to have made gains in the conservation status of vertebrate biodiversity in recent decades (Rodrigues *et al.*, 2014). The island has lost many species since colonisation by humans in the 17th century, and is a microcosm of threats affecting species worldwide. However, since the 1970s targeted conservation efforts have been successful in preventing extinctions. Future environmental change may threaten the gains made through these resource-intensive conservation programmes. Anecdotal observations for some species in Mauritius suggest that they are impacted by extreme events. Declines have been noted after cyclones in some bird populations in Mauritius (Jones, 1987). However, the long-term demographic impacts of such events on these species have not been investigated in detail before now.

There are already clear signs of climate change in Mauritius, with temperature increases and decreases in precipitation recorded since the mid-20th century (Republic of Mauritius, 2010, 2016). Trend analyses indicate an area of rapid warming in the central South Indian Ocean (e.g. WMO, 2018). Projections suggest that mean annual temperatures in Mauritius will increase by 1.0-2.0°C by the 2060s and by 1.1-3.4°C by the 2090s (McSweeney *et al.*, 2010a, b). Previous research indicates that rainfall has been increasing in the Bambous Mountains in eastern Mauritius (Senapathi *et al.*, 2010), although island-wide analyses suggest that rainfall has been decreasing overall (Republic of Mauritius, 2010, 2016). Projections from different models of mean annual rainfall in Mauritius vary widely, ranging from negative to positive changes during the 21st century (McSweeney *et al.*, 2010a, b).

It appears that the Indian Ocean region is already experiencing changes in the frequency and intensity of extreme events and further changes are projected in the future, although the trends are mixed. While Elsner *et al.* (2008) find evidence that the peak intensity of the strongest tropical cyclones in the Indian Ocean has increased since the early 1980s, Kuleshov *et al.* (2010) do not find robust evidence for any trends in the overall number of cyclones and number of severe cyclones in the South Indian Ocean from 1981-1982 to 2006-2007. In the Southwest Indian Ocean there has been an increasing trend in the number of severe cyclone days (with Saffir-Simpson category 3 storms and above) since the 1970s, with a steady decline in the total number of cyclones in this region since the 1960s (Malan *et al.*, 2013). Historical analysis also indicates that the formation of tropical cyclones in the South Indian Ocean shifts westward in El Niño years (Ho *et al.*, 2006), implying that Mauritius could be affected by cyclones more often if the frequency of El Niño events increases. However, in line with most global projections, high-resolution modelling by Gleixner *et al.* (2014) supports a prediction of fewer tropical cyclones occurring in the South Indian Ocean in the last three decades of the 21st century. In the vicinity of Mauritius, overall cyclone frequency is projected to decrease (Muthige *et al.*, 2018); however, there is a projected increase in very strong cyclones in the vicinity of the Mascarene archipelago and Madagascar (Bacmeister *et al.*, 2018).

Climate change could also influence the frequency and intensity of droughts and heavy rainfall affecting Mauritius. Data from countries in the western Indian Ocean, collected during the period 1961-2008, indicate a significant decrease in total annual rainfall and an increase in the number of consecutive dry days in the region, although the latter trend is not statistically significant (Vincent *et al.*, 2011). Climate modelling has shown that under a high greenhouse gas emissions scenario (RCP 8.5) the frequency of positive Indian Ocean Dipole (IOD) events (when sea surface temperatures are lower than average off the Sumatra-Java coasts and higher than average in the tropical western Indian Ocean) is projected to increase from one every 17.3 years in the 20th century, to one every 6.3 years over the 21st century, leading to increased frequency in extreme events in the Indian Ocean region, including droughts and flooding rains (Cai *et al.*, 2014). Indeed, extreme positive IOD events are projected to double in frequency under 1.5°C of warming compared to pre-industrial levels (Cai *et al.*, 2018), although the implications for Mauritius are uncertain.

This study utilises detailed and long-term individual-based datasets on two globally threatened bird species, which provide ideal case studies of climate impacts on threatened species. These species, the Mauritius kestrel (*Falco punctatus*) and echo parakeet (*Psittacula eques*), a raptor and psittacine species respectively, capture different biological characteristics, ecological requirements and environmental conditions. They also receive different levels of management that could buffer the effects of environmental conditions. Both species have recovered from extreme population bottlenecks, owing to dedicated conservation work. The intensive conservation work that these species have received has also entailed the gathering of detailed monitoring data on individual breeding attempts.

1.5 Direct climate impacts on raptor and psittacine species

It is well documented that climate has a strong influence on breeding success in many raptor species. However, many studies carried out to date rely on correlation analysis using annual summary metrics for breeding success and seasonal climate variables, and most evidence comes from populations in temperate regions of the Northern Hemisphere. The negative impacts of rainfall are well known and have been recorded in peregrine falcons (*F. peregrinus*) (Mearns and Newton, 1988; Olsen and Olsen, 1988; Bradley *et al.*, 1997; Anctil *et al.*, 2014; Lamarre *et al.*, 2018), with substantial effects from rainfall events of 8 mm day^{-1} and greater (Anctil *et al.*, 2014; Lamarre *et al.*, 2018), as well as northern goshawks (*Accipiter gentilis*) (Lehikoinen *et al.*, 2013) and common buzzards (*Buteo buteo*) (Lehikoinen *et al.*, 2009). Eurasian kestrels (*F. tinnunculus*) in Austria show higher breeding success after dry conditions early in the breeding season (Kreiderits *et al.*, 2016). However, in drier environments, rainfall prior to and early in the breeding season has a positive effect, as shown for populations of Eurasian kestrels on Tenerife in the Canary Islands (Carrillo and González-Dávila, 2010b) and in Italy (Costantini *et al.*, 2010). A positive effect from rainfall during the nestling stage has also been shown for golden eagles (*Aquila chrysaetos*) breeding in California, USA, during extreme drought conditions (Wiens *et al.*, 2018). For lesser kestrels (*F. naumanni*) breeding in south-western Spain, breeding success is impacted positively by rainfall prior to the nestling period, and negatively by rainfall during the nestling period (Rodríguez and Bustamente, 2003).

The mechanisms of negative impacts from rainfall in raptor species are thought to be through food limitation, perhaps due to decreased hunting efficiency, and direct exposure (e.g. Mearns and Newton, 1988). Peregrine falcons breeding in the Canadian Arctic showed reduced productivity and prey delivery rates during a season with increased rainfall (Robinson *et al.*, 2017). Fisher *et al.* (2015) show that burrowing owls (*Athene cunicularia*) in Canada experience reduced nest survival during extreme precipitation events (≥20 mm day^{-1}), due to the flooding of burrows. A food supplementation experiment showed that extreme precipitation also reduced nestling survival through food limitation (Fisher *et al.*, 2015). Observations of nesting ferruginous hawks (*B. regalis*) in Canada suggest that, although females alter their nest-attendance behaviour when summer rainstorms are approaching, prey delivery rates are similar before and after storms, implying that they do not compensate for lost foraging time (Laux *et al.*, 2016). In some cases, there is no evidence of an effect from rainfall, as shown for the productivity of booted eagles (*Hieraaetus pennatus*) breeding in Spain (Bosch *et al.*, 2015).

There are very few empirical studies on the effects of cyclonic storms on raptor species. Watts and Byrd (2007) show that a hurricane not only directly reduced nesting success in bald eagles (*Haliaeetus leucocephalus*) in coastal Virginia, USA, but appeared to have delayed impacts resulting in lower productivity in the following season in pairs that had been adversely impacted during the hurricane. In contrast, a study on breeding northern goshawks in France found little evidence of adverse impacts from a severe extra-tropical cyclone, suggesting an adaptive response to such disturbance (Penteriani *et al.*, 2002). Surveys following the landfall of Hurricane Patricia in Mexico in 2015 revealed lower densities of diurnal raptors in tropical forest within the area affected by the eyewall (area of strongest winds) compared to forest outside this area (Martínez-Ruiz and Renton, 2018).

Seasonal average temperature often has a positive effect on breeding success, as shown for Eurasian kestrels (Costantini *et al.*, 2010; Kreiderits *et al.*, 2016), Bonelli's eagles (*Hieraaetus fasciatus*) breeding in the western Mediterranean region (Ontiveros and Pleguezuelos, 2003) and common buzzards in Finland (Lehikoinen *et al.*, 2009). However, for lesser kestrels breeding in Portugal extreme hot days are associated with increased mortality and reduced growth rates in nestlings, especially in nest types that retain heat, perhaps due to acute dehydration (Catry *et al.*, 2011). Consideration of a broader range of climate aspects can provide a fuller picture of impacts. For example, nest survival in Mississippi kites (*Ictinia mississippiensis*) in Texas, USA, is negatively impacted by higher temperatures, severe storms, drought conditions and La Niña events (Welch *et al.*, 2017).

Raptor phenology shows influences from both temperature and precipitation, with prey availability often directly implicated. Spring rainfall often has a delaying effect on the timing of breeding, as shown in Eurasian kestrels in Italy (Costantini *et al.*, 2010) and Austria (Kreiderits *et al.*, 2016). In contrast, Eurasian kestrels inhabiting semi-arid areas on Tenerife appear to show earlier breeding in springs that follow wetter autumns (Carrillo and González-Dávila, 2010b). A meta-analysis of studies on Eurasian kestrel populations in the Western Palaearctic showed that the average egg-laying date is earlier in warmer and drier regions (Carrillo and González-Dávila, 2010a). Earlier hatching in northern goshawk nests in Finland is associated with warmer temperatures in late winter and early spring (Lehikoinen *et al.*, 2013).

Some raptor species in temperate regions have shown advances their breeding phenology, apparently in response to climate warming. Such advances have been documented in Cooper's hawks (*Accipiter cooperii*) breeding in Wisconsin, USA, over the period 1980-2015 (Rosenfield *et al.*, 2017), common buzzards in Finland between 1979 and 2004 (Lehikoinen *et al.*, 2009), and Eurasian sparrowhawks (*Accipiter nisus*) in Finland between 1979 and 2009 (Lehikoinen *et al.*, 2010). In contrast, a population of Eurasian sparrowhawks in The Netherlands showed no advancement in hatching dates between 1985 and 2004, despite advances in lower trophic levels (Both *et al.*, 2009). American kestrels (*F. sparverius*) breeding in Idaho, USA, appear to be tracking advances in crop-planting after mild winters and thus advances in prey availability (Smith *et al.*, 2016).

Much less is known empirically regarding climate impacts on psittacine species and this may be linked to a paucity of long-term ornithological studies in the tropics. Rainfall is generally thought to be an important influence on food availability, and thus drought is thought to negatively impact the demography of many species. The abundance of some parrot species in urban Sydney, Australia, has been shown to be linked with rainfall, as well as local wild fire occurrence, with increased abundances associated with decreases in rainfall (Davis *et al.*, 2011). Similarly, the spatial and temporal extent of drought conditions appear to be linked to the movements of swift parrots (*Lathamus discolor*) in Australia (Saunders *et al.*, 2016). Dynamic occupancy models show that Cape parrots (*Poicephalus robustus*) in South Africa are vulnerable to drought events (Kalle *et al.*, 2018).

Drought conditions, as linked to a La Niña event, appeared to reduce nestling survival and growth rates in burrowing parrots (*Cyanoliseus patagonus*) in Patagonia (Masello and Quillfedt, 2004). Likewise, ENSO phases, and associated patterns in rainfall, have been linked with interannual variation in productivity in lilac-crowned parrots (*Amazona finschi*) in Mexico (Renton and Salinas-Melgoza, 2004). Similarly, nest-site occupancy and productivity in breeding maroon-fronted parrots (*Rhynchopsitta terrisi*) in Mexico are lower after very dry years (Ortiz-Maciel *et al.*, 2014). In Australia, glossy black-cockatoos (*Calyptorhynchus lathami*) appear to show higher productivity when rainfall is higher in the preceding year, probably owing to increased food availability (Cameron, 2009). Temperature and its variability appear to influence nestling growth and fledging success in crimson rosella (*Platycercus elegans*) breeding attempts in nest-boxes in Australia (Larson *et al.*, 2015).

There is mixed evidence for the effects of tropical cyclones on parrot species. In the Dominican Republic, captive-reared and released Hispaniolan parrots (*Amazona ventralis*) showed increased ranging and movements following a strong hurricane, with evidence that they favoured areas with sinkholes, where topography had protected trees from wind damage and defoliation (White *et al.*, 2005). However, survival in Puerto Rican parrots (*Amazona vittata*) is negatively impacted by hurricanes (Beissinger *et al.*, 2008). Cyclones may also disrupt the seasonality of fruiting and therefore food availability in the months following the disturbance (Wunderle, 1999). Little effect from hurricanes was found in the nesting activity of maroon-fronted parrots in Mexico (Ortiz-Maciel *et al.*, 2014). Many bird species are vulnerable to direct mortality from spatially and temporally discrete severe weather events, such as hailstorms and heat waves, as recorded for the short-billed (Carnaby's) black-cockatoo (*Calyptorhynchus [Zanda] latirostris*) in Australia (Saunders *et al.*, 2011).

Evidence indicates that the timing of breeding in parrot species in western Amazonia is influenced by food availability, resulting from fruiting patterns that are linked to seasonal changes in rainfall, although this is based on the average annual cycle rather than interannual variability (Brightsmith *et al.*, 2018). The timing of egg-laying by short-billed black-cockatoos in south-western Australia is strongly linked to early autumn rainfall, probably because of the influence of rain on food availability later in the breeding season (Saunders *et al.*, 2013). Likewise, earlier breeding is favoured by increased pre-breeding rainfall in green-rumped parrotlets (*Forpus passerinus*) in Venezuela (Tarwater and Beissinger, 2013). Monk parakeets (*Myiopsitta monachus*) in Argentina show advances in the timing of egg-laying in warmer springs, with weaker evidence that breeding is delayed by more frequent rainfall (Navarro and Bucher, 1992). This implies that rainfall is not the main influence for all species.

These studies illustrate that climate impacts on raptor and psittacine species are variable and dependent upon species ecology and the local climate. More work is needed, in particular to test thresholds for extreme conditions and to investigate the impacts of tropical cyclones.

1.6 Thesis aims and chapter structure

The aim of this thesis is to improve our understanding of the factors that influence climate change vulnerability in tropical island species and how these factors could affect the design of conservation actions. Importantly, the effects of extreme events are considered in this study. The shortage of long-term datasets and studies on populations in the tropics means that this research is likely to make important contributions regarding tropical species responses to climate change. As part of this research, long-term climate trends are studied in important conservation areas in Mauritius.

The focal population of Mauritius kestrels has been reintroduced to the Bambous Mountains in eastern Mauritius. Previous research indicates that spring rainfall delays breeding and that heavy rainfall later in the breeding season negatively impacts breeding success (Nicoll, 2004; Senapathi, 2009; Cartwright, 2011; Senapathi *et al.*, 2011; Cartwright *et al.*, 2014). The impacts of extreme events and temperature on breeding Mauritius kestrels have not been studied so far, thus the present study extends previous research by considering these additional dimensions of the local climate. The echo parakeet population occupies remnant native forest in the southwest of Mauritius. Previous research has documented the effects of supplementary feeding and disease on the species' demography (Tollington *et al.*, 2015; Gath, 2018); however, climate impacts on population-level demography have not been studied in this species. The present study thus represents a first investigation into population-level climate impacts for the echo parakeet.

The findings of the present study will have relevance to the development of conservation actions for the focal species. The study will meet some of the neglected challenges identified by Butt *et al.* (2016), by investigating the sensitivity and adaptive capacity of species in addition to exposure, by including extreme events in analyses of climate impacts, and by quantifying recent climate trends and thus likely immediate impacts.

The chapters in this thesis are based around the analysis of climate trends and analysis of climate impacts on each focal population; the results are then brought together for comparison and synthesis:

Chapter 2: *General Methods*
This chapter provides an overview of the study system and the collection of ecological and meteorological data used in later analyses.

Chapter 3: *Climate trends in areas of high conservation importance in Mauritius*
This chapter examines the selection of meteorological indices for ecological impacts, and thus the identification of potential climate risks in an ecological context. Climate trends in areas with populations of conservation concern are analysed.

Chapter 4: *Phenological tracking of a seasonal climate window in a recovering tropical island bird species*
This chapter investigates climate influences on the breeding phenology and success of the Mauritius kestrel. The analyses incorporate temperature and the estimated onset of the rainy season to further our understanding of how this species is responding to climate trends and variability.

Chapter 5: *Re-scheduling to reduce climate risks in a threatened tropical bird species*
This chapter investigates climate impacts on the breeding phenology and success of the echo parakeet, including interactions with age and supplementary feeding. The use of

supplementary food is expected to buffer climate effects, while age is considered as it could mediate environmental impacts in this long-lived species.

Chapter 6: *General Discussion*

This chapter brings together the findings of the previous chapters and draws conclusions, with discussion of the results in a wider context and suggestion of directions for future research.

1.7 References

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A. and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate risks for forests. *Forest Ecology and Management,* **259**: 660–684.

Anctil, A., Franke, A. and Bêty, J. 2014. Heavy rainfall increases nestling mortality of an arctic top predator: experimental evidence and long-term trend in peregrine falcons. *Oecologia,* **174**: 1033–1043.

Bacmeister, J. T., Reed, K. A., Hannay, C., Lawrence, P., Bates, S., Truesdale, J. E., Rosenbloom, N. and Levy, M. 2018. Projected changes in tropical cyclone activity under future warming scenarios using a high-resolution climate model. *Climatic Change,* **146**: 547–560.

Bailey, L. D. and van de Pol, M. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology,* **85**: 85–96.

Barlow, J., França, F., Gardner, T. S., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J. and Graham, N. A. J. 2018. The future of hyperdiverse tropical ecosystems. *Nature,* **559**: 517–526.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. and Ferrer, E. A. 2011. Has the Earth's sixth mass extinction already arrived? *Nature,* **471**: 51–57.

Beissinger, S. R., Wunderle, J. M., Jr., Meyers, J. M., Sæther, B.-E. and Engen, S. 2008. Anatomy of a bottleneck: Diagnosing factors limiting population growth in the Puerto Rican parrot. *Ecological Monographs,* **78**: 185–203.

Bell, R., Strachan, J., Vidale, P. L., Hodges, K. and Roberts, M. 2013. Response of tropical cyclones to idealized climate change experiments in a global high-resolution coupled general circulation model. *Journal of Climate,* **26**: 7966–7980.

Bellard, C., Leclerc, C. and Courchamp, F. 2014. Impact of sea level rise on the 10 insular biodiversity hotspots. *Global Ecology and Biogeography,* **23**: 203–212.

Bellingham, P. J., Tanner, E. V. J. and Healey, J. R. 2005. Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. *Journal of Vegetation Science,* **16**: 675–684.

Bengtsson, L. H., K.; Esch, M.; Keenlyside, N.; Kornblueh, L.; Luo, J.-J.; Yamagata, T. 2007. How may tropical cyclones change in a warmer climate? *Tellus,* **59A**: 539–561.

Bhattarai, G. P. and Cronin, J. T. 2014. Hurricane Activity and the Large-Scale Pattern of Spread of an Invasive Plant Species. *PLoS One,* **9**: e98478.

Bosch, J., Martínez, J. E., Calvo, J. F., Zuberogoitia, I. and Jiménez-Franco, M. V. 2015. Does rainfall affect the productivity of the Booted Eagle (*Aquila pennata*) during the breeding period in Mediterranean environments? *Journal of Ornithology,* **156**: 1–8.

Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. and Visser, M. E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology,* **78**: 73–83.

Bradley, M., Johnstone, R., Court, G. and Duncan, T. 1997. Influence of Weather on Breeding Success of Peregrine Falcons in the Arctic. *Auk,* **114**: 786–791.

Brawn, J. D., Benson, T. J., Stager, M., Sly, N. D. and Tarwater, C. E. 2017. Impacts of changing rainfall regime on the demography of tropical birds. *Nature Climate Change,* **7**: 133–136.

Brightsmith, D. J., Hobson, E. A. and Martinez, G. 2018. Food availability and breeding season as predictors of geophagy in Amazonian parrots. *Ibis,* **160**: 112–129.

Butler, M. J., Metzger, K. L. and Harris, G. 2014. Whooping crane demographic responses to winter drought focus conservation strategies. *Biological Conservation,* **179**: 72–85.

Butt, N., Possingham, H. P., De Los Rios, C., Maggini, R., Fuller, R. A., Maxwell, S. L. and Watson, J. E. M. 2016. Challenges in assessing the vulnerability of species to climate change to inform conservation actions. *Biological Conservation,* **199**: 10–15.

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Ryu, H. Y., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., Warsi, O. and Wiens, J. J. 2012. How does climate change cause extinction? *Proceedings of the Royal Society of London, Series B,* **280**: 20121890.

Cai, W., Santoso, A., Wang, G., Weller, E., Wu, L., Ashok, K., Masumoto, Y. and Yamagata, T. 2014. Increased frequency of extreme Indian Ocean Diploe events due to greenhouse warming. *Nature,* **510**: 234–258.

Cai, W., Wang, G., Gan, B., Wu, L., Santoso, A., Lin, X., Chen, Z., Jia, F. and Yamagata, T. 2018. Stabilised frequency of extreme positive Indian Ocean Dipole under 1.5 °C warming. *Nature Communications,* **9**: 1419.

Cai, W., Wang, G., Santoso, A., McPhaden, M. J., Wu, L., Jin, F.-F., Timmermann, A., Collins, M., Vecchi, G., Lengaigne, M., England, M. H., Dommenget, D., Takahashi, K. and Guilyardi, E. 2015. Increased frequency of extreme La Niña events under greenhouse warming. *Nature Climate Change,* **5**: 132–137.

Cameron, M. 2009. The influence of climate on Glossy Black-cockatoo reproduction. *Pacific Conservation Biology,* **15**: 65–71.

Carrillo, J. and González-Dávila, E. 2010a. Geo-environmental influences on breeding parameters of the Eurasian Kestrel (*Falco tinnunculus*) in the Western Palaearctic. *Ornis Fennica,* **87**: 15–25.

Carrillo, J. and González-Dávila, E. 2010b. Impact of weather on breeding success of the Eurasian Kestrel *Falco tinnunculus* in a semi-arid island habitat. *Ardea,* **98**: 51–58.

Cartwright, S. J. 2011. Agriculture and the life histories of Mauritius kestrels. PhD Thesis. Reading, UK: University of Reading.

Cartwright, S. J., Nicoll, M. A. C., Jones, C. G., Tatayah, V. and Norris, K. 2014. Agriculture modifies the seasonal decline of breeding success in a tropical wild bird population. *Journal of Applied Ecology,* **51**: 1387–1395.

Catry, I., Franco, A. M. A. and Sutherland, W. J. 2011. Adapting conservation efforts to face climate change: Modifying nest-site provisioning for lesser kestrels. *Biological Conservation,* **144**: 1111–1119.

Charmantier, A. and Gienapp, P. 2013. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications,* **7**: 15–28.

Chen, S., Fan, Z., Roby, D. D., Lu, Y., Chen, C., Huang, Q., Cheng, L. and Zhu, J. 2015. Human harvest, climate change and their synergistic effects drove the Chinese Crested Tern to the brink of extinction. *Global Ecology and Conservation,* **4**: 137–145.

Cohen, J. M., Lajeunesse, M. J. and Rohr, J. R. 2018. A global synthesis of animal phenological responses to climate change. *Nature Climate Change,* **8**: 224–228.

Combes, C. 2008. The role of extreme events in evolution. *Comptes Rendus Geoscience,* **340**: 591–594.

Costantini, D., Carello, L. and Dell’Omo, G. 2010. Patterns of covariation among weather conditions, winter North Atlantic Oscillation index and reproductive traits in Mediterranean kestrels. *Journal of Zoology,* **280**: 177–184.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P. and van den Belt, M. 1997. The value of the world's ecosystem services and natural capital. *Nature,* **387**: 253–260.

Courchamp, F., Hoffmann, B. D., Russell, J. C., Leclerc, C. and Bellard, C. 2014. Climate change, sea-level rise, and conservation: keeping island biodiversity afloat. *Trends in Ecology & Evolution,* **29**: 127–130.

Dai, A. 2011. Drought under global warming: a review. *Wiley Interdisciplinary Reviews-Climate Change,* **2**: 45–65.

Dai, A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change,* **3**: 52–58.

Davis, A., Taylor, C. E. and Major, R. E. 2011. Do fire and rainfall drive spatial and temporal population shifts in parrots? A case study using urban parrot populations. *Landscape and Urban Planning,* **100**: 295–301.

Dawson, T. P., Jackson, S. T., House, J. L., Prentice, I. C. and Mace, G. M. 2011. Beyond predictions: Biodiversity conservation in a changing climate. *Science,* **332**: 53–58.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. and Martin, P. R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America,* **105**: 6668–6672.

Díaz, S., Fargione, J., Chapin, F. S., III and Tilman, D. 2006. Biodiversity Loss Threatens Human Well-Being. *PLoS Biology,* **4**: 1300–1305.

Donihue, C., M,, Herrel, A., Fabre, A.-C., Kamath, A., Geneva, A. J., Schoener, T. W., Kolbe, J. J. and Losos, J. B. 2018. Hurricane-induced selection on the morphology of an island lizard. *Nature,* **560**: 88–91.

Dvorak, V. 1984. Tropical cyclone intensity analysis using satellite data. NOAA Technical Report NESDIS. Washington, D.C.: National Oceanic and Atmospheric Administration.

Elsner, J. B., Kossin, J. P. and Jagger, T. H. 2008. The increasing intensity of the strongest tropical cyclones. *Nature,* **455**: 92–95.

Emanuel, K. A. 2013. Downscaling CMIP5 climate models shows increased tropical cyclone activity over the 21st century. *Proceedings of the National Academy of Sciences of the United States of America,* **110**: 12219–12224.

Feeley, K. J., Stroud, J. T. and Perez, T. M. 2016. Most 'global' reviews of species' responses to climate change are not truly global. *Diversity and Distributions,* **23**: 231–234.

Fey, S. B., Siepielski, A. M., Nussle, S., Cervantes-Yoshida, K., Hwan, J. L., Huber, E. R., Fey, M. J., Catenazzi, A. and Carlson, S. M. 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences,* **112**: 1083–1088.

Fisher, R. J., Wellicome, T. I., Bayne, E. M., Poulin, R. G., Todd, L. D. and Ford, A. T. 2015. Extreme precipitation reduces reproductive output of an endangered raptor. *Journal of Applied Ecology,* **52**: 1500–1508.

Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vie, J.-C., Akçakaya, H. R., Angulo, A., DeVantier, L. M., Gutsche, A., Turak, E., Cao, L., Donner, S. D., Katariya, V., Bernard, R., Holland, R. A., Hughes, A. F., O'Hanlon, S. E., Garnett, S. T., Şekercioğlu, Ç. H. and Mace, G. M. 2013. Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS One,* **8**: e65427.

Foley, C., Pettorelli, N. and Foley, L. 2008. Severe drought and calf survival in elephants. *Biology Letters,* **4**: 541–544.

Folke, C., Hahn, T., Olsson, P. and Norberg, J. 2005. Adaptive governance of social-ecological systems. *Annual Review of Environment and Resources,* **30**: 441–473.

Fordham, D. A. and Brook, B. W. 2010. Why tropical island endemics are acutely susceptible to global change. *Biodiversity and Conservation,* **19**: 329–342.

Friedlingstein, P., Andrew, R. M., Rogelj, J., Peters, G. P., Canadell, J. G., Knutti, R., Luderer, G., Raupach, M. R., Schaeffer, M., van Vuuren, D. P. and Le Quéré, C. 2014. Persistent growth of CO_2 emissions and implications for reaching climate targets. *Nature Geoscience,* **7**: 709–715.

Gath, H. C. 2018. Conservation Management of the Endangered Mauritius Parakeet *Psittacula echo*. PhD Dissertation. London, UK: University College London.

Giorgi, F., Coppola, E. and Raffaele, F. 2014. A consistent picture of the hydroclimatic response to global warming from multiple indices: Models and observations. *Journal of Geophysical Research - Atmospheres,* **119**: 11695–11708.

Gleixner, S., Keenlyside, N., Hodges, K. I., Tseng, W.-L. and Bengtsson, L. 2014. An inter-hemispheric comparison of the tropical storm response to global warming. *Climate Dynamics,* **42**: 2147–2157.

Goulding, W., Moss, P. T. and McAlpine, C. A. 2016. Cascading effects of cyclones on the biodiversity of Southwest Pacific islands. *Biological Conservation,* **193**: 143–152.

Grimbacher, P. S. and Stork, N. E. 2009. How do beetle assemblages respond to cyclonic disturbance of a fragmented tropical rainforest landscape? *Oecologia,* **161**: 591–599.

Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M.-S., Keatley, M. R., Woodward, C. A., Williamson, G., Duke, N. C. and Bowman, D. M. J. S. 2018. Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change,* **8**: 579–587.

Hawkins, E., Anderson, B., Diffenbaugh, N., Mahlstein, I., Betts, R., Hegerl, G., Joshi, M., Knutti, R., McNeall, D., Solomon, S., Sutton, R., Syktus, J. and Vecchi, G. 2014a. Uncertainties in the timing of unprecedented climates. *Nature,* **511**: E3–E5.

Hawkins, E., Joshi, M. and Frame, D. 2014b. Wetter then drier in some tropical areas. *Nature Climate Change,* **4**: 646–647.

Hellmann, J. J., Byers, J. E., Bierwagen, B. G. and Dukes, J. S. 2008. Five potential consequences of climate change for invasive species. *Conservation Biology,* **22**: 534–543.

Ho, C.-H., Kim, J.-H., Jeong, J.-H., Kim, H.-S. and Chen, D. 2006. Variation of tropical cyclone activity in the South Indian Ocean: El Niño-Southern Oscillation and Madden-Julian Oscillation effects. *Journal of Geophysical Research - Atmospheres,* **111**: D22101.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Boehm, M., Brooks, T. M., Butchart, S. H. M., Carpenter, K. E., Chanson, J., Collen, B., Cox, N. A., Darwall, W. R. T., Dulvy, N. K., Harrison, L. R., Katariya, V., Pollock, C. M., Quader, S., Richman, N. I., Rodrigues, A. S. L., Tognelli, M. F., Vie, J.-C., Aguiar, J. M., Allen, D. J., Allen, G. R., Amori, G., Ananjeva, N. B., Andreone, F., Andrew, P., Aquino Ortiz, A. L., Baillie, J. E. M., Baldi, R., Bell, B. D., Biju, S. D., Bird, J. P., Black-Decima, P., Blanc, J. J., Bolanos, F., Bolivar-G, W., Burfield, I. J., Burton, J. A., Capper, D. R., Castro, F., Catullo, G., Cavanagh, R. D., Channing, A., Chao, N. L., Chenery, A. M., Chiozza, F., Clausnitzer, V., Collar, N. J., Collett, L. C., Collette, B. B., Fernandez, C. F. C., Craig, M. T., Crosby, M. J., Cumberlidge, N., Cuttelod, A., Derocher, A. E., Diesmos, A. C., Donaldson, J. S., Duckworth, J. W., Dutson, G., Dutta, S. K., Emslie, R. H., Farjon, A., Fowler, S., Freyhof, J., Garshelis, D. L., Gerlach, J., Gower, D. J., Grant, T. D., Hammerson, G. A., Harris, R. B., Heaney, L. R., Hedges, S. B., Hero, J.-M., Hughes, B., Hussain, S. A., Icochea M, J., Inger, R. F., Ishii, N., Iskandar, D. T., Jenkins, R. K. B., Kaneko, Y., Kottelat, M., Kovacs, K. M., Kuzmin, S. L., La Marca, E., Lamoreux, J. F., Lau, M. W. N., Lavilla, E. O., Leus, K., Lewison, R. L., Lichtenstein, G., Livingstone, S. R., Lukoschek, V., Mallon, D. P., McGowan, P. J. K., McIvor, A., Moehlman, P. D., Molur, S., et al. 2010. The Impact of Conservation on the Status of the World's Vertebrates. *Science,* **330**: 1503–1509.

Hurrell, J. W. and Trenberth, K. E. 2010. Chapter 2. Climate Change. In *Effects of Climate Change on Birds* (eds: Møller, A. P., Fiedler, W. and Berthold, P.), pp. 9–29. Oxford, UK: Oxford University Press.

IPCC. 2014. Climate change 2014: Synthesis report. Fifth Assessment Synthesis Report. Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Jentsch, A. and Beierkuhnlein, C. 2008. Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *Comptes Rendus Geoscience,* **340**: 621–628.

Johnson, A. B. and Winker, K. 2010. Short-term hurricane impacts on a Neotropical community of marked birds and implications for early-stage community resilience. *PLoS One,* **5**: e15109.

Jones, C. G. 1987. The larger land-birds of Mauritius. In *Studies of Mascarene Island Birds* (ed: Diamond, A. W.), pp. 208–300. Cambridge, UK: Cambridge University Press.

Kalle, R., Ramesh, T. and Downs, C. T. 2018. When and where to move: Dynamic occupancy models explain the range dynamics of a food nomadic bird under climate and land cover change. *Global Change Biology,* **24**: e27–e39.

Kharin, V. V., Flato, G. M., Zhang, X., Gillett, N. P., Zwiers, F. and Anderson, K. J. 2018. Risks from Climate Extremes Change Differently from 1.5°C to 2.0°C Depending on Rarity. *Earth's Future,* **6**: 704–715.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J. and Barthlott, W. 2009. A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the United States of America,* **106**: 9322–9327.

King, A. D., Black, M. T., Min, S.-K., Fischer, E. M., Mitchell, D. M., Harrington, L. J. and Perkins-Kirkpatrick, S. E. 2016. Emergence of heat extremes attributable to anthropogenic influences. *Geophysical Research Letters,* **43**: 3438–3443.

Kishtawal, C. M., Jaiswal, N., Singh, R. and Niyogi, D. 2012. Tropical cyclone intensification trends during satellite era (1986-2010). *Geophysical Research Letters,* **39**: L10810.

Knutson, T. R., McBride, J. L., Chan, J., Emanuel, K., Holland, G., Landsea, C., Held, I., Kossin, J. P., Srivastava, A. K. and Sugi, M. 2010. Tropical cyclones and climate change. *Nature Geoscience,* **3**: 157–163.

Kossin, J. P. 2018. A global slowdown of tropical-cyclone translation speed. *Nature,* **558**: 104–107.

Kossin, J. P., Olander, T. L. and Knapp, K. R. 2013. Trend analysis with a new global record of tropical cyclone intensity. *Journal of Climate,* **26**: 9960–9976.

Kreiderits, A., Gamauf, A., Krenn, H. W. and Sumasgutner, P. 2016. Investigating the influence of local weather conditions and alternative prey composition on the breeding performance of urban Eurasian Kestrels *Falco tinnunculus*. *Bird Study,* **63**: 369–379.

Kuleshov, Y., Fawcett, R., Qi, L., Trewin, B., Jones, D., McBride, J. and Ramsay, H. 2010. Trends in tropical cyclones in the South Indian Ocean and the South Pacific Ocean. *Journal of Geophysical Research - Atmospheres,* **115**: D01101.

Lamarre, V., Legagneux, P., Franke, A., Casajus, N., Currie, D. C., Berteaux, D. and Bêty, J. 2018. Precipitation and ectoparasitism reduce reproductive success in an arctic-nesting top-predator. *Scientific Reports,* **8**: 8530.

Larson, E. R., Eastwood, J. R., Buchanan, K. L., Bennett, A. T. D. and Berg, M. L. 2015. How does nest-box temperature affect nestling growth rate and breeding success in a parrot? *Emu,* **115**: 247–255.

Laux, C. M., Nordell, C. J., Fisher, R. J., Ng, J. W., Wellicome, T. I. and Bayne, E. M. 2016. Ferruginous Hawks *Buteo regalis* alter parental behaviours in response to approaching storms. *Journal of Ornithology,* **157**: 355–362.

Lehikoinen, A., Byholm, P., Ranta, E., Saurola, P., Valkama, J., Korpimaki, E., Pietiainen, H. and Henttonen, H. 2009. Reproduction of the common buzzard at its northern range margin under climatic change. *Oikos,* **118**: 829–836.

Lehikoinen, A., Linden, A., Byholm, P., Ranta, E., Saurola, P., Valkama, J., Kaitala, V. and Linden, H. 2013. Impact of climate change and prey abundance on nesting success of a top predator, the goshawk. *Oecologia,* **171**: 283–293.

Lehikoinen, A., Saurola, P., Byholm, P., Linden, A. and Valkama, J. 2010. Life history events of the Eurasian sparrowhawk *Accipiter nisus* in a changing climate. *Journal of Avian Biology,* **41**: 627–636.

Lugo, A. E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology,* **33**: 368–398.

Lugo, A. E., Rogers, C. and Nixon, S. 2000. Hurricanes, coral reefs and rainforests: Resistance, ruin and recovery in the Caribbean. *Ambio,* **29**: 106–114.

Luja, V. H. and Rodriguez-Estrella, R. 2010. Are tropical cyclones sources of natural selection? Observations on the abundance and behavior of frogs affected by extreme climatic events in the Baja California Peninsula, Mexico. *Journal of Arid Environments,* **74**: 1345–1347.

Mahlstein, I., Knutti, R., Solomon, S. and Portmann, R. W. 2011. Early onset of significant local warming in low latitude countries. *Environmental Research Letters,* **6**: 034009.

Malan, N., Reason, C. J. C. and Loveday, B. R. 2013. Variability in tropical cyclone heat potential over the Southwest Indian Ocean. *Journal of Geophysical Research - Oceans,* **118**: 6734–6746.

Martínez-Ruiz, M. and Renton, K. 2018. Habitat heterogeneity facilitates resilience of diurnal raptor communities to hurricane disturbance. *Forest Ecology and Management,* **426**: 134–144.

Masello, J. F. and Quillfedt, P. 2004. Consequences of La Niña phase of ENSO for the survival and growth of nestling Burrowing Parrots on the Atlantic coast of South America. *Emu,* **104**: 337–346.

McSweeney, C., New, M. and Lizcano, G. 2010a. The UNDP Climate Change Country Profiles: Improving the Accessibility of Observed and Projected Climate Information for Studies of Climate Change in Developing Countries. *Bulletin of the American Meteorological Society,* **91**: 157–166.

McSweeney, C., New, M. and Lizcano, G. 2010b. UNDP Climate Change Country Profiles: Mauritius. Available from: https://www.geog.ox.ac.uk/.

Mearns, R. and Newton, I. 1988. Factors affecting breeding success of peregrines in south Scotland. *Journal of Animal Ecology,* **57**: 903–916.

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. and Post, E. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society of London, Series B,* **365**: 3177–3186.

Mitchell, S. J. 2013. Wind as a natural disturbance agent in forests: a synthesis. *Forestry,* **86**: 147–157.

Monzón, J., Moyer-Horner, L. and Palamar, M. B. 2011. Climate Change and Species Range Dynamics in Protected Areas. *BioScience,* **61**: 752–761.

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., Sanchez, J. J., Kaiser, L. R., Stender, Y. O., Anderson, J. M., Ambrosino, C. M., Fernandez-Silva, I., Giuseffi, L. M. and Giambelluca, T. W. 2013. The projected timing of climate departure from recent variability. *Nature,* **502**: 183–187.

Moreno, J. and Møller, A. P. 2011. Extreme climatic events in relation to global change and their impact on life histories. *Current Zoology,* **57**: 375–389.

Moritz, C. and Agudo, R. 2013. The future of species under climate change: Resilience or decline? *Science,* **341**: 504–508.

Murphy, H. T., Metcalfe, D. J., Bradford, M. G. and Ford, A. J. 2014. Community divergence in a tropical forest following a severe cyclone. *Austral Ecology,* **39**: 696–709.

Muthige, M. S., Malherbe, J., Englebrecht, F. A., Grab, S., Beraki, A., Maisha, T. R. and Van der Merwe, J. 2018. Projected changes in tropical cyclones over the South West Indian Ocean under different extents of global warming. *Environmental Research Letters,* **13**: 065019.

NAS. 2016. Attribution of extreme weather events in the context of climate change. Washington, D.C.: National Academy of Sciences.

Navarro, J. L. and Bucher, E. H. 1992. Annual variation in the timing of breeding of the Monk Parakeet in relation to climatic factors. *Wilson Bulletin,* **104**: 545–549.

Nicoll, M. A. C. 2004. The ecology and management of a re-introduced population of the Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Nicoll, M. A. C., Nevoux, M., Jones, C. G., Ratcliffe, N., Ruhomaun, K., Tatayah, V. and Norris, K. 2017. Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology,* **23**: 550–565.

Olsen, P. D. and Olsen, J. 1988. Breeding of the peregrine falcon *Falco peregrinus*. I. Weather, nest spacing and territory occupancy. *Emu,* **88**: 195–201.

Ontiveros, D. and Pleguezuelos, J. M. 2003. Influence of climate on Bonelli's eagle's (*Hieraaetus fasciatus* V. 1822) breeding success through the Western Mediterranean. *Journal of Biogeography,* **30**: 755–760.

Ortiz-Maciel, S. G., Salinas-Melgoza, A., Valdéz-Juárez, S. O., Lopez-Toledo, L. and Enkerlin-Hoeflich, E. 2014. Influence of stochastic processes and catastrophic events on the reproductive dynamics of the endangered Maroon-fronted Parrot *Rhynchopsitta terrisi*. *Ibis,* **156**: 299–310.

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., Corlett, R. T., Huntley, B., Bickford, D., Carr, J. A., Hoffmann, A. A., Midgley, G. F., Pearce-Kelly, P., Pearson, R. G., Williams, S. E., Willis, S. G., Young, B. and Rondinini, C. 2015. Assessing species vulnerability to climate change. *Nature Climate Change,* **5**: 215–225.

Parmesan, C., Root, T. L. and Willig, M. R. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society,* **81**: 443–450.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* **421**: 37–42.

Penteriani, V., Mathiaut, M. and Boisson, G. 2002. Immediate Species Responses to Catastrophic Natural Disturbances: Windthrow Effects on Density, Productivity, Nesting Stand Choice, and Fidelity in Northern Goshawks (*Accipiter gentilis*). *Auk,* **119**: 1132–1137.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R. J., Sumaila, U. R. and Walpole, M. 2010. Scenarios for Global Biodiversity in the 21st Century. *Science,* **330**: 1496–1501.

Pielke, R. A., Landsea, C., Mayfield, M., Laver, J. and Pasch, R. 2005. Hurricanes and global warming. *Bulletin of the American Meteorological Society,* **86**: 1571–1575.

Pimm, S. L., Russell, G. J., Gittleman, J. L. and Brooks, T. M. 1995. The Future of Biodiversity. *Science,* **269**: 347–350.

Renton, K. and Salinas-Melgoza, A. 2004. Climatic variability, nest predation, and reproductive output of lilac-crowned parrots (*Amazona finschi*) in tropical dry forest of western Mexico. *Auk,* **121**: 1214–1225.

Republic of Mauritius. 2010. Second national communication of the Republic of Mauritius under the United Nations Framework Convention on Climate Change (UNFCCC). Vacoas, Mauritius: Mauritius Meteorological Services.

Republic of Mauritius. 2016. Third National Communication: Report to the United Nations Framework Convention on Climate Change. Port Louis, Mauritius.

Risser, M. D. and Wehner, M. F. 2017. Attributable Human-Induced Changes in the Likelihood and Magnitude of the Observed Extreme Precipitation during Hurricane Harvey. *Geophysical Research Letters,* **44**: 12457–12464.

Robinson, B. G., Franke, A. and Derocher, A. E. 2017. Weather-mediated decline in prey delivery rates causes food-limitation in a top avian predator. *Journal of Avian Biology,* **48**: 748–758.

Rodrigues, A. S. L., Brooks, T. M., Butchart, S. H. M., Chanson, J., Cox, N., Hoffmann, M. and Stuart, S. N. 2014. Spatially Explicit Trends in the Global Conservation Status of Vertebrates. *PLoS One,* **9**: e113934.

Rodríguez, C. and Bustamente, J. 2003. The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines? *Journal of Animal Ecology,* **72**: 793–810.

Rogelj, J., den Elzen, M., Höhne, N., Fransen, T., Fekete, H., Winkler, H., Schaeffer, R., Sha, F., Riahi, K. and Meinshausen, M. 2016. Paris Agreement climate proposals need a boost to keep warming well below 2°C. *Nature,* **534**: 631–639.

Rosenfield, R. N., Hardin, M. G., Bielefeldt, J. and Keyel, E. R. 2017. Are life history events of a northern breeding population of Cooper's Hawks influenced by changing climate? *Ecology and Evolution,* **7**: 399–408.

Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T. L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S. and Imeson, A. 2008. Attributing physical and biological impacts to anthropogenic climate change. *Nature,* **453**: 353–357.

Royal Society. 2014. Resilience to extreme weather. London, UK: The Royal Society.

Saunders, D. A., Mawson, P. and Dawson, R. 2011. The impact of two extreme weather events and other causes of death on Carnaby's Black Cockatoo: a promise of things to come for a threatened species? *Pacific Conservation Biology,* **17**: 141–148.

Saunders, D. A., Wintle, B. A., Mawson, P. R. and Dawson, R. 2013. Egg-laying and rainfall synchrony in an endangered bird species: Implications for conservation in a changing climate. *Biological Conservation,* **161**: 1–9.

Saunders, D. L., Cunningham, R. and Heinsohn, R. 2016. Responses of Critically Endangered migratory Swift Parrots to variable winter drought. *Emu,* **116**: 350–359.

Schoener, T. W. and Spiller, D. A. 2006. Nonsynchronous recovery of community characteristics in island spiders after a catastrophic hurricane. *Proceedings of the National Academy of Sciences of the United States of America,* **103**: 2220–2225.

Seidl, R., Spies, T. A., Peterson, D. L., Stephens, S. L. and Hicke, J. A. 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology,* **53**: 120–129.

Selwood, K. E., Clarke, R. H., Cunningham, S. C., Lada, H., McGeoch, M. A. and Mac Nally, R. 2015. A bust but no boom: responses of floodplain bird assemblages during and after prolonged drought. *Journal of Animal Ecology,* **84**: 1700–1710.

Senapathi, D., Nicoll, M. A. C., Teplitsky, C., Jones, C. G. and Norris, K. 2011. Climate change and the risks associated with delayed breeding in a tropical wild bird population. *Proceedings of the Royal Society of London, Series B,* **278**: 3184–3190.

Senapathi, D., Underwood, F., Black, E., Nicoll, M. A. C. and Norris, K. 2010. Evidence for long-term regional changes in precipitation on the East Coast Mountains in Mauritius. *International Journal of Climatology,* **30**: 1164–1177.

Senapathi, G. D. 2009. Assessing the effect of changing climatic conditions in Mauritius on the population dynamics of the endemic Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Sergio, F., Blas, J. and Hiraldo, F. 2018. Animal responses to natural disturbance and climate extremes: a review. *Global and Planetary Change,* **161**: 28–40.

Smith, M. D. 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology,* **90**: 656–663.

Smith, P., Price, J., Molotoks, A., Warren, R. and Malhi, Y. 2018. Impacts on terrestrial biodiversity of moving from a 2°C to a 1.5°C target. *Philosophical Transactions of the Royal Society of London, Series A,* **376**: 20160456.

Smith, S. H., Steenhof, K., McClure, C. J. W. and Heath, J. A. 2016. Earlier nesting by generalist predatory bird is associated with human responses to climate change. *Journal of Animal Ecology,* **86**: 98–107.

Stein, B. A., Staudt, A., Cross, M. S., Dubois, N. S., Enquist, C., Griffis, R., Hansen, L. J., Hellmann, J. J., Lawler, J. J., Nelson, E. J. and Pairis, A. 2013. Preparing for and managing change: climate adaptation for biodiversity and ecosystems. *Frontiers in Ecology and the Environment,* **11**: 502–510.

Stephenson, D. B. 2008. Definition, diagnosis, and origin of extreme weather and climate events. In *Climate Extremes and Society* (eds: Diaz, H. F. and Murnane, R. J.), pp. 11–23. Cambridge, UK: Cambridge University Press.

Strauss, S. Y., Lau, J. A. and Carroll, S. P. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters,* **9**: 357–374.

Tarwater, C. E. and Beissinger, S. R. 2013. Opposing selection and environmental variation modify optimal timing of breeding. *Proceedings of the National Academy of Sciences of the United States of America,* **110**: 15365–15370.

Thibault, K. M. and Brown, J. H. 2008. Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences of the United States of America,* **105**: 3410–3415.

Tollington, S., Greenwood, A., Jones, C. G., Hoeck, P., Chowrimootoo, A., Smith, D., Richards, H., Tatayah, V. and Groombridge, J. J. 2015. Detailed monitoring of a small but recovering population reveals sublethal effects of disease and unexpected interactions with supplemental feeding. *Journal of Animal Ecology,* **84**: 969–977.

UNFCCC. 2015. Adoption of the Paris Agreement. Report No. FCCC/CP/2015/L.9.Rev.1. United Nations Framework Convention on Climate Change.

Urban, M. C. 2015. Accelerating extinction risk from climate change. *Science,* **348**: 571–573.

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., Schmitz, A., Zollner, P. A. and

Travis, J. M. J. 2016. Improving the forecast for biodiversity under climate change. *Science,* **353**: aad8466.

van de Pol, M., Jenouvrier, S., Cornelissen, J. H. C. and Visser, M. E. 2017. Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Philosophical Transactions of the Royal Society of London, Series B,* **372**: 20160134.

Vincent, L. A., Aguilar, E., Saindou, M., Hassane, A. F., Jumaux, G., Roy, D., Booneeady, P., Virasami, R., Randriamarolaza, L. Y. A., Faniriantsoa, F. R., Amelie, V., Seeward, H. and Montfraix, B. 2011. Observed trends in indices of daily and extreme temperature and precipitation for the countries of the western Indian Ocean, 1961-2008. *Journal of Geophysical Research - Atmospheres,* **116**: D10108.

Walsh, K. 2004. Tropical cyclones and climate change: unresolved issues. *Climate Research,* **27**: 77–83.

Walsh, K. J. E., McBride, J. L., Klotzbach, P. J., Balachandran, S., Camargo, S. J., Holland, G., Knutson, T. R., Kossin, J. P., Lee, T.-c., Sobel, A. and Sugi, M. 2016. Tropical cyclones and climate change. *Wiley Interdisciplinary Reviews-Climate Change,* **7**: 65–89.

Warren, R., Price, J., Graham, E., Forstenhaeusler, N. and VanDerWal, J. 2018. The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. *Science,* **360**: 791–795.

Warren, R., VanDerWal, J., Price, J., Welbergen, J. A., Atkinson, I., Ramirez-Villegas, J., Osborn, T. J., Jarvis, A., Shoo, L. P., Williams, S. E. and Lowe, J. 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change,* **3**: 678–682.

Wasko, C., Parinussa, R. M. and Sharma, A. 2016. A quasi-global assessment of changes in remotely sensed rainfall extremes with temperature. *Geophysical Research Letters,* **43**: 12659–12668.

Watts, B. D. and Byrd, M. A. 2007. Impact of Hurricane Isabel on bald eagle nests and reproductive performance in the lower Chesapeake Bay. *Condor,* **109**: 206–209.

Welch, B. C., Boal, C. W. and Skipper, B. R. 2017. Environmental influences on the nesting phenology and productivity of Mississippi Kites (*Ictinia mississippiensis*). *Condor,* **119**: 298–307.

White, T. H., Jr., Collazo, J. A., Vilella, F. J. and Guerrero, S. A. 2005. Effects of Hurricane Georges on habitat use by captive-reared Hispaniolan parrots (*Amazona ventralis*) released in the Dominican Republic. *Ornitología Neotropical,* **16**: 405–417.

Wiens, J. D., Kolar, P. S., Hunt, W. G., Hunt, T., Fuller, M. R. and Bell, D. A. 2018. Spatial patterns in occupancy and reproduction of Golden Eagles during drought: Prospects for conservation in changing environments. *Condor,* **120**: 106–124.

Williams, J. W., Jackson, S. T. and Kutzbach, J. E. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America,* **104**: 5738–5742.

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffman, A. A. and Langham, G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology,* **6**: 2621–2626.

WMO. 2018. WMO Statement on the State of the Global Climate in 2017. Geneva, Switzerland: World Meteorological Organization.

Wunderle, J. M., Jr. 1999. Pre- and Post-Hurricane Fruit Availability: Implications for Puerto Rican Parrots in the Luquillo Mountains. *Caribbean Journal of Science,* **35**: 249–264.

WWF. 2016. Living Planet Report 2016: Risk and resilience in a new era. Gland, Switzerland: WWF International.

Zalasiewicz, J., Williams, M., Haywood, A. and Ellis, M. 2011. The Anthropocene: a new epoch of geological time? *Philosophical Transactions of the Royal Society of London, Series A,* **369**: 835–841.

Zalasiewicz, J., Williams, M., Smith, A., Barry, T. L., Coe, A. L., Brown, P. R., Brenchley, P., Cantrill, D., Gale, A., Gibbard, P., Gregory, F. J., Hounslow, M. W., Kerr, A. C., Pearson, P., Knox, R., Powell, J., Waters, C., Marshall, J., Oates, M., Rawson, P. and Stone, P. 2008. Are we now living in the Anthropocene? *GSA Today,* **18**: 4–8.

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Chapter 2

General Methods

2.1 Geography and climate of Mauritius

Mauritius is an oceanic island of volcanic origin, located in the southwest Indian Ocean (SWIO) c.860 km east of Madagascar, and forms part of the Mascarene archipelago. Isotopic dating suggests that the island emerged ~8-10 million years ago (McDougall and Chamalaun, 1969; Cheke and Hume, 2008). The main island (20°17'S, 57°36'E) is 1,865 km^2 in area. Its topography is varied, with low plains in the north and east, rising up to ~400-600 m above sea-level (asl) on the Central Plateau, which runs approximately north to south in the southwest of the island (Cheke, 1987b; Cheke and Hume, 2008; Staub *et al.*, 2014). In the southwest of the plateau, its southern and western flanks descend steeply to the coastal lowlands, and the area includes the Black River Gorges, a deeply dissected river bed (Cheke, 1987b). The highest point on the island is Black River Peak, at 828 m asl (Cheke, 1987b; Cheke and Hume, 2008). Other highland areas include the Bambous Mountains in the east and Moka Mountains in the northwest (Cheke, 1987b).

The modern landscapes of Mauritius are dominated by agricultural land and development, with forest now covering around 25% of the land area, of which only 2% is native forest (MAIFS, 2015). Much of the lowlands are now covered in sugarcane plantations, which account for ~86% of the cultivated land that was harvested in 2016 (Statistics Mauritius, 2017). Tree-felling, initially for timber, began soon after permanent human settlement in 1638 (Cheke and Hume, 2008). Forest clearance is estimated to have been particularly rapid from the late 18th to the mid-19th century, when the human population and extent of sugar cane cultivation increased rapidly (Cheke, 1987a; Norder *et al.*, 2017). Land-use conversion, combined with the introduction of non-native plant species, resulted in native vegetation cover being reduced to 5% of the land area by 1993 (Safford, 1997).

The Mascarene archipelago is characterised as having a tropical seasonal climate (Safford and Hawkins, 2013), influenced by the surrounding ocean and two main weather regimes: seasonal tropical cyclones and Southeast Trade Winds (Anderson, 2012). The trade winds originate from subtropical anticyclones that travel eastward over the southern Indian Ocean (Republic of Mauritius, 2010). These winds affect Mauritius almost permanently at speeds of 1-45 km h^{-1}, with the highest wind speeds usually occurring from June to November (Anderson, 2012). The subtropical anticyclones, often preceded by cold fronts, inject relatively cold air that produces light rain over the island, mainly over the east, south and Central Plateau; in summer the subtropical anticyclones become weaker and migrate poleward (Republic of Mauritius, 2010).

Rainfall in Mauritius can be divided into two broad seasons, with the Southeast Lesser Monsoon season from June until November, and the Northwest Monsoon and cyclone season from December until May (Senapathi, 2009; Senapathi *et al.*, 2010), with daily temperatures peaking in the austral summer. In general, approximately 40% of total annual rainfall occurs in January-March, following the southward migration of the Inter-Tropical Convergence Zone (ITCZ) towards subtropical latitudes and the occurrence of tropical cyclones (Staub *et al.*, 2014). The SWIO basin experiences 11-12 tropical cyclones per year, with the regional cyclone season generally being from November to April (Malan *et al.*, 2013). The highest frequencies of tropical cyclones in the South Indian Ocean basin are distributed fairly evenly along the monsoon trough at 10-20°S (Levinson *et al.*, 2010). Rainfall in the Bambous Mountains is also influenced by sea surface temperatures in the western Indian Ocean, as well as large-scale factors including the Indian Monsoon and El Niño-Southern Oscillation (Senapathi *et al.*, 2010).

Mean annual rainfall on the main island varies longitudinally from ~1400 mm in the eastern coastal lowlands, to ~4000 mm in the highlands, and ~800 mm along the western coastal lowlands (Staub *et al.*, 2014). The Bambous Mountains in the east of the island form a trade wind belt and receive large amounts of rain relative to adjacent lowlands (Staub *et al.*, 2014). Orographic lifting takes place over the island as a result of its raised topography and has contributed to the creation of several microclimate zones, with the central uplands classed as super humid, the east and south regions classed as humid, and a small area in the west defined as semi-arid (reviewed by Anderson, 2012). The dry climate of the western lowlands is the result of a rain shadow effect caused by the position of the central uplands relative to the prevailing moist Southeast Trade Winds (Anderson, 2012).

2.2 Study species

This study utilises long-term detailed datasets on two threatened but recovering bird species that are endemic to Mauritius. These data have been collected during two of the most successful species recovery programmes ever conducted (Nicoll, 2004; Gath, 2018). The focal species serve as case studies for the factors affecting climate change vulnerability in tropical island species. Both species neared extinction in the late 20th century, but now number hundreds of individuals. The two focal species are ecologically very different and occupy contrasting study areas. The echo parakeet is a long-lived frugivore, and member of the order Psittaciformes, which is a highly threatened species group (Marsden and Royle, 2015). The data collected on the echo parakeet population provides an opportunity to gain detailed insights into climate impacts on a tropical psittacid. The Mauritius kestrel is a forest-dwelling falcon whose detailed monitoring has provided many insights into population regulatory processes and the impacts of climate and land-use (Nicoll *et al.*, 2003; Nicoll, 2004; Nicoll *et al.*, 2006; Burgess, 2008; Burgess *et al.*, 2008; Burgess *et al.*, 2009; Senapathi, 2009; Burgess *et al.*, 2011; Cartwright, 2011; Nevoux *et al.*, 2011; Senapathi *et al.*, 2011; Nevoux *et al.*, 2013; Cartwright *et al.*, 2014a, b). However, further research is needed to better understand the ways that different aspects of the climate, including extreme events, affect the species' demography.

2.2.1 Mauritius kestrel

The Mauritius kestrel (Figure 2.1) is the only surviving resident species of raptor in Mauritius, and the population is thought to have been isolated for 1.9-2.6 million years (Groombridge *et al.*, 2002). It is an Accipiter-like falcon that typically inhabits native forest (Temple, 1987; Cartwright, 2011), but has shown flexibility in occupying agricultural mosaics with a forest component (Burgess, 2008; Cartwright, 2011). It hunts a variety of introduced small birds, mammals and reptiles, and some insects, but shows a preference for native *Phelsuma* geckos (Jones, 1987; Temple, 1987; Carter and Jones, 1999). It usually forms monogamous pairs, which defend a breeding territory (Jones, 1987), and Mauritius kestrels are able to breed during their first year. Clutches of 1-5 eggs are laid from September onwards and breeding activity continues into the summer months, with the last young fledging in the middle of the summer rainy season (Nicoll, 2004; Cartwright, 2011). It nests in natural cavities in cliffs or trees. It is primarily the female that incubates the eggs and broods the nestlings, while the male provisions the family until the young have fledged (Cartwright, 2011; Jones *et al.*, 2013a). The species is usually single-brooded, but occasionally second, and rarely third, clutches are laid if the first attempt fails or a brood fledges early enough in the season (Cartwright, 2011). The breeding season spans two calendar years and is referred to using both of those years, e.g. 2014/2015.

It is thought that the species was widely distributed in pristine forested Mauritius before colonisation by humans (Jones, 1987). However, it suffered severe declines owing to habitat destruction, invasive non-native species and pesticide use. Nests and fledglings are predated by invasive mammal species, including black rats (*Rattus rattus*), small Indian mongooses (*Herpestes auropunctatus*), feral cats (*Felis catus*) and crab-eating macaques (*Macaca fascicularis*) (Cade and Jones, 1993). By 1949, when the implementation of organochlorine pesticides for malaria eradication took place, the species was already restricted to upland areas (Safford and Jones, 1997), but pesticide exposure has been implicated in a further crash in the population (Jones, 1987; Safford and Jones, 1997). By the 1960s, the species was restricted to southwestern Mauritius (Jones, 1987), the only forested area not targeted for pesticide use (Cheke, 1987a). The species experienced a severe population bottleneck and neared extinction in the mid-1970s, reaching a low of only four wild individuals, probably including only one breeding pair (Temple, 1986; Jones, 1987; Jones *et al.*, 2013a), with two more individuals in captivity (Cade and Jones, 1993). Subsequent genetic analysis provides supporting evidence of a severe population bottleneck, with a probable low of four birds (Groombridge *et al.*, 2001).

The Mauritius kestrel has since become an icon of species recovery and conservation. A recovery programme was initiated in 1973, which has involved captive breeding, cross-fostering in wild nests, releases of captive-bred and reared birds, clutch manipulation, provision of supplementary food and nest-boxes, and control of predators (Cade and Jones, 1993; Jones *et al.*, 1995). The species was reintroduced to upland forested areas in the Bambous and Moka mountain ranges, and additional birds were released to augment the remnant population in the Black River Gorges (Jones *et al.*, 1995; Nicoll, 2004; Cartwright, 2011). Following its reintroduction in 1991, the population in the Moka Mountains died out in the early 2000s (Jones *et al.*, 2013a).

Figure 2.1. Mauritius kestrel from the Bambous Mountains population.

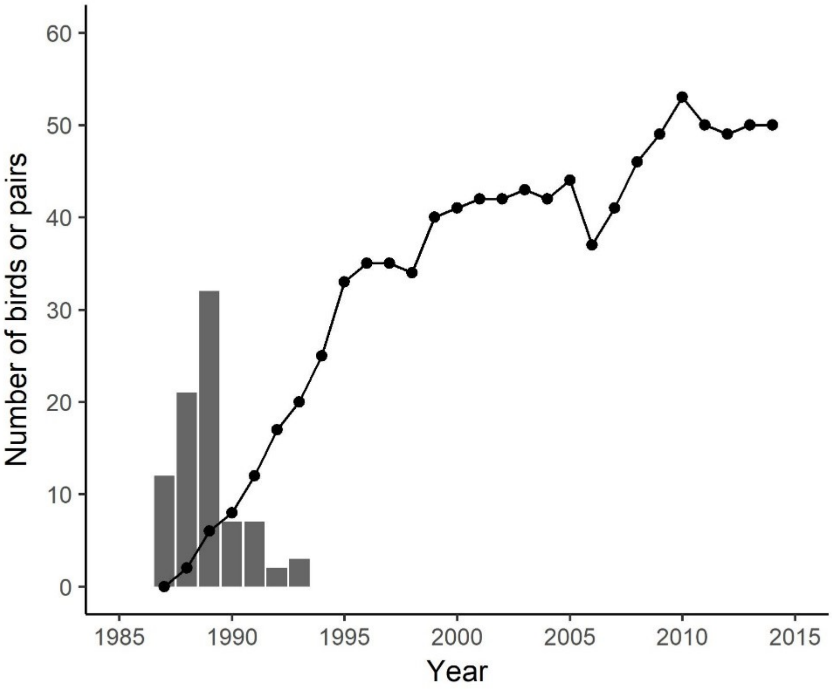

Figure 2.2. Mauritius kestrel population trend and releases in the Bambous Mountains, Mauritius, from 1987/1988 to 2014/2015: black points and lines = number of monitored breeding pairs; grey columns = number of birds released. Year indicates that of the start of the breeding season.

The species became extirpated from the Bambous Mountains in the 1950s (Cade and Jones, 1993), but was reintroduced from 1987 onwards, with releases carried out between 1987 and 1994 (Nicoll, 2004) (Figure 2.2). Intensive management of the Bambous Mountains population continued until the 1993/1994 season (Nicoll, 2004). The re-established population has since stabilised at ~50 breeding pairs (Figure 2.2). While the Bambous Mountains population is stable, the smaller extant population in the Black River Gorges has shown recent declines (BirdLife International, 2018a).

The two extant populations rely heavily on the continued provision and maintenance of artificial nest-boxes, especially in the Bambous Mountains, where there is a shortage of suitable natural cavities (Cartwright, 2011). The species shows very limited dispersal, with most birds staying within 2 km of their natal territory (Nevoux *et al.*, 2013). Natural recolonisation may be limited by conspecific attraction, in which transient non-breeders tend to occur at the margins of breeding territories, rather than occupying more remote patches of habitat (Jones *et al.*, 1995; Cartwright, 2011). This could mean that further population growth will not be possible without large-scale forest restoration (Cartwright, 2011). The two extant populations are separated by over 18 km and are effectively isolated from one-another (Cartwright, 2011). The species is now estimated to number ~250 individuals (M. A. C. Nicoll, pers. comm.). Research has confirmed that the population is inbred and has lost substantial genetic diversity, although the long-term consequences for the species are uncertain (Groombridge *et al.*, 2000; Groombridge *et al.*, 2001; Ewing *et al.*, 2008). The species is currently listed as endangered on the IUCN Red List (BirdLife International, 2018a).

Previous research has shown that the species is sensitive to variability in rainfall, with breeding success and juvenile survival negatively affected by increased rainfall in the rainy season, from December onwards (Nicoll *et al.*, 2003; Nicoll, 2004). Breeding phenology is influenced by rainfall in spring, with delayed egg-laying in response to more frequent rainfall (Nicoll, 2004; Senapathi, 2009; Senapathi *et al.*, 2011). Such delays potentially increase the exposure of broods to heavy rainfall in December, which reduces breeding success (Nicoll, 2004; Senapathi, 2009; Senapathi *et al.*, 2011). However, there is no evidence that population dynamics are affected by rainfall variability (Senapathi, 2009). Research has found spatial heterogeneity in recruitment rates (Burgess *et al.*, 2008), avoidance of agricultural areas by juveniles (Burgess *et al.*, 2009), and reduced egg to fledging survival in territories with a higher agricultural component (Burgess *et al.*, 2011). Increased exposure to agriculture worsens the seasonal decline in breeding fitness and the life-history strategies of birds are altered by exposure to a high agriculture component in their natal territory (Cartwright, 2011; Cartwright *et al.*, 2014a, b). The population has also provided opportunities to study the mechanisms through which density-dependence occurs (Nevoux *et al.*, 2011) and the individual fitness consequences of dispersal (Nevoux *et al.*, 2013).

2.2.2 Echo parakeet

The echo parakeet (Figure 2.3) is the only extant native psittacid species in Mauritius, and it may be a subspecies to an extinct taxon that occurred on Reunion (Jones *et al.*, 2013b). It feeds on plant material, including the fruit, flowers, leaves, buds and bark, of more than 50 species (Jones, 1987; Jones *et al.*, 2013b). The species is generally arboreal and forages widely, alone or in groups, visiting different areas to target a variety of plant species depending on the time of year (Jones, 1987; Jones *et al.*, 2013b). The longevity of echo parakeets is not known, but is thought to be similar to the closely related ring-necked parakeet (*P. krameri*), which may live for 25 years (Gath, 2018). This is likely, given that some breeding echo parakeets are aged between 15 and 20 years (Gath, 2018). Echo parakeets can breed at two years of age, but most transition to breeders at three years of age or older (Gath, 2018). The species is generally monogamous and usually lays one clutch per season, in a cavity in a hollow branch or tree trunk (Jones *et al.*, 2013b), with occasional re-laying after failed breeding attempts (Tollington *et al.*, 2015). However, second clutches are rare overall, with only 42 being recorded up until and including the 2013/2014 breeding season. As yet there are no records of a second clutch following a successful breeding attempt (Gath, 2018). The breeding season encompasses the austral spring and summer, stretching from August through to March. Clutches of 1-4 eggs are laid from early August onwards. The breeding season thus spans two calendar years and is referred to using both years, e.g. 2013/2014.

It is thought that the echo parakeet was widespread throughout Mauritius before human colonisation, but it has been restricted to the southwest of the island since the late 1970s, where it mainly inhabits remnant native forest in the Black River Gorges National Park (BRGNP) and adjacent areas (Jones and Owadally, 1988). It experienced a severe population bottleneck in the late 1980s, when it may have reached a low of as few as 20 individuals (Tatayah *et al.*, 2007), limited to an area of 50 km^2 of native forest (Jones and Duffy, 1993). Shortages of food and suitable nest cavities, owing to habitat destruction and degradation, are implicated in the population decline (Jones, 1987; Young, 1987). In addition, the decline has been linked to nest predation by black rats and crab-eating macaques, and competition for nest-sites with the introduced common mynah (*Acridotheres tristis*) and ring-necked parakeet, native white-tailed tropic-bird (*Phaethon lepturus*), honey bees (*Apis mellifera*), wasps (*Polistes hebraeus*) and termites (Isoptera) (Jones, 1987; Jones *et al.*, 2013b).

Figure 2.3. Male echo parakeet at a feeding hopper.

Monitoring of the echo parakeet population started in 1973, and management was intensified in 1987 (Jones *et al.*, 2013a). An official recovery programme was initiated in 1993 (Jones and Duffy, 1993), involving captive breeding and releases, nest manipulations, supplementary feeding and the provision and protection of nest-sites (Jones and Duffy, 1993). Intensive management techniques were used from 1993 until 2005, including daily monitoring of nesting attempts, medical and nutritional interventions or captive-rearing for nestlings showing poor development, and cross-fostering of eggs and nestlings (Gath, 2018). Following a successful trial in 1997, a total of 50 captive-reared echo parakeets were soft-released at Plaine Lievre in the BRGNP between 1997 and 2001, with another 49 released nearby at Bel Ombre between 2002 and 2004 (Gath, 2018) (Figures 2.4 and 2.6). An attempt to establish a third subpopulation with the release of 36 birds in 2004 was unsuccessful due to an outbreak of Psittacine Beak and Feather Disease (PBFD) (Gath, 2018).

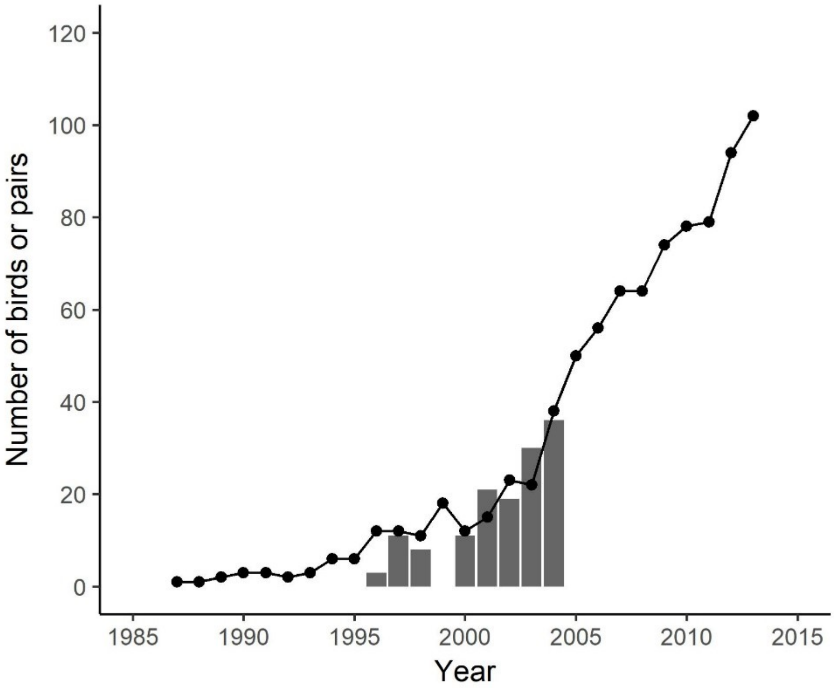

Figure 2.4. Echo parakeet population trend and releases in southwestern Mauritius, from 1987/1988 to 2013/2014: black points and lines = number of monitored breeding pairs; grey columns = number of birds released. Year indicates that of the start of the breeding season.

Attempts at providing supplementary food since 1979 were at first unsuccessful, until a revised programme started in 1997 as part of releases of captive-bred birds in which the released birds were trained to take food from hoppers; wild-bred birds subsequently learnt to use the hoppers (reviewed by Gath, 2018). Artificial food pellets and fresh fruit are provided. Consumption rates of supplementary food vary between individual birds, but 82% of the population is known to currently include it in their diet (Gath, 2018). Supplementary food use has been shown to generally increase measures of breeding success (Jones *et al.*, 2013b; Tollington *et al.*, 2015; Gath, 2018).

The reintroduction component of the recovery programme was halted and management interventions reduced in 2005, following the outbreak of PBFD (Kundu *et al.*, 2012; Jones *et al.*, 2013a; Tollington *et al.*, 2015). Nest manipulations have since been avoided unless absolutely necessary and the frequency of nest visits has been reduced (Gath 2018). The outbreak of PBFD has been linked to reduced breeding success in supplementary fed pairs, suggesting that the provision and use of supplementary food at communal feeding stations is linked to the transmission of the Beak and Feather Disease Virus (Tollington *et al.*, 2015; Gath, 2018). Survival in younger age classes of non-breeding birds has decreased since the outbreak of PBFD (Gath, 2018).

Despite the outbreak of disease, the population has increased to over 600 individuals (Gath, 2018), including over 100 breeding pairs (Figure 2.4), and this increase appears to be continuing. The extant population has been regarded as comprising three subpopulations (Tollington *et al.*, 2013), although two are recognised in this study: 1) Grande Gorge and 2) Bel Ombre, located in and around the BRGNP. Individuals have been moved between the Grande Gorge and Bel Ombre subpopulations to achieve genetic homogenisation (Jones *et al.*, 2013a). Work is now underway to establish a population in the Bambous Mountains. The species is currently listed as endangered on the IUCN Red List (BirdLife International, 2018b).

2.3 Ecological data and study sites

The recovery programmes for both study species have involved detailed monitoring protocols, resulting in the collection of data on the majority of individuals and breeding attempts.

2.3.1 Mauritius kestrel

The focal population of Mauritius kestrels is located in the Bambous Mountains (20°20’ S, 57°40’ E, Figure 2.5). The study area spans 163 km^2, across a mountain range with a 15-km spine running east to west, and a number of southward-running spurs, with elevation ranging from sea-level to 626 m (Burgess, 2008). The landscape is dominated by fragmented and heavily invaded forest, with a mosaic of cultivated fields, and is bounded by vast areas of agricultural land (Burgess, 2008; Cartwright, 2011). The forest of the Bambous Mountains is a relic of lower montane wet forest, with a very small area of dry evergreen forest at lower elevations and in the north of the area (Burgess, 2008). Large areas are dominated by invasive plant species, particularly Traveller's palm (*Ravenala madagascariensis*), strawberry guava (*Psidium cattleianum*), privet (*Ligustrum robustum*), the 'Liane Cerf' creeper (*Hiptage benghalensis*) and mango (*Mangifera indica*) (Burgess, 2008). The core range is privately owned and managed as hunting land, which is stocked with introduced Java deer (*Cervis timorensis*), and as such some areas of forest have been cleared for grazing land. There are more than 80 known previously-used Mauritius kestrel nest-sites in the study area, including natural tree and cliff cavities, and artificial nest-boxes (Cartwright, 2011). Given the species' limited dispersal and the distance to the other extant population, the Bambous Mountains population of kestrels can be considered to be a single closed system (Cartwright, 2011).

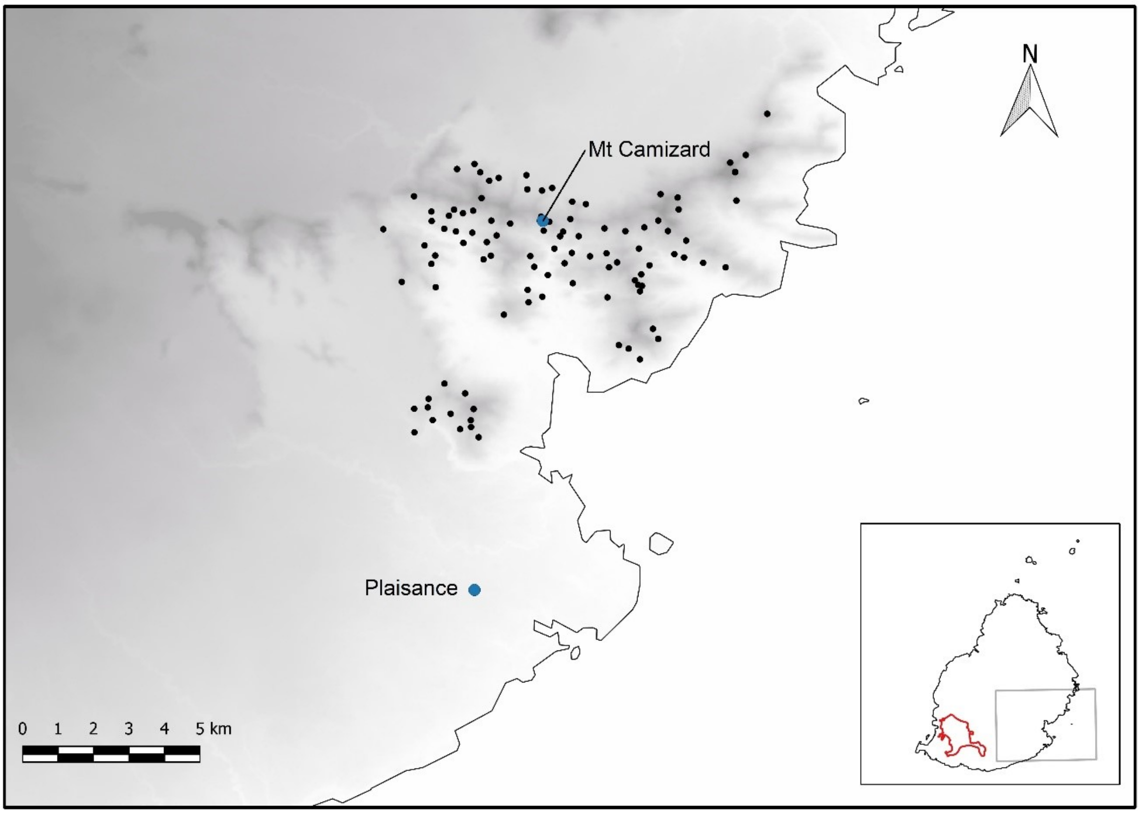

Figure 2.5. Map of Bambous Mountains study area with known Mauritius kestrel nest-sites (black points) and weather stations used in this study (blue points). Elevation data are provided by the NASA Shuttle Radar Topography Mission Version 3.0.

The majority (>90%) of birds entering the Mauritius kestrel population in the Bambous Mountains are fitted with coloured leg rings (Senapathi *et al.*, 2011) and can be identified by sight without the need for recapture. Intensive monitoring takes place in the breeding season, and teams start to visit known nest-sites in September. Inactive nest-sites are repeatedly checked to ensure that no breeding attempts are missed. Active nests are systematically monitored during the breeding season, and chicks are ringed and measured at 12-28 days of age, before they leave the nest (Nicoll, 2004). Active nests are visited as often as possible within the constraints of the availability of field workers. Data are usually collected on first egg-laying date, clutch size and number of fledglings. For the majority of clutches, visits take place at least once during the laying period and again to determine the total clutch size (Nicoll, 2004). Longer gaps between visits can create uncertainty in data on clutch size and first egg-laying date. Precise egg-laying dates are rarely recorded during fieldwork, thus standardised back calculations, based on data from a sample of nests visited daily, are used to estimate laying dates (Nicoll, 2004). These calculations are applied when a nesting attempt is discovered prior to or during laying or when the complete clutch has been laid, although not when a clutch does not hatch or the clutch size is unknown. For these calculations, the incubation period is assumed to be 29 days (based on a range of 28-30 days), with incubation assumed to start when the penultimate egg is laid and a 3-day interval assumed between the laying of each egg (Nicoll, 2004). Fieldwork continues until the end of February when the last chicks are usually fledging. The majority (>90%) of breeding pairs are located and monitored each year (Senapathi *et al.*, 2011). Where possible, the identity of the female and male are noted and from this the age and prior breeding experience of the pair can often be deduced. Data are also available on nest-site and territory characteristics. In addition to nest monitoring, a record is kept of which adult birds are re-sighted during each breeding season. The data used in this study are drawn from 911 documented breeding attempts from 1988/1989 to 2014/2015; in this study a breeding attempt is defined as the laying of at least one egg.

2.3.2 Echo parakeet

The focal population of echo parakeets is located in and around the BRGNP (20°25’ S, 57°27’ E, Figure 2.6), which includes areas of highly degraded native forest, invaded with non-native species, including strawberry guava and privet (Thorsen *et al.*, 1997). Areas of native forest are being systematically cleared of invasive species by the National Parks and Conservation Service of Mauritius. The species occurs mostly above 150 m asl (Jones *et al.*, 2013b). The two subpopulations are separated by a c.2 km-wide plateau of agricultural land and degraded habitat (Gath, 2018). Grande Gorge is the larger subpopulation, with 76 breeding pairs in the 2013/2014 season, compared with 28 pairs at Bel Ombre.

An intensive monitoring programme for the echo parakeet has accompanied the recovery programme since 1991, and was made official in 1993 (Gath, 2018). Almost all individuals (>95%) in the population are fitted with coloured leg rings, allowing them to be identified in the field. Data on supplementary food use are collected during observation periods at feeding hoppers. These 'hopper watches' are carried out on four days per week and last one hour, beginning at dawn (Gath, 2018). All birds sighted at the hoppers are identified. The hoppers at Plaine Lievre have been monitored most consistently, with more intermittent observations at Brise Fer, Mare Longue and Bel Ombre (Figure 2.6). Once a month, a full day watch at Bel Ombre is carried out (Gath, 2018).

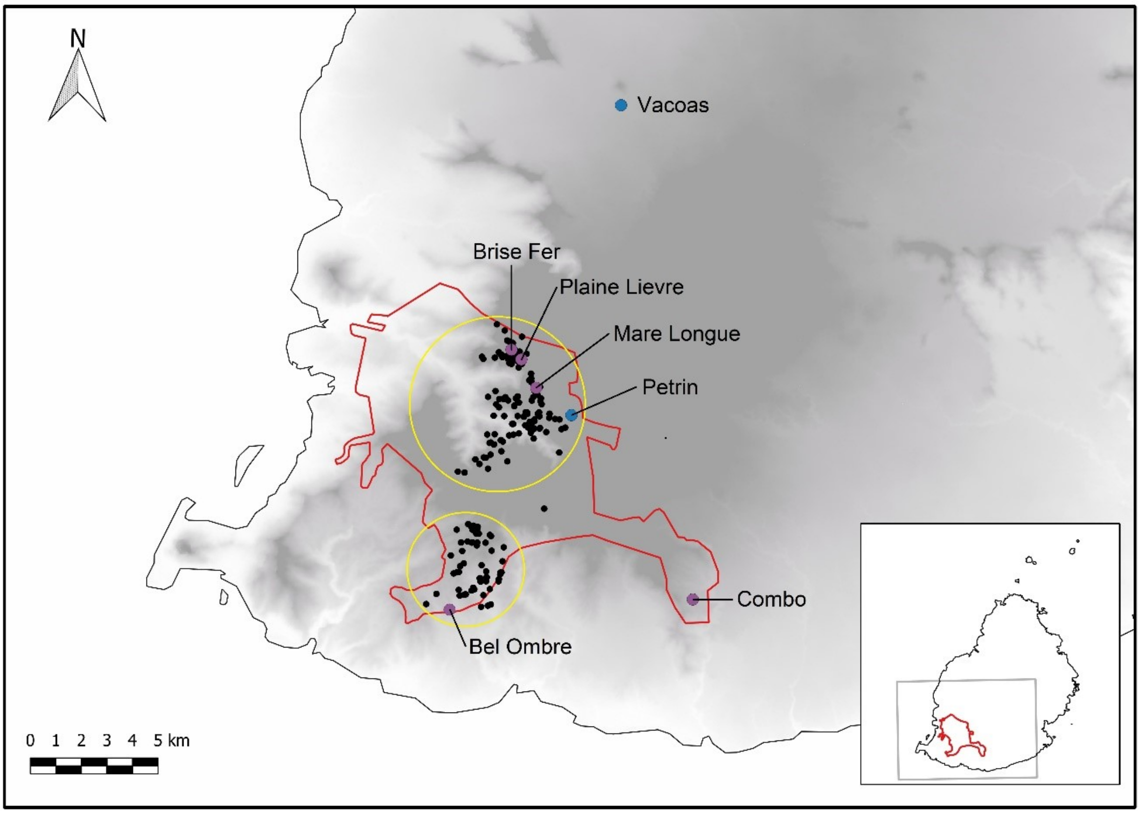

Figure 2.6. Map of the Black River Gorges area with known echo parakeet nest-sites (black points), feeding stations and release sites (purple points) and the weather stations used in this study (blue points). National park boundaries are shown in red (data provided by MWF). The two subpopulations are circled in yellow: northern subpopulation = Grande Gorge; southern subpopulation = Bel Ombre (following Gath, 2018). Elevation data are provided by the NASA Shuttle Radar Topography Mission Version 3.0.

All breeding activity is documented throughout each bird's lifetime. Data are usually collected on first egg-laying date, clutch size and number of fledglings. Known nest-sites are regularly visited at the start of the breeding season and then checked systematically until the status of any breeding pair is known. The frequency of visits to active nests has changed between seasons due to changes in monitoring protocols. In general, nest visits are kept as infrequent as possible, while scheduling to collect important data and to ring the nestlings (e.g. Henshaw *et al.*, 2015). The incubation period is assumed to be 25 days and nestlings are typically ringed when they are 13-15 days old (e.g. Henshaw *et al.*, 2015). Once a clutch had been laid, nest visits are scheduled to coincide with hatching and to ring the nestlings, with some nests visited more frequently in some seasons. Where long gaps occur between visits or the timing of hatching is not accurately predicted this increases uncertainty in the data on clutch size and first egg-laying date, and data on hatching success may be unreliable if hatching is missed. Where the first egg-laying date is not directly estimated, back calculation is used, assuming an incubation period of 25 days and the laying of eggs at 1-day intervals. Where possible, the identity of the female and male are noted and from this the age and prior breeding experience of the pair can often be calculated. Data are also available on nest-site characteristics. These data are collected in a stud book, which has been adapted for use in life-history and demographic analyses (Gath, 2018). Although population monitoring focuses on breeding birds, incidental observations of non-breeding birds have also been collected during breeding seasons (Gath, 2018). The data used in this study are drawn from the recently compiled studbook (Gath, 2018), with a total of 867 wild breeding attempts with a known clutch size from 1991/1992 to 2013/2014; in this study, a breeding attempt is defined as the laying of at least one egg.

2.4 Meteorological data

Daily weather station data and tropical cyclone tracks are used for the analysis of climate trends and impacts on the focal species. A variety of weather stations are used to collect meteorological data and observations in Mauritius. Synoptic stations are operated by Mauritius Meteorological Services (MMS) and automatically collect comprehensive weather data at fixed time intervals, reporting these via the Global Telecommunication System of the World Meteorological Organization (WMO) (MMS, 2008). Other smaller weather stations and rain gauges are operated by MMS, the Mauritius Sugar Industry Research Institute, agricultural estates and private citizens (MMS, 2008).

Data on precipitation, surface air temperature and tropical cyclone tracks for use in this study were obtained for locations relevant to the focal populations and sites of conservation importance. Rainfall data from a rain gauge in the Bambous Mountains were contributed by

Ferney Sugar Estate. These data were collected at Mt Camizard (20°20'S, 57°42'E, 21 m asl, Figure 2.5), within the range of the Bambous Mountains kestrel population, and constitute a dataset used in previous studies on the Mauritius kestrel (Nicoll *et al.*, 2003; Nicoll, 2004; Burgess, 2008; Burgess *et al.*, 2008; Burgess *et al.*, 2009; Senapathi, 2009; Senapathi *et al.*, 2010; Burgess *et al.*, 2011; Cartwright, 2011; Senapathi *et al.*, 2011; Cartwright *et al.*, 2014a, b). Rainfall data relevant to the focal population of echo parakeets were obtained from a rain gauge at Petrin (20°24'S, 57°28'E, 655 m asl, Figure 2.6) and contributed by MMS. Daily precipitation and temperature data from two synoptic stations on mainland Mauritius, at Plaisance (20°26'S, 57°41'E, 50 m asl, Figure 2.5) and Vacoas (20°17'S, 57°29'E, 424 m asl, Figure 2.6), were obtained from the National Centers for Environmental Information of the National Oceanic and Atmospheric Administration (NOAA: www.ncdc.noaa.gov) in the form of two inventories for each station: the Global Historical Climatology Network-Daily (GHCN-Daily) and Global Summary of the Day (GSOD). A complete time series of daily rainfall data from Plaisance for 1992-2015 was contributed by MMS. An incomplete time series of daily rainfall on Ile aux Aigrettes from January 2013 to April 2015 was contributed by the Mauritian Wildlife Foundation (MWF).

The GHCN-Daily data on rainfall and temperature at both synoptic stations comprise GSOD data in more recent years, thus missing values in the GHCN inventories in these years were filled with values from the GSOD inventories where available. Despite this process, the number of missing precipitation values for Vacoas limits the extent of subsequent analysis possible with this dataset. Nevertheless, the precipitation data from Vacoas form a longer-term dataset than available for Petrin, thus the Vacoas data are used to supplement the shorter-term trend analyses for Petrin when looking at climate trends in the national park. To further minimise the number of missing precipitation values and maximise the duration of the time series for Plaisance, the data from GHCN/GSOD and MMS were combined. During the process of combining these datasets, rainfall values from the MMS inventory were used to fill data gaps and replace zero values in the GHCN/GSOD data. However, it should be noted that differences between these inventories may create biases in the combined data.

Tropical cyclone tracks were downloaded as ESRI shapefiles from the International Best Track Archive for Climate Stewardship (IBTrACS v03r10) (Knapp *et al.*, 2010) via NOAA (www.ncdc.noaa.gov/ibtracs). Global best-track data comprise 6-hourly estimates of the location (latitude and longitude) and intensity (usually estimated as maximum sustained wind speed) of tropical cyclones during varying periods of record in each cyclone basin. A substantial proportion of intensity estimates are informed by the Dvorak technique, in which visible and infrared satellite data are used to study cloud features and temperatures in the eye and surrounding clouds (Dvorak, 1984). Dvorak methods were introduced into operational procedures for the SWIO region in 1982, although this was in the absence of digital imagery (Terry *et al.*, 2013). Digital imagery from orbiting weather satellites became available in 1991 for the purposes of cyclone tracking in the Indian Ocean region (Terry *et al.*, 2013). In 1998, a satellite was repositioned to provide improvements in view angle and image quality, thus resulting in a change in satellite data quality for the north and south Indian Ocean regions (Kossin *et al.*, 2013). These advances in the tracking and assessment of tropical cyclones in the SWIO have undoubtedly introduced biases into observed trends in the data (Terry *et al.*, 2013); however, these inconsistencies are difficult to remove without re-analysing satellite images (Kossin *et al.*, 2013) and this is beyond the scope of this study (see Chapter 3 for details).

2.5 References

Anderson, R. L. 2012. Rainfall erosivity attributes on central and western Mauritius. MSc Dissertation. South Africa: University of Pretoria.

BirdLife International 2018a. Species factsheet: *Falco punctatus*. http://datazone.birdlife.org. Accessed on: 31/07/2018.

BirdLife International 2018b. Species factsheet: *Psittacula eques*. http://datazone.birdlife.org. Accessed on: 19/07/2018.

Burgess, M. D. 2008. Spatial patterns and population dynamics of a reintroduced Mauritius kestrel (*Falco punctatus*) population. PhD Thesis. Reading, UK: University of Reading.

Burgess, M. D., Black, R. A., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2009. The use of agricultural, open and forest habitats by juvenile Mauritius Kestrels *Falco punctatus*. *Ibis,* **151**: 63–76.

Burgess, M. D., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2008. Restricted dispersal reduces the strength of spatial density dependence in a tropical bird population. *Proceedings of the Royal Society of London, Series B,* **275**: 1209–1216.

Burgess, M. D., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2011. Multiple environmental gradients affect spatial variation in the productivity of a tropical bird population. *Journal of Animal Ecology,* **80**: 688–695.

Cade, T. J. and Jones, C. G. 1993. Progress in restoration of the Mauritius kestrel. *Conservation Biology,* **7**: 169–175.

Carter, J. E. and Jones, M. H. 1999. Habitat composition of Mauritius Kestrel home ranges. *Journal of Field Ornithology,* **70**: 230–235.

Cartwright, S. J. 2011. Agriculture and the life histories of Mauritius kestrels. PhD Thesis. Reading, UK: University of Reading.

Cartwright, S. J., Nicoll, M. A. C., Jones, C. G., Tatayah, V. and Norris, K. 2014a. Agriculture modifies the seasonal decline of breeding success in a tropical wild bird population. *Journal of Applied Ecology,* **51**: 1387–1395.

Cartwright, S. J., Nicoll, M. A. C., Jones, C. G., Tatayah, V. and Norris, K. 2014b. Anthropogenic natal environmental effects on life histories in a wild bird population. *Current Biology,* **24**: 536–540.

Cheke, A. and Hume, J. 2008. *Lost land of the dodo*. London, UK: T & AD Poyser.

Cheke, A. S. 1987a. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. In *Studies of Mascarene Island birds* (ed: Diamond, A. W.), pp. 5–89. Cambridge, UK: Cambridge University Press.

Cheke, A. S. 1987b. The ecology of the smaller land-birds of Mauritius. In *Studies of Mascarene Island birds* (ed: Diamond, A. W.), pp. 151–207. Cambridge, UK: Cambridge University Press.

Dvorak, V. 1984. Tropical cyclone intensity analysis using satellite data. NOAA Technical Report NESDIS. Washington, D.C.: National Oceanic and Atmospheric Administration.

Ewing, S. R., Nager, R. G., Nicoll, M. A. C., Aumjaud, A., Jones, C. G. and Keller, L. F. 2008. Inbreeding and loss of genetic variation in a reintroduced population of Mauritius Kestrel. *Conservation Biology,* **22**: 395–404.

Gath, H. C. 2018. Conservation Management of the Endangered Mauritius Parakeet *Psittacula echo*. PhD Dissertation. London, UK: University College London.

Groombridge, J. J., Bruford, M. W., Jones, C. G. and Nichols, R. A. 2001. Evaluating the severity of the population bottleneck in the Mauritius kestrel *Falco punctatus* from ringing records using MCMC estimation. *Journal of Animal Ecology,* **70**: 401–409.

Groombridge, J. J., Jones, C. G., Bayes, M. K., van Zyl, A. J., Carrillo, J., Nichols, R. A. and Bruford, M. W. 2002. A molecular phylogeny of African kestrels with reference to divergence across the Indian Ocean. *Molecular Phylogenetics and Evolution,* **25**: 267–277.

Groombridge, J. J., Jones, C. G., Bruford, M. W. and Nichols, R. A. 2000. 'Ghost' alleles of the Mauritius kestrel. *Nature,* **403**: 616.

Henshaw, A., Henshaw, S., Ayady, L. and LaMont, M. 2015. Echo Parakeet (*Psittacula eques*) management report 2013/2014. Unpublished report. Vacoas, Mauritius: Mauritian Wildlife Foundation.

Jones, C. G. 1987. The larger land-birds of Mauritius. In *Studies of Mascarene Island Birds* (ed: Diamond, A. W.), pp. 208–300. Cambridge, UK: Cambridge University Press.

Jones, C. G., Burgess, M. D., Groombridge, J. J., Dale, R., Tatayah, V., Zuel, N. and Nicoll, M. A. C. 2013a. Mauritius Kestrel *Falco punctatus*. In *The Birds of Africa: Volume VIII. The Malagasy Region* (eds: Safford, R. and Hawkins, F.), pp. 300–306. London, UK: Christopher Helm.

Jones, C. G. and Duffy, K. 1993. Conservation management of the echo parakeet *Psittacula eques echo*. *Dodo,* **29**: 126–148.

Jones, C. G., Heck, W., Lewis, R. E., Mungroo, Y., Slade, G. and Cade, T. 1995. The restoration of the Mauritius kestrel *Falco punctatus* population. *Ibis,* **137**: S173–S180.

Jones, C. G., Malham, J., Reuleaux, A., Richards, H., Raisin, C., Tollington, S., Zuel, N., Chowrimootoo, A. and Tatayah, V. 2013b. Echo Parakeet *Psittacula eques*. In *The Birds of Africa: Volume VIII. The Malagasy Region* (eds: Safford, R. and Hawkins, F.), pp. 517–522. London, UK: Christopher Helm.

Jones, C. G. and Owadally, A. 1988. The life histories and conservation of the Mauritius kestrel *Falco punctatus*, pink pigeon *Columba mayeri*, and echo parakeet *Psittacula eques*. *Proceedings of the Royal Society of Arts and Sciences of Mauritius,* **5**: 79–129.

Knapp, K. R., Kruk, M. C., Levinson, D. H., Diamond, H. J. and Neumann, C. J. 2010. The International Best Track Archive for Climate Stewardship (IBTrACS): Unifying Tropical Cyclone Data. *Bulletin of the American Meteorological Society,* **91**: 363–376.

Kossin, J. P., Olander, T. L. and Knapp, K. R. 2013. Trend analysis with a new global record of tropical cyclone intensity. *Journal of Climate,* **26**: 9960–9976.

Kundu, S., Faulkes, C. G., Greenwood, A. G., Jones, C. G., Kaiser, P., Lyne, O. D., Black, S. A., Chowrimootoo, A. and Groombridge, J. J. 2012. Tracking Viral Evolution during a Disease Outbreak: the Rapid and Complete Selective Sweep of a Circovirus in the Endangered Echo Parakeet. *Journal of Virology,* **86**: 5221–5229.

Levinson, D. H., Knapp, K. R., Kruk, M. C., Diamond, H. J. and Kossin, J. P. 2010. The International Best Track Archive for Climate Stewardship (IBTrACS) Project: Overview of Methods and Indian Ocean Statistics. In *Indian Ocean Tropical Cyclones and Climate Change* (ed: Charabi, Y.), pp. 215–221. Dordrecht, Netherlands: Springer.

MAIFS. 2015. Fifth national report on the Convention on Biological Diversity. Port Louis, Mauritius: Ministry of Agro-Industry and Food Security, Republic of Mauritius.

Malan, N., Reason, C. J. C. and Loveday, B. R. 2013. Variability in tropical cyclone heat potential over the Southwest Indian Ocean. *Journal of Geophysical Research - Oceans,* **118**: 6734–6746.

Marsden, S. J. and Royle, K. 2015. Abundance and abundance change in the world's parrots. *Ibis,* **157**: 219–229.

McDougall, I. and Chamalaun, F. H. 1969. Isotopic dating and geomagnetic polarity studies on volcanic rocks from Mauritius, Indian Ocean. *Geological Society of America Bulletin,* **80**: 1419–1442.

MMS. 2008. Monthly bulletin of climatological summaries, May 2008. Vacoas, Mauritius: Mauritius Meteorological Services.

Nevoux, M., Arlt, D., Nicoll, M., Jones, C. and Norris, K. 2013. The short- and long-term fitness consequences of natal dispersal in a wild bird population. *Ecology Letters,* **16**: 438–445.

Nevoux, M., Gimenez, O., Arlt, D., Nicoll, M., Jones, C. and Norris, K. 2011. Population regulation of territorial species: both site dependence and interference mechanisms matter. *Proceedings of the Royal Society of London, Series B,* **278**: 2173–2181.

Nicoll, M. A. C. 2004. The ecology and management of a re-introduced population of the Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Nicoll, M. A. C., Jones, C. G. and Norris, K. 2003. Declining survival rates in a reintroduced population of the Mauritius kestrel: evidence for non-linear density dependence and environmental stochasticity. *Journal of Animal Ecology,* **72**: 917–926.

Nicoll, M. A. C., Jones, C. G. and Norris, K. 2006. The impact of harvesting on a formerly endangered tropical bird: insights from life-history theory. *Journal of Applied Ecology,* **43**: 567–575.

Norder, S. J., Seijmonsbergen, A. C., Rughooputh, S. D. D. V., van Loon, E. E., Tatayah, V., Kamminga, A. T. and Rijsdijk, K. F. 2017. Assessing temporal couplings in social-ecological island systems: historical deforestation and soil loss on Mauritius (Indian Ocean). *Ecology and Society,* **22**: 29.

Republic of Mauritius. 2010. Second national communication of the Republic of Mauritius under the United Nations Framework Convention on Climate Change (UNFCCC). Vacoas, Mauritius: Mauritius Meteorological Services.

Safford, R. and Hawkins, F. 2013. *The Birds of Africa: Volume VIII. The Malagasy Region*. London, UK: Christopher Helm.

Safford, R. J. 1997. A survey of the occurrence of native vegetation remnants on Mauritius in 1993. *Biological Conservation,* **80**: 181–188.

Safford, R. J. and Jones, C. G. 1997. Did organochlorine pesticide use cause declines in Mauritian forest birds? *Biodiversity and Conservation,* **6**: 1445–1451.

Senapathi, D., Nicoll, M. A. C., Teplitsky, C., Jones, C. G. and Norris, K. 2011. Climate change and the risks associated with delayed breeding in a tropical wild bird population. *Proceedings of the Royal Society of London, Series B,* **278**: 3184–3190.

Senapathi, D., Underwood, F., Black, E., Nicoll, M. A. C. and Norris, K. 2010. Evidence for long-term regional changes in precipitation on the East Coast Mountains in Mauritius. *International Journal of Climatology,* **30**: 1164–1177.

Senapathi, G. D. 2009. Assessing the effect of changing climatic conditions in Mauritius on the population dynamics of the endemic Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Statistics Mauritius. 2017. Digest of agricultural statistics 2016. Port Louis, Mauritius: Ministry of Finance & Economic Development, Republic of Mauritius.

Staub, C. G., Stevens, F. R. and Waylen, P. R. 2014. The geography of rainfall in Mauritius: Modelling the relationship between annual and monthly rainfall and landscape characteristics on a small volcanic island. *Applied Geography,* **54**: 222–234.

Tatayah, R. V. V., Malham, J., Haverson, M. J., Reuleaux, A. and Van de Wetering, J. 2007. Design and provision of nest boxes for echo parakeets *Psittacula eques* in Black River Gorges National Park, Mauritius. *Conservation Evidence,* **4**: 16–19.

Temple, S. A. 1986. Recovery of the endangered Mauritius kestrel from an extreme population bottleneck. *Auk,* **103**: 632–633.

Temple, S. A. 1987. Foraging ecology of the Mauritius kestrel (*Falco punctatus*). *Biotropica,* **19**: 2–6.

Terry, J. P., Kim, I.-H. and Jolivet, S. 2013. Sinuosity of tropical cyclone tracks in the South West Indian Ocean: Spatio-temporal patterns and relationships with fundamental storm attributes. *Applied Geography,* **45**: 29–40.

Thorsen, M., Shorten, R., Buchanan, G., Williams, S., Jones, V., Swinnerton, K., de Ravel, F., Webb, J., Lam, R. and Schellander, H. 1997. Echo parakeet (*Psittacula eques*) management report 1997. Unpublished report. Vacoas, Mauritius: Mauritian Wildlife Foundation and National Parks and Conservation Service.

Tollington, S., Greenwood, A., Jones, C. G., Hoeck, P., Chowrimootoo, A., Smith, D., Richards, H., Tatayah, V. and Groombridge, J. J. 2015. Detailed monitoring of a small but recovering population reveals sublethal effects of disease and unexpected interactions with supplemental feeding. *Journal of Animal Ecology,* **84**: 969–977.

Tollington, S., Jones, C. G., Greenwood, A., Tatayah, V., Raisin, C., Burke, T., Dawson, D. A. and Groombridge, J. J. 2013. Long-term, fine-scale temporal patterns of genetic diversity in the restored Mauritius parakeet reveal genetic impacts of management and associated demographic effects on reintroduction programmes. *Biological Conservation,* **161**: 28–38.

Young, G. 1987. Notes on the nesting behaviour of the echo parakeet *Psittacula eques echo*. *Dodo,* **24**: 102–111.

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Chapter 3

Climate trends in areas of high conservation importance in Mauritius

3.1 Abstract

Projected climate change is expected to result in changes to overall climate regimes and the frequency and severity of extreme events. The definition of extreme events in ecological studies is a subject of ongoing discussion, with choices between standard meteorological approaches, biological thresholds and hybrid approaches that combine these. Trends in the exposure of ecosystems and species to climate risks can vary on local scales, particularly in topographically complex areas. In Mauritius, rainfall trends appear to vary locally, but it is not known if extremes follow the same patterns or if this local variation is relevant to species conservation. To study this I selected ecologically-relevant climate indices based on meteorological approaches, including for extremes, and studied trends in three areas of high conservation importance. These recent trends may indicate recent pressures on species and future climate risks. The trend analyses indicate that average temperatures and extreme heat events have increased since the 1950s at two locations with relevant data available. Patterns in the occurrence of tropical cyclones since 1980 show decadal variation and no significant trends. The analysis of precipitation trends show that the Bambous Mountains in eastern Mauritius have received increases in overall and extreme rainfall since the 1960s, while Ile aux Aigrettes, a small offshore island occupied by populations of other threatened species and located within 6 km, has experienced some decreases in rainfall since the 1950s and potentially an increasing risk of drought. This local-scale variation in rainfall trends, including for some extreme indices, may result from differences in local orography and perhaps a shift in the direction of prevailing weather patterns. It is recommended that climate change vulnerability assessments and management strategies for important conservation areas and very restricted-range species should account for such local variation in climate trends and impacts and should be adapted over local scales. The use of meteorological indices in ecological studies arguably increases relevance to policy-makers and general climate research.

3.2 Introduction

Global biodiversity is under threat from a variety of anthropogenic processes, including habitat loss and degradation, overexploitation, the introduction of non-native species, pollution, global climate change, and the synergistic interactions of these processes (IUCN 2016). Insular species are particularly susceptible to these threats, owing to their often limited geographic range and population, and their isolated evolution (Berglund *et al.*, 2009; Fordham and Brook, 2010). Island-endemic species are generally expected to be highly vulnerable to climate change, based on high exposure and sensitivity and low adaptive capacity. Their inherently limited distribution constrains range shifts and increases the exposure of the population to climate risks (Foden *et al.*, 2013), and small population size may limit genetic diversity and the possibility of evolutionary adaptation to new pressures (Strauss *et al.*, 2006). Yet, tropical islands harbour biotas with very high endemism (Kier *et al.*, 2009), such that large numbers of highly distinct island species could be under serious threat from climate change.

Projections of the ecological impacts of climate change ideally incorporate species vulnerability assessments, including relevant information on exposure, sensitivity and adaptive capacity (Williams *et al.*, 2008; Dawson *et al.*, 2011; Foden *et al.*, 2013; Moritz and Agudo, 2013). An aspect that is often overlooked in projections of ecological impacts from climate change is the occurrence of changes in extreme weather and climate events, hereafter referred to as extreme events. Evidence indicates that projected climate change is likely to result in changes to the frequency, intensity, extent, duration and timing of extreme events (IPCC, 2014), which are typically defined by their rarity and severity (Stephenson, 2008). Evidence already exists to indicate that the frequency, intensity and duration of some extreme events have been changing as the climate system has warmed (NAS, 2016).

It has been argued that changes in the frequency and intensity of extreme events pose a greater threat to ecosystem functioning than shifts in global average temperatures and precipitation regimes (Jentsch and Beierkuhnlein, 2008). Increases in the frequency, severity and duration of extreme events can trigger resource bottlenecks that act as powerful demographic constraints on species (Maron *et al.*, 2015), and often exacerbate other human-induced pressures such as land-use change (Parmesan *et al.*, 2000; Maron *et al.*, 2015). The ecological consequences of changes in extreme events are often overlooked owing to gaps in our knowledge of how they affect species and ecosystems. Extreme events are difficult to study because such events are rare and their rarity and severity are very context-dependent (Smith, 2011). This has resulted in a lack of consistency in how extremes are defined in ecological studies, ranging from the use of meteorological definitions of rarity and intensity, or biological definitions based on impacts, to proposed hybrid definitions that incorporate both meteorological and biological thresholds (Smith, 2011; Bailey and van de Pol, 2016; van de Pol *et al.*, 2017). In addition, an extreme event may be defined on the basis of its abruptness (a function of magnitude over duration) relative to the life cycle of the species being studied (Jentsch *et al.*, 2007). There have been calls for more research on the ecological impacts of extreme events, including for species vulnerability studies (Chapman *et al.*, 2014) and spatial conservation prioritisation (Jones *et al.*, 2016), and there remains a need for more studies that are long term and cover multiple events (Bailey and van de Pol, 2016; van de Pol *et al.*, 2017).

Another aspect that is often overlooked in studies of species vulnerability to climate change is the potential for local-scale variation in long-term climate trends. Similar climate risks may be assumed for all species on a small island or all subpopulations of a restricted-range species. However, climate trends, especially those concerning precipitation, can vary in sign and magnitude over small scales, especially in areas of complex topography, were orography is an important influence on local precipitation (Kittel *et al.*, 2015). While spatial variation in microclimate has received much attention (e.g. Suggitt *et al.*, 2018), the ecological implications of fine-scale variation in long-term climate trends are often overlooked.

A major aim of this thesis is to study vulnerability to climate change, including to changes in extreme events, in threatened species endemic to the topographically varied island of Mauritius (1,865 km^2). Mauritius provides an opportunity to explore climate impacts on threatened species because there are long-term meteorological datasets available and it harbours endemic species of high conservation concern. This country is emblematic of tropical island biodiversity and the loss of species, which has occurred primarily due to hunting, habitat loss and degradation, and the introduction of non-native species (Cheke and Hume, 2008). However, during the late 20th century the investment of substantial funds and effort into intensive conservation work has been successful in averting the extinction of some of the country's native species (Cheke and Hume, 2008; Rodrigues *et al.*, 2014). These achievements are potentially jeopardised by climate change, including changes in the occurrence of extreme events.

Existing evidence indicates that in Mauritius there has been a general trend of decreasing rainfall (Republic of Mauritius, 2016), although in the Bambous Mountains of eastern Mauritius total rainfall and rainfall frequency have been increasing (Senapathi *et al.*, 2010). While there is strong evidence of increases in total rainfall and the number of raindays, trends in the occurrence of extreme events have not been studied in the Bambous Mountains.

I set out to study whether these apparently contrasting climate trends in Mauritius are relevant to species conservation and whether trends in extremes follow the same patterns. I hypothesised that trends in extremes will follow the trends shown in previous analyses, with extreme rainfall expected to be increasing in the Bambous Mountains and drought risk expected to be increasing elsewhere on the island. Such trends could have implications for the conservation of threatened species. The Bambous Mountains harbour a reintroduced population of the Mauritius kestrel (*Falco punctatus*) and the area is the subject of other threatened species reintroduction projects. There are important insurance populations of threatened species, located nearby on an offshore islet, Ile aux Aigrettes, which may be assumed to be experiencing the same rainfall trends as the Bambous Mountains; however, long-term climate trends have not been studied there. Arguably the most important area for biodiversity conservation in Mauritius is the Black River Gorges National Park (BRGNP), which harbours remnant populations of several threatened species, including the echo parakeet (*Psittacula eques*), and remnant fragments of native forest. Long-term climate trends, relevant to the threatened species occurring there, have not been studied for the national park. These knowledge gaps regarding climate trends at sites of conservation importance in Mauritius constrain the ability of conservation managers and policy-makers to develop informed strategies for future conservation work. The aims of this chapter are to develop ecologically-relevant indices for meteorological conditions, including for extreme events, and to quantify past trends in these indices in areas of high conservation importance in Mauritius. Such knowledge will assist conservation managers, who may need to adapt future conservation strategies.

3.3 Methods

3.3.1 Study system

Mauritius is an oceanic island state of volcanic origin, located in the Southwest Indian Ocean (SWIO), c.860 km east of Madagascar, and forms part of the Mascarene archipelago. The main island (20°17'S, 57°36'E) is 1,865 km^2 in area and features a central plateau at 400-600 m elevation and several mountain ranges (Staub *et al.*, 2014). Forest on the main island of Mauritius now covers around 25% of the land area, of which only 2% is native forest, following extensive land-use change for agriculture and development (MAIFS, 2015).

The Mascarene islands have a tropical seasonal climate (Safford and Hawkins, 2013), influenced by the surrounding ocean and two main weather regimes: seasonal tropical cyclones and the Southeast Trade Winds (Anderson, 2012). The Bambous Mountains in eastern Mauritius form a trade wind belt, and experience some of the highest annual rainfall amounts on the island (Staub *et al.*, 2014). Rainfall in Mauritius can be divided into two broad seasons, with the Southeast Lesser Monsoon season from June until November, and the Northwest Monsoon and cyclone season from December until May (Senapathi, 2009; Senapathi *et al.*, 2010) (see Figures 3.2-3.4), with daily temperatures peaking in the austral summer (see Figures 3.5 and 3.6). In general, approximately 40% of total annual rainfall occurs in January-March, following the southward migration of the Inter-Tropical Convergence Zone (ITCZ) towards subtropical latitudes and the occurrence of tropical cyclones (Staub *et al.*, 2014). The SWIO basin experiences 11-12 tropical cyclones per year, with the cyclone season generally being from November to April (Malan *et al.*, 2013). Rainfall in the Bambous Mountains on the east coast of Mauritius is also influenced by sea surface temperatures in the western Indian Ocean, as well as large-scale factors including the Indian Monsoon and El Niño-Southern Oscillation (Senapathi *et al.*, 2010).

Mean annual rainfall varies longitudinally, from ~1400 mm in the eastern coastal lowlands, to ~4000 mm in the highlands, and ~800 mm along the western coastal lowlands (Staub *et al.*, 2014). Orographic lifting takes place over the island as a result of its raised topography and has contributed to the creation of several microclimate zones, with the central uplands classed as super humid, the eastern and southern regions classed as humid, and a small area in the west defined as semi-arid (reviewed by Anderson, 2012).

3.3.2 Areas of high conservation importance

In this study, climate trends are analysed in three areas, selected on the basis of the threatened species populations that occur there and thus their importance to biodiversity conservation. They represent climatically and topographically distinct areas, with representation of uplands, intermediate mountains and hills, and coastal lowlands. The Black River Gorges National Park harbours remnant fragments of native forest on Mauritius, although much of it is invaded with non-native plant and animal species. Several threatened vertebrate species have important populations within the national park, including the echo parakeet, Mauritius kestrel, pink pigeon (*Nesoenas mayeri*), Mauritius cuckoo-shrike (*Coracina typica*), Mauritius olive white-eye (*Zosterops chloronothos*) and Mauritius fody (*Foudia rubra*). The national park comprises upland areas and areas of steep topography, descending to the south-western coastal lowlands, and holds fragments of degraded native forest. In Chapter 5, climate impacts on the echo parakeet in upland areas will be explored in more detail. The Bambous Mountains in eastern Mauritius hold a reintroduced population of the Mauritius kestrel, and other species are being reintroduced into the area, including the pink pigeon, echo parakeet and Mauritius cuckoo-shrike. The area is dominated by hunting land and farmland, with remnant fragments of native forest. The topography comprises lowlands, hills and low mountains. In Chapter 4, climate impacts on the Bambous Mountains population of Mauritius kestrels are explored. Ile aux Aigrettes (IAA) is a low-lying coralline islet, located ~625 m off the coast of south-eastern Mauritius, and is within 6 km of the Bambous Mountains. This island is kept free of predators and is the subject of ongoing habitat restoration. Insurance populations of several threatened species have been established on the islet, including the Mauritius fody, Mauritius olive white-eye, pink pigeon, Telfair’s skink (*Leiolopisma telfairii*) and Günther’s gecko (*Phelsuma guentheri*).

3.3.3 Selection of meteorological datasets

Data on precipitation, surface air temperature and tropical cyclone tracks were obtained from a variety of sources (Table 3.1) for locations relevant to the focal areas of conservation importance (Figure 3.1). Rainfall data from a rain gauge in the Bambous Mountains were contributed by Ferney Sugar Estate. These data were collected at Mt Camizard (20°20’S, 57°42’E, 21 m asl), within the range of the Bambous Mountains kestrel population, and constitute a dataset used in previous studies on the Mauritius kestrel (Nicoll *et al.*, 2003; Nicoll, 2004; Burgess, 2008; Burgess *et al.*, 2008; Burgess *et al.*, 2009; Senapathi, 2009; Senapathi *et al.*, 2010; Burgess *et al.*, 2011; Cartwright, 2011; Senapathi *et al.*, 2011; Cartwright *et al.*, 2014a, b). Rainfall data relevant to focal populations in and around the BRGNP were obtained from a rain gauge at Petrin (20°24’S, 57°28’E, 655 m asl) and contributed by Mauritius Meteorological Services (MMS). Based on the spatial modelling of rainfall (see Staub *et al.*, 2014), this gauge is thought to occupy a microclimate zone similar to most echo parakeet nest-sites, and is located within 10 km of all spatially-referenced nest-sites. Daily precipitation and temperature data from the two synoptic stations on mainland Mauritius, at Plaisance (20°26’S, 57°41’E, 50 m asl, c.5 km from IAA and c.11 km from Mt

Camizard) and Vacoas (20°17'S, 57°29'E, 424 m asl, c.12 km from Petrin) were downloaded from the National Centers for Environmental Information of the National Oceanic and Atmospheric Administration (NOAA: www.ncdc.noaa.gov) in the form of two inventories for each station: the Global Historical Climatology Network-Daily (GHCN-Daily) and Global Summary of the Day (GSOD). A complete time series of daily rainfall data from Plaisance for 1992-2015 was contributed by MMS.

The GHCN-Daily data on rainfall and temperature from the Plaisance and Vacoas synoptic stations comprise GSOD data in more recent years, thus missing values in the GHCN inventories in these years were filled with values from the GSOD inventories where available. The number of missing precipitation values for Vacoas causes difficulties in calculating reliable values for extreme indices and limits the extent of subsequent analysis possible with this dataset. Despite this, the precipitation data from Vacoas form a longer-term dataset than available for Petrin, thus the Vacoas data are used for trend analyses for some indices when looking at climate trends in the national park. To further minimise the number of missing precipitation values and maximise the duration of the time series for Plaisance, the data from GHCN-Daily and MMS were combined. During the process of combining these datasets, rainfall values from the MMS inventory were used to fill data gaps and replace zero values in the GHCN/GSOD data. However, differences between the inventories could create biases. In addition, an incomplete time series of daily rainfall on IAA from January 2013 to April 2015 was contributed by the Mauritian Wildlife Foundation (MWF); however, the short time span and proportion of missing values render these data inappropriate for use in computing meteorological indices for the study of ecological impacts.

Tropical cyclone tracks and accompanying data were downloaded as ESRI shapefiles from the International Best Track Archive for Climate Stewardship (IBTrACS v03r10) (Knapp *et al.*, 2010) via NOAA (www.ncdc.noaa.gov/ibtracs). Global best-track data comprise 6-hourly estimates of the location (latitude and longitude) and intensity (usually estimated as maximum sustained wind speed) of every recorded tropical cyclone during varying periods of record in each world region. For the SWIO region, 1982 saw the introduction of Dvorak methods for intensity estimation (Dvorak, 1984) in operational procedures, although this was in the absence of digital imagery (Terry *et al.*, 2013). Periodic advances in the tracking and assessment of tropical cyclones in the SWIO, through the introduction of digital imagery in 1991 (Terry *et al.*, 2013) and repositioning of a satellite in 1998 (Elsner *et al.*, 2008; Kossin *et al.*, 2013), have undoubtedly introduced biases into observed trends in the data (Terry *et al.*, 2013). It is expected that these changes are more likely to result in biases in intensity estimation rather than position estimation. Prior to the improvement of the view angle in

1998, intensity estimates for the tropical Indian Ocean used a more oblique view angle and were likely biased high for some cyclones due to lower estimates of cloud-top temperatures from infrared brightness (Elsner *et al.*, 2008; Kossin *et al.*, 2013), and biased low for some cyclones due to difficulty in identifying the development of an eye (Kossin *et al.*, 2013). This makes it challenging to adjust for inhomogeneities without re-selecting the satellite imagery used for intensity estimates, as carried out by Kossin *et al.* (2013). It is beyond the scope of this study to use such methods to improve the homogeneity of intensity estimates; however, potential inhomogeneities should be borne in mind when interpreting subsequent analyses.

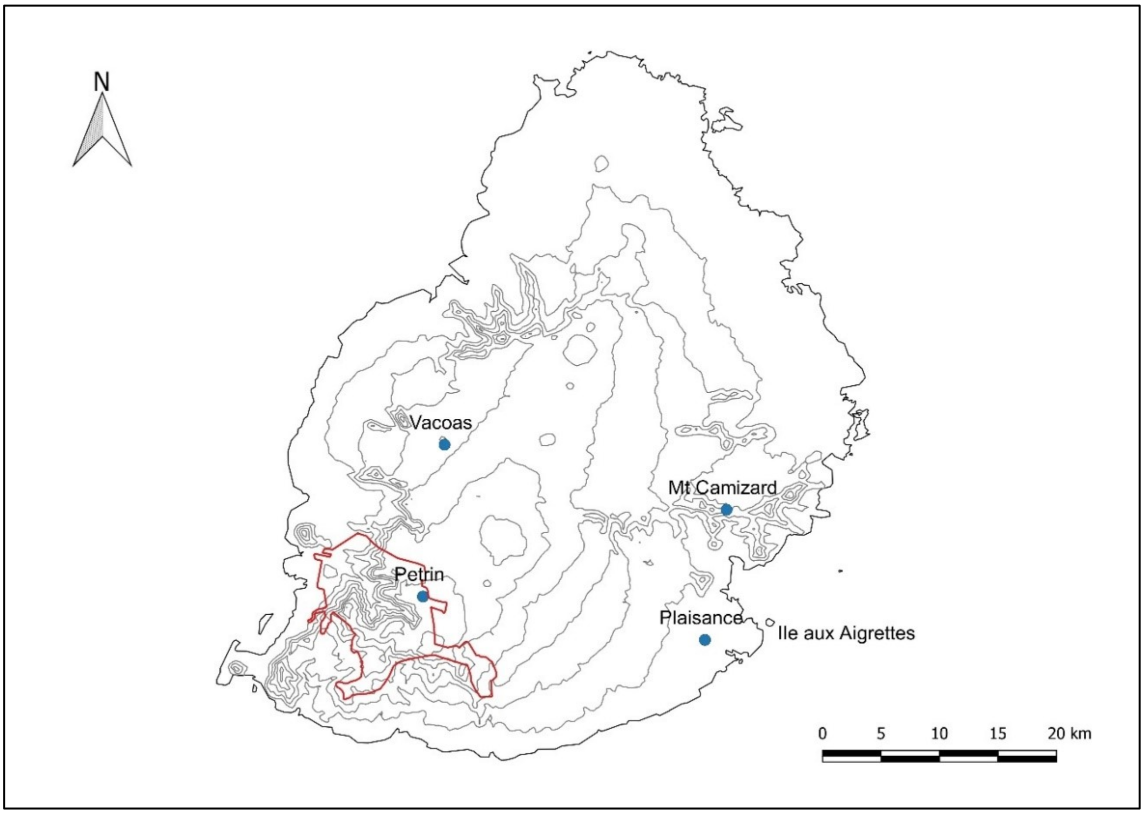

Figure 3.1. Map of mainland Mauritius showing the weather stations used in this study (blue points). Red lines indicate the borders of the Black River Gorges National Park. Contour lines show 100 m contours.

3.3.4 Identification of proxy data

Sufficient rain gauge data were not available from the rain gauge on IAA for use in this study, so the combined rain gauge data from Plaisance were compared to daily data collected on IAA to ascertain whether rainfall at Plaisance could be used as a proxy of rainfall on IAA. Data from IAA were only available for the period January 2013 to April 2015 inclusive, and values for 299 days (35.2%) were missing, thus limiting the number of options available for the comparison of these data with those from Plaisance. The two gauges were compared on a monthly basis, with two measures used; (1) probability of rainfall (≥1 mm) on days with data available, and (2) mean rainfall (mm) on raindays (≥1 mm). This was carried out using all days for which data were available from each station. Kendall's tau was used for comparisons of monthly data at the two stations. This process was carried out to assess the strength of the correlation between the two rain gauges, although this does not examine the occurrence of extremes at the two locations. Throughout this study, a rainday is defined as a day on which at least 1 mm on rain was recorded. This threshold is widely used in meteorological research and accounts for the possibility of condensation in rain gauges and difficulty in measuring rain amounts of less than 1 mm, which are sometimes not reported (Zhang *et al.*, 2011).

3.3.5 Data quality control

Artificial inhomogeneities in weather data time series can result from changes in equipment, methodology and personnel over time (WMO, 2003). Homogeneity tests typically include the comparison of data from one weather station with those from a group of neighbouring stations. In this study, data are only available from a limited number of stations, making comparisons difficult and potentially unreliable; therefore homogeneity was tested for each station independently using break point tests. These were carried out on rainfall and temperature time series data using package 'iki.dataclim' (Orlowsky, 2015) in the R statistical environment (version 3.4.4, R Core Team, 2018). Four tests were applied as described in the Algorithm Theoretical Basis Document of the European Climate Assessment and Dataset project (ECAD and KNMI, 2013): the Standard Normal Homogeneity test, the Buishand Range test, the Pettitt test and the Von Neumann Ratio test. These tests were applied to annual total rainfall at Mt Camizard, Plaisance and Vacoas, and annual mean daily maximum temperature at Plaisance and Vacoas (based on 12-month periods running from June to May; see section 3.3.6 for details), for runs of at least 20 consecutive years without missing annual values (where >36 days missing in a year). The Plaisance temperature data show a significant break point in 1975-1976 or 1985 (see Appendix Table A3.1). Following a conservative approach to inhomogeneity adjustments, and owing to substantial challenges in the adjustment of daily data (WMO, 2003), no changes were carried out on the basis of the test results. These homogeneity tests could not be applied to rainfall data from Petrin owing to the number of missing values, and it is recognised that artificial inhomogeneities could exist in these data.

The reliability of rainfall data is also affected by outliers, which may be erroneous and are sometimes removed or adjusted before other analyses are carried out (e.g. Zhang *et al.*, 2005a; Vincent *et al.*, 2011). However, this study is concerned with extreme values, thus the removal or adjustment of outliers could affect the utility of the data for this purpose. Indices for extremes have been selected that reduce the influence of absolute values where extremes occur. Consecutive repeat values in rain gauge data are problematic, as they are unlikely to occur naturally and are often due to human error or data processing errors (e.g. Durre *et al.*, 2010; Funk *et al.*, 2015). These data were detected using a bespoke function in the R statistical environment that flagged repeat values on consecutive raindays (≥1 mm), but not when rainfall was 0.1-0.9 mm, as consecutive repeats are common near zero (Nie *et al.*, 2012). The repeated values were subsequently treated as missing data (following Gallego *et al.*, 2011). Day-to-day temperature variation is often limited on tropical islands (Zhang *et al.*, 2011) so the threshold for suspect runs of consecutive repeat values was set at 10 days. None of the temperature data were flagged as a result of this check. All meteorological indices were only calculated for time periods with values missing on no more than 10% of days (i.e., months with values missing on no more than 3 days, and quarters with values missing on no more than 9 days).

3.3.6 Time windows for climate indices

Peak breeding activity in most of the relevant study species is known to be not completely coincident with peaks in annual rainfall, and some populations, such as the Mauritius fody population on IAA, show almost year-round breeding, thus meteorological indices in this study are calculated on a quarterly basis to capture important times of year for all of the study species, as well as following fairly well-defined periods of seasonal precipitation changes. Indices are computed for September-November (spring; hereafter SON), which is the peak nesting phase for Mauritius kestrels and echo parakeets and the late dry season, December-February (summer; hereafter DJF), which is the peak fledging phase in kestrels and parakeets and the early rainy and cyclone season, March-May (autumn; hereafter MAM), which is the post-fledging period in kestrels and parakeets and the late rainy and cyclone season, and June-August (winter; hereafter JJA), which is the pre-nesting period in kestrels and parakeets and the early dry season. For these analyses, the annual climate and ecological cycle is defined as June to May, which captures important seasons, including the dry season (generally JJASON), kestrel and parakeet breeding seasons (SONDJF) and rainy and cyclone season (generally DJFMAM). The start and end of the year is thus defined around the transition of the rainy season into the dry season during the austral autumn and winter. The use of standardised time periods for the calculation of indices allows the inter-comparison of temporal trends at different sites and between this study and other meteorological research, and the choice of quarterly rather than monthly time frames increases the number of extreme events that are captured by the time windows.

3.3.7 Reference period for climate indices

The components of climate indices, such as quantile thresholds and averages, may be derived from an entire time series of data, perhaps spanning many decades, potentially maximising the reliability of those values. However, there is evidence that the current climate is nonstationary, probably owing to anthropogenic influences (e.g. IPCC 2014), thus a data series of many decades may be influenced by the climate change signal (Russo *et al.*, 2013). Furthermore, datasets may differ in length and thus exhibit different amounts of influence from climate change, making inter-comparisons difficult when utilising all data from each time series.

The use of a standard reference period or base period is often employed in meteorology to derive climatological normals (WMO, 2007). A reference or base period of at least 30 years is usually recommended, especially for rainfall data (WMO, 2007), as this is thought to provide reliable estimates of quantile thresholds and monthly averages (Guttman, 1994; WMO, 2007). The previous recommended base period for climatological normals was 1961-1990, which has since been replaced with a new recommended base period of 1981-2010 (Baddour, 2011). However, data are not available for these recommended base periods for all of the locations of interest in this study, with the precipitation data from Petrin covering fewer than 30 years. Reference periods shorter than 30 years, and as short as 10 years, have been shown to produce representative averages and probability distributions in meteorological datasets (WMO, 2007). Therefore, a 25-year reference period of 1990/1991-2014/2015 (based on a year running from June to May) is used in this study, as data are available for this period from all of the study locations, and these years correspond to the period for which appropriate ecological data are available for the focal species studied in later chapters. This period therefore represents the extreme weather regime that the focal species were exposed to when the ecological data used in this study were collected. This reference period includes a strong El Niño event in 1997-1998 which may affect the values derived; however, the actual weather and climate regime experienced by the focal species is of interest here, thus data from these years are not removed and the influence of El Niño is not controlled-for when using this reference period.

3.3.8 Selection of meteorological indices

The analysis of weather and climate extremes has received substantial attention among meteorological researchers, primarily because of impacts on human society, and as a consequence a wide range of indices exist. To address the issue of inconsistency in the use of indices and methods in meteorological research, and to provide better input to the IPCC Fourth Assessment Report (IPCC, 2007), the joint WMO CCI/CLIVAR Expert Team on Climate

Change Detection, Monitoring and Indices (ETCCDMI) coordinated the development of a suite of indices for climate extremes (Easterling *et al.*, 2003; Zhang *et al.*, 2005a). The ETCCDMI recommended a total of 27 core indices with the primary focus on extremes to be derived from daily data from weather stations. These indices can be computed using a package in the R statistical environment, developed at the Climate Research Branch of the Meteorological Services of Canada on behalf of the ETCCDMI.

Many of the indices used in the present study are based on and adapted from the ETCCDMI indices, hereafter referred to as the Climdex indices (www.climdex.org). A selection of meteorological indices that were considered for use in this study and not chosen are shown in Table A3.2 (see Appendix). As well as a selection of indices for extreme meteorological events, general indices for total and average precipitation and average temperature are also derived from the datasets in this study (Table 3.2). This allows the comparison of ecological impacts from extreme events and overall conditions. Evidence already exists that indicates that breeding phenology, breeding productivity and juvenile survival in the Mauritius kestrel are influenced by total rainfall and the number of raindays in some months of the year (Nicoll *et al.*, 2003; Nicoll, 2004; Senapathi, 2009; Senapathi *et al.*, 2011). Hydroclimatic Intensity (HY-INT; Giorgi *et al.*, 2011; Giorgi *et al.*, 2014) is an index that incorporates mean daily rainfall intensity and mean dry spell duration to provide a characterisation of the climate context in which extreme events occur. For HY-INT, mean dry spell length was calculated using a bespoke function in the R statistical environment. This was carried out with all missing rainfall values coded as raindays and then coded as dry days, with the mean of these outputs for each season being used for the index calculation.

Table 3.1. Meteorological datasets used in this study on ecological impacts in Mauritius.

Weather attribute	**Type of data**	**Location**	**Data source or inventory***	**Time period with applicable data, based on complete seasons**	**Percentage of days with missing data****	**Percentage of days in 1990/1991-2014/2015 with missing data****
Precipitation	Daily rainfall totals from rain gauge measurements	Mt Camizard (20°20’S, 57°42’E, 21 m asl)	Ferney Sugar Estate	03/1962 – 02/2016	1.51	1.45
		Petrin (20°24’S, 57°28’E, 655 m asl)	MMS	03/1987 – 11/2015	4.22	4.42
		Plaisance Synoptic Station (20°26’S, 57°41’E, 50 m asl)	Combined time series from GHCN-Daily and GSOD (1951 – 2015) and MMS (1992 – 2015)	03/1951 – 11/2015	0.66	0.96
		Vacoas Synoptic Station (20°17’S, 57°29’E, 424 m asl)	Combined time series from GHCN-Daily and GSOD	03/1961 – 11/2015	4.17	8.64

Table 3.1 continued:

Weather attribute	**Type of data**	**Location**	**Data source or inventory***	**Time period with applicable data, based on complete seasons**	**Percentage of days with missing data****	**Percentage of days in 1990/1991-2014/2015 with missing data****
Surface air temperature	Thermometer readings of daily minimum and maximum air temperature	Plaisance Synoptic Station (20°26'S, 57°41'E, 50 m asl)	Combined time series from GHCN-Daily and GSOD	03/1951 – 11/2015	0.01	0.00
		Vacoas Synoptic Station (20°17'S, 57°29'E, 424 m asl)	Combined time series from GHCN-Daily and GSOD	03/1961 – 11/2015	1.86	4.05
Tropical cyclones	Tracks and intensities derived from satellite data	Global and South Indian Ocean basin	IBTrACS v03r10	12/1980 – 05/2015	NA	NA

***Data sources and inventories:** GHCN = Global Historical Climatology Network, available via NOAA (www.ncdc.noaa.gov); GSOD = Global Summary of the Day, available via NOAA (www.ncdc.noaa.gov); IBTrACS = International Best Track Archive for Climate Stewardship, available via NOAA (www.ncdc.noaa.gov/ibtracs); MMS = Mauritius Meteorological Services.

**Following quality control processes (see main text).

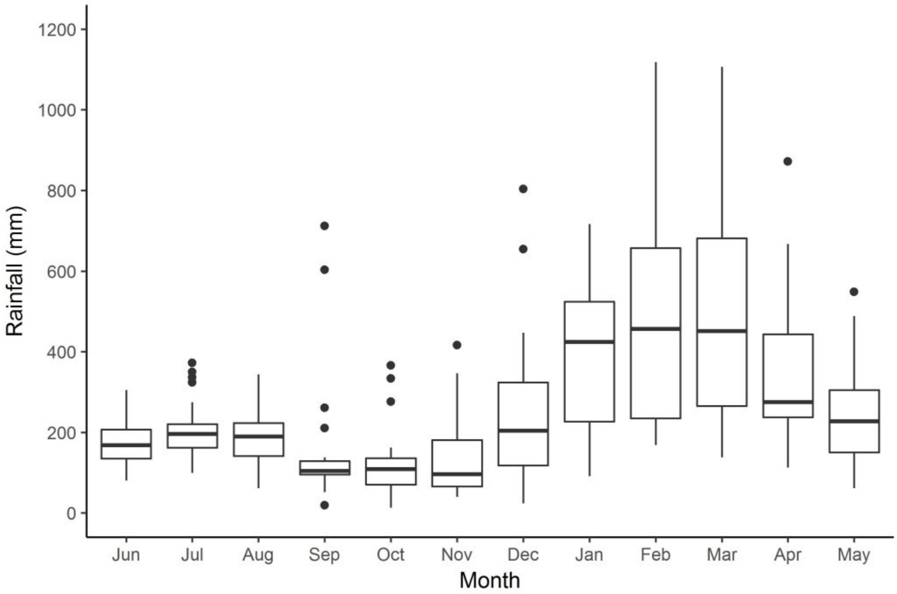

Figure 3.2. Boxplot of accumulated monthly rainfall on raindays (≥1 mm) at Mt Camizard, Mauritius, using data from June 1990 to May 2015. Horizontal bars represent median values. Boxes show interquartile range. The 'whiskers' show 1.5-3 times the interquartile range of outliers; data points show remaining outliers.

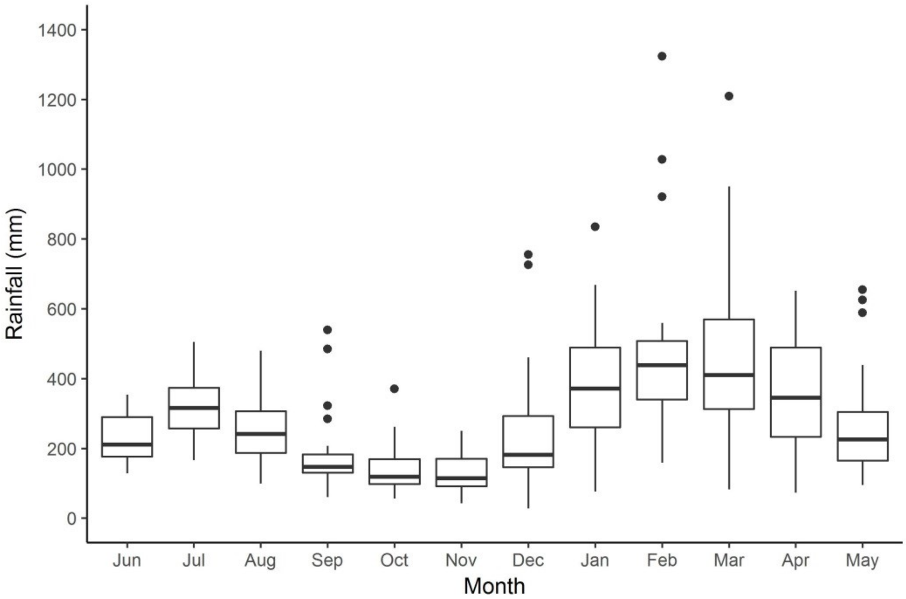

Figure 3.3. Boxplot of accumulated monthly rainfall on raindays (≥1 mm) at Petrin, Mauritius, using data from June 1990 to May 2015. Horizontal bars represent median values. Boxes show interquartile range. The 'whiskers' show 1.5-3 times the interquartile range of outliers; data points show remaining outliers.

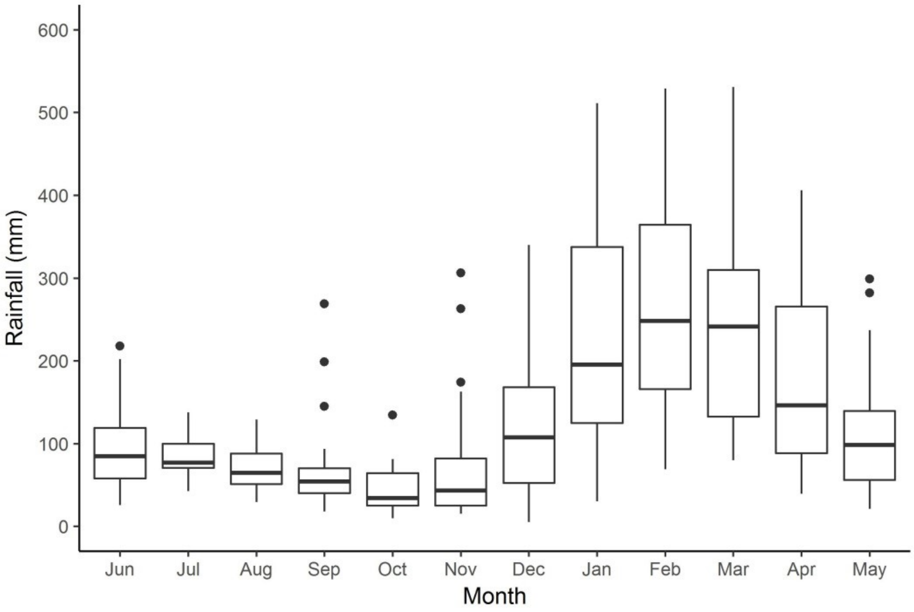

Figure 3.4. Boxplot of accumulated monthly rainfall on raindays (≥1 mm) at Plaisance, Mauritius, using data from June 1990 to May 2015. Horizontal bars represent median values. Boxes show interquartile range. The 'whiskers' show 1.5-3 times the interquartile range of outliers; data points show remaining outliers.

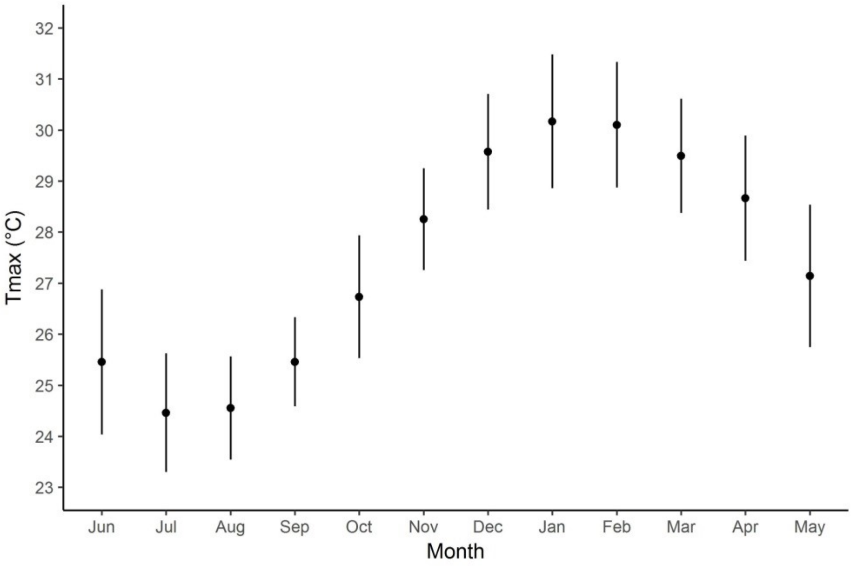

Figure 3.5. Monthly means of daily maximum temperature (Tmax, °C) at Plaisance, Mauritius, using data from June 1990 to May 2015. Error bars show ±1SD.

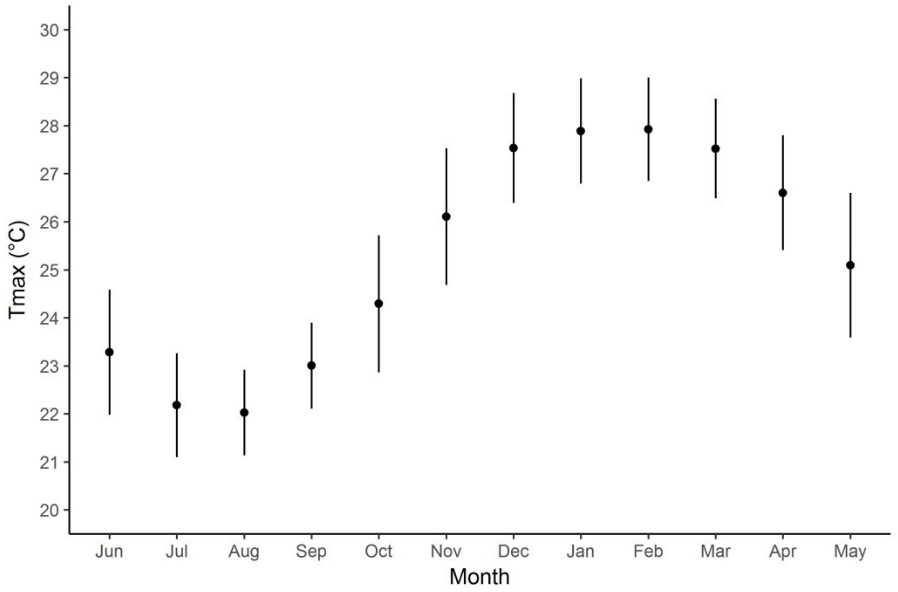

Figure 3.6. Monthly means of daily maximum temperature (Tmax, °C) at Vacoas, Mauritius, using data from June 1990 to May 2015. Error bars show ±1SD.

In calculating temperature indices, it is noted that the synoptic station at Vacoas is 231 m lower in elevation than the weather station at Petrin. The environmental lapse rate of 6.5°C/1000 m implies that temperatures at Petrin are ~1.5°C cooler than at Vacoas, although in reality this will be highly variable and affected by other factors such as differences in local humidity and wind speed. Because of this uncertainty, temperature indices calculated for Vacoas are not altered when relating them to populations in the BRGNP. The synoptic station at Plaisance is at 50 m asl, compared with 21 m asl for the Mt Camizard rain gauge, thus temperature indices calculated for Plaisance are not adjusted when relating them to populations in the Bambous Mountains. However, differences in humidity and wind patterns between the two locations will result in temperature differences.

Table 3.2. General climate indices chosen for use in this study.

Climate attribute	Index	Description	Units
Precipitation	Rainfall	Total daily rainfall on raindays (≥1 mm).	mm
	Raindays	Total number of days on which ≥1 mm of rain was recorded.	days
	SDII	Simple Daily Intensity Index: Average daily rainfall on raindays (≥1 mm).	mm
	HY-INT	Hydroclimatic Intensity: The product of the normalised SDII and normalised average dry spell length (Giorgi *et al.* 2011, 2014). Normalisations are carried out using averages from the standard reference period of 1990/1991-2014/2015.	NA
Temperature	Mean Tmax	Average daily maximum temperature.	°C

Thresholds for extreme rainfall in ecological studies may be set arbitrarily or based on prior knowledge of impacts. However, little relevant information is available for the focal populations in the present study. Regarding the Mauritius kestrel, limited information is available for some other raptor species. Breeding success by peregrine falcons (*Falco peregrinus*) in Canada was found to be impacted by heavy rainstorms, which were defined as rainfall of at least 8 mm day^{-1} (Anctil *et al.*, 2014), with another study in the same area showing an impact on chick mortality from rainfall amounts during periods of at least three consecutive days of rain (Bradley *et al.*, 1997). However, depending on the local climate context, such thresholds may not prove to be statistically extreme, and impacts may be substantial at the individual nest level but not necessarily at the population level. Owing to the limited information available on the focal populations and similar species, and the objective of this study to test the impacts of events that can be considered extreme, the indices for precipitation extremes used in the present study are based on quantiles, which provide a more objective characterisation of extreme events (Table 3.3). Extreme weather and climate events are a natural part of the climate system, but true extremes are rare events (Easterling *et al.*, 2016). Because of this rarity researchers often relax the definition of extremes to increase the number of observations that can be used in a statistical analysis

(Easterling *et al.*, 2016). The thresholds for extreme daily precipitation events in the present study are chosen as the 90th and 95th percentiles. The Intergovernmental Panel on Climate Change (IPCC) defines extreme events as those that are normally as rare or rarer than the 10th or 90th percentile of values in the probability density function (e.g. IPCC, 2014). Many of the events that exceed these thresholds are not truly extreme (Easterling *et al.*, 2016), or may be classed as 'moderate extremes' (Klein Tank *et al.*, 2009); however, their inclusion generally makes analyses more statistically robust (Alexander, 2016). This approach is also based on the assumption that a given species is adapted to the contemporary climate within its geographic range, thus changes in the frequency or temporal distribution of rare events would be expected to affect the fitness of individuals in that species' population.

In this study, quantile thresholds are calculated empirically using all raindays at each site during the standard reference period (1990/1991-2014/2015), either for each season separately or for all seasons amalgamated. Two of the extreme rain indices (Raindays90 and Raindays95) are based on seasonal percentiles because overall rainfall and extreme thresholds vary between seasons and the focal populations are at different stages in their annual cycles in each season. However, the influence of these indices cannot be compared between seasons, thus another index (Rainfall90) is calculated as the total rainfall on days over the 90th percentile threshold for all seasons combined. Many of the indices in the present study were calculated in the R statistical environment with the aid of package 'climdex.pcic' (Bronaugh, 2015).

The use of a reference period taken from a longer time series to calculate percentiles can create biases when analysing trends in exceedance indices over the entire time series (Zhang *et al.*, 2005b). This occurs because a given percentile threshold calculated from a sample of days within the reference period will not be exactly the same as in years immediately outside the reference period. This can result in an artificial jump in exceedances between in-reference and out-of-reference years, generally because of a positive bias in exceedances in years outside the reference period (Zhang *et al.*, 2005b). In the present study, the potential for such biases is reduced by calculating percentile thresholds for quarters over a 25-year reference period, thus sampling data from up to 2275 days for each quarterly percentile index. No other techniques are used to reduce these biases.

Table 3.3. Indices for extreme rainfall chosen for use in this study.

Index	**Description**	**Units**
Raindays90	Total number of days exceeding the seasonal 90th percentile threshold of raindays (in each season). Percentile thresholds are calculated empirically using all raindays (≥1 mm) for a given season during the standard reference period of 1990/1991-2014/2015.	days
Raindays95	Total number of days exceeding the seasonal 95th percentile threshold of raindays (in each season). Percentile thresholds are calculated empirically using all raindays (≥1 mm) for a given season during the standard reference period of 1990/1991-2014/2015.	days
Max Rain Spell	Maximum number of consecutive days when ≥1 mm of rainfall was recorded. Spells cannot cross into adjacent seasons.	days
Rainfall90	Total accumulated rainfall (mm) on raindays exceeding the overall 90th percentile of all raindays (in all seasons). Percentile thresholds are calculated empirically using all raindays (≥1 mm) during the standard reference period of 1990/1991-2014/2015.	mm

Droughts are the costliest form of natural disaster, causing billions of dollars (US$) of damages each year globally and affect more people than any other type of natural disaster (Wilhite, 2000). Considerable effort has therefore been invested in the monitoring, measurement and prediction of drought. However, the study of drought has long suffered from the lack of an adequate and consistent definition (Heim, 2002). The development of drought indices has evolved during the last two centuries, from basic approaches that use measures of rainfall deficiency to more complex models (Heim, 2002). More than 100 drought indices have so far been proposed (Zargar *et al.*, 2011), characterising different aspects and types of droughts.

Physical droughts can be defined as meteorological, hydrological or agricultural, based on precipitation, water supply sources and soil moisture for plant growth respectively (reviewed by Keyantash and Dracup, 2002). Among the most widely used indices is the Palmer Drought Severity Index (PDSI) (Palmer, 1965) and modified versions (reviewed by Hayes *et al.*, 1999), which requires data on precipitation, temperature and local soil moisture conditions, and is based on the supply and demand concept of the water balance equation (Hayes *et al.*, 1999).

In the early 1990s, the Standardised Precipitation Index (SPI) (McKee *et al.*, 1993; McKee *et al.*, 1995) was designed as a relatively simple, year-round index applicable to water supply conditions (Hayes *et al.*, 1999). This index has become one of the most widely-used globally and is accompanied by a substantial literature base (see WMO, 2012 for overview). Its main strengths are that it can be calculated for a variety of timescales and it requires only precipitation data. In the calculation of SPI, the probability distribution of precipitation data is determined from the long-term record by fitting a function to the data (Hayes *et al.*, 1999). The cumulative distribution is then transformed using equal probability to a normal distribution with a mean of zero and standard deviation of one (Edwards and McKee, 1997). A particular precipitation total for a specified time period is then identified with a particular SPI value consistent with probability (Hayes *et al.*, 1999). SPI has also been adapted to incorporate evapotranspiration by utilising local temperature data (Standardised Precipitation and Evapotranspiration Index: SPEI; Vicente-Serrano *et al.*, 2010).

Established drought indices designed to measure impacts relevant to human society, such as PDSI and SPI, have also been used to study impacts on ecosystems and wild populations (e.g. Albright *et al.*, 2010; Duncan *et al.*, 2012; Reichert *et al.*, 2012; Cruz-McDonnell and Wolf, 2016; Ross *et al.*, 2016). In the present study, the choice of which drought index to apply is influenced mainly by data availability. Soil moisture data are not available and temperature data are limited and not available for all study sites. As precipitation data are the only relevant data that are available for all study areas, SPI is chosen as the index to be applied to the study areas in Mauritius (Table 3.4).

It is advised that SPI be applied to at least 20-30 years of continuous precipitation data (WMO, 2012), in order to capture representative monthly means and the probability distribution of precipitation. However, it is more widely recommended that at least 30 years of data be used (McKee *et al.*, 1993; Hayes *et al.*, 1999; WMO, 2012), with some researchers recommending the use of 50-60 years (or more) of data, owing to considerable natural variability in precipitation (Guttman, 1994; WMO, 2012). However, the use of more than 30 years of data may fail to account for non-stationary climates, in which the climate change signal could be significant over such time periods (Russo *et al.*, 2013).

In the present study, not all precipitation datasets cover the commonly-used minimum of 30 years, thus SPI at all sites is standardised by the 25-year reference period of 1990/1991-

2014/2015, which corresponds to the period for which appropriate ecological data are available for the focal species. The use of the same reference period for all study sites also allows the comparison of index values between sites. The use of a reference period of fewer than 30 years is not unprecedented, and some studies have shown that SPI calculated using fewer than 30 years, and even fewer than 20 years, can produce useful results (Patel *et al.*, 2007; Naumann *et al.*, 2012; Bowden *et al.*, 2016; Kumar *et al.*, 2016). However, it should be noted when interpreting the SPI values in this study that the statistical stability of the index could be influenced by the relatively short reference period used, thus the SPI values may have weaker confidence (WMO, 2012). SPI is calculated for 3-month and 6-month periods (Table 3.4) to test for trends in different drought durations, but not for longer time periods such as 12 months, as missing data start to increasingly limit the number of seasons for which the index can be reliably calculated. SPI was computed using package 'SPEI' (Beguería and Vicente-Serrano, 2015) in the R statistical environment. In addition to SPI, the maximum dry spell (consecutive days <1 mm rainfall) is also applied, as this widely used index may characterise conditions that are ecologically relevant.

Table 3.4. Drought indices chosen for use in this study.

Index	Description	Units
SPI-3	Standardised Precipitation Index for 3-month periods: Monthly rainfall totals are fitted to a (Gamma) probability distribution, which is then transformed to a Gaussian distribution to produce an index centred on zero (WMO 2012). The standard reference period of 1990/1991-2014/2015 is used to produce the probability distribution, and SPI values are calculated on a quarterly basis.	NA
SPI-6	Standardised Precipitation Index for 6-month periods: Monthly rainfall totals are fitted to a (Gamma) probability distribution, which is then transformed to a Gaussian distribution to produce an index centred on zero (WMO 2012). The standard reference period of 1990/1991-2014/2015 is used to produce the probability distribution, and SPI values are calculated for 6-month periods, i.e. the quarter being studied plus the preceding quarter.	NA
Max Dry Spell	The maximum number of consecutive days on which <1 mm of rain was recorded. Spells cannot cross into adjacent seasons.	days

Extreme temperature indices may be based on prior knowledge about impact thresholds where existing empirical research or observations provide relevant information. In an ecological context this involves threshold temperatures beyond which known fitness costs are incurred by the species of interest, an approach that has been applied to bird species in South Africa (Cunningham *et al.*, 2013). Arbitrary thresholds, perhaps based in part on prior knowledge of the local climate, can also be tested against ecological data where sufficient temporal resolution is available, such as daily or near-daily nest survival data (Conrey *et al.*, 2016). Thresholds may also be based on studies of evaporative water loss and survival times, thermoregulatory capacity or heat stress (McKechnie and Wolf, 2010; Whitfield *et al.*, 2015), although extreme temperature events that meet such thresholds will be most common in arid regions in the current climate, and ecological impacts are likely to start at lower thresholds.

There is very little information available that is relevant to impact thresholds for the focal species in this study or for similar species, which must show taxonomic, morphological and environmental similarities. A study by Catry *et al.* (2011) suggests that the growth rate of lesser kestrel (*Falco naumanni*) chicks in southern Portugal declines above air temperatures of ~31°C. In this case, there is a taxonomic affinity with the Mauritius kestrel, and mean maximum air temperatures at the study site in southern Portugal during the lesser kestrel nesting phase (26-34°C) are comparable to those on the southeast coast of Mauritius during the Mauritius kestrel breeding season. However, without more evidence of temperature thresholds in similar species it may be more appropriate to test for the impact of statistically rare events.

In the present study, the 10th and 90th percentiles are used as thresholds for cold days and hot days (Table 3.5) in order to increase statistical robustness in subsequent analyses, while recognising that not all values exceeding these thresholds are truly extreme (Klein Tank *et al.*, 2009; Alexander, 2016; Easterling *et al.*, 2016). The approach of using quantiles also means that data can be used from weather stations that are some distance from the study populations in question or at different elevations. In the present study, temperature data are only available for the synoptic stations at Plaisance and Vacoas, c.5-12 km away from the focal populations, thus the number of relatively hot or cold days experienced by the study species can be estimated by calculating the number of relatively hot or cold days at the nearest synoptic station.

The method of deriving extreme temperature indices depends on the intended application. Many temperature percentile indices are computed using moving windows to account for the mean annual temperature cycle, thus identifying extremes relative to each calendar day;

however, percentile indices based on aggregated annual or seasonal data may be more suitable for some impact studies (Zhang *et al.*, 2011). In this study, temperature percentiles are calculated from aggregated seasonal data to identify the overall hottest 10% and coldest 10% of temperatures recorded in those seasons. The moving window approach is considered to be less relevant, as a hot day relative to variability in early spring may not have the same impact as a hot day relative to variability in late spring, when average conditions are warmer. It should be noted that biases can arise from the calculation of temperature exceedance indices where the data are of low precision and there is limited day-to-day variation in temperature, as on tropical islands (Zhang *et al.*, 2011). In this study, the precision of the temperature data was 0.1°C, as recommended by the WMO, and no further adjustments were made to reduce the potential for such bias. Temperature indices were computed with the aid of package 'climdex.pcic' in the R statistical environment.

It should be noted that in this study extreme indices are not computed from daily minimum temperature (Tmin) from the GSOD data, as GSOD data from Mauritius are reported at approximately 04:00 MUT and daily temperature minima can potentially occur within a few hours before and after this time, meaning that the number of cold nights cannot be reliably identified using these data.

Table 3.5. Indices for temperature extremes chosen for use in this study.

Index	**Description**	**Units**
Tmax90 Days	Total number of days on which daily maximum temperature exceeded the 90th percentile. Percentile thresholds are calculated using aggregated seasonal data from the standard reference period of 1990/1991-2014/2015.	days
Tmax10 Days	Total number of days on which daily maximum temperature was below the 10th percentile. Percentile thresholds are calculated using aggregated seasonal data from the standard reference period of 1990/1991-2014/2015.	days

Tropical cyclones can have disastrous impacts on human society, thus numerous categorisation schemes and indices have been developed to characterise annual and seasonal cyclone activity and the potential for societal impacts. Sustained wind speed and gusts can be estimated for a given location relative to a given tropical cyclone by use of equations for the radial wind profile of cyclones (e.g. Holland, 1980; Holland *et al.*, 2010). However, such modelling requires an estimate for the radius of maximum winds, which is often missing in cyclone data.

Basin-wide indices that quantify annual cyclone activity include Accumulated Cyclone Energy (ACE; Bell *et al.*, 2000), based on the maximum sustained wind speed squared, and Power Dissipation Index (PDI; Emanuel, 2005), based on the maximum sustained wind speed cubed. PDI is thought to be more relevant to the destructive potential of cyclones because it scales closely with economic losses (Emanuel, 2005). A storm activity index (SAI), such as ACE or PDI, can be written in a general form (following Wu *et al.*, 2008):

$$\mathrm{SAI}=\sum_{0}^{\mathrm{N}}\sum_{0}^{\mathrm{t}}\mathrm{V}_{\mathrm{max}}^{\mathrm{n}}$$

where $\mathrm{V}_{\mathrm{max}}$ is the maximum sustained wind speed of the tropical cyclone and n is an integer. When n = 2 the SAI becomes ACE and when n = 3 the SAI becomes PDI. The two $\sum$ denote the summations over the lifetime (t) of each tropical cyclone at 6-h increments and for all tropical cyclones (N) that occur in the time period and spatial extent of interest.

In this study, indices for cyclone activity in and around Mauritius are calculated from data in the IBTrACS database (r03v10) (following Nicoll *et al.*, 2017; Table 3.6). This approach provides more detail than simply counting days on which cyclones affect Mauritius. Maximum sustained wind speed estimates from the World Meteorological Organization (WMO) centre in Reunion were converted from 10-minute to 1-minute sustained winds by dividing the values by a factor of 0.93 (Harper *et al.*, 2008). Estimates of maximum 1-minute sustained wind speeds from Reunion and the Joint Typhoon Warning Center (JTWC) were then combined, with mean values calculated for storms where both centres provided estimates. All cyclones of at least tropical storm strength (maximum 1-minute sustained winds of at least 34 knots) and within 300 km of the weather stations at Mt Camizard, Petrin and Plaisance were selected. Previous research and anecdotal observations, including from Mauritius, indicate that cyclone winds and rain regularly impact areas within 275-300 km (~150 nm) of the storm centre (Cheke, 1987; Shepherd *et al.*, 2007; Neerunjun, 2015; Nicoll *et al.*, 2017). Tropical storms are included to increase the number of events in subsequent analyses, while recognising that these will not necessarily equate to true extremes. This spatial analysis was carried out in QGIS (version 2.18.20). Weather stations were used as the centre of these buffer areas, as the indices are also used to calculate cyclonic rainfall from rain gauge data at these locations. Maximum sustained wind estimates for these storms were then squared for ACE and cubed for PDI and summed for each season. Only cyclone seasons from March 1980 onwards are considered in this analysis owing to the lack of wind speed data for many cyclones in the 1970s and earlier. The number of Cyclone Days is also derived from this analysis and Cyclone Rainfall is derived from data on Cyclone Days and daily rainfall (Table 3.6). It should be noted that many tropical depressions are missing from the best track data, thus these systems are not considered in this study.

Table 3.6. Tropical cyclone indices chosen for use in this study.

Index	**Description**	**Units**
Cyclone Days	The total number of days on which the centre of at least one cyclone of tropical storm strength or higher (at least 34 knots) was located within 300 km of the study locations.	days
ACE 300km	Maximum sustained wind speed squared and summed for all cyclones of at least tropical storm strength (at least 34 knots) whose centre was located within 300 km of the study locations. The resulting values are divided by 1,000 to produce a more manageable scale.	1×10^3 kts^2
PDI 300km	Maximum sustained wind speed cubed and summed for all cyclones of at least tropical storm strength (at least 34 knots) whose centre was located within 300 km of the study locations. The resulting values are divided by 10,000 to produce a more manageable scale.	1×10^4 kts^3
Cyclone Rainfall	Total accumulated rainfall (mm) on days when the centre of at least one cyclone of tropical storm strength or higher (at least 34 knots) was located within 300 km of the study locations.	mm

3.3.9 Trend analysis for climate indices

Trends for indices at each study location were analysed using the Mann-Kendall correlation test (Mann, 1945), which incorporates Kendall's rank correlation tau (Kendall, 1938). This method and similar approaches using Kendall's tau are commonly applied to climate indices (Easterling *et al.*, 2016), including the Climdex indices (Zhang *et al.*, 2005a; Pal and Al-

Tabbaa, 2009; Vincent *et al.*, 2011; Sheikh *et al.*, 2015), other temperature indices (Ceccherini *et al.*, 2015), drought indices including SPI (Mallya *et al.*, 2016), and cyclone indices such as PDI (Wu *et al.*, 2008). This nonparametric test was used because it does not assume that the data follow a particular probability distribution and it is robust to missing data and the effect of outliers (Zhang *et al.*, 2005a; Pal and Al-Tabbaa, 2009; Vincent *et al.*, 2011; Ceccherini *et al.*, 2015). The Mann-Kendall test assumes that variables are independent; however, climate indices from adjacent time periods can show auto-correlation. In this study, trends for indices in adjacent seasons are not analysed. 'Pre-whitening' was not carried out, as the sample sizes of most time series in this analysis are >50 years, and pre-whitening can reduce the detection of real trends in some cases (Yue and Wang, 2002). The test was applied using package 'Kendall' (McLeod, 2011) in the R statistical environment. Trends are considered statistically significant where $P < 0.05$.

3.4 Results

3.4.1 Identification of proxy data

The two monthly measures of rainfall (probability of rainfall (≥1 mm) and mean rainfall (mm) on raindays (≥1 mm)) at IAA and Plaisance are positively correlated between the two stations (Figures 3.7 and 3.8), although Plaisance appears to be drier overall. The probability of a rainday is strongly correlated between the two sites (Kendall's tau = 0.592, $P < 0.0001$, $N = 28$), as is mean rainfall on raindays (Kendall's tau = 0.698, $P < 0.0001$, $N = 28$).

Any correlation between monthly rainfall indices from the two stations could simply be a result of both sites experiencing the same annual precipitation cycle and thus the same rainy and dry seasons. This would be expected given the proximity of the two weather stations. However, the strength of the correlations shown here suggests that the sites not only show the same rainfall seasonality, but also show similarities at finer temporal scales.

Ideally, correlations between the two stations would be tested for each season separately, but this is precluded by the limited availability of data for IAA, which cover only 28 months. Following this analysis, the combined data from Plaisance are judged to be an adequate proxy for rainfall on IAA and are used as such hereafter. It should be noted, however, that the analysis presented here is limited by the short time period for which data from IAA are available and may be biased due to the number of days with data missing for IAA.

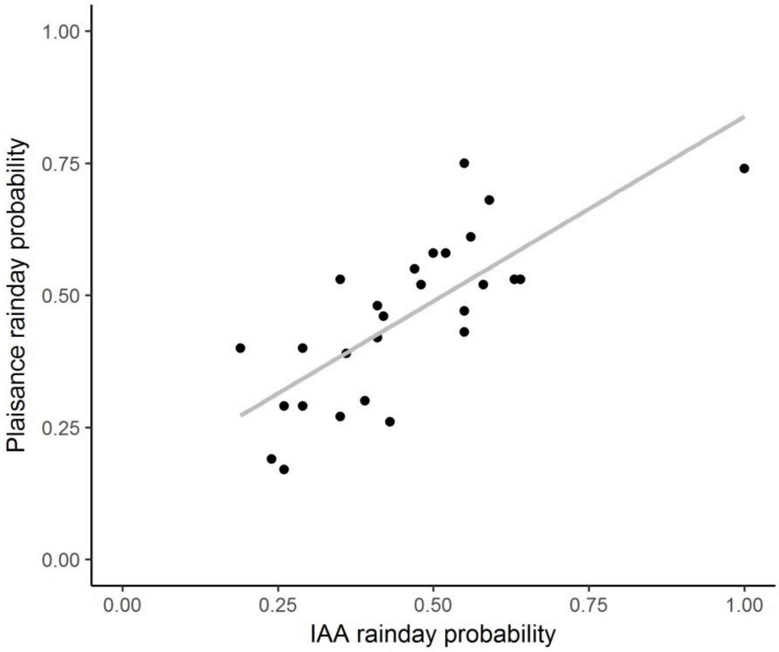

Figure 3.7. Rainday (≥1 mm) probability by month, at Ile aux Aigrettes (IAA) and Plaisance, southeastern Mauritius, using rain gauge data collected from January 2013 until April 2015 inclusive. Trend line fitted using least squares regression (*b*=0.699, R^2=0.574, *N*=28).

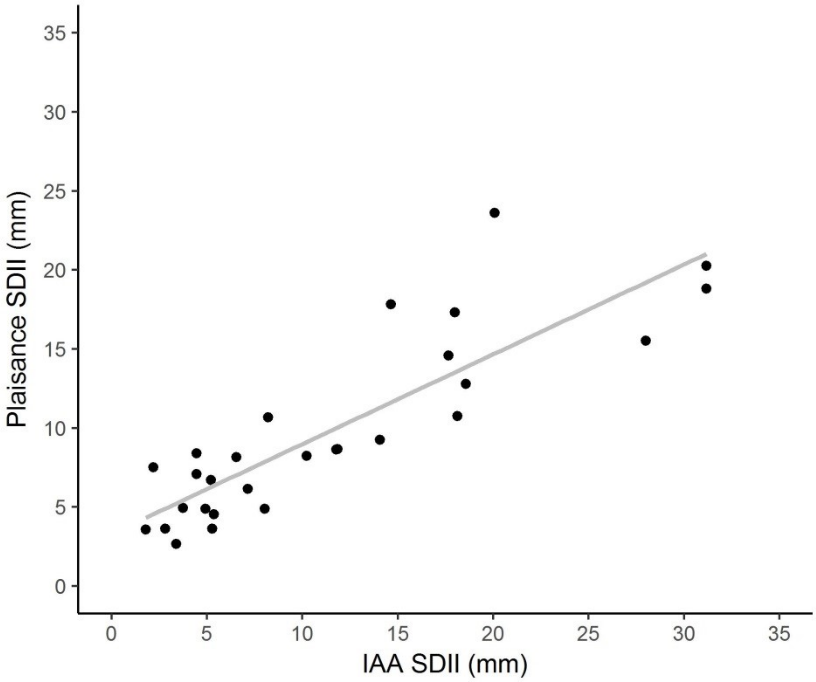

Figure 3.8. Mean daily rainfall (Standard Daily Intensity Index: SDII) (mm) on raindays (≥1 mm) averaged by month at Ile aux Aigrettes (IAA) and Plaisance, southeastern Mauritius, using rain gauge data collected from January 2013 until April 2015 inclusive. Trend line fitted using least squares regression (*b*=0.568, R^2=0.741, *N*=28).

3.4.2 Trends in precipitation and drought indices

Trend analysis indicates overall increases in precipitation at Mt Camizard (Table 3.7), with significant positive trends in Rainfall and Raindays in all seasons. Increases have also occurred in the numbers of extreme rainfall events at Mt Camizard, with significant positive trends in Raindays90 in JJA, SON and DJF, and Raindays95 in SON (Figure 3.9). These patterns are accompanied by significant increases in the duration of Max Rain Spells in all seasons, and significant decreases in the duration of Max Dry Spells in JJA and DJF. Significant positive trends in SPI in all seasons (Table 3.7; see Figure 3.10) imply a long term decrease in the occurrence of drought conditions and increase in the frequency of very rainy seasons.

In contrast to signs of increasing rainfall at Mt Camizard, there are signs of decreases in rainfall at Plaisance (Table 3.8), including significant negative trends in Rainfall and Raindays in JJA and a significant negative trend in Raindays in MAM. There is also a significant negative trend in SPI-3 and SPI-6 in JJA (Table 3.8; Figure 3.11), suggesting that drought conditions in the dry season have become more likely at Plaisance.

The method used to combine different daily rainfall inventories for Plaisance could cause biases in climate indices, so an alternative method was employed in which the MMS inventory was used for all data from 1 January 1992 and the GHCN/GSOD inventory was used for all data prior to this date. The trend analyses for indices derived from this alternative method (Table A3.3) give similar results to those from the original method, with stronger negative trends in JJA and MAM rainfall indices. This suggests that the original method for combining the inventories is relatively conservative regarding the biases that are incorporated. As with the original method, all homogeneity tests for the annual rainfall data using the alternative method are non-significant, implying that both methods for combining the inventories avoid creating inhomogeneties.

There are few significant trends in the precipitation and drought indices at Petrin (Table 3.9), perhaps owing in part to the relatively short time span for which data are available; however, there are significant decreases in Raindays in SON and MAM. SON also shows a significant increase in HY-INT and significant decrease in Max Rain Spell. Long-term trends at Vacoas indicate decreasing rainfall, especially in JJA (Table 3.10).

The analysis of correlations between climate indices for each location and season (Tables A3.4-A3.19) show that in all seasons at all locations Rainfall is more strongly correlated with SDII than with Raindays, indicating that changes in total seasonal rainfall are driven by changes in daily average rainfall intensity more so than by changes in the frequency of rainfall.

Table 3.7. Trends (Kendall's tau) and 2-tailed significance levels for rainfall and drought indices at Mt Camizard, 1962-2015, based on Mann-Kendall tests. *$P < 0.05$, **$P < 0.01$.

Index	**JJA**	**SON**	**DJF**	**MAM**
Rainfall	0.292**	0.219*	0.230*	0.222*
Raindays	0.478**	0.277**	0.402**	0.283**
SDII	0.080	0.019	0.125	0.069
HY-INT	-0.105	-0.089	-0.027	0.040
Max Rain Spell	0.278**	0.241*	0.197*	0.275**
Raindays90	0.278**	0.220*	0.270**	0.082
Raindays95	0.190	0.210*	0.187	0.075
Rainfall90	0.165	0.169	0.245**	0.150
SPI-3	0.302**	0.221*	0.225**	0.198*
SPI-6	0.283**	0.345**	0.258**	0.297**
Max Dry Spell	-0.252*	-0.133	-0.256**	-0.063

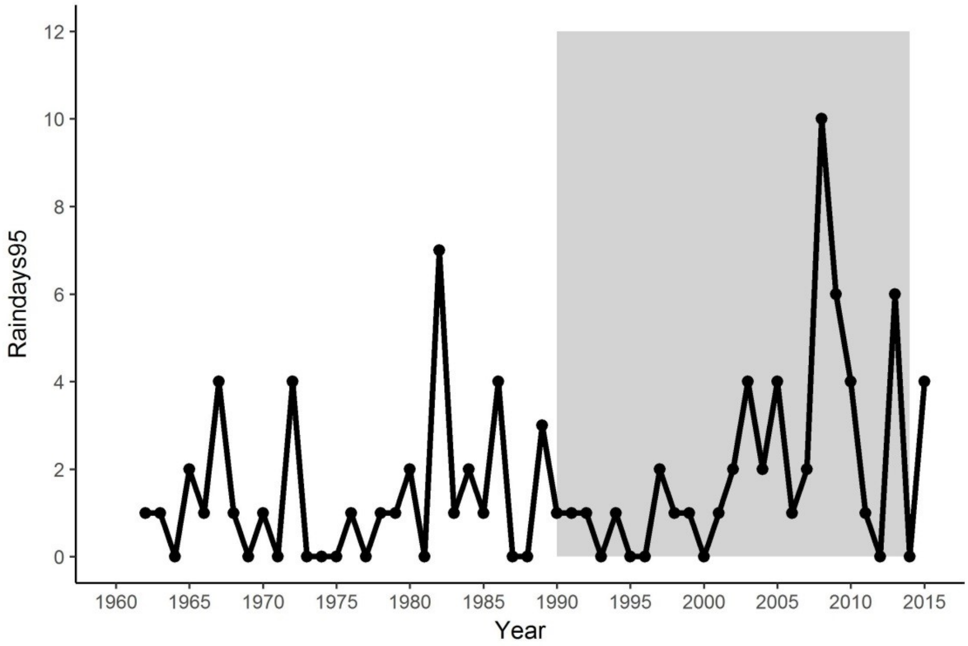

Figure 3.9. Trend in number of raindays exceeding the seasonal 95th percentile threshold (Raindays95) in SON at Mt Camizard, Mauritius. The shaded area shows the reference period from which percentile thresholds are calculated and the time span for which ecological data are available.

Table 3.8. Trends (Kendall's tau) and 2-tailed significance levels for rainfall and drought indices at Plaisance, 1951-2015, based on Mann-Kendall tests. *$P < 0.05$, **$P < 0.01$.

Index	**JJA**	**SON**	**DJF**	**MAM**
Rainfall	-0.189*	-0.077	0.074	-0.135
Raindays	-0.185*	-0.032	-0.034	-0.295**
SDII	-0.144	-0.068	0.072	-0.052
HY-INT	-0.107	-0.025	0.144	0.075
Max Rain Spell	-0.223*	0.031	0.150	-0.040
Raindays90	-0.225*	-0.095	0.112	-0.194*
Raindays95	-0.059	-0.012	0.068	-0.160
Rainfall90	-0.054	-0.055	0.115	-0.083
SPI-3	-0.189*	-0.076	0.074	-0.138
SPI-6	-0.176*	-0.159	0.073	-0.070
Max Dry Spell	0.069	-0.072	0.149	0.126

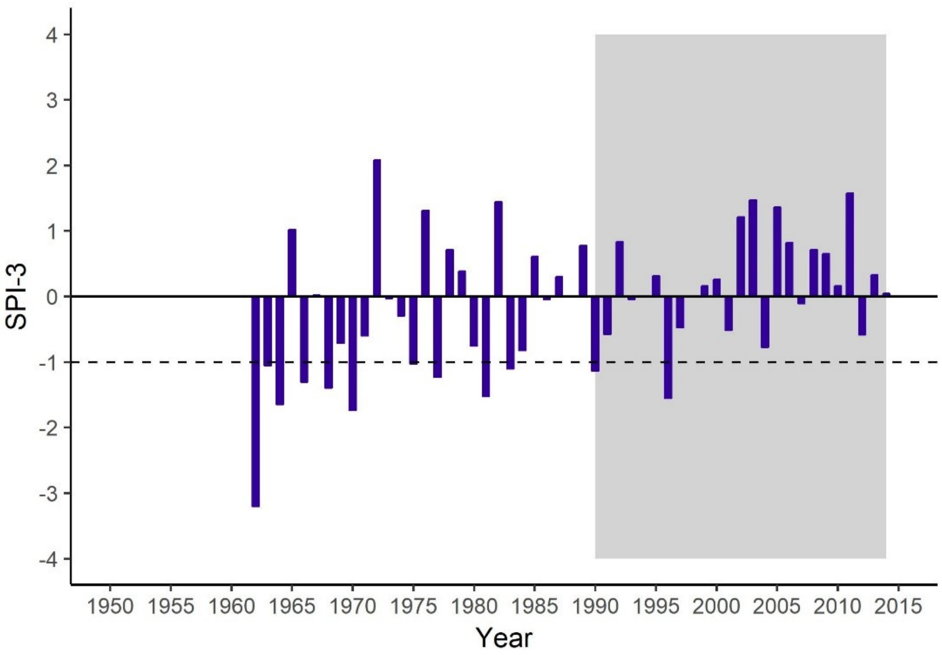

Figure 3.10. Three-month Standardised Precipitation Index (SPI-3) for June-August (JJA) at Mt Camizard, Mauritius. The shaded area shows the reference period with which the index was standardised and also the time span within which ecological data are available. Values below -1 are deemed to indicate drought conditions (McKee *et al.*, 1993).

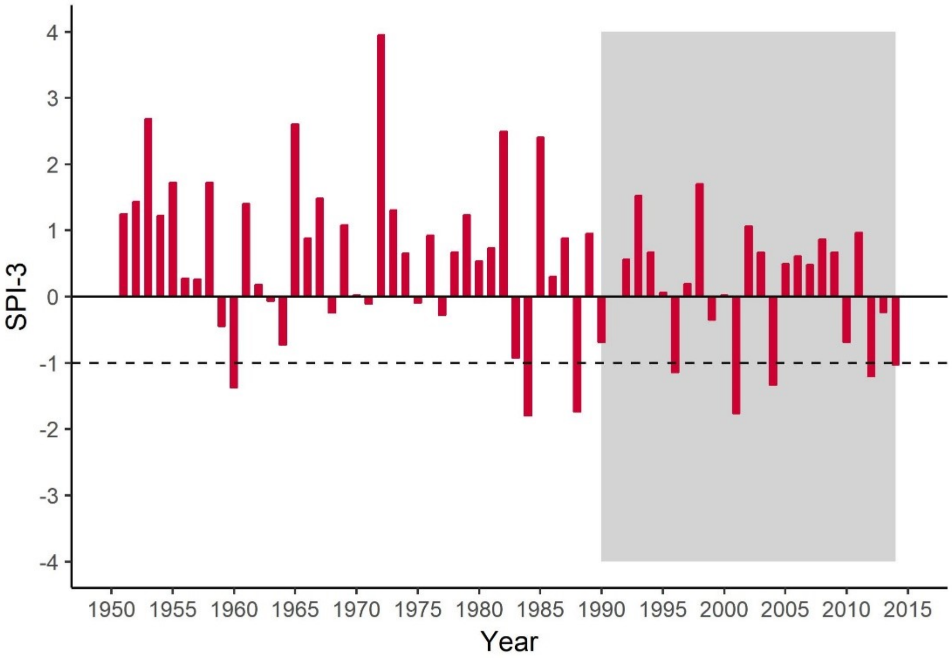

Figure 3.11. Three-month Standardised Precipitation Index (SPI-3) for June-August (JJA) at Plaisance, Mauritius. The shaded area shows the reference period with which the index was standardised and also the time span within which ecological data are available. Values below -1 are deemed to indicate drought conditions (McKee *et al.*, 1993).

Table 3.9. Trends (Kendall's tau) and 2-tailed significance levels for rainfall and drought indices at Petrin, 1987-2015, based on Mann-Kendall tests. *$P < 0.05$, **$P < 0.01$.

Index	**JJA**	**SON**	**DJF**	**MAM**
Rainfall	0.003	-0.071	-0.151	-0.175
Raindays	-0.147	-0.387**	-0.154	-0.319*
SDII	0.145	0.174	-0.046	-0.101
HY-INT	0.140	0.348*	0.074	0.107
Max Rain Spell	-0.130	-0.311*	-0.101	-0.251
Raindays90	-0.047	0.000	0.013	-0.137
Raindays95	-0.124	0.056	-0.162	0.003
Rainfall90	-0.052	0.163	-0.169	-0.069
SPI-3	0.003	-0.028	-0.151	-0.167
SPI-6	-0.063	-0.104	-0.073	-0.210
Max Dry Spell	0.147	0.211	0.153	0.153

Table 3.10. Trends (Kendall's tau) and 2-tailed significance levels for rainfall indices at Vacoas, 1961-2015, based on Mann-Kendall tests. *$P < 0.05$, **$P < 0.01$.

Index	**JJA**	**SON**	**DJF**	**MAM**
Rainfall	-0.279**	-0.082	-0.188	-0.047
Raindays	-0.328**	-0.212*	-0.193	-0.150
SDII	-0.182	-0.009	-0.121	0.032
Max Rain Spell	-0.244*	-0.144	-0.076	-0.054
Max Dry Spell	0.000	0.056	0.289**	0.121

3.4.3 Trends in temperature indices

The trend analysis for temperature indices at Plaisance (Table 3.11) and Vacoas (Table 3.12) indicate overall increases in both Mean Tmax and Tmax90 Days, with decreases in Tmax10 Days (see Figures 3.12 and 3.13). All seasons at both sites exhibit significant positive trends in Mean Tmax. Analysis of correlations between climate indices for each location and season (Tables A3.4-A3.19) indicate that the strength and sign of correlations between rainfall and temperature indices vary among stations and seasons, although this may only reflect differences between the weather stations and seasons in the direction of trends shown by rainfall indices.

Table 3.11. Trends (Kendall's tau) and 2-tailed significance levels for temperature indices at Plaisance, 1951-2015, based on Mann-Kendall tests *$P < 0.05$, **$P < 0.01$.

Index	**JJA**	**SON**	**DJF**	**MAM**
Mean Tmax	0.461**	0.479**	0.389**	0.441**
Tmax90 Days	0.347**	0.274**	0.119	0.237**
Tmax10 Days	-0.445**	-0.467**	-0.417**	-0.356**

Table 3.12. Trends (Kendall's tau) 2-tailed significance levels for temperature indices at Vacoas, 1961-2015, based on Mann-Kendall tests. *$P < 0.05$, **$P < 0.01$.

Index	**JJA**	**SON**	**DJF**	**MAM**
Mean Tmax	0.438**	0.372**	0.410**	0.273**
Tmax90 Days	0.358**	0.374**	0.509**	0.163
Tmax10 Days	-0.413**	-0.306**	-0.309**	-0.247*

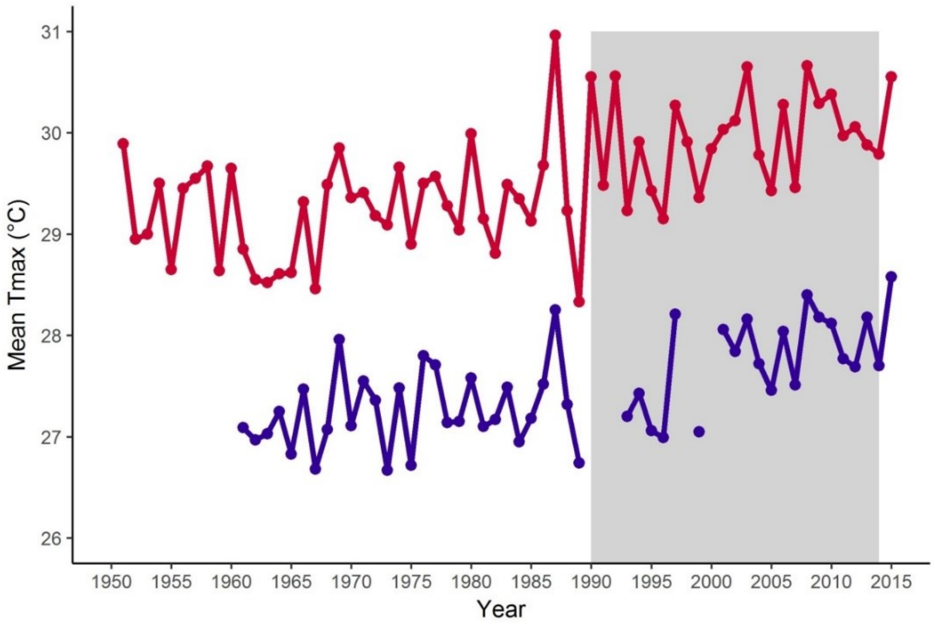

Figure 3.12. Mean daily maximum temperature (Mean Tmax, °C) in December-February (DJF) at Plaisance (red data points) and Vacoas (blue data points), Mauritius. The shaded area shows the time span for which ecological data are available.

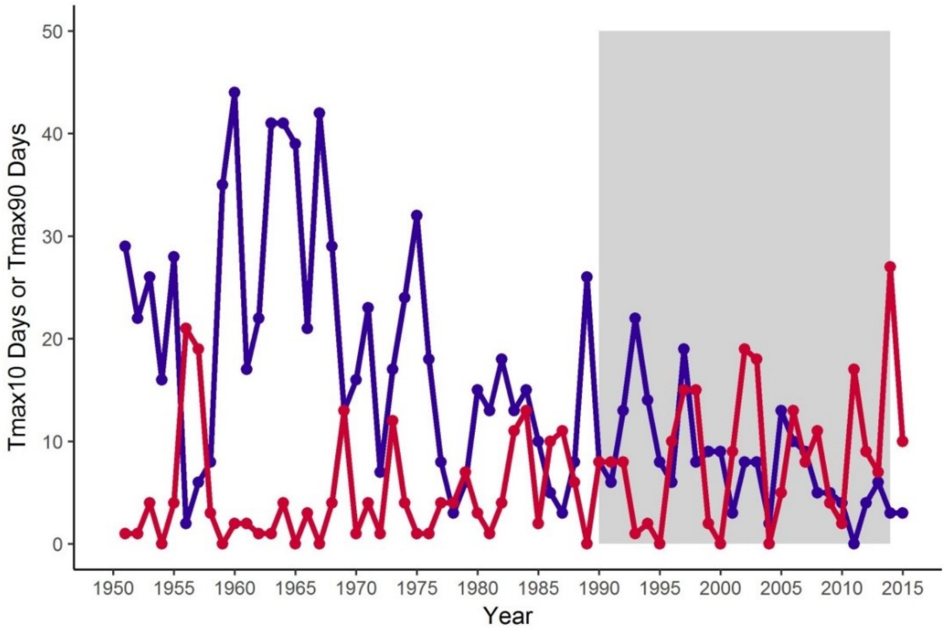

Figure 3.13. Number of days below the 10th percentile (Tmax10 Days, blue data points) and exceeding the 90th percentile (Tmax90 Days, red data points) of daily maximum temperature in September-November (SON) at Plaisance, Mauritius. The shaded area shows the time span from which percentile thresholds were calculated and the period for which ecological data are available.

3.4.4 Trends in tropical cyclone indices

There are no significant trends in the tropical cyclone indices, although all of the non-significant trends are negative (Table 3.13). These data series exhibit strong decadal variability (Figure 3.14). However, this 35-year time span is a short period over which to analyse cyclone data, owing to the tendency for decadal variation. Most cyclone activity occurs in DJF, with DJF 2001-2002 showing particularly high activity (Figure 3.14).

Table 3.13. Trends for tropical cyclone indices at Mt Camizard, Plaisance and Petrin, 1980/1981-2014/2015, based on Mann-Kendall tests.

Location	**Index**	**DJF**	**MAM**
Mt Camizard	Cyclone Days	-0.155	-0.061
	ACE 300km	-0.196	-0.075
	PDI 300km	-0.206	-0.065
	Cyclone Rainfall	-0.189	-0.090
Petrin	Cyclone Days	-0.146	-0.073
	ACE 300km	-0.150	-0.075
	PDI 300km	-0.157	-0.080
	Cyclone Rainfall	-0.140	-0.221
Plaisance	Cyclone Days	-0.114	-0.053
	ACE 300km	-0.164	-0.058
	PDI 300km	-0.164	-0.053
	Cyclone Rainfall	-0.206	-0.074

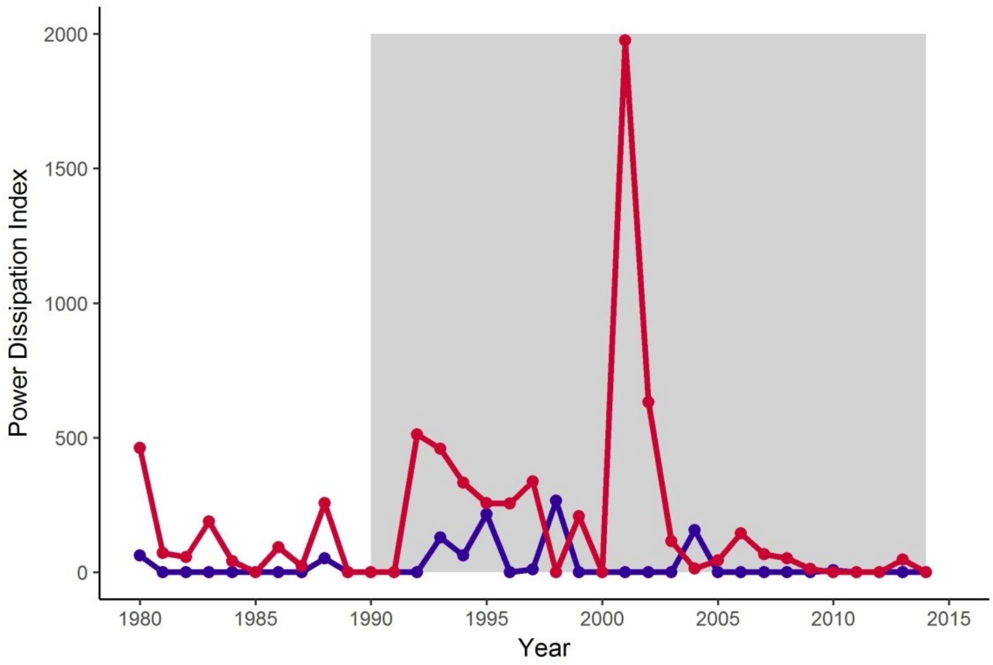

Figure 3.14. Power Dissipation Index (1×10⁴ kts³) for tropical storms and cyclones whose centre was located within 300 km of Mt Camizard, Mauritius, during December-February (DJF, red data points) and March-May (MAM, blue data points). The shaded area shows the time span for which ecological data are available.

3.5 Discussion

3.5.1 Trends in meteorological indices in Mauritius

The assumption that this study is being conducted in the context of a nonstationary climate is supported by the trend analysis of temperature indices, although trends in precipitation indices vary by location and season. Long-term increases in precipitation indices in the Bambous Mountains (Mt Camizard) contrast to some extent with concomitant decreases in some seasons on the Central Plateau (Vacoas) and southeastern lowlands (Plaisance) since the mid-20th century. The patterns of decreasing precipitation at Plaisance and Vacoas, and to some extent at Petrin, correspond with longer-term trends found in previous analyses for the entire island. Comparisons of the normal rainfall distributions between 1931-1960 and 1971-2000 and between 1951-1980 and 1981-2010 show a decline in the amount of rainfall, particularly on the Central Plateau (Republic of Mauritius, 2010, 2016). Annual rainfall over mainland Mauritius has decreased by about 63 mm per decade over the past century (1905-2007) (Republic of Mauritius, 2010), with more pronounced drying in the north and west of the island (Republic of Mauritius, 2016). The positive trends noted here in seasonal rainfall indices at Mt Camizard also correspond well with patterns found for multiple rain gauges in the Bambous Mountains in previous research (Senapathi, 2009; Senapathi *et al.*, 2010). As expected, indices for extreme rainfall broadly followed similar trends to those shown by general rainfall indices. It should be noted that the potential for undetected inhomogeneities in the Petrin rainfall data could affect the results of trend analyses.

Mauritius is located in an ocean region that climate models indicate is on the border between areas that are characterised by increasing precipitation to the east and decreasing precipitation to the west (Polson *et al.*, 2016). However, the contrasting trends on Mauritius imply that a particular set of smaller-scale processes are influencing local conditions. In the absence of changes to circulation patterns and relative humidity, thermodynamic factors suggest that extreme precipitation intensity should increase with increasing global mean surface temperature, scaling at about 7% per 1°C increase, as governed by the Clausius-Clapeyron equation, which describes the capacity of the atmosphere to hold moisture. However, some studies report a scaling of extreme precipitation above this rate (Allan *et al.*, 2010; Wasko *et al.*, 2016). For example, Benestad (2013) found that rainday 95th percentiles worldwide have been influenced by global mean temperature, consistent with an accelerated hydrological cycle caused by global warming. In reality, the local influence of climate change on precipitation will be mediated by local and mesoscale processes, as well as synoptic scale changes. Important among these is the effect of orography on local precipitation (Houze, 2012). Seasonal trends in Mauritius show variation, implying that synoptic-scale patterns are also having an influence.

Contrasting trends in precipitation have been noted in other topographically varied continental regions (Kittel *et al.*, 2015) and on islands, as shown for the Canary Islands (García-Herrera *et al.*, 2003) and the Hawaiian Islands (Chu *et al.*, 2010; Chen and Chu, 2014; Frazier and Giambelluca, 2017), with weather stations in the same island group and on the same island sometimes showing opposite trends in precipitation (García-Herrera *et al.*, 2003; Chu *et al.*, 2010; Chen and Chu, 2014). Changes in mountain climates can differ substantially from those in adjacent lowlands and wider regional signals, as seen in both observations and model simulations (Beniston *et al.*, 1997; Giorgi *et al.*, 1997; Fyfe and Flato, 1999; Urrutia and Vuille, 2009; Rangwala and Miller, 2012; Pepin *et al.*, 2015). Within mountain systems, locations that differ in terms of elevation and position relative to mountain crests have been shown to exhibit different long-term trends in precipitation (Rangwala *et al.*, 2009; Kittel *et al.*, 2015). Important topographic characteristics include the elevation, orientation and slope of mountain features relative to the direction of moisture-bearing atmospheric flow (Roe, 2005; Daly *et al.*, 2008; Kittel *et al.*, 2015). Orographic precipitation on islands in the trade wind belt is also influenced by the strength of trade winds, as shown for Dominica (Smith *et al.*, 2012). Idealised simulations have been used to study the response of orographic precipitation extremes to climate warming, showing that there are higher fractional changes in precipitation extremes on the climatological leeward slope of midlatitude mountains compared to the windward slope (Siler and Roe, 2014; Shi and Durran, 2015).

The analysis of precipitation indices in this study has uncovered unexpected differences in trends at Mt Camizard and Plaisance, which are located <15 km apart on the southeastern coast. This could be due to a shift in the prevailing direction of weather fronts or trade winds that affect the southeast coast of Mauritius, combined with the orographic effects of the Bambous Mountains compared to the lowlands surrounding Plaisance. The decreasing trend in precipitation at Vacoas on the Central Plateau might indicate that a change in prevailing circulation patterns is the main driver of the contrasting trends at the two stations on the southeastern coast, and that this is mediated by differences in orography. However, it is beyond the scope of this study to investigate this further.

The precipitation data from Petrin cover a brief period in which few significant climate trends are detected, although there are some signs of decreases in rainfall. The long-term declines in precipitation at Vacoas suggest that populations in the BRGNP are experiencing decreases in rainfall and potentially an increasing risk of drought. Such patterns could impact echo parakeets if food availability is affected; significant changes in precipitation during the nesting phase may impact breeding success and changes in precipitation in the post-nesting phase could impact juvenile survival. This population receives supplementary food, thus birds that use the supplementary food least may be the most impacted.

Both synoptic stations show significant increases in the frequency of hot days and decreases in cold days, including during SON when kestrels and parakeets have their peaks in nesting activity. Breeding success could be impacted by these trends in temperature extremes during the nesting phase. The increasing frequency of extreme heat events has been linked to anthropogenic changes to the climate. For example, King *et al.* (2016) found a significant human contribution to the probability of record-breaking global temperature events as early as the 1930s, with all of the last 16 record-breaking hot years globally since then having an anthropogenic contribution to their probability of occurrence. Previous analyses of temperature data over the period 1950-2007 for several stations in Mauritius and over the Outer Islands shows that the mean temperature is rising by about 0.16°C per decade, and on average, temperatures have increased over the region by 0.74-1.2°C since 1950 (Republic of Mauritius, 2010). It should be noted that the weather station at Vacoas is situated in an urban area and temperature trends there are likely to have been affected by increasing urbanisation. It should also be borne in mind that inhomogeneities detected in the Plaisance temperature data could affect the results of trend analyses. This is also true regarding biases created by the standard reference period (Zhang *et al.*, 2005b; Zhang *et al.*, 2011).

Tropical cyclone indices show particularly high cyclone activity in DJF 2001, with fairly high activity in the 1990s. High cyclone activity in DJF could potentially impact fledging and juvenile survival in Mauritius kestrels and echo parakeets, while cyclone activity in DJF or MAM could disrupt breeding activity in the pink pigeon and Mauritius fody populations on Ile aux Aigrettes, which are less seasonal (Bambini *et al.*, 2011; Concannon, 2014).

3.5.2 Species management implications

Given the influence of topography on climate trends, it is important that conservationists account for variation in local trends in climate risks, such as droughts and extreme rainfall, especially for insular and montane species. The present study highlights a dichotomy of trends in the weather regimes experienced by focal populations in Mauritius. The trend analyses imply that populations on IAA are experiencing decreases in precipitation and are at increasing risk of drought. The reintroduced population of Mauritius kestrels in the Bambous Mountains is, however, experiencing increasing rainfall and increasingly frequent extreme rain events. Studies on other raptor species show that, in general, precipitation has negative impacts on productivity (reviewed in Chapter 1). Previous research on the Mauritius kestrel has shown that increased rainfall before and during the breeding season influences breeding phenology and productivity, such that egg-laying is delayed and breeding success is reduced (Nicoll, 2004; Senapathi, 2009; Senapathi *et al.*, 2011), and that rainfall in the cyclone season negatively impacts the survival of juvenile birds (Nicoll *et al.*, 2003; Nicoll, 2004). Positive trends in overall rainfall and heavy rain events in the Bambous Mountains imply that the focal kestrel population could be experiencing worsening impacts on breeding success and juvenile survival. Management actions in response could involve the re-designing of nest-boxes and responsive supplementary feeding during periods of intense and more frequent rainfall. It may also be necessary to bolster and establish other populations of this species in drier parts of the island. Insectivorous and frugivorous species in the Bambous Mountains, such as the newly re-introduced populations of echo parakeet and Mauritius cuckoo-shrike, may benefit from increasing rainfall. Indeed, the Bambous Mountains may be more suitable for the echo parakeet than the BRGNP, where rainfall appears to be decreasing. Research on other psittacine species indicates that rainfall variability and drought events have important influences on phenology and demography, probably through effects on food availability (reviewed in Chapter 1).

Populations on IAA, such as the Mauritius fody, Mauritius olive white-eye and pink pigeon, which are generally frugivorous and insectivorous, appear to be at increasing risk from droughts. Some of these populations may be buffered by management actions, including the provision of supplementary food and water; however, a key question will be whether such management will be sufficient to buffer against drought impacts if the trends of decreasing precipitation continue. Severe drought conditions on Ile aux Aigrettes, as noted in the 2010-2011 breeding season, cause the extensive defoliation of vegetation and declines in invertebrate density, and may also negatively impact Mauritius fody breeding activity (Bambini *et al.*, 2011). In contrast, it appears that rainfall does not strongly influence survival and recruitment in the pink pigeon population on IAA (Concannon, 2014). The Mauritius olive white-eye is highly nectivorous, but also consumes invertebrates and fruit, and on IAA they show a decrease in their consumption of supplementary nectar and fruit during rainy conditions (Maggs, 2016), suggesting that they have a greater need for these artificial resources during dry weather. Overall, it appears that the occurrence of more frequent and more severe droughts on IAA could have negative demographic effects, thus populations there may require additional supplementary food and water, especially during severe drought events.

3.5.3 Definition of meteorological extremes for ecological studies

The definition of meteorological extremes presents a substantial challenge for ecologists, especially where sufficient prior knowledge and data from which to define thresholds are lacking. The use of meteorological approaches for the definition of extremes provides a starting point for ecological analysis and the opportunity to set ecological research in the context of wider meteorological and climate research, including the study of societal impacts. Setting ecological research in the context of societal impacts and climate research arguably makes such research more relevant to decision-makers, who typically must prioritise human needs and see research outputs through the prism of human impacts. Most meteorological research naturally focusses on the use of meteorological concepts for defining and characterising extremes, thus if ecological studies are framed in the same context and use similar methods, future meteorological research and climate projections can be related directly to those ecological studies.

A potential problem with the approach of defining extreme meteorological events based solely on ecological impact thresholds is that inferring causality for any one or number of variables can be difficult. Extreme ecological impacts, e.g. mass mortality or breeding failure, could be the result of an accumulation of conditions, potentially including both extreme events and changes in average conditions, or could be a product of undetected intrinsic factors. Defining extremes first and testing their impact in models that incorporate other factors allows the research questions to be addressed around prior definitions of extremes based on societal impacts or statistical rarity and how these relate to the evolution of the species and past selection pressures.

In this study, established meteorological indices have been adapted to make them more relevant to the study species and local climate cycle. The relatively short time spans for which there are ecological data in this study places immediate limitations on the number of truly extreme events that can be studied, therefore the definition of statistically extreme events has been relaxed to provide a larger number of observations for study and to increase the statistical robustness of subsequent analysis. This also places limitations on the scope of climate variability captured in the study.

3.5.4 Conclusions

This chapter has explored the definition of extreme meteorological events for ecological research. In the context of very limited prior knowledge of impact thresholds for the study species or system it is argued that established meteorological indices for extreme events, often based on statistical rarity, provide a useful methodology and framework with which to characterise events that are likely to have ecological impacts. This also facilitates direct links to be drawn between ecological studies and research in meteorology and climate change.

Overall, the analysis of precipitation data from four sites and temperature data from two sites provides strong evidence of a climate change signal in Mauritius since the mid-20th century, and implies that species in Mauritius are experiencing changes in average conditions and extreme events. However, trends vary by location and season. The analysis demonstrates spatial variation in long-term (>50 years) precipitation changes, with differences in the changing risk of extreme rainfall and drought over spatial scales of <15 km. This fine-scale variation has important implications for the climate change vulnerability and conservation of very restricted-range species. Local variation in climate trends should prompt conservation management to be adapted over local scales. Furthermore, climate change vulnerability assessments for restricted-range species should combine detailed analyses of sensitivity with analyses of local trends in climate risks.

3.6 References

Albright, T. P., Pidgeon, A. M., Rittenhouse, C. D., Clayton, M. K., Wardlow, B. D., Flather, C. H., Culbert, P. D. and Radeloff, V. C. 2010. Combined effects of heat waves and droughts on avian communities across the conterminous United States. *Ecosphere,* **1**: 12.

Alexander, L. V. 2016. Global observed long-term changes in temperature and precipitation extremes: A review of progress and limitations in IPCC assessments and beyond. *Weather and Climate Extremes,* **11**: 4–16.

Allan, R. P., Soden, B. J., John, V. O., Ingram, W. and Good, P. 2010. Current changes in tropical precipitation. *Environmental Research Letters,* **5**: 025205.

Anctil, A., Franke, A. and Bêty, J. 2014. Heavy rainfall increases nestling mortality of an arctic top predator: experimental evidence and long-term trend in peregrine falcons. *Oecologia,* **174**: 1033–1043.

Anderson, R. L. 2012. Rainfall erosivity attributes on central and western Mauritius. MSc Dissertation. South Africa: University of Pretoria.

Baddour, O. 2011. Climate normals (Commission for Climatology Management Group Meeting). Denver, USA: World Meteorological Organization.

Bailey, L. D. and van de Pol, M. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology,* **85**: 85–96.

Bambini, L., Ferrière, C., Hotopp, K., Jones, L., McMurdo-Hamilton, T., Morgan, S., Morris, P., Ormsby, L., Vercoe, A. and Zuël, N. 2011. Mauritius Fody Recovery Programme Annual Report 2010-2011. Unpublished report. Vacoas, Mauritius: Mauritian Wildlife Foundation.

Beguería, S. and Vicente-Serrano, S. M. 2015. Package 'SPEI', Calculation of the Standardised Precipitation-Evapotranspiration Index, version 1.6.

Bell, G. D., Halpert, M. S., Schnell, R. C., Higgins, R. W., Lawrimore, J., Kousky, V. E., Tinker, R., Thiaw, W., Chelliah, M. and Artusa, A. 2000. Climate assessment for 1999. *Bulletin of the American Meteorological Society,* **81**: S1–S50.

Benestad, R. E. 2013. Association between trends in daily rainfall percentiles and the global mean temperature. *Journal of Geophysical Research - Atmospheres,* **118**: 10802–10810.

Beniston, M., Diaz, H. F. and Bradley, R. S. 1997. Climatic change at high elevation sites: An overview. *Climatic Change,* **36**: 233–251.

Berglund, H., Jaremo, J. and Bengtsson, G. 2009. Endemism predicts intrinsic vulnerability to nonindigenous species on islands. *American Naturalist,* **174**: 94–101.

Bowden, J. H., Talgo, K. D., Spero, T. L. and Nolte, C. G. 2016. Assessing the Added Value of Dynamical Downscaling Using the Standardized Precipitation Index. *Advances in Meteorology,* **2016**: 8432064.

Bradley, M., Johnstone, R., Court, G. and Duncan, T. 1997. Influence of Weather on Breeding Success of Peregrine Falcons in the Arctic. *Auk,* **114**: 786–791.

Bronaugh, D. 2015. Package 'climdex.pcic', PCIC Implementation of Climdex Routines, version 1.1-6.

Burgess, M. D. 2008. Spatial patterns and population dynamics of a reintroduced Mauritius kestrel (*Falco punctatus*) population. PhD Thesis. Reading, UK: University of Reading.

Burgess, M. D., Black, R. A., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2009. The use of agricultural, open and forest habitats by juvenile Mauritius Kestrels *Falco punctatus*. *Ibis,* **151**: 63–76.

Burgess, M. D., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2008. Restricted dispersal reduces the strength of spatial density dependence in a tropical bird population. *Proceedings of the Royal Society of London, Series B,* **275**: 1209–1216.

Burgess, M. D., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2011. Multiple environmental gradients affect spatial variation in the productivity of a tropical bird population. *Journal of Animal Ecology,* **80**: 688–695.

Cartwright, S. J. 2011. Agriculture and the life histories of Mauritius kestrels. PhD Thesis. Reading, UK: University of Reading.

Cartwright, S. J., Nicoll, M. A. C., Jones, C. G., Tatayah, V. and Norris, K. 2014a. Agriculture modifies the seasonal decline of breeding success in a tropical wild bird population. *Journal of Applied Ecology,* **51**: 1387–1395.

Cartwright, S. J., Nicoll, M. A. C., Jones, C. G., Tatayah, V. and Norris, K. 2014b. Anthropogenic natal environmental effects on life histories in a wild bird population. *Current Biology,* **24**: 536–540.

Catry, I., Franco, A. M. A. and Sutherland, W. J. 2011. Adapting conservation efforts to face climate change: Modifying nest-site provisioning for lesser kestrels. *Biological Conservation,* **144**: 1111–1119.

Ceccherini, G., Russo, S., Ameztoy, I., Romero, C. P. and Carmona-Moreno, C. 2015. Magnitude and frequency of heat and cold waves in recent decades: the case of South America. *Natural Hazards and Earth System Sciences,* **3**: 7379–7409.

Chapman, S., Mustin, K., Renwick, A. R., Segan, D. B., Hole, D. G., Pearson, R. G. and Watson, J. E. M. 2014. Publishing trends on climate change vulnerability in the conservation literature reveal a predominant focus on direct impacts and long time-scales. *Diversity and Distributions,* **20**: 1221–1228.

Cheke, A. and Hume, J. 2008. *Lost land of the dodo*. London, UK: T & AD Poyser.

Cheke, A. S. 1987. The ecology of the smaller land-birds of Mauritius. In *Studies of Mascarene Island birds* (ed: Diamond, A. W.), pp. 151–207. Cambridge, UK: Cambridge University Press.

Chen, Y. R. and Chu, P.-S. 2014. Trends in precipitation extremes and return levels in the Hawaiian Islands under a changing climate. *International Journal of Climatology,* **34**: 3913–3925.

Chu, P.-S., Chen, Y. R. and Schroeder, T. A. 2010. Changes in Precipitation Extremes in the Hawaiian Islands in a Warming Climate. *Journal of Climate,* **23**: 4881–4900.

Concannon, L. 2014. Managing threatened species: Understanding the factors limiting the recovery of the endangered pink pigeon. PhD Thesis. Reading, UK: University of Reading.

Conrey, R. Y., Skagen, S. K., Adams, A. A. Y. and Panjabi, A. O. 2016. Extremes of heat, drought and precipitation depress reproductive performance in shortgrass prairie passerines. *Ibis,* **158**: 614–629.

Cruz-McDonnell, K. K. and Wolf, B. O. 2016. Rapid warming and drought negatively impact population size and reproductive dynamics of an avian predator in the arid southwest. *Global Change Biology,* **22**: 237–253.

Cunningham, S. J., Kruger, A. C., Nxumalo, M. P. and Hockey, P. A. R. 2013. Identifying biologically meaningful hot-weather events using threshold temperatures that affect life-history. *PLoS One,* **8**: e82492.

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J. and Pasteris, P. P. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology,* **28**: 2031–2064.

Dawson, T. P., Jackson, S. T., House, J. L., Prentice, I. C. and Mace, G. M. 2011. Beyond predictions: Biodiversity conservation in a changing climate. *Science,* **332**: 53–58.

Duncan, C., Chauvenet, A. L. M., McRae, L. M. and Pettorelli, N. 2012. Predicting the future impact of droughts on ungulate populations in arid and semi-arid environments. *PLoS One,* **7**: e51490.

Durre, I., Menne, M. J., Gleason, B. E., Houston, T. G. and Vose, R. S. 2010. Comprehensive automated quality assurance of daily surface observations. *Journal of Applied Meteorology and Climatology,* **49**: 1615–1633.

Dvorak, V. 1984. Tropical cyclone intensity analysis using satellite data. NOAA Technical Report NESDIS. Washington, D.C.: National Oceanic and Atmospheric Administration.

Easterling, D. R., Alexander, L. V., Mokssit, A. and Detemmerman, V. 2003. CCI/CLIVAR workshop to develop priority climate indices. *Bulletin of the American Meteorological Society,* **84**: 1403–1407.

Easterling, D. R., Kunkel, K. E., Wehner, M. F. and Sun, L. 2016. Detection and attribution of climate extremes in the observed record. *Weather and Climate Extremes,* **11**: 17–27.

ECAD and KNMI. 2013. Algorithm theoretical basis document. European Climate Assessment & Dataset and Royal Netherlands Meteorological Institute.

Edwards, D. C. and McKee, T. B. 1997. Characteristics of 20th century drought in the United States at multiple time scales. In *Atmospheric Science Paper No. 634/Climatology Report No. 97-2*. Fort Collins, CO: Department of Atmospheric Science, Colorado State University.

Elsner, J. B., Kossin, J. P. and Jagger, T. H. 2008. The increasing intensity of the strongest tropical cyclones. *Nature,* **455**: 92–95.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature,* **436**: 686–688.

Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vie, J.-C., Akçakaya, H. R., Angulo, A., DeVantier, L. M., Gutsche, A., Turak, E., Cao, L., Donner, S. D., Katariya, V., Bernard, R., Holland, R. A., Hughes, A. F., O'Hanlon, S. E., Garnett, S. T., Şekercioğlu, Ç. H. and Mace, G. M. 2013. Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS One,* **8**: e65427.

Fordham, D. A. and Brook, B. W. 2010. Why tropical island endemics are acutely susceptible to global change. *Biodiversity and Conservation,* **19**: 329–342.

Frazier, A. G. and Giambelluca, T. W. 2017. Spatial trend analysis of Hawaiian rainfall from 1920 to 2012. *International Journal of Climatology,* **37**: 2522–2531.

Funk, C., Nicholson, S. E., Landsfeld, M., Klotter, D., Peterson, P. and Harrison, L. 2015. The Centennial Trends Greater Horn of Africa precipitation dataset. *Scientific Data,* **2**: 150050.

Fyfe, J. C. and Flato, G. M. 1999. Enhanced climate change and its detection over the Rocky Mountains. *Journal of Climate,* **12**: 230–243.

Gallego, M. C., Trigo, R. M., Vaquero, J. M., Brunet, M., García, J. A., Sigró, J. and Valente, M. A. 2011. Trends in frequency indices of daily precipitation over the Iberian Peninsula during the last century. *Journal of Geophysical Research - Atmospheres,* **116**: D02109.

García-Herrera, R., Gallego, D., Hernandez, E., Gimeno, L., Ribera, P. and Calvo, N. 2003. Precipitation trends in the Canary Islands. *International Journal of Climatology,* **23**: 235–241.

Giorgi, F., Coppola, E. and Raffaele, F. 2014. A consistent picture of the hydroclimatic response to global warming from multiple indices: Models and observations. *Journal of Geophysical Research - Atmospheres,* **119**: 11695–11708.

Giorgi, F., Hurrell, J. W., Marinucci, M. R. and Beniston, M. 1997. Elevation dependency of the surface climate change signal: A model study. *Journal of Climate,* **10**: 288–296.

Giorgi, F., Im, E. S., Coppola, E., Diffenbaugh, N. S., Gao, X. J., Mariotti, L. and Shi, Y. 2011. Higher hydroclimatic intensity with global warming. *Journal of Climate,* **24**: 5309–5324.

Guttman, N. B. 1994. On the sensitivity of sample-L moments to sample-size. *Journal of Climate,* **7**: 1026–1029.

Harper, B. A., Kepert, J. D. and Ginger, J. D. 2008. Guidelines for converting between various wind averaging periods in tropical cyclone conditions. Geneva, Switzerland: World Meteorological Organization.

Hayes, M. J., Svoboda, M. D., Wilhite, D. A. and Vanyarkho, O. V. 1999. Monitoring the 1996 drought using the Standardized Precipitation Index. *Bulletin of the American Meteorological Society,* **80**: 429–438.

Heim, R. R., Jr. 2002. A review of twentieth-century drought indices used in the United States. *Bulletin of the American Meteorological Society,* **83**: 1149–1165.

Holland, G. J. 1980. An analytic model of the wind and pressure profiles in hurricanes. *Monthly Weather Review,* **108**: 1212–1218.

Holland, G. J., Belanger, J. I. and Fritz, A. 2010. A revised model for radial profiles of hurricane winds. *Monthly Weather Review,* **138**: 4393–4401.

Houze, R. A., Jr. 2012. Orographic effects on precipitating clouds. *Reviews of Geophysics,* **50**: RG1001.

IPCC. 2007. Climate Change 2007. Fourth Assessment Report (AR4). Geneva, Switzerland: Intergovernmental Panel on Climate Change.

IPCC. 2014. Climate change 2014: Synthesis report. Fifth Assessment Synthesis Report. Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Jentsch, A. and Beierkuhnlein, C. 2008. Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *Comptes Rendus Geoscience,* **340**: 621–628.

Jentsch, A., Kreyling, J. and Beierkuhnlein, C. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment,* **5**: 365–374.

Jones, K. R., Watson, J. E. M., Possingham, H. P. and Klein, C. J. 2016. Incorporating climate change into spatial conservation prioritisation: A review. *Biological Conservation,* **194**: 121–130.

Kendall, M. G. 1938. A new measure of rank correlation. *Biometrika,* **30**: 81–93.

Keyantash, J. and Dracup, J. A. 2002. The quantification of drought: An evaluation of drought indices. *Bulletin of the American Meteorological Society,* **83**: 1167–1180.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J. and Barthlott, W. 2009. A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the United States of America,* **106**: 9322–9327.

King, A. D., Black, M. T., Min, S.-K., Fischer, E. M., Mitchell, D. M., Harrington, L. J. and Perkins-Kirkpatrick, S. E. 2016. Emergence of heat extremes attributable to anthropogenic influences. *Geophysical Research Letters,* **43**: 3438–3443.

Kittel, T. G. F., Williams, M. W., Chowanski, K., Hartman, M., Ackerman, T., Losleben, M. and Blanken, P. D. 2015. Contrasting long-term alpine and subalpine precipitation trends in a mid-latitude North American mountain system, Colorado Front Range, USA. *Plant Ecology & Diversity,* **8**: 607–624.

Klein Tank, A. M. G., Zwiers, F. W. and Zhang, X. 2009. Guidelines on analysis of extremes in a changing climate in support of informed decisions for adaptation. Geneva, Switzerland: World Meteorological Organization.

Knapp, K. R., Kruk, M. C., Levinson, D. H., Diamond, H. J. and Neumann, C. J. 2010. The International Best Track Archive for Climate Stewardship (IBTrACS): Unifying Tropical Cyclone Data. *Bulletin of the American Meteorological Society,* **91**: 363–376.

Kossin, J. P., Olander, T. L. and Knapp, K. R. 2013. Trend analysis with a new global record of tropical cyclone intensity. *Journal of Climate,* **26**: 9960–9976.

Kumar, R., Musuuza, J. L., Van Loon, A. F., Teuling, A. J., Barthel, R., Ten Broek, J., Mai, J., Samaniego, L. and Attinger, S. 2016. Multiscale evaluation of the Standardized Precipitation Index as a groundwater drought indicator. *Hydrology and Earth System Sciences,* **20**: 1117–1131.

Maggs, G. 2016. The ecology and conservation of wild and reintroduced populations of the critically endangered Mauritius olive white-eye *Zosterops chloronothos*. PhD Dissertation. London, UK: University College London.

MAIFS. 2015. Fifth national report on the Convention on Biological Diversity. Port Louis, Mauritius: Ministry of Agro-Industry and Food Security, Republic of Mauritius.

Malan, N., Reason, C. J. C. and Loveday, B. R. 2013. Variability in tropical cyclone heat potential over the Southwest Indian Ocean. *Journal of Geophysical Research - Oceans,* **118**: 6734–6746.

Mallya, G., Mishra, V., Niyogi, D., Tripathi, S. and Govindaraju, R. S. 2016. Trends and variability of droughts over the Indian monsoon region. *Weather and Climate Extremes,* **12**: 43–68.

Mann, H. B. 1945. Nonparametric tests against trend. *Econometrica,* **13**: 245–259.

Maron, M., McAlpine, C. A., Watson, J. E. M., Maxwell, S. and Barnard, P. 2015. Climate-induced resource bottlenecks exacerbate species vulnerability: a review. *Diversity and Distributions,* **21**: 731–743.

McKechnie, A. E. and Wolf, B. O. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters,* **6**: 253–256.

McKee, T. B., Doesken, N. J. and Kleist, J. 1993. The relationship of drought frequency and duration to time scales. In *8th Conference on Applied Climatology*. pp. 179–184. Anaheim, California.

McKee, T. B., Doesken, N. J. and Kleist, J. 1995. Drought monitoring with multiple time scales. In *9th Conference on Applied Climatology*. pp. 233–236. Dallas, Texas.

McLeod, A. I. 2011. Package 'Kendall', Kendall rank correlation and Mann-Kendall trend test, version 2.2.

Moritz, C. and Agudo, R. 2013. The future of species under climate change: Resilience or decline? *Science,* **341**: 504–508.

NAS. 2016. Attribution of extreme weather events in the context of climate change. Washington, D.C.: National Academy of Sciences.

Naumann, G., Barbosa, P., Carrao, H., Singleton, A. and Vogt, J. 2012. Monitoring drought conditions and their uncertainties in Africa using TRMM data. *Journal of Applied Meteorology and Climatology,* **51**: 1867–1874.

Neerunjun, H. H. 2015. Rainfall variability on the east coast of Mauritius. MSc Dissertation. Reading, UK: University of Reading.

Nicoll, M. A. C. 2004. The ecology and management of a re-introduced population of the Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Nicoll, M. A. C., Jones, C. G. and Norris, K. 2003. Declining survival rates in a reintroduced population of the Mauritius kestrel: evidence for non-linear density dependence and environmental stochasticity. *Journal of Animal Ecology,* **72**: 917–926.

Nicoll, M. A. C., Nevoux, M., Jones, C. G., Ratcliffe, N., Ruhomaun, K., Tatayah, V. and Norris, K. 2017. Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology,* **23**: 550–565.

Nie, S.-P., Luo, Y., Li, W.-P., Wu, T.-W., Shi, X.-L. and Wang, Z.-Z. 2012. Quality control and analysis of global gauge-based daily precipitation dataset from 1980 to 2009. *Advances in Climate Change Research,* **3**: 45–53.

Orlowsky, B. 2015. Package 'iki.dataclim', Consistency, Homogeneity and Summary Statistics of Climatological Data, version 1.0.

Pal, I. and Al-Tabbaa, A. 2009. Trends in seasonal precipitation extremes - An indicator of 'climate change' in Kerala, India. *Journal of Hydrology,* **367**: 62–69.

Palmer, W. C. 1965. Meteorological Drought. Weather Bureau Research Paper No. 45. Washington, D. C.: US Department of Commerce.

Parmesan, C., Root, T. L. and Willig, M. R. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society,* **81**: 443–450.

Patel, N. R., Chopra, P. and Dadhwal, V. K. 2007. Analyzing spatial patterns of meteorological drought using standardized precipitation index. *Meteorological Applications,* **14**: 329–336.

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schoener, W., Severskiy, I., Shahgedanova, M., Wang, M. B., Williamson, S. N. and Yang, D. Q. 2015. Elevation-dependent warming in mountain regions of the world. *Nature Climate Change,* **5**: 424–430.

Polson, D., Hegerl, G. C. and Solomon, S. 2016. Precipitation sensitivity to warming estimated from long island records. *Environmental Research Letters,* **11**: 074024.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rangwala, I. and Miller, J. R. 2012. Climate change in mountains: a review of elevation-dependent warming and its possible causes. *Climatic Change,* **114**: 527–547.

Rangwala, I., Miller, J. R. and Ming, X. 2009. Warming in the Tibetan Plateau: Possible influences of the changes in surface water vapour. *Geophysical Research Letters,* **36**: L06703.

Reichert, B. E., Cattau, C. E., Fletcher, R. J., Jr., Kendall, W. L. and Kitchens, W. M. 2012. Extreme weather and experience influence reproduction in an endangered bird. *Ecology,* **93**: 2580–2589.

Republic of Mauritius. 2010. Second national communication of the Republic of Mauritius under the United Nations Framework Convention on Climate Change (UNFCCC). Vacoas, Mauritius: Mauritius Meteorological Services.

Republic of Mauritius. 2016. Third National Communication: Report to the United Nations Framework Convention on Climate Change. Port Louis, Mauritius.

Rodrigues, A. S. L., Brooks, T. M., Butchart, S. H. M., Chanson, J., Cox, N., Hoffmann, M. and Stuart, S. N. 2014. Spatially Explicit Trends in the Global Conservation Status of Vertebrates. *PLoS One,* **9**: e113934.

Roe, G. H. 2005. Orographic precipitation. *Annual Review of Earth and Planetary Sciences,* **33**: 645–671.

Ross, B. E., Haukos, D. A., Hagen, C. A. and Pitman, J. C. 2016. Landscape composition creates a threshold influencing Lesser Prairie-Chicken population resilience to extreme drought. *Global Ecology and Conservation,* **6**: 179–188.

Russo, S., Dosio, A., Sterl, A., Barbosa, P. and Vogt, J. 2013. Projection of occurrence of extreme dry-wet years and seasons in Europe with stationary and nonstationary Standardized Precipitation Indices. *Journal of Geophysical Research - Atmospheres,* **118**: 7628–7639.

Safford, R. and Hawkins, F. 2013. *The Birds of Africa: Volume VIII. The Malagasy Region*. London, UK: Christopher Helm.

Senapathi, D., Nicoll, M. A. C., Teplitsky, C., Jones, C. G. and Norris, K. 2011. Climate change and the risks associated with delayed breeding in a tropical wild bird population. *Proceedings of the Royal Society of London, Series B,* **278**: 3184–3190.

Senapathi, D., Underwood, F., Black, E., Nicoll, M. A. C. and Norris, K. 2010. Evidence for long-term regional changes in precipitation on the East Coast Mountains in Mauritius. *International Journal of Climatology,* **30**: 1164–1177.

Senapathi, G. D. 2009. Assessing the effect of changing climatic conditions in Mauritius on the population dynamics of the endemic Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Sheikh, M. M., Manzoor, N., Ashraf, J., Adnan, M., Collins, D., Hameed, S., Manton, M. J., Ahmed, A. U., Baidya, S. K., Borgaonkar, H. P., Islam, N., Jayasinghearachchi, D., Kothawale, D. R., Premalal, K. H. M. S., Revadekar, J. V. and Shrestha, M. L. 2015. Trends in extreme daily rainfall and temperature indices over South Asia. *International Journal of Climatology,* **35**: 1625–1637.

Shepherd, J. M., Grundstein, A. and Mote, T. L. 2007. Quantifying the contribution of tropical cyclones to extreme rainfall along the coastal southeastern United States. *Geophysical Research Letters,* **34**: L23810.

Shi, X. and Durran, D. R. 2015. Estimating the Response of Extreme Precipitation over Midlatitude Mountains to Global Warming. *Journal of Climate,* **28**: 4246–4262.

Siler, N. and Roe, G. 2014. How will orographic precipitation respond to surface warming? An idealized thermodynamic perspective. *Geophysical Research Letters,* **41**: 2606–2613.

Smith, M. D. 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology,* **90**: 656–663.

Smith, R. B., Minder, J. R., Nugent, A. D., Storelvmo, T., Kirshbaum, D. J., Warren, R., Lareau, N., Palany, P., James, A. and French, J. 2012. Orographic precipitation in the tropics - the Dominica Experiment. *Bulletin of the American Meteorological Society,* **93**: 1567–1579.

Staub, C. G., Stevens, F. R. and Waylen, P. R. 2014. The geography of rainfall in Mauritius: Modelling the relationship between annual and monthly rainfall and landscape characteristics on a small volcanic island. *Applied Geography,* **54**: 222–234.

Stephenson, D. B. 2008. Definition, diagnosis, and origin of extreme weather and climate events. In *Climate Extremes and Society* (eds: Diaz, H. F. and Murnane, R. J.), pp. 11–23. Cambridge, UK: Cambridge University Press.

Strauss, S. Y., Lau, J. A. and Carroll, S. P. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters,* **9**: 357–374.

Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie, J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D., Walker, K. J. and Maclean, I. M. D. 2018. Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change,* **8**: 713–717.

Terry, J. P., Kim, I.-H. and Jolivet, S. 2013. Sinuosity of tropical cyclone tracks in the South West Indian Ocean: Spatio-temporal patterns and relationships with fundamental storm attributes. *Applied Geography,* **45**: 29–40.

Urrutia, R. and Vuille, M. 2009. Climate change projections for the tropical Andes using a regional climate model: Temperature and precipitation simulations for the end of the 21st century. *Journal of Geophysical Research - Atmospheres,* **114**: D02108.

van de Pol, M., Jenouvrier, S., Cornelissen, J. H. C. and Visser, M. E. 2017. Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Philosophical Transactions of the Royal Society of London, Series B,* **372**: 20160134.

Vicente-Serrano, S. M., Beguería, S. and López-Moreno, J. I. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate,* **23**: 1696–1717.

Vincent, L. A., Aguilar, E., Saindou, M., Hassane, A. F., Jumaux, G., Roy, D., Booneeady, P., Virasami, R., Randriamarolaza, L. Y. A., Faniriantsoa, F. R., Amelie, V., Seeward, H. and Montfraix, B. 2011. Observed trends in indices of daily and extreme temperature and precipitation for the countries of the western Indian Ocean, 1961-2008. *Journal of Geophysical Research - Atmospheres,* **116**: D10108.

Wasko, C., Parinussa, R. M. and Sharma, A. 2016. A quasi-global assessment of changes in remotely sensed rainfall extremes with temperature. *Geophysical Research Letters,* **43**: 12659–12668.

Whitfield, M. C., Smit, B., McKechnie, A. E. and Wolf, B. O. 2015. Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *Journal of Experimental Biology,* **218**: 1705–1714.

Wilhite, D. A. 2000. Drought as a natural hazard: Concepts and definitions. In *Drought: A global assessment* (ed: Wilhite, D. A.), pp. 3–18. London, UK: Routledge.

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffman, A. A. and Langham, G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology,* **6**: 2621–2626.

WMO. 2003. Guidelines on climate metadata and homogenization. Geneva, Switzerland: World Meteorological Organization.

WMO. 2007. The role of climatological normals in a changing climate. Geneva, Switzerland: World Meteorological Organization.

WMO. 2012. Standardized Precipitation Index User Guide. Geneva, Switzerland: World Meteorological Organization.

Wu, L., Bin, W. and Braun, S. A. 2008. Implications of tropical cyclone power dissipation index. *International Journal of Climatology,* **28**: 727–731.

Yue, S. and Wang, C. Y. 2002. Applicability of prewhitening to eliminate the influence of serial correlation on the Mann-Kendall test. *Water Resources Research,* **38**: 1068.

Zargar, A., Sadiq, R., Naser, B. and Khan, F. I. 2011. A review of drought indices. *Environmental Reviews,* **19**: 333–349.

Zhang, X., Alexander, L., Hegerl, G. C., Jones, P., Tank, A. K., Peterson, T. C., Trewin, B. and Zwiers, F. W. 2011. Indices for monitoring changes in extremes based on daily temperature and precipitation data. *Wiley Interdisciplinary Reviews-Climate Change,* **2**: 851–870.

Zhang, X. B., Aguilar, E., Sensoy, S., Melkonyan, H., Tagiyeva, U., Ahmed, N., Kutaladze, N., Rahimzadeh, F., Taghipour, A., Hantosh, T. H., Albert, P., Semawi, M., Ali, M. K., Al-Shabibi, M. H. S., Al-Oulan, Z., Zatari, T., Khelet, I. A., Hamoud, S., Sagir, R., Demircan, M., Eken, M., Adiguzel, M., Alexander, L., Peterson, T. C. and Wallis, T. 2005a. Trends in Middle East climate extreme indices from 1950 to 2003. *Journal of Geophysical Research - Atmospheres,* **110**: D22104.

Zhang, X. B., Hegerl, G., Zwiers, F. W. and Kenyon, J. 2005b. Avoiding inhomogeneity in percentile-based indices of temperature extremes. *Journal of Climate,* **18**: 1641–1651.

3.7 Appendix

Table A3.1. Results (significance levels) of homogeneity analysis using four tests: the Standard Normal Homogeneity test (SNH), the Buishand Range test (BHR), the Pettitt test (PET) and the Von Neumann Ratio test (VON). NS = Not significant.

Type of data	Location	Time period	SNH	BHR	PET	VON
Annual (June-May) Rainfall (mm)	Mt Camizard	1962-2014	<0.01	<0.05	<0.05	<0.01
	Plaisance	1951-2014	NS	NS	NS	NS
	Vacoas	1961-1989	<0.05	NS	NS	NS
Annual (June-May) Mean Tmax (°C)	Plaisance	1951-2014	<0.01	<0.01	<0.01	<0.01
	Vacoas	1961-1989	<0.05	NS	<0.05	<0.01

Table A3.2. Meteorological indices considered for use in this study but not selected.

Meteorological event	Metrics	Notes
Extreme and heavy rainfall	Percentage of total seasonal or annual rain falling on heavy or extreme raindays	In this study it is expected that the absolute number of rare events or their absolute severity will be more informative of ecological impacts than the relative proportion of seasonal rainfall (which varies annually) that falls on extreme raindays.
	Maximum rainfall during a defined number of consecutive days	This metric can identify high rainfall over a pre-defined number of days, but ignores other rain events in a season, as well as ignoring variation within the events identified.
	Number of days or accumulated rainfall on days when rainfall exceeds an arbitrary threshold	In this study subjectively choosing thresholds is difficult given the level of knowledge for the study species and for similar species around the world; by using percentiles, thresholds can be more objectively based on the rarity of events.
Drought	Drought indices that require temperature data (e.g. Standardised Precipitation and Evapotranspiration Index: SPEI) and soil moisture data (e.g. Palmer Drought Severity Index: PDSI)	Air temperature and soil moisture data are not available for all of the locations of interest in this study, thus these indices cannot be applied directly to all of the study locations.

Table A3.2 continued:

Meteorological event	**Metrics**	**Notes**
Temperature extremes	Means of daily temperature data for moving windows of consecutive days	In this study temperature data are not available for the study locations, and are only available from two synoptic stations in mainland Mauritius. Therefore the use of absolute temperature values in extreme metrics is not ideal, as temperature thresholds based on direct impacts cannot be reliably inferred; in this case relative extremes identified using percentile thresholds are preferred.

Table A3.3. Trends (Kendall's tau) and 2-tailed significance levels for rainfall and drought indices at Plaisance, using inventory data combined using different methods (see Results section), 1951-2015 (1980/1981-2014/2015 for Cyclone Rainfall), based on Mann-Kendall tests. *$P < 0.05$, **$P < 0.01$.

Index	**JJA**	**SON**	**DJF**	**MAM**
Rainfall	-0.244**	-0.114	0.065	-0.177*
Raindays	-0.284**	-0.104	-0.096	-0.347**
SDII	-0.145	-0.059	0.082	-0.092
HY-INT	-0.029	0.033	0.194*	0.053
Max Rain Spell	-0.302**	-0.092	0.107	-0.080
Raindays90	-0.194*	-0.049	0.092	-0.170
Raindays95	-0.089	-0.009	0.067	-0.156
Rainfall90	-0.102	-0.073	0.093	-0.141
SPI-3	-0.243**	-0.114	0.063	-0.178*
SPI-6	-0.227**	-0.203*	0.052	-0.107
Max Dry Spell	0.135	-0.022	0.188*	0.140
Cyclone Rainfall	-	-	-0.199	-0.089

Table A3.4. Correlations (Kendall's tau) among JJA rainfall indices at Mt Camizard and temperature indices at Plaisance.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00													
Raindays	0.38	1.00												
SDII	0.63	0.01	1.00											
HY-INT	0.28	-0.28	0.61	1.00										
Raindays90	0.71	0.20	0.70	0.43	1.00									
Raindays95	0.72	0.15	0.76	0.48	0.78	1.00								
Rainfall90	0.71	0.15	0.73	0.43	0.68	0.82	1.00							
Max Rain Spell	0.34	0.61	0.06	-0.10	0.20	0.10	0.15	1.00						
Max Dry Spell	-0.07	-0.42	0.18	0.40	0.10	0.13	0.09	-0.23	1.00					
SPI-3	1.00	0.40	0.64	0.28	0.70	0.72	0.71	0.34	-0.07	1.00				
SPI-6	0.54	0.29	0.41	0.25	0.50	0.48	0.43	0.27	-0.01	0.54	1.00			
Mean Tmax	0.19	0.27	0.07	-0.03	0.16	0.14	0.15	0.17	-0.15	0.20	0.22	1.00		
Tmax90	0.17	0.16	0.12	0.05	0.22	0.18	0.15	0.18	-0.06	0.18	0.35	0.55	1.00	
Tmax10	-0.14	-0.27	-0.04	0.07	-0.13	-0.12	-0.13	-0.15	0.16	-0.15	-0.16	-0.80	-0.41	1.00

Table A3.5. Correlations (Kendall's tau) among SON rainfall indices at Mt Camizard and temperature indices at Plaisance.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00													
Raindays	0.44	1.00												
SDII	0.60	0.04	1.00											
HY-INT	0.23	-0.31	0.59	1.00										
Raindays90	0.65	0.26	0.63	0.34	1.00									
Raindays95	0.63	0.22	0.63	0.39	0.60	1.00								
Rainfall90	0.64	0.17	0.67	0.41	0.60	0.81	1.00							
Max Rain Spell	0.34	0.54	0.12	-0.07	0.29	0.23	0.17	1.00						
Max Dry Spell	-0.27	-0.43	-0.08	0.23	-0.20	-0.13	-0.09	-0.14	1.00					
SPI-3	1.00	0.44	0.61	0.24	0.65	0.63	0.64	0.34	-0.28	1.00				
SPI-6	0.65	0.35	0.51	0.22	0.50	0.60	0.54	0.23	-0.22	0.65	1.00			
Mean Tmax	-0.01	0.07	-0.16	-0.13	-0.07	0.04	0.02	0.04	-0.02	-0.01	0.14	1.00		
Tmax90	-0.05	0.00	-0.08	-0.05	-0.06	0.02	-0.01	-0.03	-0.01	-0.05	0.02	0.50	1.00	
Tmax10	-0.10	-0.17	0.06	0.12	-0.03	-0.10	-0.09	-0.13	0.08	-0.10	-0.20	-0.71	-0.31	1.00

Table A3.6. Correlations (Kendall's tau) among DJF rainfall and cyclone indices at Mt Camizard and temperature indices at Plaisance.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10	Cyclone Days	ACE 300km	PDI 300km	Cyclone Rainfall
Rainfall	1.00																	
Raindays	0.42	1.00																
SDII	0.79	0.21	1.00															
HY-INT	0.45	-0.08	0.62	1.00														
Raindays90	0.77	0.42	0.66	0.36	1.00													
Raindays95	0.75	0.32	0.74	0.46	0.69	1.00												
Rainfall90	0.86	0.34	0.81	0.48	0.78	0.77	1.00											
Max Rain Spell	0.37	0.39	0.29	0.23	0.29	0.30	0.33	1.00										
Max Dry Spell	-0.24	-0.55	-0.08	0.24	-0.26	-0.16	-0.17	-0.17	1.00									
SPI-3	1.00	0.42	0.80	0.47	0.77	0.75	0.86	0.38	-0.23	1.00								
SPI-6	0.77	0.40	0.70	0.44	0.64	0.69	0.71	0.35	-0.21	0.78	1.00							
Mean Tmax	0.04	0.17	0.00	-0.04	0.07	-0.03	0.06	0.01	-0.14	0.04	0.05	1.00						
Tmax90	0.13	0.16	0.10	0.07	0.10	0.06	0.13	0.09	-0.18	0.12	0.12	0.57	1.00					
Tmax10	0.02	-0.10	0.07	0.10	-0.01	0.09	-0.01	0.02	0.07	0.01	0.01	-0.75	-0.39	1.00				
Cyclone Days	-0.02	-0.12	0.05	0.05	0.04	0.03	0.04	-0.31	0.15	-0.02	-0.09	-0.06	-0.02	0.07	1.00			
ACE 300km	-0.05	-0.07	0.00	0.02	0.04	-0.01	-0.02	-0.28	0.12	-0.05	-0.12	0.00	0.07	0.07	0.74	1.00		
PDI 300km	-0.07	-0.03	-0.03	0.00	0.02	-0.03	-0.04	-0.25	0.11	-0.08	-0.14	0.00	0.06	0.07	0.68	0.93	1.00	
Cyclone Rainfall	0.10	-0.06	0.16	0.17	0.16	0.16	0.16	-0.16	0.17	0.10	0.02	-0.10	-0.03	0.14	0.81	0.63	0.60	1.00

Table A3.7. Correlations (Kendall's tau) among MAM rainfall and cyclone indices at Mt Camizard and temperature indices at Plaisance.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10	Cyclone Days	ACE 300km	PDI 300km	Cyclone Rainfall
Rainfall	1.00																	
Raindays	0.32	1.00																
SDII	0.73	0.05	1.00															
HY-INT	0.44	-0.19	0.65	1.00														
Raindays90	0.71	0.23	0.68	0.45	1.00													
Raindays95	0.69	0.14	0.72	0.47	0.70	1.00												
Rainfall90	0.84	0.21	0.78	0.52	0.76	0.75	1.00											
Max Rain Spell	0.20	0.49	-0.01	-0.04	0.12	0.01	0.11	1.00										
Max Dry Spell	-0.19	-0.45	-0.01	0.30	-0.10	-0.09	-0.09	-0.16	1.00									
SPI-3	1.00	0.28	0.73	0.46	0.71	0.69	0.84	0.17	-0.14	1.00								
SPI-6	0.44	0.29	0.31	0.17	0.30	0.40	0.37	0.22	-0.18	0.44	1.00							
Mean Tmax	0.16	0.32	0.02	0.00	0.11	0.02	0.09	0.28	-0.08	0.12	0.24	1.00						
Tmax90	0.12	0.32	-0.02	-0.03	0.10	0.03	0.07	0.27	-0.09	0.10	0.16	0.57	1.00					
Tmax10	-0.13	-0.28	0.03	0.04	-0.05	-0.06	-0.08	-0.22	0.05	-0.11	-0.25	-0.62	-0.28	1.00				
Cyclone Days	-0.09	-0.08	-0.05	-0.06	0.01	-0.08	-0.03	-0.10	0.15	-0.11	-0.27	-0.06	0.13	0.07	1.00			
ACE 300km	-0.09	-0.14	-0.05	-0.04	0.00	-0.09	-0.03	-0.14	0.19	-0.13	-0.28	-0.09	0.07	0.08	0.91	1.00		
PDI 300km	-0.09	-0.14	-0.05	-0.04	0.00	-0.09	-0.03	-0.14	0.20	-0.13	-0.28	-0.10	0.06	0.08	0.89	0.99	1.00	
Cyclone Rainfall	-0.05	-0.10	-0.01	-0.02	0.05	-0.03	0.01	-0.11	0.15	-0.09	-0.25	-0.10	0.07	0.11	0.91	0.90	0.89	1.00

Table A3.8. Correlations (Kendall's tau) among JJA climate indices at Plaisance.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00													
Raindays	0.39	1.00												
SDII	0.74	0.12	1.00											
HY-INT	0.46	-0.13	0.67	1.00										
Raindays90	0.70	0.28	0.66	0.49	1.00									
Raindays95	0.62	0.23	0.64	0.48	0.59	1.00								
Rainfall90	0.66	0.19	0.70	0.48	0.46	0.66	1.00							
Max Rain Spell	0.10	0.35	-0.02	-0.05	0.03	0.04	0.01	1.00						
Max Dry Spell	-0.11	-0.40	0.06	0.25	-0.08	-0.07	-0.04	-0.18	1.00					
SPI-3	1.00	0.39	0.74	0.46	0.70	0.62	0.66	0.10	-0.10	1.00				
SPI-6	0.53	0.41	0.40	0.23	0.43	0.34	0.37	0.15	-0.16	0.53	1.00			
Mean Tmax	-0.11	-0.13	-0.10	-0.08	-0.10	-0.07	-0.08	-0.25	0.04	-0.11	-0.11	1.00		
Tmax90	0.05	-0.01	0.04	0.01	0.05	0.05	0.00	-0.12	0.04	0.05	0.08	0.54	1.00	
Tmax10	0.19	0.17	0.16	0.11	0.17	0.15	0.16	0.25	-0.04	0.18	0.16	-0.77	-0.37	1.00

Table A3.9. Correlations (Kendall's tau) among SON climate indices at Plaisance.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00													
Raindays	0.41	1.00												
SDII	0.72	0.13	1.00											
HY-INT	0.36	-0.22	0.61	1.00										
Raindays90	0.62	0.22	0.66	0.43	1.00									
Raindays95	0.67	0.27	0.68	0.43	0.64	1.00								
Rainfall90	0.69	0.19	0.71	0.49	0.49	0.76	1.00							
Max Rain Spell	0.30	0.49	0.13	-0.04	0.16	0.28	0.19	1.00						
Max Dry Spell	-0.20	-0.46	-0.02	0.26	-0.08	-0.14	-0.12	-0.29	1.00					
SPI-3	1.00	0.41	0.72	0.36	0.62	0.67	0.69	0.30	-0.20	1.00				
SPI-6	0.55	0.24	0.49	0.27	0.36	0.40	0.53	0.17	-0.14	0.55	1.00			
Mean Tmax	-0.27	-0.30	-0.15	-0.01	-0.14	-0.10	-0.17	-0.20	0.12	-0.27	-0.26	1.00		
Tmax90	-0.29	-0.29	-0.19	-0.03	-0.15	-0.16	-0.25	-0.15	0.12	-0.29	-0.23	0.55	1.00	
Tmax10	0.17	0.22	0.08	-0.03	0.07	0.03	0.09	0.13	-0.08	0.17	0.20	-0.75	-0.38	1.00

Table A3.10. Correlations (Kendall's tau) among DJF climate indices at Plaisance.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10	Cyclone Days	ACE 300km	PDI 300km	Cyclone Rainfall
Rainfall	1.00																	
Raindays	0.41	1.00																
SDII	0.70	0.10	1.00															
HY-INT	0.42	-0.13	0.67	1.00														
Raindays90	0.75	0.37	0.62	0.38	1.00													
Raindays95	0.61	0.17	0.66	0.47	0.62	1.00												
Rainfall90	0.84	0.29	0.79	0.51	0.76	0.69	1.00											
Max Rain Spell	0.39	0.36	0.22	0.19	0.29	0.23	0.32	1.00										
Max Dry Spell	-0.14	-0.38	0.02	0.29	-0.07	-0.03	-0.08	-0.06	1.00									
SPI-3	1.00	0.41	0.70	0.42	0.75	0.61	0.84	0.40	-0.15	1.00								
SPI-6	0.78	0.38	0.62	0.37	0.67	0.59	0.75	0.33	-0.13	0.78	1.00							
Mean Tmax	-0.13	-0.20	-0.07	0.06	-0.04	-0.08	-0.07	-0.09	0.18	-0.13	-0.16	1.00						
Tmax90	-0.03	-0.17	0.05	0.16	-0.01	-0.01	0.02	0.02	0.14	-0.03	-0.07	0.54	1.00					
Tmax10	0.16	0.19	0.10	0.01	0.08	0.12	0.12	0.07	-0.21	0.16	0.20	-0.76	-0.36	1.00				
Cyclone Days	0.03	-0.01	0.13	0.12	0.04	0.13	0.08	0.11	0.06	0.01	-0.03	-0.06	-0.03	0.07	1.00			
ACE 300km	0.03	-0.04	0.14	0.12	0.01	0.13	0.04	0.02	-0.07	0.01	-0.04	0.02	0.07	0.07	0.75	1.00		
PDI 300km	0.03	-0.04	0.14	0.10	0.01	0.14	0.04	0.03	-0.10	0.01	-0.04	0.00	0.04	0.08	0.71	0.95	1.00	
Cyclone Rainfall	0.19	0.05	0.26	0.24	0.15	0.25	0.19	0.19	-0.01	0.18	0.16	-0.16	-0.06	0.18	0.75	0.66	0.62	1.00

Table A3.11. Correlations (Kendall's tau) among MAM climate indices at Plaisance.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10	Cyclone Days	ACE 300km	PDI 300km	Cyclone Rainfall
Rainfall	1.00																	
Raindays	0.37	1.00																
SDII	0.71	0.07	1.00															
HY-INT	0.37	-0.22	0.63	1.00														
Raindays90	0.66	0.28	0.59	0.35	1.00													
Raindays95	0.68	0.20	0.69	0.41	0.67	1.00												
Rainfall90	0.84	0.25	0.78	0.47	0.68	0.72	1.00											
Max Rain Spell	0.09	0.41	-0.09	-0.11	0.07	-0.09	0.04	1.00										
Max Dry Spell	-0.38	-0.46	-0.19	0.13	-0.29	-0.30	-0.32	-0.12	1.00									
SPI-3	1.00	0.37	0.71	0.37	0.66	0.68	0.85	0.09	-0.38	1.00								
SPI-6	0.52	0.25	0.46	0.24	0.36	0.38	0.48	0.06	-0.37	0.51	1.00							
Mean Tmax	-0.05	-0.11	0.00	0.04	-0.07	-0.07	-0.01	0.02	0.07	-0.06	-0.07	1.00						
Tmax90	-0.02	0.05	-0.04	-0.02	-0.01	-0.05	-0.03	0.13	-0.01	-0.02	0.00	0.54	1.00					
Tmax10	0.08	0.19	0.00	-0.01	0.08	0.07	0.01	0.07	-0.10	0.08	0.04	-0.62	-0.24	1.00				
Cyclone Days	0.13	0.20	0.06	0.03	0.05	0.09	0.14	0.25	-0.07	0.13	-0.01	-0.05	0.12	0.03	1.00			
ACE 300km	0.12	0.20	0.03	0.01	0.04	0.08	0.12	0.24	-0.08	0.12	-0.02	-0.07	0.06	0.03	0.92	1.00		
PDI 300km	0.12	0.20	0.03	0.00	0.03	0.08	0.12	0.24	-0.09	0.12	-0.01	-0.08	0.05	0.03	0.91	0.99	1.00	
Cyclone Rainfall	0.14	0.19	0.07	0.04	0.08	0.12	0.15	0.22	-0.08	0.14	0.01	-0.08	0.06	0.04	0.91	0.93	0.92	1.00

Table A3.12. Correlations (Kendall’s tau) among JJA rainfall indices at Petrin and temperature indices at Vacoas.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00													
Raindays	0.47	1.00												
SDII	0.69	0.15	1.00											
HY-INT	0.21	-0.27	0.47	1.00										
Raindays90	0.66	0.32	0.59	0.31	1.00									
Raindays95	0.43	0.26	0.46	0.32	0.61	1.00								
Rainfall90	0.56	0.31	0.56	0.34	0.63	0.81	1.00							
Max Rain Spell	0.25	0.32	0.11	0.07	0.39	0.24	0.25	1.00						
Max Dry Spell	-0.29	-0.51	-0.06	0.34	-0.22	0.00	-0.05	-0.18	1.00					
SPI-3	1.00	0.47	0.69	0.21	0.66	0.43	0.56	0.25	-0.29	1.00				
SPI-6	0.24	0.12	0.23	0.06	0.25	0.22	0.25	0.07	-0.12	0.24	1.00			
Mean Tmax	-0.16	-0.32	-0.07	0.08	-0.23	-0.33	-0.27	-0.08	0.07	-0.16	-0.32	1.00		
Tmax90	0.18	-0.21	0.32	0.41	0.21	0.11	0.13	-0.01	0.01	0.18	-0.18	0.49	1.00	
Tmax10	0.14	0.20	0.10	0.02	0.14	0.27	0.14	0.08	0.03	0.14	0.17	-0.67	-0.24	1.00

Table A3.13. Correlations (Kendall's tau) among SON rainfall indices at Petrin and temperature indices at Vacoas.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00													
Raindays	0.36	1.00												
SDII	0.62	-0.03	1.00											
HY-INT	0.33	-0.30	0.63	1.00										
Raindays90	0.67	0.16	0.72	0.50	1.00									
Raindays95	0.63	0.11	0.68	0.52	0.65	1.00								
Rainfall90	0.60	0.05	0.71	0.57	0.62	0.76	1.00							
Max Rain Spell	0.26	0.48	0.00	-0.05	0.12	0.08	0.06	1.00						
Max Dry Spell	-0.13	-0.48	0.11	0.40	-0.01	0.10	0.08	-0.26	1.00					
SPI-3	1.00	0.34	0.60	0.36	0.66	0.62	0.62	0.28	-0.09	1.00				
SPI-6	0.47	0.38	0.26	0.10	0.36	0.43	0.39	0.25	-0.19	0.47	1.00			
Mean Tmax	0.03	-0.34	0.25	0.36	0.20	0.07	0.15	-0.35	0.08	0.01	-0.20	1.00		
Tmax90	0.02	-0.30	0.18	0.31	0.09	0.18	0.24	-0.31	0.18	0.01	-0.27	0.48	1.00	
Tmax10	-0.05	0.17	-0.18	-0.16	-0.20	-0.08	-0.16	0.24	-0.03	-0.04	0.03	-0.59	-0.19	1.00

Table A3.14. Correlations (Kendall's tau) among DJF rainfall and cyclone indices at Petrin and temperature indices at Vacoas.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10	Cyclone Days	ACE 300km	PDI 300km	Cyclone Rainfall
Rainfall	1.00																	
Raindays	0.40	1.00																
SDII	0.71	0.10	1.00															
HY-INT	0.37	-0.20	0.65	1.00														
Raindays90	0.74	0.26	0.77	0.49	1.00													
Raindays95	0.60	0.19	0.63	0.44	0.72	1.00												
Rainfall90	0.82	0.28	0.75	0.44	0.81	0.72	1.00											
Max Rain Spell	0.38	0.54	0.16	0.07	0.28	0.23	0.34	1.00										
Max Dry Spell	-0.31	-0.63	-0.03	0.29	-0.15	-0.11	-0.20	-0.40	1.00									
SPI-3	1.00	0.40	0.71	0.37	0.74	0.60	0.82	0.38	-0.31	1.00								
SPI-6	0.78	0.38	0.65	0.38	0.70	0.59	0.71	0.40	-0.25	0.78	1.00							
Mean Tmax	-0.26	-0.42	-0.04	0.23	-0.19	-0.24	-0.27	-0.23	0.39	-0.26	-0.13	1.00						
Tmax90	-0.13	-0.27	0.04	0.30	-0.08	-0.06	-0.10	0.10	0.23	-0.13	-0.02	0.54	1.00					
Tmax10	0.27	0.35	0.06	-0.15	0.16	0.25	0.24	0.33	-0.32	0.27	0.14	-0.74	-0.38	1.00				
Cyclone Days	0.12	-0.09	0.21	0.17	0.11	0.22	0.13	-0.28	0.02	0.12	0.04	-0.12	-0.18	0.00	1.00			
ACE 300km	0.20	-0.01	0.25	0.15	0.14	0.27	0.22	-0.10	-0.06	0.20	0.09	-0.10	-0.04	0.02	0.74	1.00		
PDI 300km	0.22	-0.01	0.26	0.15	0.17	0.31	0.25	-0.09	-0.09	0.22	0.12	-0.08	-0.02	0.00	0.70	0.95	1.00	
Cyclone Rainfall	0.32	-0.01	0.36	0.23	0.29	0.36	0.34	-0.15	-0.01	0.32	0.19	-0.13	-0.09	0.06	0.78	0.79	0.76	1.00

Table A3.15. Correlations (Kendall's tau) among MAM rainfall and cyclone indices at Petrin and temperature indices at Vacoas.

	Rainfall	Raindays	SDII	HY-INT	Raindays90	Raindays95	Rainfall90	Max Rain Spell	Max Dry Spell	SPI-3	SPI-6	Mean Tmax	Tmax90	Tmax10	Cyclone Days	ACE 300km	PDI 300km	Cyclone Rainfall
Rainfall	1.00																	
Raindays	0.36	1.00																
SDII	0.78	0.13	1.00															
HY-INT	0.48	-0.12	0.60	1.00														
Raindays90	0.62	0.10	0.66	0.52	1.00													
Raindays95	0.58	-0.01	0.70	0.55	0.58	1.00												
Rainfall90	0.75	0.14	0.85	0.55	0.68	0.73	1.00											
Max Rain Spell	0.33	0.56	0.20	-0.06	0.04	0.16	0.25	1.00										
Max Dry Spell	0.02	-0.45	0.18	0.38	0.22	0.10	0.19	-0.29	1.00									
SPI-3	1.00	0.36	0.78	0.48	0.62	0.58	0.75	0.33	0.03	1.00								
SPI-6	0.49	0.29	0.44	0.34	0.48	0.41	0.45	0.26	-0.05	0.49	1.00							
Mean Tmax	-0.23	-0.27	-0.22	-0.10	-0.27	-0.27	-0.26	-0.23	0.14	-0.23	-0.32	1.00						
Tmax90	-0.02	-0.06	-0.04	-0.12	-0.03	-0.21	-0.13	-0.10	0.06	-0.02	-0.02	0.43	1.00					
Tmax10	0.41	0.11	0.44	0.27	0.60	0.43	0.46	0.07	0.03	0.41	0.42	-0.52	-0.03	1.00				
Cyclone Days	-0.03	-0.13	-0.03	0.04	0.02	-0.13	-0.07	-0.29	0.20	-0.03	0.10	-0.06	0.34	0.21	1.00			
ACE 300km	-0.04	-0.14	-0.04	0.05	0.00	-0.11	-0.08	-0.29	0.20	-0.04	0.10	-0.08	0.33	0.24	0.93	1.00		
PDI 300km	-0.05	-0.15	-0.05	0.05	-0.02	-0.13	-0.09	-0.31	0.22	-0.05	0.08	-0.06	0.33	0.22	0.90	0.98	1.00	
Cyclone Rainfall	0.12	0.01	0.12	0.15	0.14	0.03	0.08	-0.18	0.14	0.12	0.27	-0.18	0.23	0.32	0.85	0.84	0.82	1.00

Table A3.16. Correlations (Kendall's tau) among JJA climate indices at Vacoas.

	Rainfall	Raindays	SDII	Max Rain Spell	Max Dry Spell	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00							
Raindays	0.47	1.00						
SDII	0.73	0.19	1.00					
Max Rain Spell	0.19	0.41	0.04	1.00				
Max Dry Spell	-0.16	-0.32	-0.02	-0.02	1.00			
Mean Tmax	-0.17	-0.29	-0.02	-0.09	0.01	1.00		
Tmax90	0.03	-0.17	0.14	-0.03	0.01	0.64	1.00	
Tmax10	0.12	0.22	0.01	0.05	0.00	-0.70	-0.39	1.00

Table A3.17. Correlations (Kendall's tau) among SON climate indices at Vacoas.

	Rainfall	Raindays	SDII	Max Rain Spell	Max Dry Spell	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00							
Raindays	0.47	1.00						
SDII	0.68	0.14	1.00					
Max Rain Spell	0.16	0.46	-0.02	1.00				
Max Dry Spell	-0.41	-0.48	-0.21	-0.10	1.00			
Mean Tmax	-0.17	-0.38	-0.03	-0.19	0.20	1.00		
Tmax90	-0.21	-0.38	-0.06	-0.13	0.23	0.46	1.00	
Tmax10	0.11	0.23	0.01	0.18	-0.10	-0.67	-0.24	1.00

Table A3.18. Correlations (Kendall's tau) among DJF climate indices at Vacoas.

	Rainfall	Raindays	SDII	Max Rain Spell	Max Dry Spell	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00							
Raindays	0.32	1.00						
SDII	0.76	0.08	1.00					
Max Rain Spell	0.28	0.40	0.16	1.00				
Max Dry Spell	-0.09	-0.34	0.02	0.08	1.00			
Mean Tmax	-0.13	-0.21	-0.04	-0.08	0.15	1.00		
Tmax90	-0.14	-0.19	-0.07	-0.11	0.24	0.54	1.00	
Tmax10	0.10	0.19	0.02	0.12	-0.09	-0.67	-0.29	1.00

Table A3.19. Correlations (Kendall's tau) among MAM climate indices at Vacoas.

	Rainfall	Raindays	SDII	Max Rain Spell	Max Dry Spell	Mean Tmax	Tmax90	Tmax10
Rainfall	1.00							
Raindays	0.25	1.00						
SDII	0.64	-0.12	1.00					
Max Rain Spell	0.14	0.47	-0.09	1.00				
Max Dry Spell	-0.19	-0.44	0.03	-0.21	1.00			
Mean Tmax	-0.07	-0.21	0.00	-0.14	-0.05	1.00		
Tmax90	0.15	0.05	0.08	0.12	-0.22	0.52	1.00	
Tmax10	0.26	0.32	0.08	0.22	-0.02	-0.56	-0.14	1.00

Chapter 4

Phenological tracking of a seasonal climate window in a recovering tropical island bird species

4.1 Abstract

Shifts in the reproductive timing of plants and animals in temperate regions are widespread and have potential consequences for individual fitness and population dynamics if reproduction becomes mistimed relative to favourable biotic or abiotic conditions. Very little is known about these processes in the highly speciose tropics. Tropical island species are expected to be particularly vulnerable to climate change. However, changes in phenology represent one potential mode of adaptation. Here, I explore these issues by quantifying climate change impacts on the phenology and demography of the Mauritius kestrel (*Falco punctatus*); a tropical raptor and iconic conservation success story, having recovered from a severe population bottleneck. I show that the timing of egg-laying is advancing in response to increases in late winter-early spring temperatures, at rates similar to temperate bird populations, with individual females showing plasticity to increases in temperature. Fledgling production is reduced when nesting overlaps with the summer rainy season, especially during heavy rainfall. As the timing of egg-laying advances, the risk of rainy season overlap should decrease, but this trend is not evident because rainy season onset is also advancing in recent years. This suggests that the breeding phenology of Mauritius kestrels is tracking changes in a seasonal window of favourable climate conditions. These results show how a threatened island-endemic species may adapt to a changing climate. The mechanism of changing seasonal windows may be widespread in the tropics, and climate change may result in new seasonal windows to which species must synchronise their life-history events.

4.2 Introduction

Understanding the vulnerability of species to climate change, based on their exposure, sensitivity and adaptive capacity, is vital for informing policies on mitigation, adaptation and conservation (Williams *et al.*, 2008; Dawson *et al.*, 2011; Foden *et al.*, 2013; Moritz and Agudo, 2013). Species adaptation to climate change may involve physiological and behavioural plasticity, spatial or elevational range shifts or evolutionary changes, without which local extirpation or complete extinction are increasingly likely and management interventions are needed (Williams *et al.*, 2008; Dawson *et al.*, 2011; Bellard *et al.*, 2012; Moritz and Agudo, 2013). Changes in phenology (the timing of seasonal life-history events) are among the most frequently cited examples of ecological response to climate change (Forrest and Miller-Rushing, 2010; Post *et al.*, 2018). The vast majority of biological phenomena have annual cycles and these temporal patterns, resulting from trade-offs among life-history characteristics and environmental conditions, underpin many aspects of ecology and evolution (Forrest and Miller-Rushing, 2010). The advancement of spring phenology, such as flowering times in plants and the timing of breeding in animals, has been documented for a range of taxonomic groups and life-history traits, most frequently in temperate regions of the Northern Hemisphere (Parmesan and Yohe, 2003; Parmesan, 2006; Chambers *et al.*, 2013; IPCC, 2014; Cohen *et al.*, 2018; Post *et al.*, 2018). Evidence indicates that phenological advancement is generally more rapid at higher latitudes, owing largely to the increasing velocity of warming as latitude increases (Both *et al.*, 2004; Parmesan, 2007; IPCC, 2014; Post *et al.*, 2018).

The timing of reproduction is a life-history decision with major fitness consequences for individuals (Visser *et al.*, 2006; Visser *et al.*, 2009), as it mediates the relationship between environmental conditions and reproductive fitness (Visser and Both, 2005). While there are exceptions, the population demographic effects of phenological changes in species are likely to emerge in reproduction before affecting other life-history stages, owing to the energy requirements of reproduction, the tendency for adult survival to be prioritised and the vulnerability of very young offspring to adverse conditions (Miller-Rushing *et al.*, 2010). In a changing climate, species that rely on climate cues for the timing of pre-emptive physiological changes (Dawson, 2008) risk mistiming their activities relative to peaks in important resources (Harrington *et al.*, 1999; Visser and Both, 2005; Visser *et al.*, 2012) or to a window of favourable abiotic conditions (Miller-Rushing *et al.*, 2010). The phenological responses of species to climate change appear to differ between trophic levels, with species in higher trophic levels generally being less responsive, thus increasing the risk of trophic mismatch, population declines and disruption to ecosystem functioning (Both *et al.*, 2009; Thackery *et al.*, 2010; Thackery *et al.*, 2016). However, there is mixed evidence of causal links between phenological shifts and population trends and the mechanisms by which these occur (Both *et al.*, 2010; Reed *et al.*, 2013; Dunn and Møller, 2014; Franks *et al.*, 2017).

Bird populations in temperate regions have provided model systems for the study of climate change impacts on phenology and trophic mismatch, but very little is known about the implications of climate change for the phenology of bird species in the tropics (Charmantier and Gienapp, 2013). Photoperiod is thought to be the principal environmental cue in the phenology of birds, even near the equator (Hau *et al.*, 1998; Beebe *et al.*, 2005; Dawson, 2007), with physiological plasticity allowing other short-term cues to fine-tune timing (Wikelski *et al.*, 2000; Dawson, 2008). In tropical regions, seasons and peaks in resources may be less pronounced (Hau, 2001), and species are adapted to a relatively narrow range of temperature conditions (Janzen, 1967; Ghalambor *et al.*, 2006; Gill *et al.*, 2016). While temperature is the dominant climate influence on phenology in temperate regions, variation in precipitation is thought to become increasingly important at lower latitudes (Forrest and Miller-Rushing, 2010; Pearce-Higgins and Green, 2014; Cohen *et al.*, 2018). However, the influence of temperature on tropical species is not always tested and compared to that of precipitation. Many tropical bird species breed seasonally (Hau *et al.*, 1998), and have phenological patterns that are influenced by climate (Komdeur, 1996; Wikelski *et al.*, 2000; Moore *et al.*, 2005; Moore *et al.*, 2006; Senapathi *et al.*, 2011; Cavalcanti *et al.*, 2016; Shaw, 2017). Temporal variation in biotic and abiotic conditions may therefore be sufficient for climate change to impact the phenology, individual fitness and population dynamics of tropical species (Komdeur, 1996; Senapathi *et al.*, 2011; Şekercioğlu *et al.*, 2012), but these processes are poorly understood.

The ecological significance of climate change is likely to vary in time and space, including across latitudes (La Sorte *et al.*, 2018). While the velocity of warming has been most rapid at higher latitudes, tropical regions, with their more limited climate variability, especially in relation to temperature, are projected to be among the first to emerge from recent variability into relatively novel climate regimes (IPCC, 2007; Mora *et al.*, 2013; Hawkins *et al.*, 2014; La Sorte *et al.*, 2018). These areas also harbour globally important concentrations of biodiversity (Barlow *et al.*, 2018). Species adapted to environments with low intra- and interannual variability may have low capacity for adaptation to even small shifts in climate, thus the greatest biological risks of climate change may be where biodiversity is at its richest (Deutsch *et al.*, 2008). However, a shortage of long-term detailed datasets and studies on the demographic impacts of climate change in tropical species constrains the projection of future impacts at low latitudes (Brawn *et al.*, 2017). Further research into climate change impacts on the phenology and demography of wild populations in the speciose tropics is urgently needed, as large concentrations of biodiversity could be at risk. Within the tropics, islands harbour high endemism (Kier *et al.*, 2009), and island-endemic species are particularly vulnerable to global change (Fordham and Brook, 2010). The limited distributions of island species increase population-level exposure to climate risks and limit the scope for spatial shifts (Foden *et al.*, 2013). Small population size may limit genetic diversity and the potential for evolutionary adaptation to new pressures (Parmesan *et al.*, 2000; Strauss *et al.*, 2006). The impacts of human activities, such as land-use change and the introduction of invasive species, are particularly acute on islands (Gillespie *et al.*, 2008; Kier *et al.*, 2009), and occur in synergy with the effects of climate, potentially reducing adaptive capacity to climate change (Parmesan *et al.*, 2000). For example, the effects of island area and human activities may disrupt adaptive phenological shifts in island populations (Gordo and Doi, 2012). It is vital, therefore, that further research be conducted into the climate change vulnerability of tropical island species, including potential modes of adaptation such as phenological changes.

Here, I address these issues using an extraordinarily detailed, individual-based dataset on a reintroduced population of a tropical wild bird, the Mauritius kestrel. This species was once one of the rarest birds in the world, but a successful recovery program has averted its extinction. Indeed, Mauritius is one of the few countries to have achieved a net gain in the conservation status of its vertebrate biodiversity in recent decades (Rodrigues *et al.*, 2014). Conservation gains in Mauritius and other countries represent important contributions to the protection of global biodiversity; however, climate change potentially threatens these achievements. Mauritius has a tropical climate with a summer rainy season, as influenced by tropical cyclones and orographic rain brought by the Southeast Trade Winds (Senapathi *et al.*, 2010; Staub *et al.*, 2014). The focal population occupies the Bambous Mountains in eastern Mauritius, which form a trade wind belt and receive high rainfall relative to most parts of the island (Staub *et al.*, 2014). The birds start to breed in the dry austral spring, with many young fledging early in the summer rainy season. Mauritius kestrels exhibit limited dispersal and the focal population is effectively isolated, allowing the monitoring of virtually all individuals and breeding attempts. These data enable the combination of individual life-history data on the timing of breeding and its fitness consequences with climate records spanning >20 years. Specifically, I address three broad questions: (1) how is breeding phenology (timing of egg-laying) responding to a changing climate, (2) how does climate impact breeding success; and (3) what are the fitness consequences of changes in breeding phenology? The analyses reveal a novel ecological mechanism in a tropical species, in which the birds appear to be breeding within a changing seasonal window defined by warming temperatures in spring when they are egg-laying, coupled with changes in rainfall patterns later in the season that affect breeding success.

4.3 Methods

4.3.1 Study system

The Mauritius kestrel is a diurnal, accipiter-like falcon (Temple, 1987), endemic to Mauritius. It is a monogamous and territorial cavity-nester, and tends to favour native forest (Jones, 1987), although it also occupies agricultural areas (Burgess *et al.*, 2008, 2011; Cartwright *et al.*, 2014). Its principal prey are endemic arboreal day geckos (*Phelsuma* species) (Temple, 1987), but it will also hunt native and introduced small birds, introduced small mammals, introduced reptiles and some insects (Jones, 1987; Temple, 1987; Carter and Jones, 1999). The species has been the subject of an intensive recovery programme since it suffered a severe population bottleneck and neared extinction in the wild in the 1970s. Threats have included habitat destruction, introduced invasive species and pesticide pollution (Jones *et al.*, 1995). Management strategies used in the recovery programme include captive-breeding and releases, cross-fostering, provision of nest-boxes, supplementary feeding and control of invasive species (Jones *et al.*, 1995). The species became locally extinct in the Bambous Mountains in the 1950s, but was reintroduced from 1987 onwards (Jones *et al.*, 1995). Following re-establishment, the Bambous Mountains population has stabilised at ~50 breeding pairs. There is a smaller and declining remnant population in the Black River Gorges area of southwestern Mauritius. Dispersal is very limited, with most birds staying within 2 km of their natal territory (Nevoux *et al.*, 2013), thus the two extant populations, located c.18 km apart, are effectively isolated (Cartwright *et al.*, 2014). The current Bambous Mountains population is significantly inbred and has lost substantial genetic diversity, although the consequences for the species are unclear (Groombridge *et al.*, 2000; Ewing *et al.*, 2008). The vast majority of the population is colour-ringed and monitored during each breeding season, with nest-sites checked regularly. Egg-laying starts in September and the last chicks fledge in January or February (Cartwright *et al.*, 2014).

4.3.2 Meteorological data

Rain gauge data from Mt Camizard (20°20’ S, 57°42’ E, 21 m asl) for the period January 1962 - March 2016 were contributed by Ferney Sugar Estate. The Mt Camizard rain gauge is situated in a central location in the Bambous Mountains range of the Mauritius kestrel and has been shown to be representative of seasonal rainfall trends in other parts the Bambous Mountains area (Senapathi *et al.*, 2010). Temperature data from the nearest available weather station at Plaisance (20°26’ S, 57°41’ E, 50 m asl; c.11 km from Mt Camizard) for the period January 1951 – January 2016 were obtained via the US National Oceanic and Atmospheric Administration (NOAA) in the form of the GHCN (Global Historical Climatology Network) and GSOD (Global Summary of the Day) inventories. These inventories were merged to minimise the number of days with missing data. Quality control was carried out on the rainfall and temperature data, including homogeneity tests and removal of consecutive repeat precipitation values (following Gallego *et al.*, 2011). Homogeneity tests on annual rainfall and temperature indices identified a break point in the Plaisance temperature data in 1975-1976 or 1985. No adjustments were made to the data following homogeneity tests, as such adjustments are challenging and inhomogeneities could be caused by genuine climate variability (WMO, 2003). Tropical cyclone tracks and accompanying data were downloaded as ESRI shapefiles from the International Best Track Archive for Climate Stewardship (IBTrACS v03r10) (Knapp *et al.*, 2010) via NOAA (www.ncdc.noaa.gov/ibtracs). Global best-track data comprise 6-hourly estimates of the location (latitude and longitude) and intensity (usually estimated as maximum sustained wind speed) of every recorded tropical cyclone during varying periods of record in each world region. Inhomogeneities in intensity estimation in the Indian Ocean dataset exist owing to the repositioning of a satellite and thus improvement of the view angle in 1998 (Elsner *et al.*, 2008; Kossin *et al.*, 2013). These inconsistencies are difficult to remove without re-analysing satellite images (Kossin *et al.*, 2013), and they may affect the cyclone indices used in this study.

4.3.3 Breeding success and phenology

Exploratory analyses of climate impacts on breeding success and phenology were carried out using (generalised) linear mixed effects models. All exploratory analyses followed two stages: First, a base (or background) model (e.g. Öberg *et al.*, 2015) was chosen by running a selection of candidate models incorporating potentially important variables, based in part on prior evidence; and second, climate indices were incorporated into the selected base model to test for their effect. Table 4.1 shows the variables incorporated into the candidate base models for fledgling production, egg survival, clutch size and timing of breeding. Measures of prior breeding experience and age were included as linear terms and quadratic terms, as spline analysis and previous studies indicated quadratic relationships. All candidate base models for fledgling production, egg survival and clutch size included first egg-laying date (FED) because it is known to directly affect breeding success and influence the exposure of each breeding attempt to weather conditions (see Table 4.1). Once a base model had been selected, it was run again with one of a selection of climate indices systematically included as additive effects. Nest-level time windows for climate indices were adopted for use in the analyses of impacts on breeding success. It should be noted that nest-level climate indices for temporally overlapping nests are not truly independent, as they are derived from the same weather station data. Nevertheless, they serve to estimate the exposure of each nest to certain conditions. All continuous climate indices were added as a linear term only and with a quadratic term. Annual population density has been shown to be an important influence on clutch size and fledgling production (Nicoll, 2004; Nevoux *et al.*, 2011), although this pattern may be a consequence of more lower-quality territories becoming occupied as population density has increased (Nevoux *et al.*, 2011). Cartwright *et al.* (2014) found that local density for each territory did not have an important influence on egg survival. In the present analyses, year is included as a random effect in place of annual density as a fixed effect, as the identification of influential nest-level climate variables could be compounded by the inclusion of a season-level fixed effect variable such as density.

Climate indices were chosen and developed based on expected and plausible impacts on breeding Mauritius kestrels. In all nest-level indices, extreme rainfall events are defined as those exceeding the 90th percentile of all raindays (≥1 mm) in the season of interest, aggregated from the base period 1990/1991-2014/2015. The 90th percentile (rather than the 95th or 99th) is chosen to maximise the number of days sampled in the statistical analysis. In order to detect the influence of seasonal drought conditions on breeding success, binary indices were included to identify breeding attempts initiated during years when drought conditions occurred in the dry season (June-November). Droughts were identified as periods with a Standardised Precipitation Index value of ≤ -1.0 for total seasonal rainfall (McKee *et al.*, 1993), based on mean seasonal rainfall for the base period 1990/1991-2014/2015. Hot days were defined as those exceeding the seasonal 90th percentile of all days in the same 25-year base period. Binary indices are included to identify the overlap of nesting activity with one or more days on which the centre of a tropical storm or cyclone (maximum 1-minute sustained wind ≥ 34 knots) was located within 300 km of Mt Camizard (analysed using QGIS version 2.18.20). Previous research and anecdotal observations, including from Mauritius, indicate that cyclone winds and rain regularly impact areas within 275-300 km (~150 nm) of the storm centre (Shepherd *et al.*, 2007; Nicoll *et al.*, 2017). Climate indices were calculated where no more than 10% of days had missing data in the time window of interest.

Climate indices of interest were defined for an 80-day period relevant to each breeding attempt for the fledgling production analysis, the estimated brood phase of each nest for the egg survival analysis, and a 10-day window just prior to the FED for the clutch size analysis (Table 4.2). Indices are also calculated for the three-month period July-September (Table 4.3), as conditions in this period at the start of the breeding season have been shown to be influential on the timing of egg-laying (Nicoll, 2004; Senapathi *et al.*, 2011). August rainfall frequency has been shown to be important (Senapathi *et al.*, 2011), but JAS indices are used here as Tmax is also analysed, and conditions in July and September may influence the onset of courtship and egg-laying by later breeders respectively. The 80-day indices start 10 days before the FED. In clutches of three or more eggs, incubation is usually initiated on the day when the third egg is laid and eggs are laid at three-day intervals (M. A. C. Nicoll pers. obs.), thus for clutches of 1-2 eggs the incubation delay is assumed to be three days, and for clutches of 3-5 eggs the delay is assumed to be six days. In the case of the 80-day climate indices, the maximum delay of six days is assumed for all nests. The incubation period is assumed to be 29 days in all nests, as this usually ranges from 28 to 30 days and 29 days is used for the back calculation and estimation of the FED from field observations. Brood periods are known to range from 32 to 35 days (Cartwright *et al.*, 2014), but the maximum of 35 days is assumed here for all nests to account for delays in the fledging of the youngest nestling in broods of three or more. The relevant time window may be overestimated for smaller clutches because of their shorter laying delay, but most clutches in the exploratory analyses for breeding success (379/403) number three or more eggs. For the calculation of brood phase climate indices, the expected hatch day (EHD) of the first egg in each clutch was estimated. The EHD was estimated from the FED by adding the assumed incubation delay, based on the clutch size, and then the assumed incubation period of 29 days for all nests. Once the EHD of a clutch had been estimated, the brood period was assumed to be 35 days including the EHD. For the analysis of climate impacts on clutch size, indices were calculated for a 10-day window immediately prior to the FED.

The analyses of fledgling production, egg survival and clutch size include 403 unmanaged first clutches from the 1990/1991 to 2014/2015 seasons, for which there are complete data for the variables of interest, including important variables identified in previous research and the climate indices to be tested. Second and third clutches were excluded because of the likely costs incurred during the breeding attempts that preceded relays (e.g. Hansson *et al.*, 2000). The mixed-model analysis of FED includes 356 unmanaged first clutches in the 1994/1995-2014/2015 seasons, for which there are complete data for the variables of interest, with at least 10 clutches per season. All data subsets are thus extracted from the period 1990/1991 to 2014/2015. Overall trends in the timing of breeding were analysed using data from 489 unmanaged first clutches in 20 seasons from the 1994/1995 to the 2014/2015 seasons (in which there are at least 10 such clutches per season with sufficient data). There are insufficient samples of unmanaged nests to study timing in earlier years.

4.3.4 Phenological plasticity

The exploratory analysis of climate impacts on the timing of egg-laying combines both the variance observed within individuals and between individuals. To disentangle these two sources of variance a method known as within-subject centring (van de Pol and Verhulst, 2006; van de Pol and Wright, 2009) was applied to the most parsimonious climate index. The analysis of within- and between-individual phenological responses of Mauritius kestrels to spring rainfall has been carried out in previous research (Senapathi *et al.*, 2011). In the present study, the dataset used in the FED analyses was subset so that it contained only females with data on at least two breeding attempts. The same base model for the FED analyses was used again in these analyses. Additional models were constructed in which the mean of climate conditions experienced by each female across multiple years was used to describe the between-individual variance; the difference between this mean value for each female and the conditions in each year was used to describe the within-individual variance. To determine if the difference between the within- and between-individual variance is significant, as model was constructed including the original climate variable and the new variable for between-individual variance. To test whether there is any between-individual variation in the slopes of within-individual responses (reaction norms), a model was constructed in which a random slope for the within-individual response was added to the random intercept for female identity.

4.3.5 Rainy season onset

Previous research has identified December rainfall as influential on breeding success in Mauritius kestrels (Nicoll, 2004; Senapathi *et al.*, 2011; Cartwright *et al.*, 2014). To test this pattern further, recently developed methods (Liebmann *et al.*, 2012; Dunning *et al.*, 2016) were used to identify the onset and cessation of the rainy season (RS) in the Bambous Mountains. The onset and cessation of rainy seasons in the Bambous Mountains were analysed using the Mt Camizard rain gauge data, and identified from accumulated daily rainfall anomalies (Liebmann *et al.*, 2012; Dunning *et al.*, 2016). Leap days were removed, but daily values that were removed in the quality control processes were retained in the gauge time series, as treating missing values as zeros would strongly bias the results. First, harmonic analysis was used to confirm the occurrence of one or two rainy seasons per year. The period in which the RS usually occurs, termed the climatological water season, was then identified in order to account for rainy seasons that span calendar years. To identify this period, the climatological mean rainfall on each day of the calendar year was calculated and from this the climatological cumulative daily rainfall anomaly was derived. The minimum of these values indicates the start and the maximum indicates the end of the climatological water season. For each year in turn the daily cumulative rainfall anomaly was then computed. The onset and cessation dates were determined by finding the minimum and maximum respectively in the cumulative daily rainfall anomaly. This anomaly increases when daily rainfall is above the climatological mean daily rainfall and decreases when daily rainfall is below this amount.

The analysis of RS onset and cessation shows that the mean (±1SD) duration of the RS over the period 1963/1964-2014/2015 is 99.4 ± 55.2 days. The RS durations identified for the years 1963/1964, 1964/1965, 1965/1966, 1983/1984, 1993/1994 and 1998/1999 were more than 1.5 standard deviations below the mean (z-score < -1.5, duration < 17 days) and treated as completely missing seasons in terms of potential impacts on kestrel breeding success. The RS in all other years ranged from 26 days (in 1989/1990) to 209 days (in 2014/2015). The impact of rainy season onset on breeding success was analysed using a sample of 433 unmanaged first clutches for which data were available on the FED, clutch size, fledgling production and identity of the female, and in years with at least 10 clutches with these data. Over this period the duration of the RS varied from 52 to 209 days. The notional overlap of nests with rainy season onset was estimated by calculating the expected fledging day (EHD + 35 days) of each clutch relative to the day of onset. The effect of overlap with onset was tested with linear, quadratic and cubic terms to test for nonlinearity in the effect on breeding success.

4.3.6 Statistical analyses

The R statistical environment (version 3.4.4; R Core Team, 2018) was used for all statistical analyses. Linear models, linear mixed models and generalised linear mixed models (GLMMs) were run with package 'lme4' (Bates *et al.*, 2018). Model ranking and selection were carried out using package 'MuMIn' (Barton, 2018). The effects of explanatory variables were studied with the 'effects' package (Fox *et al.*, 2018). The error distribution of response variables was assessed with the aid of histograms and Cullen and Frey graphs using the 'fitdistrplus' package (Delignette-Muller *et al.*, 2017). FED and clutch size were assumed to follow a Gaussian error distribution. In fledgling production models a Poisson error distribution was assumed and the log-linear link function used, and in the egg survival models a binomial error distribution was assumed and logit link function used. Egg survival to fledging was modelled as two-vector matrix of eggs that fledged and eggs that failed in each nest, following Cartwright *et al.* (2014). All mixed-effects models incorporated female identity and year as random effects in order to control for repeated (non-independent) observations from the same individuals and repeated season-level conditions not included in the fixed effects. All continuous predictor variables in the mixed-effects models were centred and scaled, and the BOBYQA (Bound Optimisation By Quadratic Approximation) optimiser (Powell, 2009) was used in all GLMMs to facilitate model convergence. All simple fixed effects included in mixed models showed (generalised) variance inflation factors of < 3 (see Zuur *et al.*, 2010).

In correlation and trend analyses, Kendall's tau and the Mann-Kendall test were used where the assumptions of parametric tests were not sufficiently met. Interannual trends in climate indices were analysed with Mann-Kendall trend tests using the package 'Kendall' (McLeod, 2011). Kendall's tau is robust to the influence of outliers and missing data, and thus can be applied to a range of climate indices (e.g. Vincent *et al.*, 2011). For trend analyses the results were considered significant where $P < 0.05$. Akaike's Information Criterion corrected for sample size (AICc) was used for comparison of mixed-effects models. The threshold of ΔAICc < 2 was used to guide stringent model selection and interpretation while recognising that a threshold of ΔAICc < 7 might be more appropriate for identifying all models that are informative (Burnham *et al.*, 2011). Marginal and conditional Pseudo-R^2 values (Nakagawa and Schielzeth, 2013) were calculated for mixed models using the 'MuMIn' package.

Table 4.1. Explanatory variables included in candidate base models for Mauritius kestrel first egg-laying date (FED), fledgling production (FP), egg survival to fledging (ES) and clutch size (CS), based on prior research.

Variable	**Base model**	**Description**	**References**
FED	FP, ES, CS	First Egg-laying Date (days from 1 September)	Burgess *et al.* (2011); Senapathi *et al.* (2011); Cartwright *et al.* (2014)
Agriculture	FP, ES	Percentage of territory classed as agricultural land	Burgess *et al.* (2011); Cartwright *et al.* (2014)
Elevation	FED, FP, ES	Elevation (m asl) of territory	Burgess *et al.* (2011); Cartwright *et al.* (2014)
Cavity type	FP, ES	Two-level factor for natural and artificial cavities	Nicoll (2004); Cartwright *et al.* (2014)
Clutch size	ES	Number of eggs in clutch	Burgess *et al.* (2011); Cartwright *et al.* (2014)
Female Age	FED	Age (years) of female in pair	Senapathi *et al.* (2011)
Male Age	FED	Age (years) of male in pair	Senapathi *et al.* (2011)
Male PBE	FED, FP, ES	Prior breeding experience (years) of male in pair	Burgess *et al.* (2008); Burgess *et al.* (2011); Cartwright *et al.* (2014)
Pair PBE	FP, ES, CS	Prior breeding experience (years) of pair together	Nicoll (2004)

Table 4.2. Nest-level climate indices incorporated into models for breeding success in Mauritius kestrels. Time windows: FP = 80-day period for fledgling production; ES = 35-day period for egg survival to fledging; CS = 10-day period for clutch size. Percentile thresholds and standardised precipitation index (SPI) were calculated from the standard reference period 1990/1991-2014/2015.

Climate index	**Analysis and time window**	**Description**
Rainfall	FP, ES, CS	Total rainfall (mm) on raindays (≥1 mm)
Raindays	FP, ES, CS	Total number of days with ≥ 1 mm rain
Rainfall90	FP, ES, CS	Total rainfall (mm) on days that exceed the SONDJF 90th percentile (40.7 mm)
Raindays90	FP, ES, CS	Total number of raindays that exceed the SONDJF 90th percentile (40.7 mm)
Max Dry Spell	FP, ES, CS	Maximum number of consecutive dry days (< 1mm rainfall)
Max Rain Spell	FP, ES, CS	Maximum number of consecutive raindays (≥1 mm rainfall)
Mean Tmax	FP, ES	Mean daily maximum temperature (°C)
Tmax90 Days	FP, ES	Total number of days with maximum temperature over the SONDJF 90th percentile (30.9°C)
Cyclone	FP, ES	Binary factor to indicate if there were one or more days when the centre of a tropical storm (≥ 34 knots) or cyclone was located within 300 km of Mt Camizard
Drought	FP, ES, CS	Binary factor to indicate if the breeding attempt coincided with drought in the dry season (June-November), defined as a Standardised Precipitation Index value of -1.0 or lower.

Table 4.3. July-September (JAS) climate indices incorporated into models for timing (first egg-laying date) in Mauritius kestrel breeding attempts. Percentile thresholds and standardised precipitation index (SPI) were calculated from the standard reference period 1990/1991-2014/2015.

Climate index	**Description**
Rainfall	Total rainfall (mm) on raindays (≥1 mm)
Raindays	Total number of days with ≥1 mm rainfall
Rainfall90	Total rainfall during JAS on days exceeding the JAS 90th percentile (20.4 mm)
Raindays90	Total number of raindays during JAS exceeding the JAS 90th percentile (20.4 mm)
Max Rain Spell	Maximum number of consecutive raindays (≥1 mm)
Mean Tmax	Mean daily maximum temperature (°C)

4.4 Results

4.4.1 How is breeding phenology responding to a changing climate?

If the breeding phenology of the Mauritius kestrel is responding to a changing climate, systematic shifts in the timing of egg-laying would be expected. The data on the FED of 489 unmanaged first clutches show that the timing of egg-laying has significantly advanced at the rate of ~0.7 days year^{-1} over the period 1994-2014 (N = 20 years, 13-30 clutches per year), based on annual mean values of FED (b = -0.675 ± 0.163, R^2 = 0.488, P = 0.0006, Figure 4.1) and annual median values of FED (b = -0.719 ± 0.148, R^2 = 0.569, P = 0.0001, Figure 4.1). Trends in FED for a sample of 453 of clutches with female identity recorded were nearly identical for annual means (b = -0.642 ± 0.168, R^2 = 0.449, P = 0.0012) and medians (b = -0.695 ± 0.146, R^2 = 0.557, P = 0.0002).

Phenological shifts by breeding kestrels imply that timing is responding to an aspect of the local climate that also shows a systematic trend. The exploratory analysis indicates that the timing of egg-laying is changing in response to July-September mean maximum temperature (JAS mean Tmax), although the frequency of raindays during the same period (JAS raindays) also has a delaying influence (Table A4.2) (also see Senapathi *et al.*, 2011). A model incorporating quadratic terms for both JAS mean Tmax and JAS raindays shows stronger support (AICc = 2804.987) than a model with JAS mean Tmax only (AICc = 2810.139, Table A4.2), although JAS mean Tmax retains a dominant influence on FED in the model with both indices included (Figure 4.2). There is no support for an interaction between linear terms for JAS mean Tmax and JAS raindays (AICc = 2808.019) compared with an additive model with the same terms (AICc=2808.779). Mixed models incorporating Year as a continuous variable, to control for potentially confounding correlations with time (see Iler *et al.*, 2017), confirm that mean Tmax and raindays are influencing FED (Table A4.3). Annual median values in mean Tmax 10 days before FED in the 489 clutches for which timing is analysed show no directional trend (b = -0.005 ± 0.017, R^2 = 0.005, P = 0.762, Figure 4.3). This provides strong evidence that kestrels are tracking late winter-early spring warming. Mean maximum temperature in JAS shows an increase between 1951 and 2015 (Mann-Kendall tau = 0.482, 2-tailed P < 0.001, N = 65, Figure 4.4), with a warming rate of 0.020°C year^{-1} estimated by least squares regression. The warming trend is also evident over the period 1994-2014 (Mann-Kendall tau = 0.455, 2-tailed P = 0.003, N = 21), for which kestrel phenology is studied here, with an increase of 0.035°C year^{-1}.

Further analysis to test if the advancement of egg-laying is due to within-individual plasticity in female kestrels using within-subject centring (van de Pol and Verhulst, 2006; van de Pol and Wright, 2009), as previously applied to Mauritius kestrel phenology in response to spring rainfall (Senapathi *et al.*, 2011), shows that the population-level response to late winter-early spring temperature arises from both within-individual and between-individual responses (Table 4.4). These results confirm the presence of phenological plasticity in response to temperature changes. The variance between females in their within-individual responses is quite low (variance component = 0.810, standard deviation = 0.900), indicating that there is limited variation between individuals in their response to temperature changes (reaction norms).

Table 4.4. Model comparison and parameter estimates in the analysis of plasticity in first egg-laying dates of Mauritius kestrels in response to July-September mean maximum temperature (Mean Tmax). The models test the significance of within-individual responses (Within-ind.), between-individual responses (Between-ind.) and the difference between the within- and between-individual responses (Within-Betw. Difference). *N* = 308 unmanaged first clutches (1994/1995-2014/2015). The base model includes female age and male age (years) as continuous fixed effects, both with quadratic terms. All models include female identity and year as random effects, except where the random effects have within-individual responses nested in female identity (Within|Fem). ln(L) = log-likelihood.

Model	**ln(L)**	**AICc**	**Fixed effect**	**Coefficient estimate (±SE)**	***P*-value**
Base + Tmax + Difference	-1182.013	2384.767	Mean Tmax	-3.222 ± 1.020	0.005
			Within-Betw. Difference	-2.174 ± 1.039	0.041
Base + Within + Between	-1182.299	2385.338	Within-ind.	-2.455 ± 0.778	0.005
			Between-ind.	-4.256 ± 0.860	<0.001
Base + Within + Between + (Within|Fem)	-1181.724	2388.505	Within-ind.	-2.463 ± 0.770	0.004
			Between-ind.	-4.275 ± 0.848	<0.001
Base + Tmax	-1185.016	2388.636	Mean Tmax	-4.474 ± 0.921	<0.001

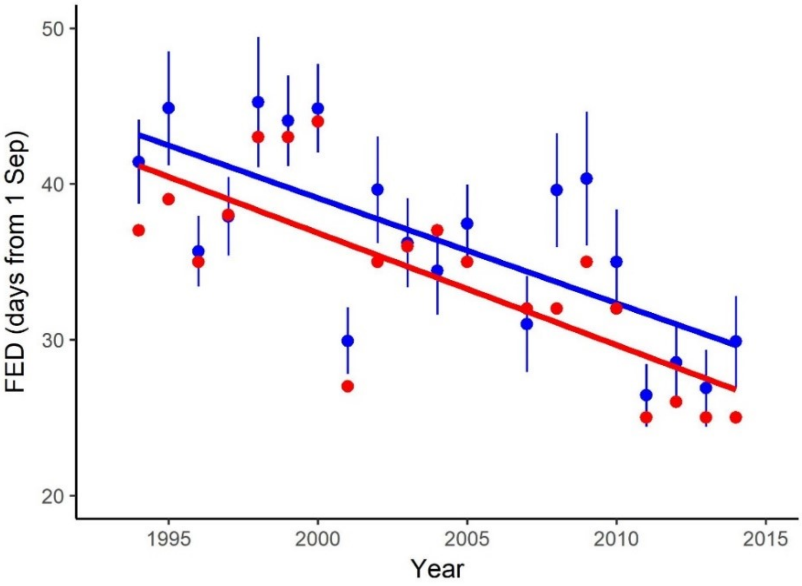

Figure 4.1. Trend in mean (±SE) (blue) and median (red) first egg-laying dates (FED, days from 1 September) by year between 1994 and 2014. *N* = 20 years, 489 clutches, 13-30 clutches per year. Trend lines fitted using least squares regression.

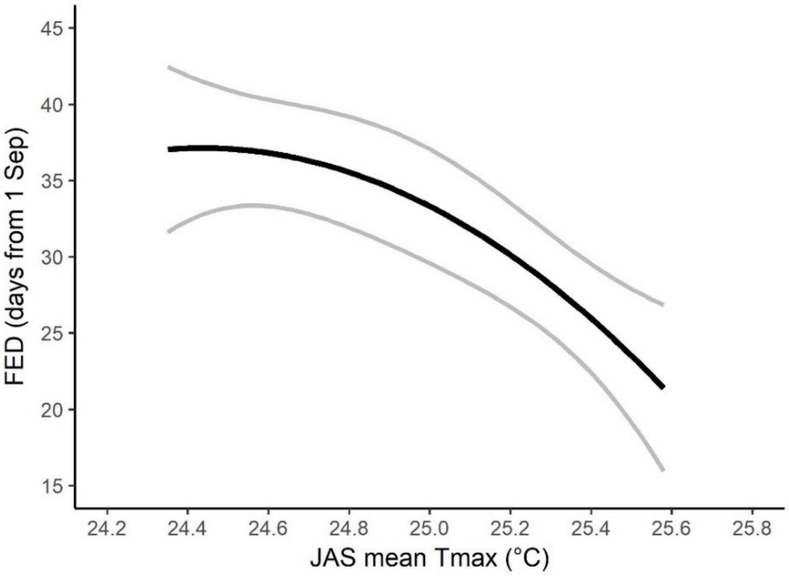

Figure 4.2. Effect plot of first egg-laying date (FED, days from 1 September) (with 95% confidence intervals) in relation to July-September mean maximum temperature (JAS mean Tmax, °C), extracted from a model incorporating the effects of female age^2, male age^2 and JAS raindays^2; with female identity and year as random effects. *N* = 356 clutches (1994/1995-2014/2015).

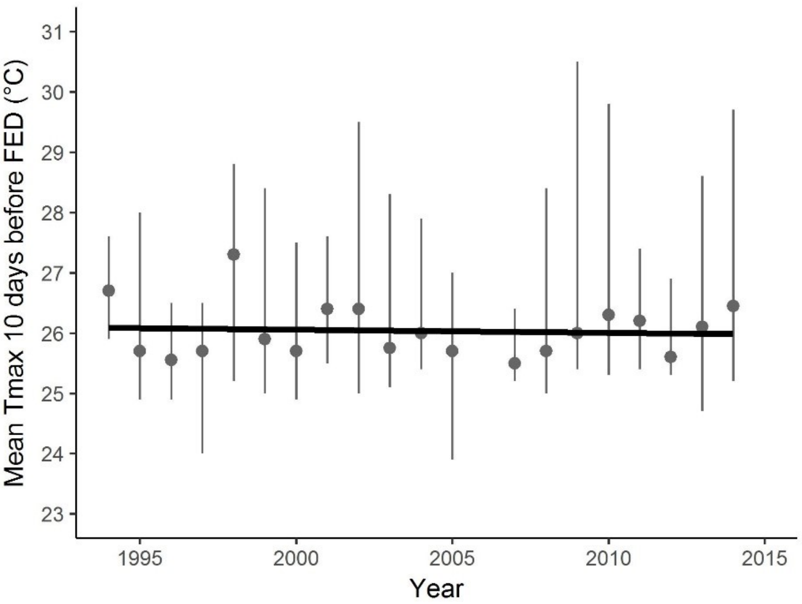

Figure 4.3. Trend in annual median values (with minimum and maximum shown) of mean maximum temperature (Mean Tmax, °C) 10 days before first egg-laying date (FED), between 1994 and 2014. *N* = 20 years, 489 clutches, 13-30 clutches per year. Trend line fitted using least squares regression.

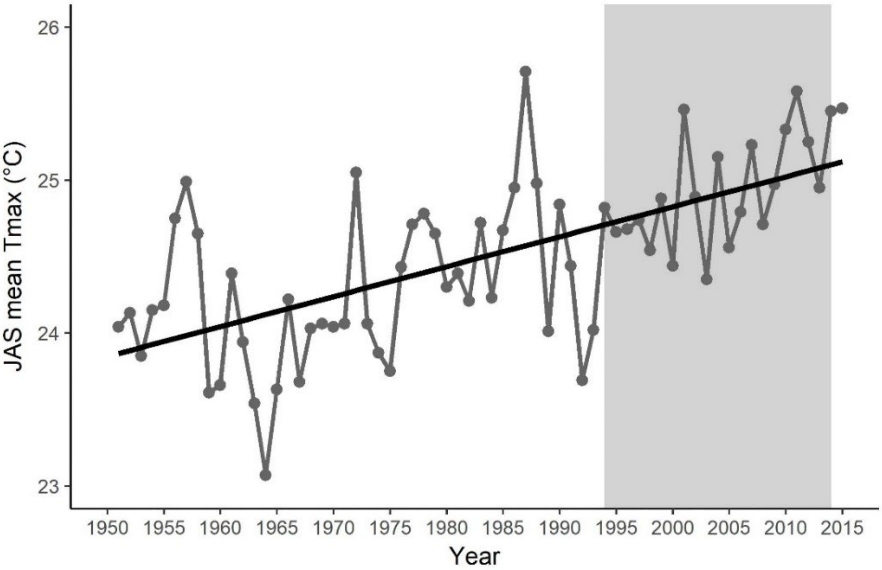

Figure 4.4. Trend in July-September mean maximum temperature (JAS mean Tmax, °C) by year between 1951 and 2015. *N* = 65 years. Trend line fitted using least squares regression. The shaded area indicates the period for which the impacts of rainy season onset on breeding success are analysed in this study.

4.4.2 How does climate impact breeding success?

Previous research has identified rainfall in December, when there is a population-level peak in the brood phase of nests, as a key influence on fledgling production and egg to fledging survival in this species (Senapathi *et al.*, 2011; Cartwright *et al.*, 2014), thus rainfall exposure at the nest-level and brood-level is expected to affect breeding success. Analysis of nest-level and brood-level climate influences on breeding success in 403 unmanaged first clutches (1990/1991-2014/2015) indicate that rainfall indices are the most parsimonious and that increasing rainfall exposure throughout the active phase of nesting attempts and during the brood phase of nests has a negative impact on the production of fledglings and survival of eggs to fledging (Tables A4.4-4.7; Figure 4.5). Models incorporating total rainfall, rather than indices for extreme raindays only (> seasonal 90th percentile), are slightly better supported, suggesting that all raindays or days exceeding a threshold below the 90th percentile are contributing to the negative impact.

Population density was originally omitted from these analyses, although the base models for fledgling production (AICc = 1240.650) and egg survival (AICc = 1148.417) are improved when density is added (AICc = 1231.124 and 1140.459 respectively). However, when FED is omitted from the base models (AICc = 1268.581 and 1185.098 respectively), adding density does not improve them (AICc = 1268.346 and 1184.875 respectively). This could occur because of the potentially confounding effect of systematic changes in the timing of breeding, which could result in a pattern of declining breeding success across years, and apparent negative density dependence, when FED is held constant. When FED is omitted from the base models for fledgling production and egg survival, the addition of rainfall still improves the models substantially (AICc = 1260.183 and 1166.911 respectively), implying that these results are not artefacts created by holding FED constant. There is no evidence to support climate impacts on clutch size (Table A4.9). Likewise, there is no evidence that JAS mean Tmax alters the seasonal decline in clutch size, as a model including only fixed effects for FED^2 (AICc = 775.313) is not improved by JAS mean Tmax as an additive effect (AICc = 781.237) or by an interaction between FED^2 and JAS mean Tmax (AICc = 795.268).

If increasing exposure to rainfall has a negative impact on breeding success, temporal overlaps with the summer RS would be expected to reduce fledgling production, possibly as a nonlinear function of the amount of overlap. The analysis of RS onset and cessation using the Mt Camizard rain gauge data indicates that the climatological water season, in which the RS usually occurs and which is based on the climatological mean rainfall for each calendar day, runs from 19 December to 4 May. The impact of RS timing on kestrel breeding success was studied for 19 years in the period 1994/1995-2014/2015, with 1998/1999 excluded due to a missed rainy season (duration = 3 days) and 2006/2007 excluded due to insufficient data on kestrel nests. The notional overlap with RS onset was calculated as the expected fledging day of each clutch relative to the day of onset and ranged from –122 days to 76 days. Analyses show that the notional overlap of nesting with RS onset has a negative impact on fledgling production and that this relationship is nonlinear (Table 4.5, Figure 4.6). The extent of the negative impact of overlap with onset is mediated by the amount of rainfall during the first 50 days of the RS and the amount of rainfall 50 days before onset (Table 4.5, Figure 4.7).

The seasonal decline in clutch size (Figure 4.8) could influence this pattern, so I also tested the effect of the number of days of overlap with the RS (where no overlap = 0 days) on fledgling production and egg survival as an additive effect in mixed models that include FED. For fledgling production, a model including only a fixed effect for FED (AICc = 1318.171) is improved by the inclusion of an additive term for the number of days of overlap with the RS (AICc = 1315.128). Likewise, a model for egg survival including only FED (AICc = 1236.396) is improved by the same additive term for the amount of overlap (AICc = 1232.411). These analyses support the finding that overlap with the RS influences the decline in productivity within seasons. Breeding kestrels therefore incur reproductive fitness costs when nesting activity coincides with RS onset.

As RS onset usually occurs later in the breeding season, earlier breeders would be expected to show less overlap with the RS. The data show that later breeding increases overlap with the onset of the RS (Kendall's tau = 0.323, $P < 0.0001$, $N = 433$, Figure 4.9), indicating one of the mechanisms through which earlier breeding pairs tend to show higher breeding success (Figure 4.10). As overlap generally leads to a non-linear decrease in fledgling production, I compared the mean annual fledgling production, as estimated using a generalised linear mixed model with female identity as a random effect, in years showing no overlap ($N = 5$) with years in which at least some nesting attempts overlapped with the RS ($N = 15$). Years in which the sample of nests does not overlap with the RS tend to show higher mean fledgling production (median of years: 1.620, range: 1.389-2.186) than years with some overlap (median of years: 1.421, range: 1.176-1.807), although the difference is marginally non-significant (Wilcoxon-Mann-Whitney test, $U = 60$, $P = 0.053$).

Table 4.5. Effect of notional overlap with rainy season onset (Overlap, days) and rainfall (RF, mm) 50 days before and after onset on fledgling production in Mauritius kestrel breeding attempts. *N* = 433 unmanaged first clutches (1994/1995-2014/2015). All models include female identity and year as random effects. Where quadratic and cubic terms are included only the highest order term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-*R*²**	**Conditional Pseudo-*R*²**
Overlap^3 × RF 50d after onset	10	-655.377	1331.276	0.000	0.987	0.318	0.354
Overlap^3 × RF 50d before onset	10	-659.813	1340.148	8.872	0.012	0.376	0.425
Overlap^3	6	-666.096	1344.389	13.113	0.001	0.173	0.243
Overlap^2	5	-668.628	1347.396	16.120	0.000	0.119	0.202
Overlap	4	-674.832	1357.758	26.482	0.000	0.041	0.137
Null	3	-682.883	1371.822	40.546	0.000	0.000	0.116

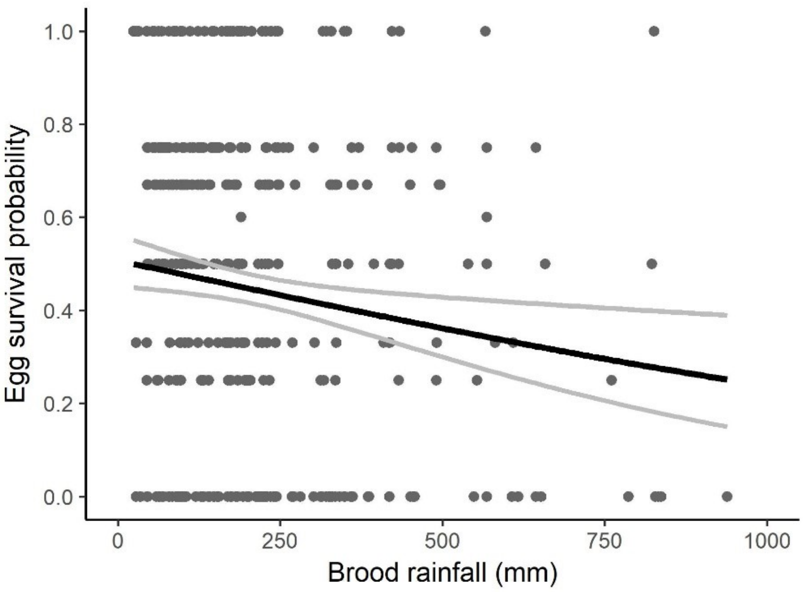

Figure 4.5. Effect plot of egg to fledging survival probability (with 95% confidence intervals) in relation to total rainfall (mm) during the brood phase of nests, extracted from a model incorporating the effects of first egg-laying date, agriculture proportion in territory, and their interaction; with female identity and year as random effects. Data points show raw data. *N* = 403 clutches (1990/1991-2014/2015).

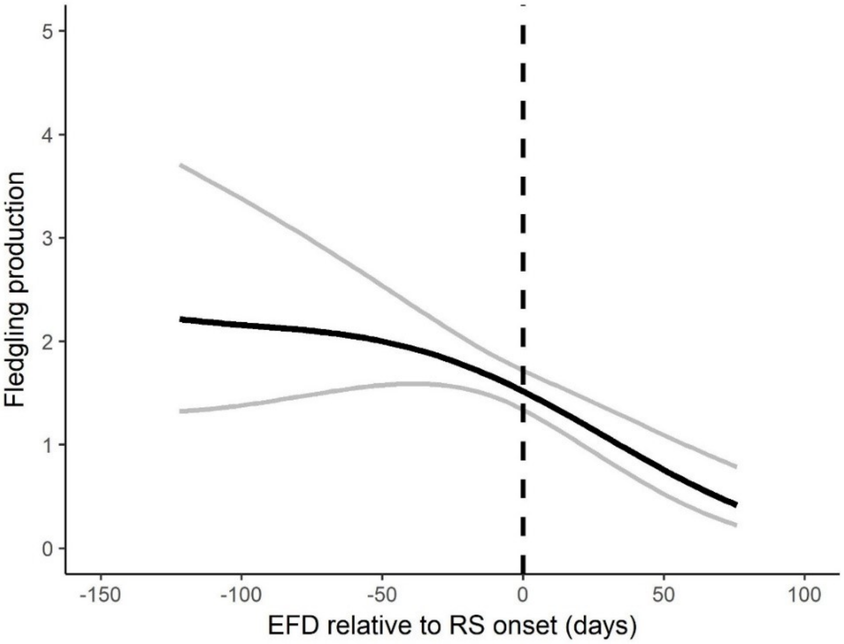

Figure 4.6. Effect plot of fledgling production (with 95% confidence intervals) in relation to expected fledging day (EFD) relative to rainy season (RS) onset (indicating notional overlap with onset in days), extracted from a model incorporating female identity and year as random effects. *N* = 433 clutches (1994/1995-2014/2015).

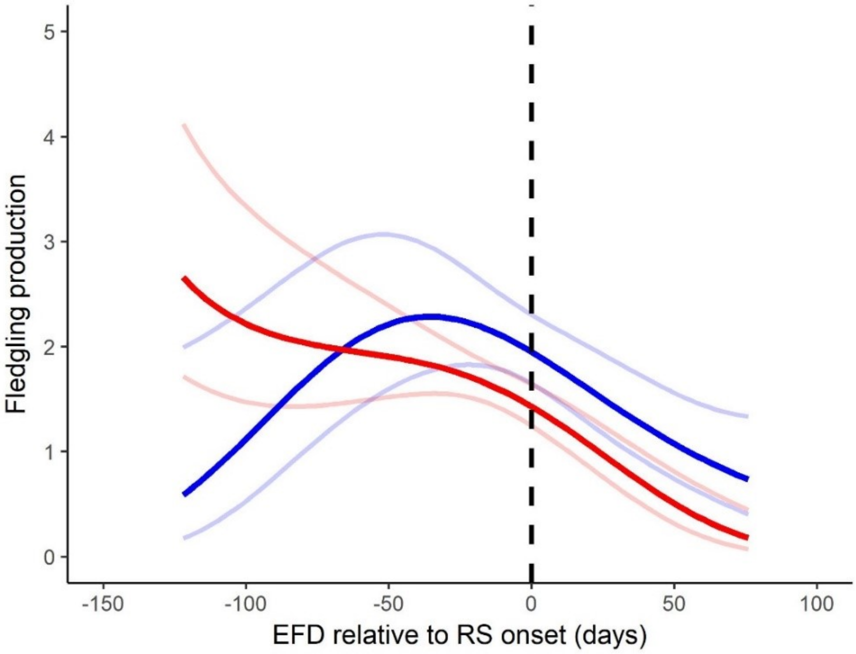

Figure 4.7. Effect plot of fledgling production (with 95% confidence intervals) in relation to expected fledging day (EFD) relative to rainy season (RS) onset (indicating notional overlap with onset in days) when there is 500 mm of rain 50 days after onset (blue line) and 1000 mm of rain 50 days after onset (red line), extracted from a model incorporating female identity and year as random effects. *N* = 433 clutches (1994/1995-2014/2015).

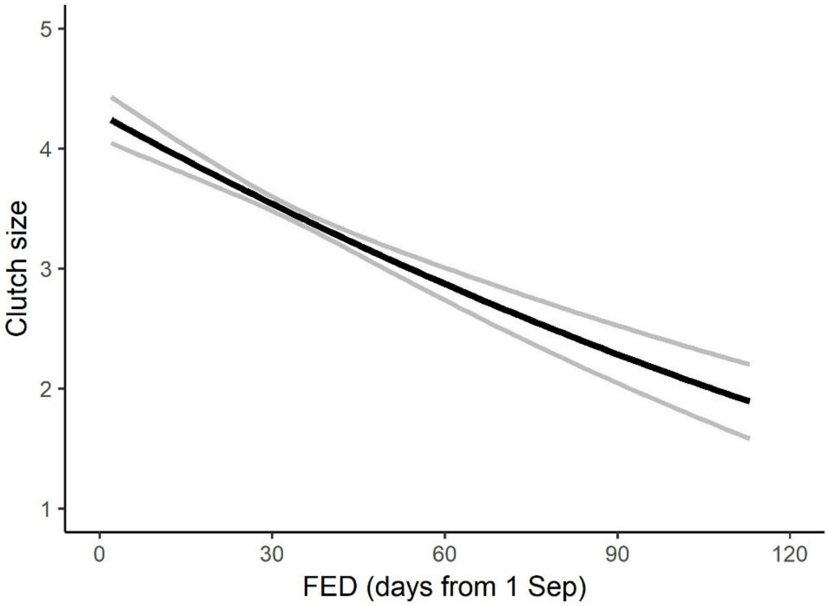

Figure 4.8. Effect plot of clutch size (with 95% confidence intervals) in relation to first egg-laying date (FED, days from 1 September) with a quadratic term, extracted from a model incorporating female identity and year as random effects. *N* = 433 clutches (1994/1995-2014/2015).

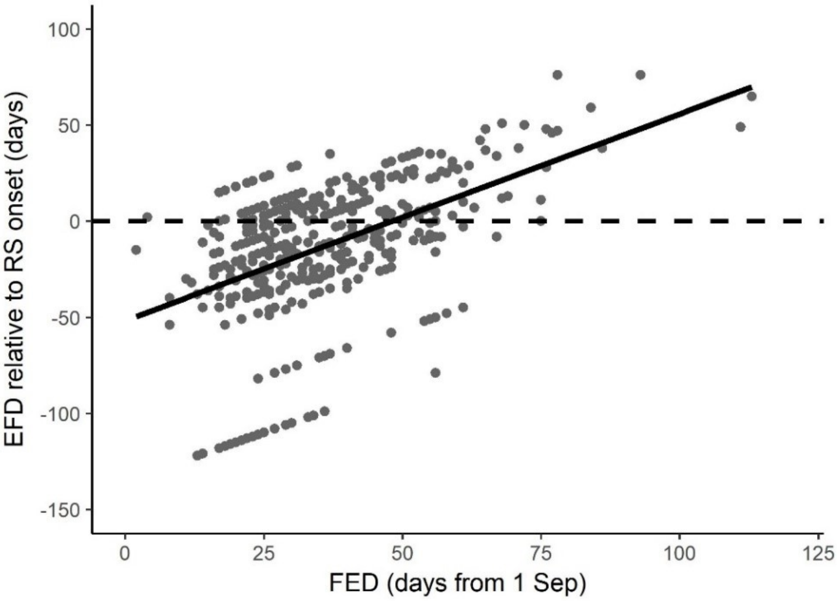

Figure 4.9. Expected fledging day (EFD) relative to rainy season (RS) onset (indicating notional overlap with onset in days) in relation to first egg-laying date (FED). *N* = 433 clutches (1994/1995-2014/2015). Trend line fitted using least squares regression.

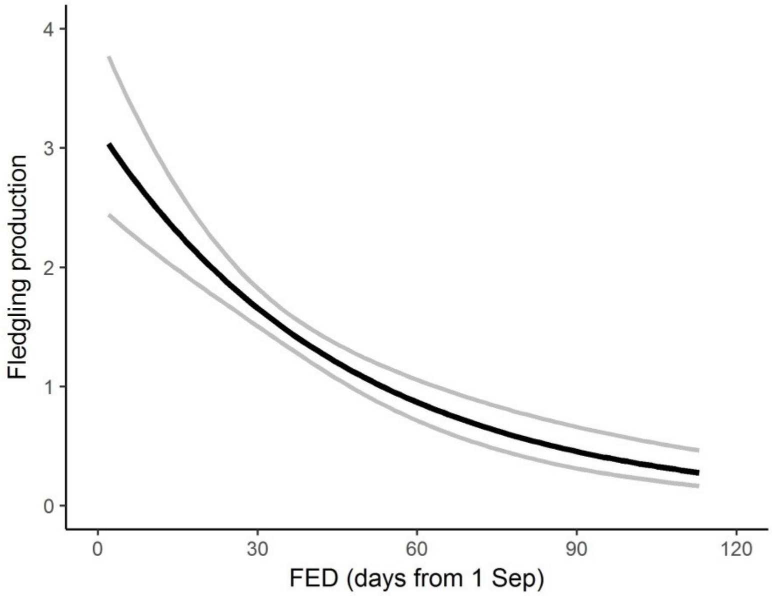

Figure 4.10. Effect plot of fledgling production in relation to first egg-laying date (FED, days from 1 September) (with 95% confidence intervals), extracted from a model incorporating female identity and year as random effects. *N* = 433 clutches (1994/1995-2014/2015).

4.4.3 What are the fitness consequences of changes in breeding phenology?

As the timing of egg-laying advances, the risk of overlap with the onset of the RS should decrease, but there is no evidence of this in the data. Years in which the population does not overlap with the RS tend to show higher mean fledgling production than years with overlap, so fledgling production might be expected to show a positive interannual trend if overlap were decreasing. However, there is no evidence of this pattern in the data, and annual mean fledgling production, as estimated using a mixed model, shows a weak non-significant decrease (Mann-Kendall tau = -0.253, 2-tailed $P = 0.127$, $N = 20$ years, Figure 4.11). This pattern seems to arise because there is no trend across years in the amount of overlap, based on annual mean expected fledging days (EFD) (Mann-Kendall tau = -0.006, $P = 1.000$, $N = 19$ years, Figure 4.12) and median EFD (Mann-Kendall tau = -0.029, $P = 0.861$, $N = 19$ years, Figure 4.12), with slopes of -0.207 and -0.266 respectively, as estimated with least squares regression. Similarly, a binomial model of overlap by at least one day shows no trend over the study years ($b = -0.008 \pm 0.016$, $z = -0.494$, $P = 0.621$, $N = 433$ clutches). This indicates that the trend towards earlier egg-laying is not significantly reducing the risk of overlap across years. The most likely explanation for these patterns is that the onset of the RS is also advancing. The onset of RS appears to be advancing at a rate of -0.431 days year^{-1} over the period 1966-2014 and -0.363 days year^{-1} over the period 1994-2014, based on least squares regression; a rate that is comparable to the rate at which the timing of egg-laying is advancing. However, there is substantial interannual variation in the estimate of RS onset, and the trends are not statistically significant over the period 1966-2014 (Mann-Kendall tau = -0.103, 2-tailed $P = 0.320$, $N = 46$ years, Figure 4.13) or 1994-2014 (Mann-Kendall tau = -0.064, 2-tailed $P = 0.721$, $N = 20$ years).

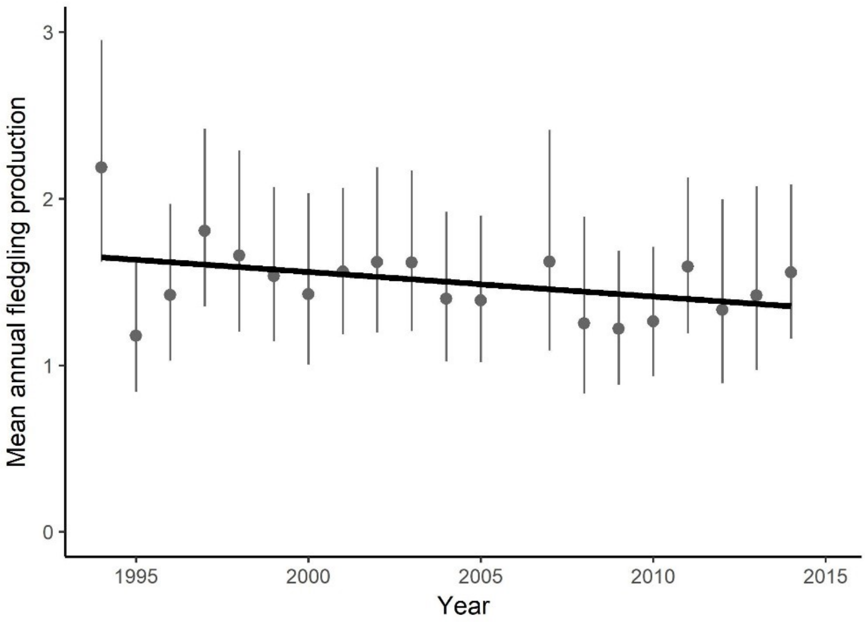

Figure 4.11. Interannual trend in mean annual fledgling production, as estimated using a generalised linear mixed model with female identity as a random effect. *N* = 20 years, 453 clutches, 13-30 clutches per year. Error bars show 95% confidence intervals. Trend line fitted using least squares regression.

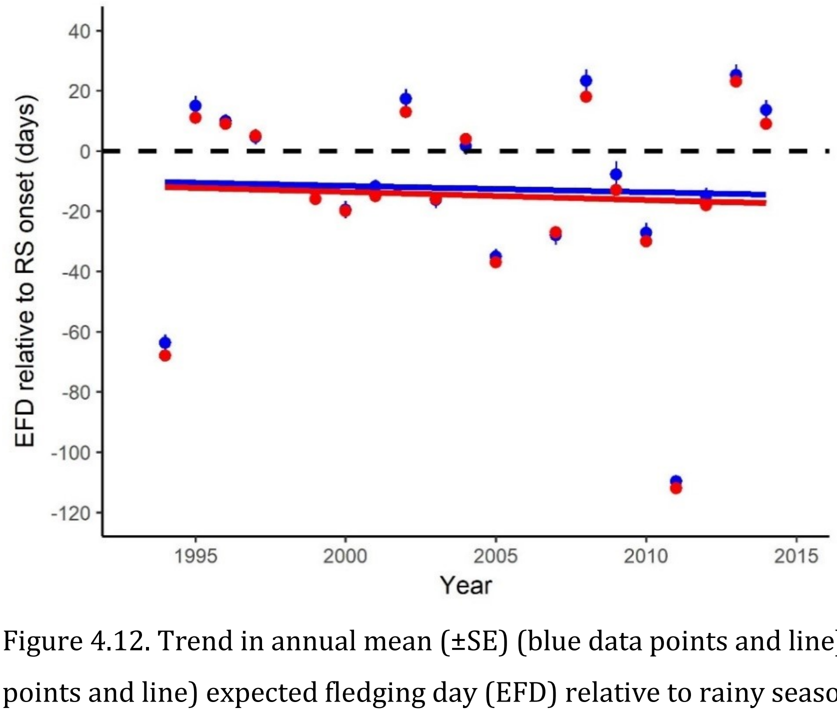

Figure 4.12. Trend in annual mean (±SE) (blue data points and line) and median (red data points and line) expected fledging day (EFD) relative to rainy season (RS) onset (indicating notional overlap with onset in days). *N* = 19 years, 433 clutches, 13-30 clutches per year. Trend lines fitted using least squares regression.

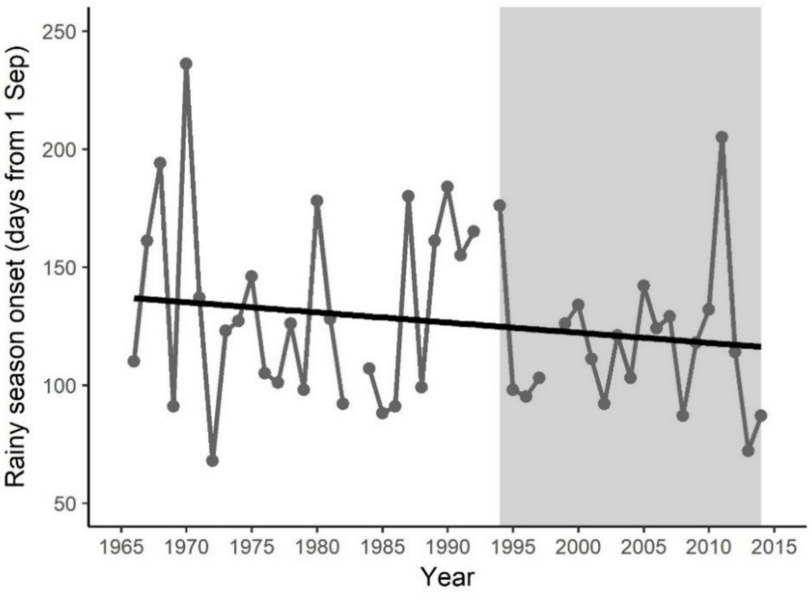

Figure 4.13. Trend in the timing of rainy season onset by year between 1966 and 2014. *N* = 46 years. Trend line fitted using least squares regression. The shaded area indicates the period for which the impacts of rainy season onset on breeding success are analysed in this study. Missing data points indicate absent rainy seasons (see Methods).

4.5 Discussion

The analyses in this study provide evidence that Mauritius kestrels in the Bambous Mountains are tracking a shifting seasonal window of favourable conditions for breeding, delimited at the start by late winter-early spring temperatures that affect the timing of egg-laying and at the end by the onset of the summer RS that affects breeding success in relation to timing (Figure 4.14). Both of these seasonal transitions appear to be advancing, although there is substantial interannual variation in the timing of RS onset. As shown in ectotherms, abiotic factors can favour seasonal reproduction in tropical animals in a similar manner to their influence on temperate species (Brown and Shine, 2006). Evidence from phenological data supports the general expectation that endotherms are less sensitive to abiotic conditions (Cohen *et al.*, 2018), and this may be assumed to be particularly true at tropical latitudes, where temperature variability is relatively limited (Pearce-Higgins and Green, 2014). However, the present study provides compelling evidence of high sensitivity to increasing temperatures in a tropical endotherm occupying a high trophic level. The rates of advancement in Mauritius kestrels are similar to those reported for some temperate bird populations (Both *et al.*, 2004; Franks *et al.*, 2017) and for animals globally (Cohen *et al.*, 2018).

These results show that temperature plays a dominant role in influencing the breeding phenology of a tropical bird species, either as a direct cue or through an influence on food availability. It is not possible in this study to ascertain whether breeding kestrels are using temperature as a direct cue or tracking earlier prey availability as temperatures increase. Timing of breeding may be related to the breeding condition of birds as influenced by food availability. Cole and Harris (2011) characterised the months May-August as the cold wet season on Ile aux Aigrettes, an offshore islet located c.5 km from the Bambous Mountains, and found that diurnal activity in day geckos was lower in these months compared to other times of year. Furthermore, gecko delivery rates by breeding Mauritius kestrels have been shown to be highest in the early afternoon (13:00-15:00), when conditions are at their warmest and geckos are probably most active (Carter, 1991). The increases in temperature may therefore influence the activity patterns of geckos and thus prey availability for kestrels. Burgess *et al.* (2011) suspected that the timing of the kestrel breeding season may be influenced by gecko densities. The monitoring of gecko density and activity patterns would provide more insights.

The results of the breeding success analyses show that early breeders tend to be more successful, in part because they avoid overlap with the onset of the RS, and hence reduce the adverse impacts of associated heavy rainfall events on fledgling production. The exploratory analyses indicate that extreme raindays are an important component of the rainfall impact, although total rainfall has more support, suggesting that the impact threshold is below the 90th percentile. This illustrates the challenges of using percentile thresholds for limited definitions of extremes in an ecological context and perhaps the need for sensitivity analysis to identify important thresholds. Heavy rainfall is likely to reduce hunting efficiency, hunting opportunities and prey availability, thus limiting the ability of adults to obtain enough food for their chicks (Carter, 1991; Senapathi *et al.*, 2011). Heavy rain may also lead to hypothermia in chicks if nests are flooded (Senapathi *et al.*, 2011). Therefore, in most years there is selection for early breeding in order to avoid an overlap of the brood phase with the onset of the rains and potentially with heavy rainfall. In this system, interannual variability in the occurrence of high impact rainfall early in the RS contributes to this abiotic selection pressure on the phenology of Mauritius kestrels. The advantage of earlier breeding is therefore amplified in years with heavy rainfall in the first weeks after the onset of the rains. A limitation of this analysis is that there are no data to investigate whether there are peaks in prey abundance that could also influence fitness and selection on timing.

Despite the genetic legacy of near-extinction, the Mauritius kestrel shows adaptive phenological plasticity to increases in late winter-early spring temperature and consequently tracking of favourable climate conditions for breeding. Plasticity is important in enabling organisms to respond to rapid changes in their environment (Donelson *et al.*, 2017). These results imply that phenological reaction norms have been retained by the population that are sufficient for the tracking of recent changes in the local climate. It is unclear whether further changes in the local climate will require responses beyond those shown by the population. It is already known that the Mauritius kestrel has suffered substantial genetic depletion and increased inbreeding since the severe bottleneck of the 1970s (Groombridge *et al.*, 2000; Ewing *et al.*, 2008). Previous research has also shown that there is very little heritable genetic variation for mean egg-laying date in this species (Senapathi, 2009). The fairly low variation in reaction norms between individual females shown in the present study also suggests that there is little in the way of standing genetic variation for plasticity. This could be a result of the population bottleneck or a small ancestral population (Senapathi, 2009), or due to purifying selection under predictable environmental variability (Oostra *et al.*, 2018). Analysis of neutral genetic variation in the Mauritius kestrel indicates that the genetic diversity of the ancestral population was high and comparable to that of mainland kestrel species (Groombridge *et al.*, 2000). In this species, phenotypic plasticity is likely to be very important under current climate change, as evolutionary adaptation to continued change may be constrained by depleted genetic diversity. The response observed so far in this Mauritius kestrel population may 'buy time' while future management actions are developed (e.g. Socolar *et al.*, 2017).

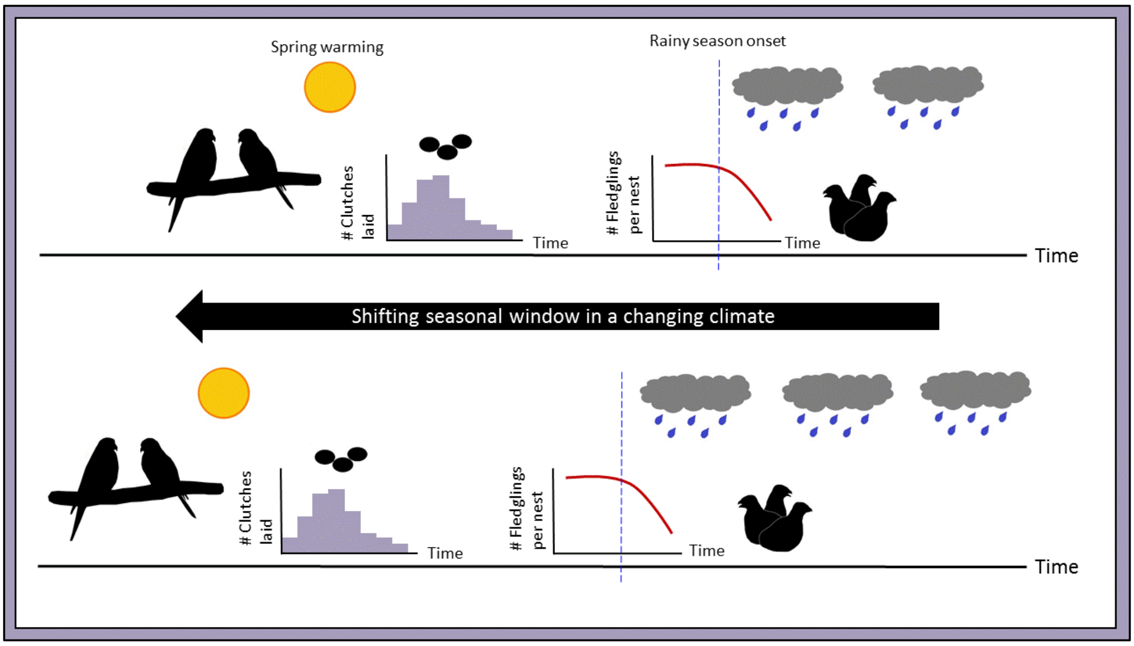

Figure 4.14. Schematic diagram of changes in the seasonal window of favourable conditions for breeding Mauritius kestrels: The species begins egg-laying in spring as temperatures warm. Early breeders tend to be more successful because they complete nesting before the onset of the summer rainy season; whereas later breeders can get exposed to heavy rainfall at the start of the rainy season, reducing the number of fledglings they produce. In a changing climate, late winter-early spring temperatures are warming, which results in birds laying their eggs progressively earlier. As a result, it might be expected that they breed more successfully as the overlap with onset of the rainy season reduces, but this appears not to be the case. Breeding success and overlap remain similar, suggesting that the onset of the summer rainy season is also advancing in recent years. The estimates of the onset of the rainy season reflect this, but are also highly variable.

These analyses might be limited by the use of weather data from only one rain gauge and one synoptic station. However, the locations of these stations should ensure that they provide reliable indications of conditions experienced by Mauritius kestrels in the Bambous Mountains. Previous research has shown that rainfall trends measured at the Mt Camizard rain gauge are representative of rainfall trends in other areas of the Bambous Mountains (Senapathi *et al.*, 2010). In addition, there are some limitations to the rainy season analysis methods used in this study. For the identification of onset and cessation, the methods require runs of consistent above-average precipitation, producing a pronounced increase in the cumulative daily anomaly, and as a consequence intermittent or light rainfall at the beginning or end of the season would not be considered part of the RS (Dunning *et al.*, 2016). In general, this methodology is particularly suited to regions that experience fairly consistent, well-defined and pronounced annual rainfall seasonality (Liebmann *et al.*, 2012). However, in the Bambous Mountains in eastern Mauritius the contrasts between rainy and dry seasons can be less pronounced. This lack of pronounced rainy and dry seasons in all years could manifest as high interannual variability in the timing of onset and cessation. Such variability may be increased through use of data from a single rain gauge. Despite this, the rate of advancement in onset timing observed in this study is likely to be ecologically significant, as it appears to be comparable to the rate of advancement in egg-laying by kestrels, there is no evidence of a trend in the amount of overlap between nesting activity and onset, and there is no trend in seasonal average breeding success. However, confidence in the estimation of the rate of advancement in onset is limited by high interannual variability.

Very little is known about the implications of climate change for the phenology of animal species in the tropics. The projected emergence of some tropical regions from recent climate variability this century (IPCC, 2007; Mora *et al.*, 2013; Hawkins *et al.*, 2014) raises the prospect of other strong phenological changes in tropical species. When two or more metrics, such as precipitation and temperature, are considered this can lead to increased estimates in the rate of departure from recent variability that may be more relevant to ecological communities (Mahony and Cannon, 2018). The occurrence of novel climates by 2100 is projected to be most prevalent in tropical and subtropical regions, based on mean temperature and precipitation in summer and winter (Williams *et al.*, 2007). Furthermore, climate research has indicated large-scale trends in the seasonality of rainfall in the tropics, with some regions seeing increasing contrast between rainy and dry seasons, while other regions experience a reduction in this seasonality (Feng *et al.*, 2013). Precipitation patterns in the tropics are projected to change substantially during this century, although there is inconsistency among models (Kent *et al.*, 2015; Chadwick *et al.*, 2016). Such changes are likely to affect phenology and alter the impacts of seasonal precipitation transitions on fitness and population dynamics.

Taken together, the results of this study suggest that Mauritius kestrels synchronise their breeding season with a seasonal window defined in spring by warming temperatures that affect the timing of egg-laying, and in summer by the onset of the rainy season, which reduces breeding success. This seasonal window is changing and appears to be advancing in time, with Mauritius kestrels appearing to be successful in synchronising their breeding season with this shift, with negligible fitness consequences. Shifting seasonal windows may be widespread phenomena through which tropical species respond to climate change. They may be particularly relevant to regions that have pronounced contrasts between rainy and dry seasons, and their prevalence may increase towards the subtropics as annual temperature cycles become more pronounced. The defining characteristics of seasonal windows will depend on the ecology and underlying seasonality of each species and the local annual climate cycle. For example, rainy season onset may have negative impacts on most raptors but positive impacts on insectivorous and frugivorous birds, which would be expected to be negatively impacted by early or prolonged dry seasons (Brawn *et al.*, 2017). Given that tropical regions will be among the first to emerge from recent variability into relatively novel climate regimes, temperature and precipitation changes in the tropics, relative to past variability, may be such that they result in the creation of new seasonal climate windows to which tropical species must synchronise their life-history events. For example, increases in the magnitude of rainy seasons could cause rainy season onset to become an important influence on fitness and demographic rates in some species. Similarly, temperature increases could result in increasingly shorter windows in which conditions are suitable for the activities of some species. A better understanding of such complex dynamics in local climate, and their effects on phenology, individual fitness and demography, will be essential for safeguarding species in a changing climate.

4.6 References

Barlow, J., França, F., Gardner, T. S., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J. and Graham, N. A. J. 2018. The future of hyperdiverse tropical ecosystems. *Nature,* **559**: 517–526.

Barton, K. 2018. Package 'MuMIn', Multi-Model Inference, version 1.40.4.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G. and Green, P. 2018. Package 'lme4', Linear Mixed-Effects Models using 'Eigen' and S4, version 1.1-17.

Beebe, K., Bentley, G. E. and Hau, M. 2005. A seasonally breeding tropical bird lacks absolute photorefractoriness in the wild, despite high photoperiodic sensitivity. *Functional Ecology,* **19**: 505–512.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. and Courchamp, F. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters,* **15**: 365–377.

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Jarvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P. A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Torok, J., Winkel, W., Wright, J., Zang, H. and Visser, M. E. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London, Series B,* **271**: 1657–1662.

Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. and Visser, M. E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology,* **78**: 73–83.

Both, C., Van Turnhourt, C. A. M., Bijlsma, R. G., Siepel, H., Van Strien, A. J. V. and Foppen, R. P. B. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London, Series B,* **277**: 1259–1266.

Brawn, J. D., Benson, T. J., Stager, M., Sly, N. D. and Tarwater, C. E. 2017. Impacts of changing rainfall regime on the demography of tropical birds. *Nature Climate Change,* **7**: 133–136.

Brown, G. P. and Shine, R. 2006. Why do most tropical animals reproduce seasonally? Testing hypotheses on an Australian snake. *Ecology,* **87**: 133–143.

Burgess, M. D., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2008. Restricted dispersal reduces the strength of spatial density dependence in a tropical bird population. *Proceedings of the Royal Society of London, Series B,* **275**: 1209–1216.

Burgess, M. D., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2011. Multiple environmental gradients affect spatial variation in the productivity of a tropical bird population. *Journal of Animal Ecology,* **80**: 688–695.

Burnham, K. P., Anderson, D. R. and Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology,* **65**: 23–35.

Carter, J. E. 1991. Home range, habitat utilization, and prey delivery patterns of the Mauritius kestrel (*Falco punctatus*). MSc Dissertation. Boise, Idaho: Boise State University.

Carter, J. E. and Jones, M. H. 1999. Habitat composition of Mauritius Kestrel home ranges. *Journal of Field Ornithology,* **70**: 230–235.

Cartwright, S. J., Nicoll, M. A. C., Jones, C. G., Tatayah, V. and Norris, K. 2014. Agriculture modifies the seasonal decline of breeding success in a tropical wild bird population. *Journal of Applied Ecology,* **51**: 1387–1395.

Cavalcanti, L. M. P., de Paiva, L. V. and França, L. F. 2016. Effects of rainfall on bird reproduction in a semi-arid Neotropical region. *Zoologia,* **33**: e20160018.

Chadwick, R., Good, P., Martin, G. and Rowell, D. P. 2016. Large rainfall changes consistently projected over substantial areas of tropical land. *Nature Climate Change,* **6**: 177–181.

Chambers, L. E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L. J., Crawford, R. J. M., Durant, J. M., Hughes, L., Keatley, M. R., Low, M., Morellato, P. C., Poloczanska, E. S., Ruoppolo, V., Vanstreels, R. E. T., Woehler, E. J. and Wolfaardt, A. C. 2013. Phenological changes in the Southern Hemisphere. *PLoS One,* **8**: e75514.

Charmantier, A. and Gienapp, P. 2013. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications,* **7**: 15–28.

Cohen, J. M., Lajeunesse, M. J. and Rohr, J. R. 2018. A global synthesis of animal phenological responses to climate change. *Nature Climate Change,* **8**: 224–228.

Cole, N. C. and Harris, S. 2011. Environmentally-induced shifts in behavior intensify indirect competition by an invasive gecko in Mauritius. *Biological Invasions,* **13**: 2063–2075.

Dawson, A. 2007. Seasonality in a temperate zone bird can be entrained by near equatorial photoperiods. *Proceedings of the Royal Society of London, Series B,* **274**: 721–725.

Dawson, A. 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society of London, Series B,* **363**: 1621–1633.

Dawson, T. P., Jackson, S. T., House, J. L., Prentice, I. C. and Mace, G. M. 2011. Beyond predictions: Biodiversity conservation in a changing climate. *Science,* **332**: 53–58.

Delignette-Muller, M.-L., Dutang, C., Pouillot, R., Denis, J.-B. and Siberchicot, A. 2017. Package 'fitdistrplus', Help to Fit of a Parametric Distribution to Non-Censored or Censored Data, version 1.0-9.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. and Martin, P. R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America,* **105**: 6668–6672.

Donelson, J. M., Salinas, S., Munday, P. L. and Shama, L. N. S. 2017. Transgenerational plasticity and climate change experiments: Where do we go from here? *Global Change Biology,* **21**: 2954–2962.

Dunn, P. O. and Møller, A. P. 2014. Changes in breeding phenology and population size of birds. *Journal of Animal Ecology,* **83**: 729–739.

Dunning, C. M., Black, E. C. L. and Allan, R. P. 2016. The onset and cessation of seasonal rainfall over Africa. *Journal of Geophysical Research - Atmospheres,* **121**: 11405–11424.

Elsner, J. B., Kossin, J. P. and Jagger, T. H. 2008. The increasing intensity of the strongest tropical cyclones. *Nature,* **455**: 92–95.

Ewing, S. R., Nager, R. G., Nicoll, M. A. C., Aumjaud, A., Jones, C. G. and Keller, L. F. 2008. Inbreeding and loss of genetic variation in a reintroduced population of Mauritius Kestrel. *Conservation Biology,* **22**: 395–404.

Feng, X., Porporato, A. and Rodriguez-Iturbe, I. 2013. Changes in rainfall seasonality in the tropics. *Nature Climate Change,* **3**: 811–815.

Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vie, J.-C., Akçakaya, H. R., Angulo, A., DeVantier, L. M., Gutsche, A., Turak, E., Cao, L., Donner, S. D., Katariya, V., Bernard, R., Holland, R. A., Hughes, A. F., O'Hanlon, S. E., Garnett, S. T., Şekercioğlu, Ç. H. and Mace, G. M. 2013. Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS One,* **8**: e65427.

Fordham, D. A. and Brook, B. W. 2010. Why tropical island endemics are acutely susceptible to global change. *Biodiversity and Conservation,* **19**: 329–342.

Forrest, J. and Miller-Rushing, A. J. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society of London, Series B,* **365**: 3101–3112.

Fox, J., Weisberg, S., Friendly, M., Hong, J., Andersen, R., Firth, D., Taylor, S. and R Core Team. 2018. Package 'effects', Effect Displays for Linear, Generalized Linear, and Other Models, version 4.0-1.

Franks, S. E., Pearce-Higgins, J. W., Atkinson, S., Bell, J. R., Botham, M. S., Brereton, T. M., Harrington, R. and Leech, D. I. 2017. The sensitivity of breeding songbirds to changes in seasonal timing is linked to population change but cannot be directly attributed to the effects of trophic asynchrony on productivity. *Global Change Biology,* **24**: 957–971.

Gallego, M. C., Trigo, R. M., Vaquero, J. M., Brunet, M., García, J. A., Sigró, J. and Valente, M. A. 2011. Trends in frequency indices of daily precipitation over the Iberian Peninsula during the last century. *Journal of Geophysical Research - Atmospheres,* **116**: D02109.

Ghalambor, C. K., Huey, R. B., Martin, P. R., Tewksbury, J. J. and Wang, G. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology,* **46**: 5–17.

Gill, B. A., Kondratieff, B. C., Casner, K. L., Encalada, A. C., Flecker, A. S., Gannon, D. G., Ghalambor, C. K., Guayasamin, J. M., Poff, N. L., Simmons, M. P., Thomas, S. A., Zamudio, K. R. and Funk, W. C. 2016. Cryptic species diversity reveals biogeographic support for the 'mountain passes are higher in the tropics' hypothesis. *Proceedings of the Royal Society of London, Series B,* **283**: 20160553.

Gillespie, R. G., Claridge, E. M. and Roderick, G. K. 2008. Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. *Molecular Ecology,* **17**: 45–57.

Gordo, O. and Doi, H. 2012. Spring phenology delays in an insular subtropical songbird: is response to climate change constrained by population size? *Journal of Ornithology,* **153**: 355–366.

Groombridge, J. J., Jones, C. G., Bruford, M. W. and Nichols, R. A. 2000. 'Ghost' alleles of the Mauritius kestrel. *Nature,* **403**: 616.

Hansson, B., Bensch, S. and Hasselquist, D. 2000. The quality and the timing hypotheses evaluated using data on great reed warblers. *Oikos,* **90**: 575–581.

Harrington, R., Woiwod, I. and Sparks, T. 1999. Climate change and trophic interactions. *Trends in Ecology & Evolution,* **14**: 146–150.

Hau, M. 2001. Timing of breeding in variable environments: Tropical birds as model systems. *Hormones and Behavior,* **40**: 281–290.

Hau, M., Wikelski, M. and Wingfield, J. C. 1998. A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proceedings of the Royal Society of London, Series B,* **265**: 89–95.

Hawkins, E., Anderson, B., Diffenbaugh, N., Mahlstein, I., Betts, R., Hegerl, G., Joshi, M., Knutti, R., McNeall, D., Solomon, S., Sutton, R., Syktus, J. and Vecchi, G. 2014. Uncertainties in the timing of unprecedented climates. *Nature,* **511**: E3–E5.

Iler, A. M., Inouye, D. W., Schmidt, N. M. and Høye, T. T. 2017. Detrending phenological time series improves climate-phenology analyses and reveals evidence of plasticity. *Ecology,* **98**: 647–655.

IPCC. 2007. Climate Change 2007. Fourth Assessment Report (AR4). Geneva, Switzerland: Intergovernmental Panel on Climate Change.

IPCC. 2014. Climate change 2014: Impacts, adaptation, and vulnerability. Fifth Assessment Report. Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *American Naturalist,* **101**: 233–249.

Jones, C. G. 1987. The larger land-birds of Mauritius. In *Studies of Mascarene Island Birds* (ed: Diamond, A. W.), pp. 208–300. Cambridge, UK: Cambridge University Press.

Jones, C. G., Heck, W., Lewis, R. E., Mungroo, Y., Slade, G. and Cade, T. 1995. The restoration of the Mauritius kestrel *Falco punctatus* population. *Ibis,* **137**: S173–S180.

Kent, C., Chadwick, R. and Rowell, D. P. 2015. Understanding uncertainties in future projections of seasonal tropical precipitation. *Journal of Climate,* **28**: 4390–4413.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J. and Barthlott, W. 2009. A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the United States of America,* **106**: 9322–9327.

Knapp, K. R., Kruk, M. C., Levinson, D. H., Diamond, H. J. and Neumann, C. J. 2010. The International Best Track Archive for Climate Stewardship (IBTrACS): Unifying Tropical Cyclone Data. *Bulletin of the American Meteorological Society,* **91**: 363–376.

Komdeur, J. 1996. Seasonal timing of reproduction in a tropical bird, the Seychelles warbler: A field experiment using translocation. *Journal of Biological Rhythms,* **11**: 333–346.

Kossin, J. P., Olander, T. L. and Knapp, K. R. 2013. Trend analysis with a new global record of tropical cyclone intensity. *Journal of Climate,* **26**: 9960–9976.

La Sorte, F. A., Fink, D. and Johnston, A. 2018. Seasonal associations with novel climates for North American migratory bird populations. *Ecology Letters,* **21**: 845–856.

Liebmann, B., Blade, I., Kiladis, G. N., Carvalho, L. M. V., Senay, G. B., Allured, D., Leroux, S. and Funk, C. 2012. Seasonality of African Precipitation from 1996 to 2009. *Journal of Climate,* **25**: 4304–4322.

Mahony, C. R. and Cannon, A. J. 2018. Wetter summers can intensify departures from natural variability in a warming climate. *Nature Communications,* **9**: 783.

McKee, T. B., Doesken, N. J. and Kleist, J. 1993. The relationship of drought frequency and duration to time scales. In *8th Conference on Applied Climatology*. pp. 179–184. Anaheim, California.

McLeod, A. I. 2011. Package 'Kendall', Kendall rank correlation and Mann-Kendall trend test, version 2.2.

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. and Post, E. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society of London, Series B,* **365**: 3177–3186.

Moore, I. T., Bentley, G. E., Wotus, C. and Wingfield, J. C. 2006. Photoperiod-independent changes in Immunoreactive Brain Gonadotropin-releasing hormone (GnRH) in a free-living, tropical bird. *Brain, Behavior and Evolution,* **68**: 37–44.

Moore, I. T., Bonier, F. and Wingfield, J. C. 2005. Reproductive asynchrony and population divergence between two tropical bird populations. *Behavioral Ecology,* **16**: 755–762.

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., Sanchez, J. J., Kaiser, L. R., Stender, Y. O., Anderson, J. M., Ambrosino, C. M., Fernandez-Silva, I., Giuseffi, L. M. and Giambelluca, T. W. 2013. The projected timing of climate departure from recent variability. *Nature,* **502**: 183–187.

Moritz, C. and Agudo, R. 2013. The future of species under climate change: Resilience or decline? *Science,* **341**: 504–508.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution,* **4**: 133–142.

Nevoux, M., Arlt, D., Nicoll, M., Jones, C. and Norris, K. 2013. The short- and long-term fitness consequences of natal dispersal in a wild bird population. *Ecology Letters,* **16**: 438–445.

Nevoux, M., Gimenez, O., Arlt, D., Nicoll, M., Jones, C. and Norris, K. 2011. Population regulation of territorial species: both site dependence and interference mechanisms matter. *Proceedings of the Royal Society of London, Series B,* **278**: 2173–2181.

Nicoll, M. A. C. 2004. The ecology and management of a re-introduced population of the Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Nicoll, M. A. C., Nevoux, M., Jones, C. G., Ratcliffe, N., Ruhomaun, K., Tatayah, V. and Norris, K. 2017. Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology,* **23**: 550–565.

Öberg, M., Arlt, D., Pärt, T., Laugen, A. T., Eggers, S. and Low, M. 2015. Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecology and Evolution,* **5**: 345–356.

Oostra, V., Saastamoinen, M., Zwaan, B. J. and Wheat, C. W. 2018. Strong phenotypic plasticity limits potential for evolutionary responses to climate change. *Nature Communications,* **9**: 1005.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics,* **37**: 637–669.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology,* **13**: 1860–1872.

Parmesan, C., Root, T. L. and Willig, M. R. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society,* **81**: 443–450.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* **421**: 37–42.

Pearce-Higgins, J. W. and Green, R. E. 2014. *Birds and Climate Change: Impacts and Conservation Responses*. Cambridge, UK: Cambridge University Press.

Post, E., Steinman, B. A. and Mann, M. E. 2018. Acceleration of phenological advance and warming with latitude over the past century. *Scientific Reports,* **8**: 3927.

Powell, M. J. D. 2009. The BOBYQA algorithm for bound constrained optimization without derivatives. Cambridge, UK: Centre for Mathematical Sciences, University of Cambridge.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B.-E. and Visser, M. E. 2013. Population growth in a wild bird is buffered against phenological mismatch. *Science,* **340**: 488–491.

Rodrigues, A. S. L., Brooks, T. M., Butchart, S. H. M., Chanson, J., Cox, N., Hoffmann, M. and Stuart, S. N. 2014. Spatially Explicit Trends in the Global Conservation Status of Vertebrates. *PLoS One,* **9**: e113934.

Şekercioğlu, Ç. H., Primack, R. B. and Wormworth, J. 2012. The effects of climate change on tropical birds. *Biological Conservation,* **148**: 1–18.

Senapathi, D., Nicoll, M. A. C., Teplitsky, C., Jones, C. G. and Norris, K. 2011. Climate change and the risks associated with delayed breeding in a tropical wild bird population. *Proceedings of the Royal Society of London, Series B,* **278**: 3184–3190.

Senapathi, D., Underwood, F., Black, E., Nicoll, M. A. C. and Norris, K. 2010. Evidence for long-term regional changes in precipitation on the East Coast Mountains in Mauritius. *International Journal of Climatology,* **30**: 1164–1177.

Senapathi, G. D. 2009. Assessing the effect of changing climatic conditions in Mauritius on the population dynamics of the endemic Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Shaw, P. 2017. Rainfall, leafing phenology and sunrise time as potential Zeitgeber for the bimodal, dry season laying pattern of an African rain forest tit (*Parus fasciiventer*). *Journal of Ornithology,* **158**: 263–275.

Shepherd, J. M., Grundstein, A. and Mote, T. L. 2007. Quantifying the contribution of tropical cyclones to extreme rainfall along the coastal southeastern United States. *Geophysical Research Letters,* **34**: L23810.

Socolar, J. B., Epanchin, P. N., Beissinger, S. R. and Tingley, M. W. 2017. Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences of the United States of America,* **114**: 12976–12981.

Staub, C. G., Stevens, F. R. and Waylen, P. R. 2014. The geography of rainfall in Mauritius: Modelling the relationship between annual and monthly rainfall and landscape characteristics on a small volcanic island. *Applied Geography,* **54**: 222–234.

Strauss, S. Y., Lau, J. A. and Carroll, S. P. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters,* **9**: 357–374.

Temple, S. A. 1987. Foraging ecology of the Mauritius kestrel (*Falco punctatus*). *Biotropica,* **19**: 2–6.

Thackery, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T., Duck, C., Edwards, M., Elliott, J. M., Hall, S. J. G., Harrington, R., Pearce-Higgins, J. W., Høye, T. T., Kruuk, L. E. B., Pemberton, J. M., Sparks, T. H., Thompson, P. M., White, I., Winfield, I. J. and Wanless, S. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature,* **535**: 241–245.

Thackery, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalhos, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., Roy, D. B., Scott, A., Smith, M., Smithers, R. J., Winfield, I. J. and Wanless, S. 2010. Trophic level synchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology,* **16**: 3304–3313.

van de Pol, M. and Verhulst, S. 2006. Age-Dependent Traits: A New Statistical Model to Separate Within- and Between-Individual Effects. *American Naturalist,* **167**: 766–773.

van de Pol, M. and Wright, J. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour,* **77**: 753–758.

Vincent, L. A., Aguilar, E., Saindou, M., Hassane, A. F., Jumaux, G., Roy, D., Booneeady, P., Virasami, R., Randriamarolaza, L. Y. A., Faniriantsoa, F. R., Amelie, V., Seeward, H. and Montfraix, B. 2011. Observed trends in indices of daily and extreme temperature and precipitation for the countries of the western Indian Ocean, 1961-2008. *Journal of Geophysical Research - Atmospheres,* **116**: D10108.

Visser, M. E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London, Series B,* **272**: 2561–2569.

Visser, M. E., Holleman, L. J. M. and Caro, S. P. 2009. Temperature has a causal effect on avian timing of reproduction. *Proceedings of the Royal Society of London, Series B,* **276**: 2323–2331.

Visser, M. E., Holleman, L. J. M. and Gienapp, P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impacts on the breeding biology of an insectivorous bird. *Oecologia,* **147**: 164–172.

Visser, M. E., te Marvelde, L. and Lof, M. E. 2012. Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology,* **153**: S75–S84.

Wikelski, M., Hau, M. and Wingfield, J. C. 2000. Seasonality of reproduction in a Neotropical rain forest bird. *Ecology,* **81**: 2458–2472.

Williams, J. W., Jackson, S. T. and Kutzbach, J. E. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America,* **104**: 5738–5742.

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffman, A. A. and Langham, G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology,* **6**: 2621–2626.

WMO. 2003. Guidelines on climate metadata and homogenization. Geneva, Switzerland: World Meteorological Organization.

Zuur, A. F., Ieno, E. N. and Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution,* **1**: 3–14.

4.7 Appendix

Table A4.1. Results of candidate base model analysis for first egg-laying date, using data from 356 Mauritius kestrel breeding attempts (1994/1995-2014/2015). All models include female identity and year as random effects. Where linear and quadratic terms are included, only the quadratic term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Female Age^2 + Male Age^2	8	-1404.290	2824.996	0.000	0.936	0.181	0.427
Female Age^2 + Male PBE^2	8	-1407.353	2831.121	6.125	0.044	0.167	0.406
Male Age^2	6	-1410.213	2832.667	7.671	0.020	0.163	0.415
Male PBE^2	6	-1414.758	2841.757	16.761	0.000	0.143	0.390
Female Age^2	6	-1427.019	2866.279	41.283	0.000	0.091	0.360
Female Age + Male Age	6	-1429.154	2870.548	45.552	0.000	0.086	0.331
Female Age + Male PBE	6	-1430.114	2872.469	47.473	0.000	0.080	0.330
Male Age	5	-1432.931	2876.033	51.037	0.000	0.072	0.337
Male PBE	5	-1434.442	2879.055	54.059	0.000	0.063	0.335
Female Age	5	-1436.474	2883.119	58.123	0.000	0.054	0.300
Elevation	5	-1445.941	2902.053	77.057	0.000	0.004	0.296
Null	4	-1447.328	2902.771	77.775	0.000	0.000	0.278

Table A4.2. Results of July-September climate impacts analysis on first egg-laying date, using data from 356 Mauritius kestrel breeding attempts (1994/1995-2014/2015). Base model: Female Age^2 + Male Age^2. All models include female identity and year as random effects. Where linear and quadratic terms are included, only the quadratic term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-*R*^{2}**	**Conditional Pseudo-*R*^{2}**
Base + Mean Tmax^2	-4.367/-0.778	10	-1394.751	2810.139	0.000	0.543	0.285	0.437
Base + Mean Tmax	-4.582	9	-1396.003	2810.526	0.387	0.448	0.282	0.436
Base + Raindays^2	2.494/-0.500	10	-1400.186	2821.010	10.871	0.002	0.203	0.430
Base + Raindays	2.561	9	-1401.326	2821.171	11.032	0.002	0.204	0.426
Base + Rainfall90^2	-1.684/1.109	10	-1401.489	2823.616	13.477	0.001	0.181	0.435
Base + Max Rain Spell^2	-1.158/0.702	10	-1401.530	2823.698	13.559	0.001	0.180	0.437
Base + Rainfall^2	0.255/0.299	10	-1401.783	2824.204	14.065	0.001	0.177	0.436
Base + Max Rain Spell	-0.669	9	-1402.854	2824.228	14.089	0.001	0.180	0.431
Base + Rainfall	0.711	9	-1402.900	2824.320	14.181	0.001	0.179	0.431
Base + Raindays90^2	-0.388/0.013	10	-1401.856	2824.350	14.211	0.000	0.178	0.438
Base + Raindays90	-0.376	9	-1402.955	2824.429	14.290	0.000	0.181	0.432
Base + Rainfall90	0.056	9	-1403.028	2824.576	14.437	0.000	0.179	0.432
Base	-	8	-1404.290	2824.996	14.857	0.000	0.181	0.427

Table A4.3. Results of July-September climate impacts analysis on de-trended first egg-laying date, using data from 356 Mauritius kestrel breeding attempts (1994/1995-2014/2015). All models include female identity and year as random effects. Where linear and quadratic terms are included, only the quadratic term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised Year coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**
Base + Year + Mean Tmax^2 + Raindays^2	-3.477	11	-1388.281	2799.330	0.000
Base + Year + Raindays	-4.701	10	-1391.437	2803.511	4.181
Base + Year + Mean Tmax	-3.043	10	-1391.637	2803.911	4.581
Base + Year + Raindays^2	-4.701	11	-1390.608	2803.984	4.654
Base + Year + Mean Tmax^2	-2.963	11	-1390.656	2804.079	4.749
Base + Year	-4.726	9	-1395.998	2810.516	11.186

Table A4.4. Results of candidate base model analysis for fledgling production, using data from 403 Mauritius kestrel breeding attempts (1990/1991-2014/2015). All models include female identity and year as random effects. Where linear and quadratic terms are included, only the quadratic term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
FED + Elevation	5	-615.842	1241.835	0.000	0.276	0.160	0.202
FED + Pair PBE^2	6	-615.053	1242.317	0.482	0.217	0.157	0.208
FED + Agriculture	5	-616.359	1242.869	1.034	0.165	0.156	0.213
FED × Agriculture	6	-615.443	1243.099	1.264	0.147	0.183	0.235
FED + Male PBE^2	6	-616.394	1244.999	3.164	0.057	0.150	0.208
FED + Cavity Type	5	-617.483	1245.117	3.282	0.053	0.152	0.212
FED + Male PBE	5	-617.676	1245.503	3.668	0.044	0.149	0.210
FED + Pair PBE	5	-617.740	1245.630	3.795	0.041	0.148	0.209
Null	3	-640.290	1286.641	44.806	0.000	0.000	0.105

Table A4.5. Results from the analysis of nest-level climate impacts (during an 80-day period) on fledgling production, using data from 403 Mauritius kestrel breeding attempts (1990/1991-2014/2015). All models include female identity and year as random effects. The base model is a combination of the four highest ranking models in the candidate selection analysis and includes elevation, pair PBE^2, agriculture and the FED × agriculture interaction. Where linear and quadratic terms are included, only the quadratic term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base + Rainfall	-0.104	10	-608.639	1237.840	0.000	0.221	0.222	0.231
Base + Rainfall90	-0.087	10	-609.306	1239.174	1.334	0.113	0.214	0.225
Base + Raindays90	-0.086	10	-609.393	1239.346	1.506	0.104	0.214	0.225
Base + Rainfall^2	-0.092/-0.013	11	-608.586	1239.848	2.008	0.081	0.230	0.239
Base + Raindays90^2	-0.058/-0.046	11	-608.691	1240.057	2.217	0.073	0.246	0.259
Base + Rainfall90^2	-0.043/-0.040	11	-608.766	1240.208	2.368	0.068	0.239	0.251
Base	-	9	-611.096	1240.650	2.810	0.054	0.198	0.220
Base + Cyclone	-0.245	10	-610.275	1241.111	3.271	0.043	0.206	0.228
Base + Raindays	-0.054	10	-610.345	1241.252	3.412	0.040	0.209	0.233
Base + Max Dry Spell^2	0.046/-0.072	11	-609.505	1241.686	3.846	0.032	0.209	0.232
Base + Raindays^2	-0.040/-0.046	11	-609.587	1241.850	4.010	0.030	0.224	0.248
Base + Max Rain Spell	-0.032	10	-610.870	1242.302	4.462	0.024	0.203	0.224

Table A4.5 continued:

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base + Max Rain Spell^2	-0.008/-0.031	11	-609.876	1242.428	4.588	0.022	0.241	0.259
Base + Tmax90 Days	0.020	10	-611.033	1242.626	4.786	0.020	0.197	0.218
Base + Drought	-0.053	10	-611.054	1242.668	4.828	0.020	0.198	0.221
Base + Mean Tmax	0.013	10	-611.079	1242.719	4.879	0.019	0.198	0.221
Base + Max Dry Spell	-0.007	10	-611.082	1242.725	4.885	0.019	0.198	0.220
Base + Tmax90 Days^2	0.072/-0.026	11	-610.667	1244.009	6.169	0.010	0.217	0.236
Base + Mean Tmax^2	0.009/-0.017	11	-610.960	1244.596	6.756	0.007	0.205	0.228

Table A4.6. Results of candidate base model analysis for egg survival to fledging, using data from 403 Mauritius kestrel breeding attempts (1990/1991-2014/2015). All models include female identity and year as random effects. Where linear and quadratic terms are included, only the quadratic term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
FED × Agriculture	6	-568.102	1148.417	0.000	0.384	0.079	0.223
FED + Agriculture	5	-569.387	1148.926	0.509	0.297	0.067	0.219
FED + Elevation	5	-570.537	1151.225	2.808	0.094	0.066	0.204
FED + Pair PBE^2	6	-569.507	1151.227	2.810	0.094	0.062	0.203
FED + Male PBE^2	6	-570.277	1152.765	4.348	0.044	0.060	0.207
FED + Pair PBE	5	-571.800	1153.751	5.334	0.027	0.059	0.210
FED + Male PBE	5	-571.934	1154.019	5.602	0.023	0.059	0.207
FED + Cavity Type	5	-572.077	1154.305	5.888	0.020	0.059	0.206
FED + Clutch Size	5	-572.248	1154.647	6.230	0.017	0.057	0.206
Null	3	-592.526	1191.113	42.696	0.000	0.000	0.152

Table A4.7. Results from the analysis of brood-level climate impacts (during a 35-day period) on egg survival to fledging, using data from 403 Mauritius kestrel breeding attempts (1990/1991-2014/2015). Base model: FED × Agriculture. All models include female identity and year as random effects. Where linear and quadratic terms are included, only the quadratic term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base + Rainfall	-0.193	7	-565.606	1145.495	0.000	0.199	0.085	0.222
Base + Raindays90	-0.170	7	-566.031	1146.345	0.850	0.130	0.082	0.221
Base + Rainfall90	-0.165	7	-566.167	1146.617	1.122	0.114	0.082	0.221
Base + Max Dry Spell^2	0.257/-0.116	8	-565.467	1147.299	1.804	0.081	0.086	0.226
Base + Rainfall^2	-0.194/0.001	8	-565.606	1147.576	2.081	0.070	0.085	0.222
Base + Raindays90^2	-0.116/-0.046	8	-565.687	1147.739	2.244	0.065	0.084	0.224
Base + Rainfall90^2	-0.106/-0.038	8	-565.929	1148.224	2.729	0.051	0.083	0.223
Base	-	6	-568.102	1148.417	2.922	0.046	0.079	0.223
Base + Mean Tmax	0.154	7	-567.206	1148.695	3.200	0.040	0.081	0.226
Base + Raindays^2	-0.059/-0.099	8	-566.417	1149.200	3.705	0.031	0.086	0.230
Base + Drought	-0.355	7	-567.676	1149.635	4.140	0.025	0.079	0.224
Base + Tmax90 Days	0.086	7	-567.685	1149.654	4.159	0.025	0.078	0.221
Base + Cyclone	-0.291	7	-567.710	1149.703	4.208	0.024	0.080	0.223
Base + Raindays	-0.066	7	-567.825	1149.933	4.438	0.022	0.080	0.223
Base + Max Dry Spell	0.052	7	-567.890	1150.063	4.568	0.020	0.080	0.224

Table A4.7 continued:

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base + Mean Tmax^2	0.139/0.044	8	-566.900	1150.165	4.670	0.019	0.080	0.224
Base + Max Rain Spell	0.050	7	-567.970	1150.224	4.729	0.019	0.078	0.224
Base + Tmax90 Days^2	0.132/-0.017	8	-567.580	1151.526	6.031	0.010	0.079	0.222
Base + Max Rain Spell^2	0.107/-0.028	8	-567.641	1151.648	6.153	0.009	0.083	0.228

Table A4.8. Results of candidate base model analysis for clutch size, using data from 403 Mauritius kestrel breeding attempts (1990/1991-2014/2015). All models include female identity and year as random effects. Where linear and quadratic terms are included, only the quadratic term is shown in the model notation for brevity. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-*R*^{2}**	**Conditional Pseudo-*R*^{2}**
FED^2	6	-348.882	709.977	0.000	0.486	0.189	0.342
FED	5	-350.122	710.395	0.418	0.394	0.166	0.337
FED^2 + Pair PBE	7	-349.906	714.096	4.119	0.062	0.194	0.343
FED + Pair PBE	6	-351.061	714.334	4.357	0.055	0.172	0.339
FED + Pair PBE^2	7	-353.519	721.321	11.344	0.002	0.172	0.344
FED^2 + Pair PBE^2	8	-352.578	721.521	11.544	0.001	0.194	0.347
Null	4	-382.451	773.003	63.026	0.000	0.000	0.224

Table A4.9. Results from the analysis of climate impacts (during a 10-day pre-laying period) on clutch size, using data from 403 Mauritius kestrel breeding attempts (1990/1991-2014/2015). Base model: FED^2. All models include female identity and year as random effects. Only models <7 ΔAICc compared to the base model are shown. DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base	-	6	-348.882	709.977	0.000	0.590	0.189	0.342
Base + Drought	0.167	7	-349.264	712.812	2.835	0.143	0.191	0.347
Base + Raindays	-0.063	7	-349.577	713.437	3.460	0.105	0.202	0.326
Base + Max Rain Spell	-0.047	7	-350.380	715.044	5.067	0.047	0.197	0.329
Base + Mean Tmax	0.047	7	-350.545	715.373	5.396	0.040	0.194	0.345
Base + Max Dry Spell	0.019	7	-351.314	716.912	6.935	0.018	0.191	0.337

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Chapter 5

Re-scheduling to reduce climate risks in a threatened tropical bird species

5.1 Abstract

Threatened species conservation is expected to become more challenging under future climate change and managers require tools to respond to new risks. However, there are substantial knowledge gaps around the potential for existing management actions, such as supplementary food (SF) provision, to alleviate the impacts of climate change. I investigate these issues for reproduction in the echo parakeet (*Psittacula eques*), a long-lived recovering species, endemic to Mauritius. I show that breeding success in older females is reduced when their nesting attempt coincides with a tropical cyclone, therefore disrupting the age advantage in breeding productivity and possibility representing the mediation of reproductive senescence by extreme weather. Delayed egg-laying after dry conditions in late winter-early spring is most pronounced in younger females, probably owing to a combination of reduced food availability and less experience in younger birds. Delays increase exposure to cyclones, which tend to occur earlier after dry springs, so the window of favourable conditions for breeding narrows in some years. SF use advances breeding and reduces overlap with cyclones. Altering resource availability, for example through the provision of SF, represents a potentially important strategy for reducing climate risks associated with timing.

5.2 Introduction

Future climate change is projected to progress at rates faster than those experienced for 10,000 years (Hurrell and Trenberth, 2010). Such changes will threaten many species and ecosystems, with the number of species that are vulnerable to climate change projected to increase (Foden *et al.*, 2013). Species that are unable to adapt to a changing climate, through physiological and behavioural plasticity, spatial or elevational range shifts, or evolutionary changes, are increasingly likely to face local extirpation or complete extinction (Williams *et al.*, 2008; Dawson *et al.*, 2011; Bellard *et al.*, 2012; Moritz and Agudo, 2013). Species conservation and the continued protection and recovery of species that are already threatened are expected to become increasingly challenging under climate change (Dawson *et al.*, 2011). The problem is exacerbated by poor understanding of the vulnerability of many species to climate change, as usually assessed through a framework of exposure, sensitivity and adaptive capacity (Williams *et al.*, 2008; Dawson *et al.*, 2011; Foden *et al.*, 2013; Moritz and Agudo, 2013; Butt *et al.*, 2016). Species that are already threatened may be at particularly high risk, as their capacity to adapt to changes in climate is often undermined by other threats, such as habitat fragmentation and invasive species (Parmesan *et al.*, 2000; Strauss *et al.*, 2006).

The issue of poor knowledge regarding climate change vulnerability is particularly serious in the tropics, where at least 78% of species are found (Barlow *et al.*, 2018) and the climate change signal is projected to emerge from recent variability in many areas this century (Williams *et al.*, 2007; Mora *et al.*, 2013; Hawkins *et al.*, 2014). Large concentrations of biodiversity in tropical regions are already under acute threat from a range of anthropogenic processes (Brodie *et al.*, 2012; Barlow *et al.*, 2018), but they may also be particularly vulnerable to a changing climate, as they are typically adapted to a relatively narrow range of temperature conditions (Deutsch *et al.*, 2008; Bonebrake and Mastrandrea, 2010). Yet, a shortage of detailed long-term datasets and demographic analyses on tropical species constrains the projection of future impacts (Brawn *et al.*, 2017). The implications of climate change for species conservation and management in the tropics therefore urgently requires further research.

Species management in the face of climate change will likely necessitate adaptive management strategies (Hulme, 2005; Heller and Zavaleta, 2009; Stein *et al.*, 2013), which aim to adjust natural systems to expected climates (IPCC, 2014). These strategies can be generally classed as those aimed at facilitating shifts or expansions in species' distributions, and in-situ strategies aimed at improving species' capacities to cope with less favourable conditions within their original range (Heller and Zavaleta, 2009; Correia *et al.*, 2015). In-situ management actions are likely to play an important role in the future conservation of species unable to sufficiently adapt to climate change (Correia *et al.*, 2015). In a changing climate, conservation managers will need to leverage adaptive capacity to the advantage of populations (Hulme, 2005; Dawson *et al.*, 2011). For most species, in-situ management will be the preferred and most cost-effective option, and for some species it will be the only feasible option. For example, the possibilities for assisted range shifts are very limited for many island species.

It is well established that management interventions can buffer populations against environmental change and variability; however, the potential for current management to mitigate the impacts of future climate change is rarely tested (Correia *et al.*, 2015). Management strategies will be needed that respond not only to changes in average conditions, but also changes in extreme weather and climate events, which may pose a greater threat to ecosystem functioning than changes in overall climate regimes (Jentsch and Beierkuhnlein, 2008). Future responses of species and ecosystems are difficult to predict and generalise, but a deeper understanding of biological responses to extreme events is essential to inform management interventions (Harris *et al.*, 2018). The interacting effects of gradual climate change and the occurrence of extreme events add weight to the need for adaptive management approaches (Harris *et al.*, 2018).

Supplementary food (SF) provision is a widely-used and globally important management strategy in threatened species conservation, and is generally cost-effective; however, its potential use for buffering the impacts of a changing climate is largely untested (Correia *et al.*, 2015). It has the potential to buffer against the impacts of climate change on food availability, which is likely to be an important mechanism through which a changing climate affects species (Correia *et al.*, 2015). SF provision results in the availability of safe food sources, improves vital rates, alters phenology and leads to population growth (Robb *et al.*, 2008; Martínez-Abraín and Oro, 2013; Correia *et al.*, 2015). There is a shortage of empirical studies on how the expected benefits of SF on species viability may be influenced by climate change (Correia *et al.*, 2015). It has been shown, however, that SF will likely function to buffer the impacts of increases in heavy rainfall and rainfall variability on a population of the hihi (*Notiomystis cincta*), although it is unlikely to prevent local extirpation as temperatures increase (Correia *et al.*, 2015). This study on the hihi estimated the future effects of SF under climate change but did not include indices for extreme events when looking at interactions with climate.

Here, I investigate climate impacts, including those from extreme events, and interactions with age and supplementary feeding, on the breeding demography and phenology of the echo parakeet (*Psittacula eques*), a threatened and long-lived Psittacid that is endemic to Mauritius and now restricted to the southwest of the island. Anecdotal evidence for the echo parakeet implies that feeding behaviour is influenced by droughts (Jones, 1987), that breeding success is reduced in cold and rainy conditions (Jones *et al.*, 2013), and that survival is negatively impacted by tropical cyclones (Jones, 1987). This species has recovered from a low of around 20 individuals in the late 1980s (Tatayah *et al.*, 2007) owing to intensive management, and now numbers over 600 birds (Gath, 2018). This achievement contributes to net improvements in the conservation status of vertebrate biodiversity made by Mauritius in recent decades (Rodrigues *et al.*, 2014). However, such gains could be jeopardised by future climate change. The species is the focus of a dedicated monitoring programme, with nearly the entire population marked, and nearly every breeding attempt recorded (Gath, 2018). Data are available on the distribution of management actions in the population, allowing in-depth analysis of their effects (Tollington *et al.*, 2015; Gath, 2018). I show that the species' breeding phenology is re-scheduled through the provision of SF. This potentially reduces the impacts of tropical cyclones late in the breeding season, especially in years of delayed breeding.

5.3 Methods

5.3.1 Study species

The echo parakeet is a medium-sized psittacid that is only found on Mauritius, although the remnant population may represent a subspecies to an extinct taxon that once occurred on Reunion (see Jones *et al.*, 2013). The species is reliant upon native forest, and feeds on plant material, including the fruit, flowers, leaves, buds and bark of more than 50 species (Jones, 1987; Jones *et al.*, 2013). It is thought to have been widespread throughout Mauritius before human colonisation in the 17th century, but has been restricted to the southwest of the island since the late 1970s, where it mainly inhabits remnant native forest in the Black River Gorges National Park (BRGNP) and adjacent areas (Jones and Owadally, 1988). It is currently listed as endangered owing to its small range and threats to its habitat (BirdLife International, 2018).

The species experienced a severe population bottleneck in the late 1980s, when it may have reached a low of 20 individuals (Tatayah *et al.*, 2007). The main threats have included habitat destruction and invasive non-native species (Jones *et al.*, 2013). A recovery programme was initiated in 1993 (Jones and Duffy, 1993), involving captive breeding and releases, nest manipulations, supplementary feeding and the provision and protection of nest-sites (Jones and Duffy, 1993; Jones *et al.*, 2013). SF has been used by individuals in the population since 1997, when captive-bred birds that were released were trained to use feeding hoppers (reviewed by Jones *et al.*, 2013). During the years of the present study, the number of feeding stations increased from one to five. The reintroduction component of the recovery programme was halted in 2005, following an outbreak of Psittacine Beak and Feather Disease (PBFD) (Kundu *et al.*, 2012; Tollington *et al.*, 2015). The outbreak of PBFD has been linked to reduced breeding success in supplementary fed (SFed) pairs during some seasons, suggesting that the provision and use of SF at communal feeding stations is linked to the transmission of the Beak and Feather Disease Virus (BFDV) (Tollington *et al.*, 2015; Gath, 2018).

The species has been regarded as having three putative subpopulations (Tollington *et al.*, 2013), although two are recognised in this study: 1) Grande Gorge and 2) Bel Ombre, located in and around the BRGNP. Echo parakeets can breed at two years of age, but most transition to breeders at three years of age or older (Gath, 2018). The species' longevity in the wild is not known, but it is thought to be similar to the closely-related ring-necked parakeet (*P. krameri*), which lives for up to 25 years (Gath, 2018). This is regarded as likely, given that several breeding echo parakeets are aged over 15 years. The breeding season spans from the austral spring into summer, stretching from August through to March; as such it encompasses two calendar years and is referred to using both years, e.g. 2005/2006. At 53-69 days old the nestlings fledge, after which they may accompany their parents for 2-3 months (Jones, 1987; Young, 1987; Thorsen *et al.*, 1997).

5.3.2 Study area

This study focuses on both subpopulations of the echo parakeet in southwestern Mauritius. Grande Gorge is the larger subpopulation, with 76 breeding pairs in the 2013/2014 season, compared with 28 pairs at Bel Ombre. The two subpopulations are separated by a c.2 km-wide plateau of agricultural land and degraded habitat (Gath, 2018). The area is topographically varied and parakeet nest-sites are estimated to range from 199 to 724 m asl, based on location coordinates and a 30-m resolution digital elevation model (NASA SRTM version 3.0). The area holds most of the remnant native forest in Mauritius, although much of it has been invaded by non-native species, such as strawberry guava (*Psidium cattleianum*) and privet (*Ligustrum robustum*) (Thorsen *et al.*, 1997). Large areas of forest are now being cleared of invasive species. Vegetation types range from upland scrub and dwarf forest at high elevations to dry tropical forest at lower elevations. Spatial rainfall modelling by Staub *et al.* (2014) indicates that the highest elevation areas of the Black River Gorges region receive large rainfall totals compared to most areas of the island.

Mauritius has a tropical seasonal climate (Safford and Hawkins, 2013), influenced by the Southeast Trade Winds and summer cyclone season. Rainfall in Mauritius can be divided into two broad seasons, with the Southeast Lesser Monsoon from June until November, and the Northwest Monsoon and cyclone season from December until May (Senapathi *et al.*, 2010). In general, ~40% of total annual rainfall occurs in January-March (Staub *et al.*, 2014).

5.3.3 Ecological data

An intensive monitoring programme for the echo parakeet has accompanied the recovery programme since 1991, and was made official in 1993 (Gath, 2018). The monitoring programme was intensified in 2005 when management intensity was reduced following the outbreak of PBFD. Almost all individuals (>95%) in the population are fitted with coloured leg rings, allowing them to be identified in the field. Data on SF use are collected during regular observations at feeding stations. Observations at feeding stations are carried out on four days per week and last one hour, beginning at dawn (Gath, 2018). The main feeding station at Plaine Lievre has been monitored most consistently, with more intermittent observations at Brise Fer, Mare Longue and Bel Ombre. Once a month, a full day watch at Bel Ombre is carried out (Gath, 2018).

Data on individual nesting attempts are collected as part of the species recovery programme. The majority of breeding attempts are found and documented. Data are usually collected on first egg-laying date (FED), clutch size and number of fledglings. Where possible, the identity of the female and male are noted and from this the age and prior breeding experience of the pair can often be calculated. Data are also available on nest-site characteristics. The data used in this study are drawn from a recently compiled studbook (Gath, 2018), with a total of 867 wild breeding attempts with known clutch size from 1991/1992 to 2013/2014; in this study, a breeding attempt is defined as the laying of at least one egg. The analyses of timing of breeding and breeding success in the present study include first clutches for which there are complete data for the variables of interest, including known clutch size, and complete data for all of the climate variables of interest. Only first clutches are included because the success of second clutches may be affected by the costs incurred by parent birds during the previous breeding attempt (following Tollington *et al.*, 2015). Second clutches are rare, with only 42 recorded up until and including the 2013/2014 breeding season.

5.3.4 Meteorological data

Rain gauge data from Petrin (20°24’S, 57°28’E, 655 m asl) (contributed by Mauritius Meteorological Services) are used to assess direct impacts on breeding echo parakeets. The Petrin rain gauge is situated close to nest sites and feeding stations in the Black River Gorges area, with all spatially-referenced nest sites located within 10 km of the rain gauge. Mean annual rainfall at Petrin is ~3500 mm. Spatial modelling by Staub *et al.* (2014) indicates that the Bel Ombre population experiences less rainfall overall; however, the next nearest rain gauge (Bel Ombre settlement) is located in a drier area, thus the data from Petrin are applied to the entire population. Daily temperature data and additional daily rainfall data were obtained from the nearest available synoptic weather station at Vacoas (20°17’S, 57°29’E, 424 m asl) via NOAA (US National Oceanic and Atmospheric Administration) in the form of the GHCN (Global Historical Climatology Network) and GSOD (Global Summary of the Day) inventories, which were merged to minimise the number of days with missing data. Quality control of rainfall and temperature data included homogeneity tests, as well as removal of consecutive repeat precipitation values (following Gallego *et al.*, 2011). None of the datasets showed inhomogeneities, although the rainfall time series for Petrin was too short for these tests. It should be noted that the weather station at Vacoas is located in an urban area; however, the temperature data have not been adjusted for these analyses as they still provide evidence of relative temperature variation across days and seasons that may affect parakeets. Tropical cyclone best track data were obtained in the form of ESRI shapefiles from the IBTrACS (International Best Track Archive for Climate Stewardship) database (Knapp *et al.*, 2010) via NOAA. These data include 6-hourly positions and intensity estimates.

Inhomogeneities in intensity estimation in the Indian Ocean dataset exist owing to the repositioning of a satellite and thus improvement of the view angle in 1998 (Elsner *et al.*, 2008; Kossin *et al.*, 2013), although these are difficult to remove without re-analysing satellite images (Kossin *et al.*, 2013). These inhomogeneities may affect the cyclone data used in this study, although the analyses of cyclone impacts on parakeets are conducted using data collected after 1998.

5.3.5 Exploratory analyses

I explored the impacts of selected climate indices on 1) fledgling production, 2) egg survival, 3) clutch size and 4) timing of breeding, using (generalised) linear mixed models. Each set of exploratory analyses followed two stages; first, a base (or background) model (e.g. Öberg *et al.*, 2015) was chosen by running a selection of candidate models based on prior evidence of which variables, other than climate indices, are thought to be important to the timing of breeding or breeding success (Table 5.1); and second, climate indices (Tables 5.2 and 5.3) were incorporated into the selected base model to test for an effect. Candidate base models were formulated to represent realistic hypotheses based on prior research. All candidate base models for measures of breeding success included FED, as it has an important direct influence on fitness (Tollington *et al.*, 2015; Gath, 2018), and affects the exposure of breeding pairs to weather conditions. All candidate base models for fledgling production, egg survival and clutch size also included female age and SF use, as prior evidence indicates that they are influential on breeding success (Tollington *et al.*, 2015; Gath, 2018), and interactions of these variables with climate indices would be tested at a later stage. Population density is not included in the analyses in the present study, as there is no prior evidence of density dependence in the breeding success of this population. Mean annual productivity has shown increases as the population has increased (Jones *et al.*, 2013), suggesting that there is no negative density dependence, at least in the presence of conservation management.

Once a base model had been selected, it was run again with one of a selection of climate indices systematically included as additive effects. FED models were run with climate indices for the period July-September (JAS), at the start of the breeding season. Research on the Mauritius kestrel (*Falco punctatus*), which has a similar breeding season, has shown that conditions in JAS are influential on timing (Nicoll, 2004). Fledgling production models were run with 95-day nest-level indices to test for effects from conditions during and just prior to the active phase of each breeding attempt. Incubation and brood climate indices were applied to egg to fledging survival, as conditions during the incubation and brood phases were expected to have strong effects on the survival of eggs and nestlings. Indices for a period of 10 days prior to egg-laying were applied to the analysis of clutch size. It should be noted that nest-level climate indices for temporally overlapping nests are not truly independent, as they are based on the same weather station data. Nevertheless, they serve to estimate the exposure of each nest to certain conditions. All indices were added as a linear term only and with a quadratic term to test for non-linear effects. Interactions of climate indices were tested with SF use and female age, as these were judged as likely to modify climate influences. Echo parakeets receive other management interventions, such as the provision of artificial nest-boxes; however, only interactions of climate with SF use are tested here. This is because any effect of nest type on climate impacts is most likely to be detected using climate data of very high spatial resolution, which are not available, whereas climate interactions with SF use are more readily testable with data from a single weather station, as most of the population utilises a limited number of feeding stations and climate variation is expected to influence natural food availability for the entire population. Climate impacts on this long-lived species have not been studied previously at the population level, so interactions with female age were included to test for climate effects on age-dependent reproductive success. Age is defined as a two-level factor, for females aged 2-5 years and those aged 6+ years, based on the average age of ~6 years for breeding females in the study period. This division of age classes allows relatively balanced sampling in all years of the study. Female age, and not male age, is used here as there are more data available on female breeding birds and female age is expected to be more strongly linked to the breeding fitness of pairs.

I estimated the incubation and brood phases of each nest from the FED of each clutch. Egg-laying occurs at one- or two-day intervals, with incubation usually starting when the first or second egg is laid, and occasionally when the last egg is laid (Jones *et al.*, 2013). For the calculation of the incubation and brood phases of each breeding attempt it was assumed that incubation always starts when the first egg is laid. For each clutch, an incubation period of 25 days is assumed, as this is the assumption used in the back calculation of FED from field observations. The expected hatch day (EHD) was therefore always assumed to be 25 days after the FED. The brood period has been documented as varying from 50 to 69 days in wild nests (Jones *et al.*, 2013), thus for the brood-level climate indices the brood phase is always assumed to be 60 days (EHD + 59 days). It should be noted that for large clutches, not all chicks will fledge after 60 days, owing to some eggs being laid after the start of incubation. The 95-day nest level indices were calculated from the total time window including the incubation phase, brood phase and a period of 10 days prior to the FED. The expected fledging day (EFD) is always assumed to be 60 days after the EHD. Based on the data and these calculations, in the sample of 533 clutches used in the exploratory analyses of breeding success the earliest FED was 9 August and the latest EFD was 12 March. These estimates of the timing of breeding attempts were used to estimate temporal overlap with high impact events and thus test whether timing influences such impacts.

Climate indices (Tables 5.2 and 5.3) were chosen based on plausible and expected impacts on breeding echo parakeets, and include measures of extreme rainfall, rain and dry spells, droughts, cyclone conditions and cold days, as well as indices that characterise more general weather conditions such as total rainfall, number of raindays and average maximum temperature. I expected the species to be impacted by cold days, rather than hot days, because much of its current range is in high elevation areas, and anecdotal observations suggest that egg mortality during incubation is linked to cold rainy days (Jones *et al.*, 2013). Egg-laying starts in late August, with fledging typically until early March (e.g. Jones *et al.*, 2013), thus extreme raindays and temperatures are defined based on percentiles for the 25-year standard base period August-March 1990/1991-2014/2015.

For the purpose of calculating climate indices, I defined extreme rain events as those exceeding the 90th percentile of all raindays (≥1 mm) aggregated from the season of interest during the standard base period 1990/1991-2014/2015. The 90th percentile (rather than the 95th or 99th) was chosen to maximise the number of days sampled in the statistical analysis, while recognising that this includes mostly ‘moderate extremes’ (Klein Tank *et al.*, 2009; Alexander, 2016; Easterling *et al.*, 2016). Raindays were subset first so that the 90th percentile relates to rainfall events rather than to all days including dry days, as this analysis is concerned with the impacts of intensities at the extreme end of the distribution of events. The 90th percentile was calculated for the breeding season only so that this relates to extreme conditions that parakeets experience relative to conditions when they are undertaking particular behaviour. Likewise, cold days are defined as those below the 10th percentile of all days aggregated across the base period 1990/1991-2014/2015. It should be noted that the percentile thresholds for rainfall and temperature will have different return times because rainfall thresholds are based on the subset of raindays only. In order to detect the influence of seasonal drought conditions on breeding success, binary indices were included to identify breeding attempts initiated during years when drought conditions occurred in the dry season (June-November). Droughts were identified as periods with a Standardised Precipitation Index value of ≤ -1.0 for total seasonal rainfall (McKee *et al.*, 1993), based on mean seasonal rainfall for the base period 1990/1991-2014/2015. All climate indices were only calculated where no more than 10% of days had missing data in a given time window.

5.3.6 Further analyses of climate impacts on breeding success

The exploratory analyses of climate impacts on breeding success shows only weak support for an effect of mean maximum temperature (Mean Tmax) on fledgling production (Table A5.2). There is no support for effects from climate and interactions between climate, age and SF on clutch size (Table A5.6). There is strong support for effects on egg survival from an interaction between age and the occurrence of tropical storms and cyclones (hereafter referred to as cyclones), as well as from Mean Tmax (Table A5.4). Cyclone occurrence was defined as the presence of a cyclone of tropical storm strength or higher (1-minute maximum sustained wind speed ≥34 knots) whose centre was located within 300 km of the study site (analysed using QGIS version 2.18.20). Previous research and anecdotal observations, including from Mauritius, indicate that cyclone winds and rain regularly impact areas within 275-300 km (~150 nm) of the storm centre (Shepherd *et al.*, 2007; Nicoll *et al.*, 2017). I carried out further analysis to assess the effect of temporal overlap with cyclones on egg survival. For this I used a subset of 415 first clutches with breeding success data recorded in years where the centre of at least one cyclone passed within 300 km of Petrin. As cyclones are temporally discrete events that usually occur late in the parakeet breeding season, I also investigated the influence of reproductive timing on exposure to cyclones. Temporal overlap with the first cyclone of the season was calculated as the EFD relative to the first cyclone day.

5.3.7 Further analysis of climate influences on breeding phenology

Exploratory analyses of impacts from climate indices for late winter-early spring (July-September) on FED indicate that total rainfall (JAS rainfall) is the most parsimonious index (Table A5.8). FED and its relationship with JAS rainfall may be influenced by the age of birds and their use of SF. Further analyses were conducted using a subset of 568 first clutches in the period 2004/2005-2013/2014, a period in which supplementary feeding had become successful and female age was frequently recorded. In these years there are unbalanced samples of clutches representing SFed and non-SFed pairs and the age range of breeding females. JAS rainfall is therefore treated as a categorical variable, with years categorised based on the Standardised Precipitation Index (SPI) for JAS rainfall; years with SPI ≤ -1.0 are classed as 'Drought', those with SPI > -1.0 and <1.0 classed as 'Normal', and years with SPI ≥ 1.0 classed as 'Wet' (McKee *et al.*, 1993; WMO, 2012). Linear mixed models and linear quantile mixed models were used to estimate the overall influence of SF on mean and median FED when controlling for year.

5.3.8 Effects of phenology and management on exposure to climate risks

The influence of SF use on exposure to cyclones was tested using a subset of 450 first clutches in years where the centre of at least one cyclone occurred within 300 km of Petrin. Linear mixed models and quantile linear mixed models were used to estimate the overall influence of SF on the mean and median overlap with cyclones when controlling for year. I calculated the seasonal time window of favourable conditions for breeding as the number of days between the median FED and day of the first cyclone. The median FED, rather than the mean, was used because it is expected to be closer to the population-level peak in egg-laying. I carried out analyses to investigate whether JAS rainfall has any correlation with the timing of cyclones and the breeding time window.

5.3.9 Statistical analyses

The R statistical environment (version 3.4.4; R Core Team, 2018) was used for all statistical analyses. The error distribution of response variables was studied with histograms and Cullen and Frey graphs in the 'fitdistrplus' package (Delignette-Muller *et al.*, 2017). In correlation and trend analyses, where the assumptions of parametric tests were not sufficiently met the non-parametric Kendall and Mann-Kendall tests were used. Linear regression, linear mixed models and generalised linear mixed models (GLMMs) were run with package 'lme4' (Bates *et al.*, 2018). The package 'lmerTest' was used to estimate the significance of coefficients in linear mixed models based on Satterthwaite's degrees of freedom method (Kuznetsova *et al.*, 2018). Linear quantile mixed models were run with the 'lqmm' package (Geraci, 2018). The Mann-Kendall trend test was applied using the 'Kendall' package (McLeod, 2011).

Mixed models always included female identity and year as random effects to account for the replication of individual-level and season-level conditions not included in the fixed effects. In the clutch size and timing of breeding models I assumed a Gaussian error distribution. In the fledgling production models, I assumed a Poisson error distribution and used the log-linear link function, and in the egg survival models I assumed a binomial error distribution and used the logit link function. I modelled egg to fledging survival as a two-vector matrix of eggs that fledged and eggs that failed in each nest (following Cartwright *et al.*, 2014). In mixed models, all continuous explanatory variables were centred and scaled before analysis in order to aid model convergence and parameter estimation. All mixed models for fledgling production and egg survival were run with the BOBYQA (Bound Optimisation By Quadratic Approximation) optimiser (Powell, 2009) to facilitate model convergence. All simple explanatory terms showed (generalised) variance inflation factors (VIFs) of < 3 (see Zuur *et al.*, 2010), except for temperature indices in the fledgling production and egg survival models. These terms showed higher VIFs owing to correlation with FED, although all values were < 7.

Mixed model ranking and selection, and extraction of Pseudo-R^2 values (Nakagawa and Schielzeth, 2013), were carried out using package ‘MuMIn’ (Barton, 2018). Akaike’s Information Criterion corrected for sample size (AICc) was used for the comparison of mixed models. The threshold of ΔAIC < 2 is used for stringent model selection and interpretation while recognising that a threshold of ΔAIC < 7 may be more appropriate for identifying all informative models (Burnham *et al.*, 2011). The effects of explanatory variables were studied and extracted with the ‘effects’ package (Fox *et al.*, 2018).

Table 5.1. Explanatory variables included in candidate base models for echo parakeet first egg-laying date (FED), fledgling production (FP), egg survival (ES) and clutch size (CS).

Explanatory variable	**Response variables**	**Description**	**References**
FED	FP, ES, CS	First egg-laying date (days from 1 August)	Tollington *et al.* (2015); Gath (2018)
Subpop	FED, FP, ES, CS	Two-level factor identifying subpopulations (Grande Gorge and Bel Ombre)	Gath (2018)
Outbreak	FED, FP, ES, CS	PBFD Outbreak Phase: Factor for 1997/1998-2003/2004 as pre-outbreak, 2004/2005 as early outbreak, 2005/2006 as main outbreak, and 2006/2007 onwards as post-outbreak	Tollington *et al.* (2015); Gath (2018)
SF	FED, FP, ES, CS	Two-level factor for use of supplementary food	Tollington *et al.* (2015); Gath (2018)
Age	FED, FP, ES, CS	Two-level factor for the age (years) of the female in pair; 2-5 years, 6+ years	Tollington *et al.* (2015); Gath (2018)
Elevation	FED, FP, ES, CS	Elevation (m asl) of each nest site, estimated from coordinates of nest site locations and a 30m-resolution digital elevation model (NASA SRTM version 3.0)	Not previously tested for this species in published literature
Nest Type	FED, FP, ES, CS	Two-level factor to denote natural cavities and artificial nest-boxes	Unpublished analyses (see Jones *et al.*, 2013)

Table 5.2. Climate indices for nest-level time windows relating to fledgling production (FP), egg survival to fledging (ES) and clutch size (CS) in echo parakeet breeding attempts. Percentile thresholds and standardised precipitation index (SPI) were calculated from the standard reference period 1990/1991-2014/2015.

Climate index	**Response variables**	**Description**
Rainfall	FP, ES, CS	Total rainfall (mm) on raindays (≥1 mm)
Raindays	FP, ES, CS	Total number of days with ≥1 mm rain
Rainfall90	FP, ES, CS	Total rainfall on days exceeding August-March 90th percentile (37.0 mm)
Raindays90	FP, ES, CS	Total raindays exceeding August-March 90th percentile (37.0 mm)
Max Rain Spell	FP, ES, CS	Maximum number of consecutive raindays (≥1 mm)
Max Dry Spell	FP, ES, CS	Maximum number of consecutive dry days (<1 mm)
Drought	FP, ES, CS	Binary classification whether drought conditions occur during the dry season (SPI-6* for JJASON <-1.0)
Mean Tmax	FP, ES, CS	Mean daily maximum temperature (°C), using data from Vacoas
Tmax10 Days	FP, ES, CS	Number of days with maximum temperature below the August-March 10th percentile for Vacoas (21.9°C)
Cyclone	FP, ES	Binary classification of whether at least one tropical storm or cyclone (1-minute maximum sustained wind speed ≥ 34 knots) occurred (the centre was located within 300 km of Petrin)

*SPI-6 = Six-month Standardised Precipitation Index based on total rainfall.

Table 5.3. July-September (JAS) climate indices included in models for the analysis of timing of breeding in echo parakeets. Percentile thresholds and standardised precipitation index (SPI) were calculated from the standard reference period 1990/1991-2014/2015.

Climate index	**Description**
Rainfall	Total seasonal rainfall (mm) on raindays (≥1 mm)
Raindays	Total number of days in season with ≥1 mm rain
Rainfall90	Total rainfall on days exceeding the JAS 90th percentile (25.5 mm)
Raindays90	Total raindays exceeding the JAS 90th percentile (25.5 mm)
Drought	Binary classification whether drought conditions occur during JAS (SPI-3* ≤-1.0)
Max Rain Spell	Maximum number of consecutive raindays (≥1 mm)
Mean Tmax	Mean daily maximum temperature (°C) at Vacoas

*SPI-3 = Three-month Standardised Precipitation Index based on total rainfall.

5.4 Results

5.4.1 Climate impacts on breeding success

Exploratory analyses reveal that the coincidence of a cyclone with nesting attempts reduces egg to fledging survival when the breeding female is in the older age group (Figure 5.1, Table A5.4), although this interaction is not supported for fledgling production (Figure 5.2, Table A5.2). Females in the older age group lay larger clutches ($b = 0.255 \pm 0.050$, $t = 5.097$, $P < 0.0001$, $N = 533$ unmanaged first clutches, 2005/2006-2013/2014, extracted from base model, see Appendix), and the interaction effect of age and cyclone coincidence on egg survival could be linked to the additional effort needed to raise a larger clutch. However, this egg survival model (AICc = 1348.158, Table A5.4), is more parsimonious than a model in which the cyclone × age interaction is replaced by a cyclone × clutch size interaction (AICc = 1351.483) and a model with a cyclone × age × clutch size interaction (AICc = 1350.068).

The interaction between cyclone occurrence and age could arise through other interactions with correlated variables. Older females are generally more likely to nest in natural cavities, although this pattern has reduced as the population has aged (based on the dataset used here ($N = 533$) in the 2005/2006 season the mean age (± SE) of females using natural cavities was 5.21 ± 0.50 years ($N = 14$), compared with 4.12 ± 0.34 years using artificial cavities ($N = 25$); in the 2013/2014 season the mean age of females using natural cavities was 8.36 ± 1.23 years ($N = 11$), compared with 8.05 ± 0.36 years using artificial cavities ($N = 76$)) and older females are generally less likely to take SF, although again the gap has narrowed as the population has aged (in the 2005/2006 season the mean age of females in pairs not using SF was 5.67 ± 0.41 years ($N = 9$), compared with 4.17 ± 0.34 years in pairs using SF ($N = 30$); in the 2013/2014 season the mean age of females in pairs not using SF was 8.20 ± 0.90 years ($N = 20$), compared with 8.06 ± 0.37 years in pairs using SF ($N = 67$)), so interactions of cyclone occurrence with these factors were also tested. Adding nest type to the model does not improve it (AICc = 1350.132). Equivalent models in which the cyclone × age interaction is replaced by cyclone × nest type (AICc = 1354.898) and cyclone × nest type × SF use (AICc = 1353.100) are less parsimonious compared with the original cyclone × age interaction. This implies that the cyclone × age interaction is not confounded by other potential interactions.

Analysis of the effect on egg survival of the temporal overlap of nesting attempts with the first cyclone of the season reveals a non-linear change in nesting attempts by older females (Table 5.4, Figure 5.3). Data from the 2005/2006-2013/2014 seasons show that the temporal overlap with the first cyclone of the season increases as the FED gets later (Kendall's tau = 0.355, $P < 0.0001$, $N = 415$, Figure 5.4). Using the same data, it can be shown that there is decreasing overlap of breeding attempts and cyclones as the first cyclone occurs later (Kendall's tau = -0.715, $P < 0.0001$, $N = 415$, Figure 5.5).

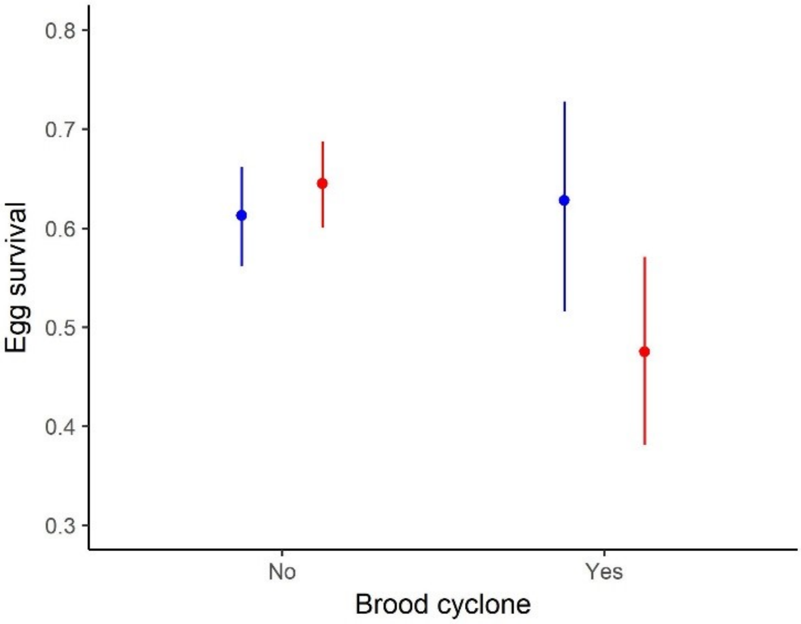

Figure 5.1. Effect of brood phase cyclone occurrence (Brood cyclone) on egg survival in clutches where the age of the female is 2-5 years (blue data points) and 6+ years (red data points), extracted from a model including first egg-laying date (FED), subpopulation, and PBFD outbreak phase × SF use, with female identity and year as random effects. $N = 533$ unmanaged first clutches (2005/2006-2013/2014). Error bars show 95% confidence intervals.

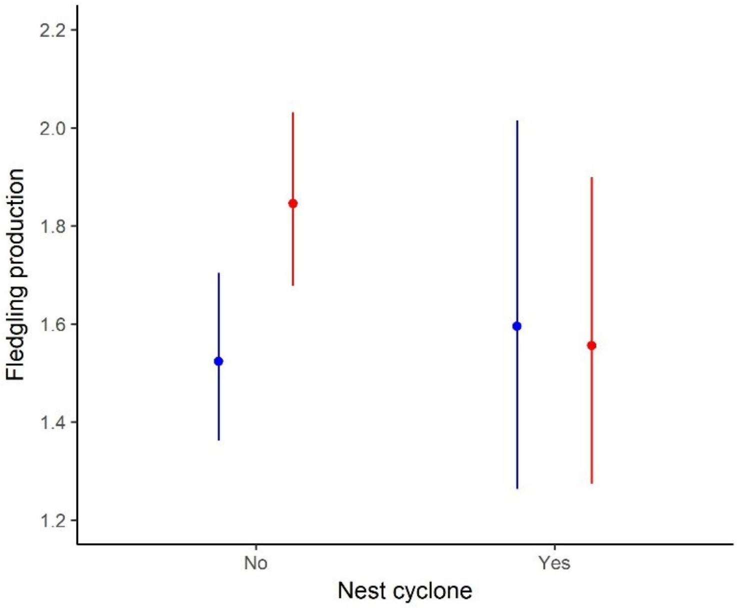

Figure 5.2. Effect of nest-level cyclone occurrence (Nest cyclone) on fledgling production in clutches where the age of the female is 2-5 years (blue data points) and 6+ years (red data points), extracted from a model including first egg-laying date (FED) and PBFD outbreak phase × SF use, with female identity and year as random effects. *N* = 533 unmanaged first clutches (2005/2006-2013/2014). Error bars show 95% confidence intervals.

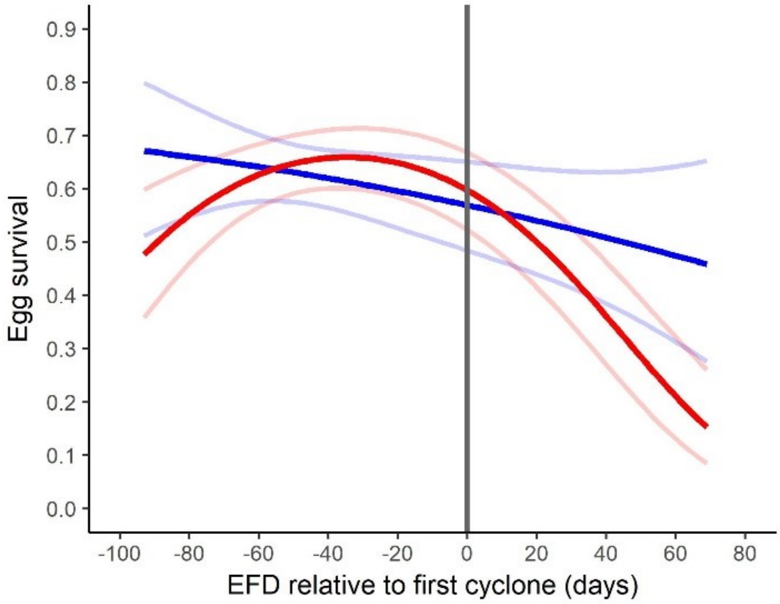

Figure 5.3. Effect of temporal overlap of nesting attempts with a cyclone (expected fledging day (EFD) relative to the first cyclone of the season) on egg survival (with 95% confidence intervals) in clutches where the age of the female is 2-5 years (blue line) and 6+ years (red line), extracted from a model with female identity and year as random effects. *N* = 415 unmanaged first clutches, 7 seasons in period 2005/2006-2013/2014.

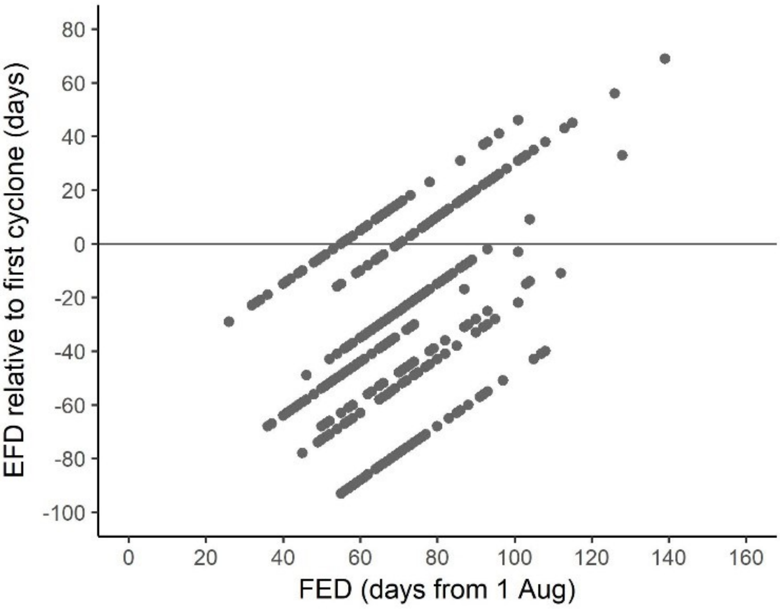

Figure 5.4. Expected fledging day (EFD) relative to first cyclone of the season plotted against first egg-laying date (FED, days from 1 August). *N* = 415 unmanaged first clutches, 7 seasons in period 2005/2006-2013/2014.

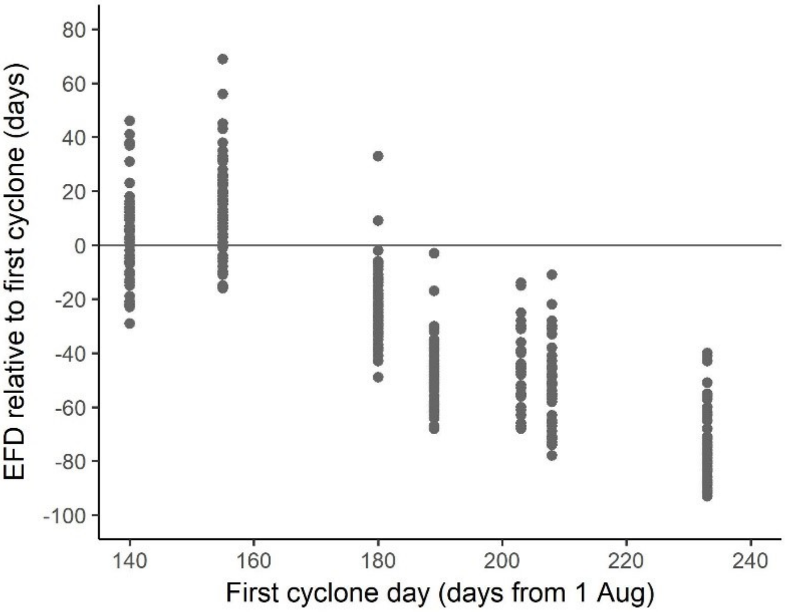

Figure 5.5. Expected fledging day (EFD) relative to first cyclone of the season plotted against first cyclone day. *N* = 415 unmanaged first clutches, 7 seasons in period 2005/2006-2013/2014.

Table 5.4. Comparison of models of egg survival in relation to temporal overlap (days) of nesting attempts with the first cyclone of the season (expected fledging day relative to first cyclone day) and interactions with female age (Age). All models include female identity and year as random effects. *N* = 415 unmanaged first clutches (2005/2006-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Cyclone overlap^2 × Age	8	-539.956	1096.267	0.000	0.821	0.064	0.259
Cyclone overlap^3 × Age	10	-539.907	1100.359	4.092	0.106	0.059	0.245
Cyclone overlap^2	5	-545.794	1101.736	5.469	0.053	0.041	0.228
Cyclone overlap^3	6	-545.772	1103.749	7.482	0.019	0.036	0.218
Cyclone overlap	4	-552.261	1112.620	16.353	0.000	0.018	0.183
Null	3	-553.970	1113.998	17.731	0.000	0.000	0.154
Cyclone overlap × Age	6	-551.073	1114.352	18.085	0.000	0.029	0.202

5.4.2 Climate influences on breeding phenology

There is no interannual trend in FED at the population level, based on annual means (Mann-Kendall tau = 0.015, 2-tailed P = 0.967) and annual medians (Mann-Kendall tau = 0.082, 2-tailed P = 0.679), with trends of 0.221 days year^{-1} and 0.181 days year^{-1} respectively, estimated using least squares regression (N = 17 years in period 1996-2013, 732 clutches in total; 11-96 clutches per year). There is, however, interannual variability in timing, with the population advancing egg-laying in some years, e.g. 1999, 2002, 2007 and 2008 (Figure 5.6). A mixed model with constant FED across years (AICc = 5532.695) is substantially improved by the inclusion of an effect for year (AICc = 5317.610). This implies that timing is responding to an aspect of the environment that shows interannual variability but no systematic trend.

Exploratory mixed-model analysis, using a subset of 658 first clutches in 1997/1998-2013/2014 for which data on female identity and late winter-early spring (July-September, JAS) weather conditions are available (Table A5.7), shows that FED is most strongly influenced by JAS rainfall with a quadratic term (AICc = 5333.814), with earlier breeding in springs with more rainfall (Figure 5.7). Interactions of rainfall with subpopulation and elevation improve the model (AICc of 5319.008 and 5331.278 respectively), which implies that rain gauge measurements at Petrin are more indicative of conditions experienced by certain parts of the population. There is no significant trend in JAS rainfall at Petrin in the period 1987-2015 (Mann-Kendall tau = -0.071, 2-tailed P = 0.617, N = 27 years, Figure 5.8) or 1996-2013 (Mann-Kendall tau = -0.170, 2-tailed P = 0.327, N = 17 years). However, Vacoas shows a negative trend in JAS rainfall between 1961 and 2015 (Mann-Kendall tau = 0.239, 2-sided P = 0.015, N = 50 years, Figure 5.8), with a trend of -1.84 mm year^{-1}, as estimated using least squares regression. It appears, therefore, that JAS rainfall in the central-western uplands of Mauritius has shown interannual variability and no clear trend since the mid-1990s, but with a longer-term decreasing trend evident since the early 1960s.

Mixed model comparisons using a smaller subset of data (Table 5.5) indicate that both SF and age modulate the response of breeding pairs to JAS rainfall. There is strong support for an interaction between SF use and JAS rainfall, but the most parsimonious model includes a three-way interaction between JAS rainfall, SF use and age (Table 5.5, Figure 5.9). These analyses show that non-SFed birds breed later in dry and normal springs, but respond more strongly to increasing rainfall so that SFed and non-SFed birds breed at similar times in springs with high rainfall. The latest breeders are non-SFed pairs with a female in the younger age group during drought years. The analyses also indicate that SF has a more marked effect on FED in the younger age group during drought and normal conditions than in the older age group.

Comparison of mean FED in SFed and non-SFed pairs shows that they breed at similar times in early years, and that delays are greater for non-SFed pairs in later years (Figure 5.10). SFed pairs show a delay of 0.556 ± 0.096 days per 1 day of delay in non-SFed pairs (t = 5.807, P = 0.0004, N = 10 years), indicating a significant difference compared to a 1:1 relationship. This demonstrates that SF use buffers the effects of environmental variability. When controlling for year, SF use advances FED by 7.718 ± 2.165 days (t = -3.565, P = 0.0005, N = 568 clutches). Quantile regression shows that median FED is advanced by 8.016 ± 3.011 days in pairs taking SF when controlling for year (P = 0.011, N = 568 clutches).

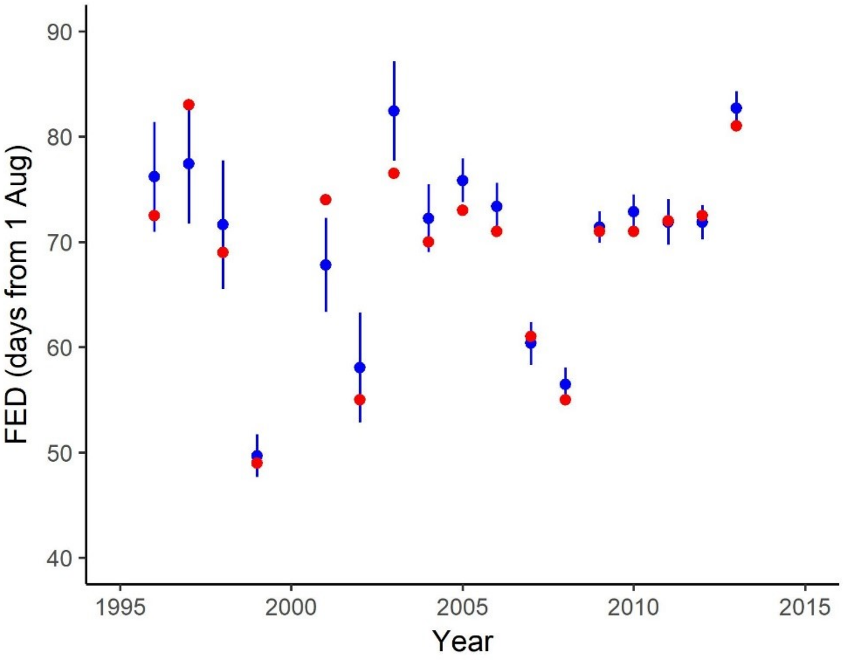

Figure 5.6. Annual overall mean (± SE) (blue data points and line) and median (red data points and line) first egg-laying date (FED, days from 1 August) in first clutches laid by echo parakeets. N = 17 years in period 1996/1997-2013/2014, 732 clutches in total; 11-96 clutches per year.

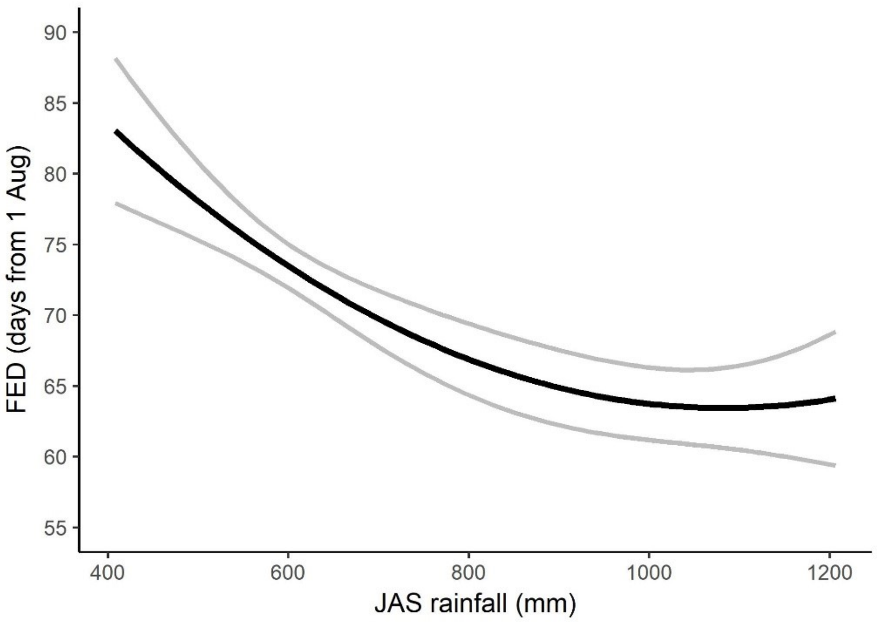

Figure 5.7. Effect of July-September rainfall (JAS rainfall, mm) on first egg-laying date (FED, days from 1 August) (with 95% confidence intervals) in echo parakeet breeding attempts, extracted from a model including PBFD outbreak phase × supplementary food use, elevation, subpopulation and nest type, with female identity and year as random effects. *N* = 658 first clutches, 1997/1998-2013/2014.

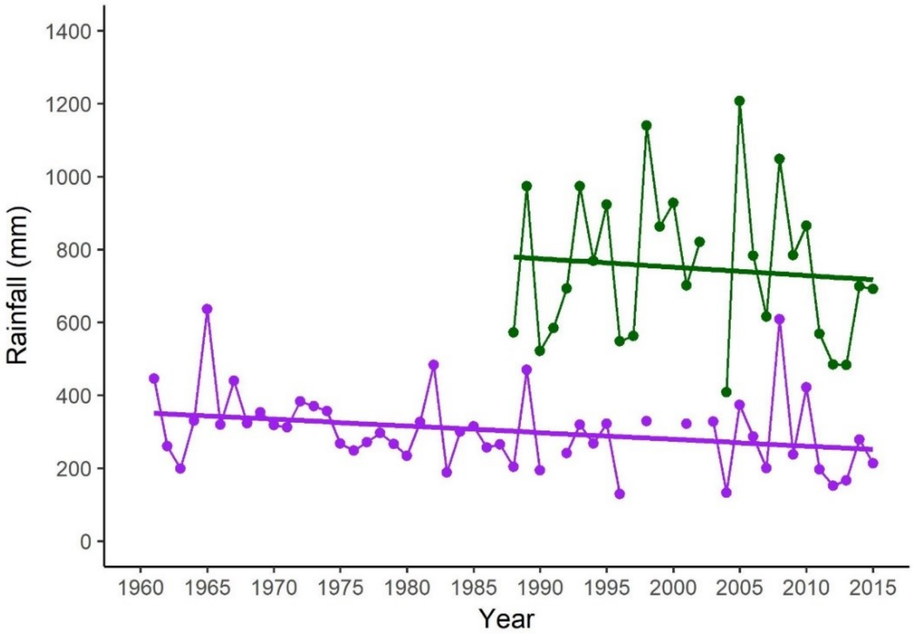

Figure 5.8. Interannual trends in July-September rainfall (mm) at Petrin (green data points and lines, *N* = 27 years) and Vacoas (purple data points and lines, *N* = 50 years). Trend lines fitted using least squares regression.

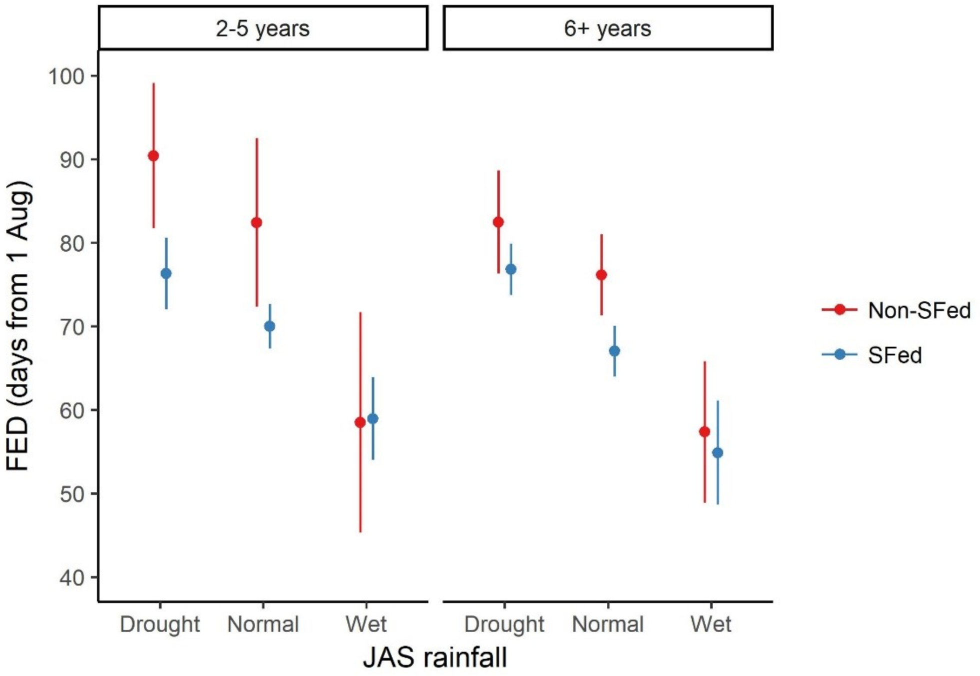

Figure 5.9. Effect of an interaction between supplementary food use (SFed, Non-Sfed), JAS rainfall and female age on first egg-laying date (FED, days from 1 August), extracted from a model including PBFD outbreak phase × SF use, elevation, subpopulation and nest type, with female identity and year as random effects. *N* = 568 first clutches (2004/2005-2013/2014). Error bars show 95% confidence intervals.

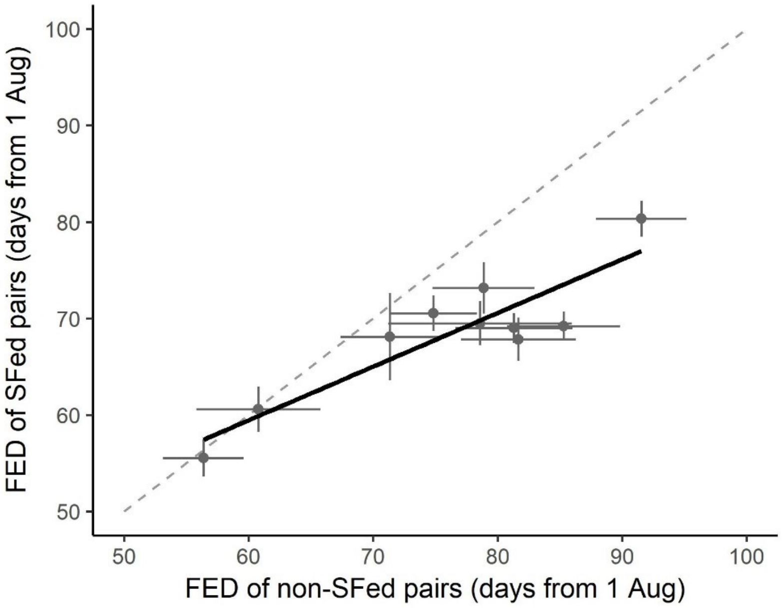

Figure 5.10. Mean first egg-laying date (FED, days from 1 August) of supplementary fed (Sfed) pairs compared to non-Sfed pairs. *N* = 568 first clutches (5-67 clutches per group by year) (2004/2005-2013/2014). Error bars show standard error.

Table 5.5. Effects of interactions between supplementary food use (SF), female age (Age), and July-September rainfall (Rain) on first egg-laying date (days from 1 August) in echo parakeet breeding attempts. The base model includes PBFD outbreak phase × SF use, elevation, subpopulation, nest type and age. All models include female identity and year as random effects. *N* = 568 first clutches (2004/2005-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base + Rain × SF × Age	22	-2236.648	4519.153	0.000	1.000	0.173	0.525
Base + Rain × SF	17	-2250.493	4536.098	16.945	0.000	0.174	0.526
Base + Rain × Age	17	-2252.444	4540.001	20.848	0.000	0.169	0.522
Base + Rain	15	-2256.905	4544.680	25.527	0.000	0.171	0.521
Base + Age × SF	14	-2262.937	4554.634	35.481	0.000	0.055	0.519
Base	13	-2265.628	4557.913	38.760	0.000	0.055	0.524
Null	4	-2294.845	4597.762	78.609	0.000	0.000	0.487

5.4.3 Effects of timing and management on exposure to climate risks

The timing of the first cyclone of the season shows a positive correlation with JAS rainfall over the period 1996/1997-2013/2014 (Kendall's tau = 0.407, *P* = 0.047, *N* = 14 years), with cyclones tending to occur earlier as rainfall decreases (Figure 5.11); however, this pattern is not significant over the entire period with data available (1988/1989-2014/2015, Kendall's tau = 0.240, *P* = 0.164, *N* = 19 years). There is a non-significant negative correlation between annual median FED and JAS rainfall (Kendall's tau = -0.332, *P* = 0.077, *N* = 16 years, Figure 5.11), thus there could be a narrowing of the time window between median FED and the first cyclone as JAS rainfall decreases. Analysis of this time window in relation to JAS rainfall shows that the window is positively correlated with rainfall (Kendall's tau = 0.451, *P* = 0.026, *N* = 14 years), thus drier conditions in JAS are associated with narrower time windows (Figure 5.12). The timing of fledging (expected fledging day, EFD) relative to the first cyclone is altered by the use of SF, as an interaction with female age and JAS rainfall (Table 5.6, Figure 5.13). When controlling for year, SF use reduces the amount of overlap with the first cyclone by 8.150 ± 2.277 days (*t* = -3.580, *P* = 0.0005, *N* = 450 clutches). Quantile regression shows that median overlap is reduced by 11.004 ± 3.403 days in pairs taking SF when controlling for year (*P* = 0.002, *N* = 450 clutches), implying that the peak in EFD is generally shifted further forwards than the mean.

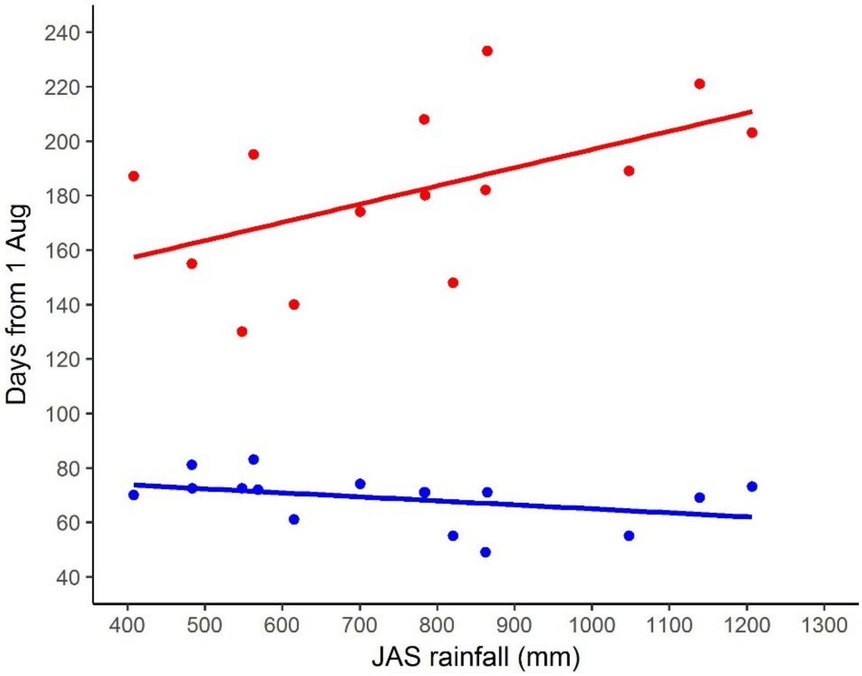

Figure 5.11. Timing (days from 1 August) of overall median first egg-laying date (FED: blue, *N* = 16 years) and first cyclone of the season (red, *N* = 14 years) plotted by JAS rainfall (mm).

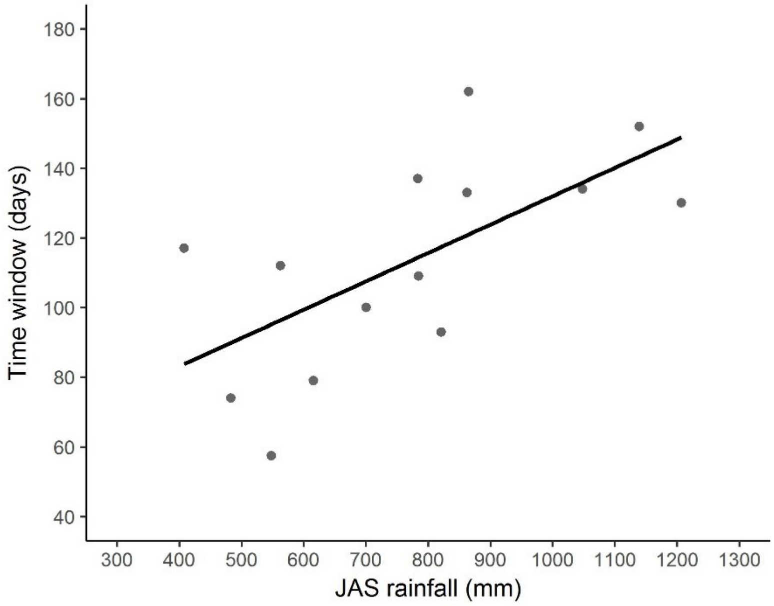

Figure 5.12. Time window (days) between overall median FED and first cyclone day plotted against JAS rainfall (mm). *N* =14 years.

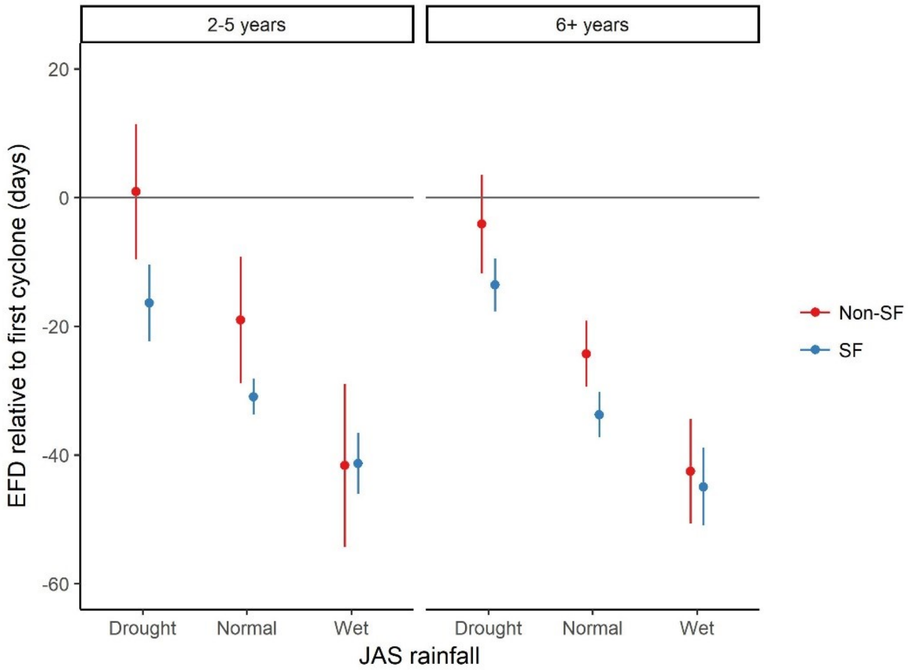

Figure 5.13. Effect of interaction of supplementary food use (SFed, Non-SFed), female age and JAS rainfall on the overlap of nesting attempts with the first cyclone of the season (expected fledging day (EFD) relative to the first cyclone day), extracted from a model including outbreak phase × SF, subpopulation, elevation, nest type and first cyclone day, with female identity and year as random effects. *N* = 450 clutches (2004/2005-2013/2014). Error bars show 95% confidence intervals.

Table 5.6. Effects of interactions between supplementary food use (SF), female age (Age), and July-September rainfall (Rain) on temporal overlap (days) with the first cyclone of the season in echo parakeet breeding attempts (expected fledging day relative to the first cyclone day). The base model includes outbreak phase × SF, subpopulation, elevation, nest type and first cyclone day. All models include female identity and year as random effects. *N* = 450 first clutches (2004/2005-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
SF × Age × Rain	15	-1794.726	3620.559	0.000	1.000	0.139	0.898
SF × Rain	9	-1809.867	3638.143	17.584	0.000	0.136	0.899
SF + Age + Rain	8	-1813.998	3644.322	23.763	0.000	0.134	0.899
SF + Rain	7	-1815.751	3645.755	25.196	0.000	0.135	0.899
Rain × Age	9	-1817.557	3653.523	32.964	0.000	0.128	0.899
SF × Age	7	-1820.926	3656.105	35.546	0.000	0.012	0.876
SF + Age	6	-1823.061	3658.311	37.752	0.000	0.011	0.876
Rain + Age	7	-1822.205	3658.664	38.105	0.000	0.126	0.899
Rain	6	-1823.604	3659.397	38.838	0.000	0.127	0.899
SF	5	-1824.808	3659.751	39.192	0.000	0.010	0.875
Age	5	-1831.286	3672.707	52.148	0.000	0.000	0.877
Null	4	-1832.682	3673.453	52.894	0.000	0.000	0.876

5.5 Discussion

Taken together, these results demonstrate that SF can be used to buffer the effects of interannual climate variability and climate risks on a threatened tropical bird population. Interannual variability in late winter-early spring rainfall and the timing of summer tropical cyclones results in year-to-year variation in a window of favourable conditions for breeding by echo parakeets. Late winter-early spring rainfall is likely to affect the availability of natural food sources, such as fruit, flowers and other plant material. For example, the intensity and species richness of fruiting in tropical forest in Madagascar are positively correlated with rainfall, particularly in the dry season (Dunham *et al.*, 2018). Phenological responses by echo parakeets are effectively maladaptive, as delayed breeding occurs in drier late winter-early spring conditions, after which cyclones also tend to be early. The correlation between late winter-early spring rainfall and the timing of cyclones is perhaps due to a link with synoptic scale weather patterns. Previous research has shown that spring (JAS, SON) synoptic-scale conditions can be used to predict the number of summer (DJFM) cyclone days near Mauritius (Jury *et al.*, 1999). Early cyclones present a risk to the realisation of high breeding success in older females. SFed pairs breed earlier than non-SFed pairs, especially in drier springs. The provision of SF therefore re-schedules breeding in a species at risk of climate impacts associated with timing. It should be noted that a limitation of this study is the availability of only nine years of comprehensive data on breeding success.

It is well established that SF provision influences the breeding phenology and demography of birds, with strong evidence that timing is advanced by the use of SF (reviewed by Robb *et al.*, 2008; Ruffino *et al.*, 2014). This probably occurs because females have fewer constraints on the energetic demands of egg development (Robb *et al.*, 2008). SF appears to be more influential on the phenology of bird species at lower latitudes (Schoech and Hahn, 2007; Dhondt, 2010; Ruffino *et al.*, 2014), perhaps because of greater underlying plasticity in timing (Ruffino *et al.*, 2014). The estimates of FED advancement in echo parakeets taking SF are in the mid-range of estimates (0-25 days) recorded for bird species from various latitudes (Dhondt, 2010). In a study on the hihi in New Zealand, it was shown that SF can buffer against the impacts of changes in rainfall on survival and recruitment, which probably occur through effects on natural food availability, such that local extirpation due to climate change would be delayed, but probably not prevented (Correia *et al.*, 2015). It has been suggested that SF could be used to adjust the reproductive timing of temperate species that are at risk of trophic mismatch in a changing climate due to constraints on phenological adaptation (Smith and Smith, 2013). The scheduling of life-history events and the relative timing of extreme events is highly influential on demography and can affect the status of threatened species. For example, later re-scheduling of nesting by Chinese crested terns (*Thalasseus bernsteini*) is caused by egg-harvesting, and this increases the exposure of broods to typhoons (Chen *et al.*, 2015). This is an example of adverse re-scheduling caused by human activities, and probably represents a synergistic effect with typhoon occurrence. The present study demonstrates the potential for SF to reduce the temporal overlap of nesting attempts with cyclones and thus reduce adverse timing relative to unfavourable abiotic conditions.

This study also provides evidence that age modulates climate impacts in the echo parakeet, with the strongest effects of late winter-early spring rainfall variation and early cyclones apparently being felt by different age classes. Climate impacts in the echo parakeet system may therefore be viewed as operating on the age axis of inexperience in youth and senescence in later life. Experience may influence the impacts of food limitation in drier springs because less experienced birds have acquired less knowledge of where to forage for food in times of drought and food shortages. Knowledge of the immediate landscape and the location of various plant species that produce food in different conditions and seasons is expected to be gained with age. This would explain why the greatest delays in breeding occur in younger non-SFed birds during dry springs. Birds in the older age class show less delay in dry springs and less influence from SF use, perhaps because experience of where to forage makes them more resilient to food shortages associated with dry weather.

The negative impacts of cyclones in older females may represent weather-mediated reproductive senescence. The majority of nests that overlapped with a tropical cyclone did so during the brood phase, thus the negative impact occurs during chick-rearing. This could occur through effects on energy budgets, foraging efficiency or behavioural responses. For example, foraging efficiency or frequency may be reduced in strong winds and heavy rain, or adult birds may prioritise their own wellbeing in such conditions relative to their investment in raising nestlings in favourable conditions. However, there is no evidence that clutch size shows the same senescence pattern, as females in the older age class lay larger clutches overall.

Some breeding echo parakeets are over 15 years of age, and the species shows high adult survival (Gath, 2018), so senescence effects may not be expected from the age of 6 years. However, age-dependent reproductive success in some species, such as the Seychelles warbler (*Acrocephallus sechellensis*), peaks before birds have reached the mid-range of ages in breeding birds (Hammers *et al.*, 2012). In blue-footed boobies (*Sula nebouxii*), nest defence peaks at around the mid-range of ages of breeding birds and then decreases later in life (Ortega *et al.*, 2017), implying that behavioural responses or investment associated with breeding change before individuals reach old age. Although egg survival is negatively impacted by cyclones in older echo parakeets, these females also lay larger clutches on average, thus their average fledgling production is only reduced to the level of younger birds. The occurrence of cyclones therefore negates the clutch size and experience advantage in older females, and a section of the population that is usually the most productive experiences a reduction in breeding success. This effect remains relatively small; however, it should be noted that the tropical cyclone events in the dataset used in this study did not cause severe conditions in Mauritius. The effects may be more pronounced when intense cyclones make landfall or pass in close proximity to Mauritius. The nonlinear decrease in egg survival with increasing temporal overlap with the first cyclone of the season implies that cyclones have a more negative impact on egg to fledging survival when they occur earlier in the nesting attempt, although the pattern may also result from exposure to additional cyclones and inclement weather soon after the first cyclone of the season.

In Mauritius, the frequency of tropical cyclones is projected to increase and then decrease as warming continues (Muthige *et al.*, 2018), with a projected increase in the number of very strong cyclones in the vicinity of the island (Bacmeister *et al.*, 2018). More frequent El Niño events could increase the number of cyclones forming in more western regions of the tropical Indian Ocean and passing close to Mauritius (Ho *et al.*, 2006). Rainfall is generally decreasing in Mauritius (Republic of Mauritius, 2010, 2016). Any trends towards stronger and earlier cyclones and continued decreases in rainfall are likely to have negative impacts on echo parakeet demography and will require adaptive management such as changing SF provision. This study demonstrates how altering resource availability can re-schedule the timing of life-history events and change exposure to climate risks. Such management techniques are likely to be important for species that are already threatened and reliant upon management.

5.6 References

Alexander, L. V. 2016. Global observed long-term changes in temperature and precipitation extremes: A review of progress and limitations in IPCC assessments and beyond. *Weather and Climate Extremes,* **11**: 4–16.

Bacmeister, J. T., Reed, K. A., Hannay, C., Lawrence, P., Bates, S., Truesdale, J. E., Rosenbloom, N. and Levy, M. 2018. Projected changes in tropical cyclone activity under future warming scenarios using a high-resolution climate model. *Climatic Change,* **146**: 547–560.

Barlow, J., França, F., Gardner, T. S., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J. and Graham, N. A. J. 2018. The future of hyperdiverse tropical ecosystems. *Nature,* **559**: 517–526.

Barton, K. 2018. Package 'MuMIn', Multi-Model Inference, version 1.40.4.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G. and Green, P. 2018. Package 'lme4', Linear Mixed-Effects Models using 'Eigen' and S4, version 1.1-17.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. and Courchamp, F. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters,* **15**: 365–377.

BirdLife International 2018. Species factsheet: *Psittacula eques*. http://datazone.birdlife.org. Accessed on: 19/07/2018.

Bonebrake, T. C. and Mastrandrea, M. D. 2010. Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proceedings of the National Academy of Sciences of the United States of America,* **107**: 12581–12586.

Brawn, J. D., Benson, T. J., Stager, M., Sly, N. D. and Tarwater, C. E. 2017. Impacts of changing rainfall regime on the demography of tropical birds. *Nature Climate Change,* **7**: 133–136.

Brodie, J., Post, E. and Laurance, W. F. 2012. Climate change and tropical biodiversity: a new focus. *Trends in Ecology & Evolution,* **27**: 145–150.

Burnham, K. P., Anderson, D. R. and Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology,* **65**: 23–35.

Butt, N., Possingham, H. P., De Los Rios, C., Maggini, R., Fuller, R. A., Maxwell, S. L. and Watson, J. E. M. 2016. Challenges in assessing the vulnerability of species to climate change to inform conservation actions. *Biological Conservation,* **199**: 10–15.

Cartwright, S. J., Nicoll, M. A. C., Jones, C. G., Tatayah, V. and Norris, K. 2014. Agriculture modifies the seasonal decline of breeding success in a tropical wild bird population. *Journal of Applied Ecology,* **51**: 1387–1395.

Chen, S., Fan, Z., Roby, D. D., Lu, Y., Chen, C., Huang, Q., Cheng, L. and Zhu, J. 2015. Human harvest, climate change and their synergistic effects drove the Chinese Crested Tern to the brink of extinction. *Global Ecology and Conservation,* **4**: 137–145.

Correia, D. L. P., Chauvenet, A. L. M., Rowcliffe, J. M. and Ewen, J. G. 2015. Targeted management buffers negative impacts of climate change on the hihi, a threatened New Zealand passerine. *Biological Conservation,* **192**: 145–153.

Dawson, T. P., Jackson, S. T., House, J. L., Prentice, I. C. and Mace, G. M. 2011. Beyond predictions: Biodiversity conservation in a changing climate. *Science,* **332**: 53–58.

Delignette-Muller, M.-L., Dutang, C., Pouillot, R., Denis, J.-B. and Siberchicot, A. 2017. Package 'fitdistrplus', Help to Fit of a Parametric Distribution to Non-Censored or Censored Data, version 1.0-9.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. and Martin, P. R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America,* **105**: 6668–6672.

Dhondt, A. A. 2010. Broodedness, not latitude, affects the response of reproductive timing of birds to food supplementation. *Journal of Ornithology,* **151**: 955–957.

Dunham, A. E., Razafindratsima, O. H., Rakotonirina, P. and Wright, P. C. 2018. Fruiting phenology is linked to rainfall variability in a tropical rain forest. *Biotropica,* **50**: 396–404.

Easterling, D. R., Kunkel, K. E., Wehner, M. F. and Sun, L. 2016. Detection and attribution of climate extremes in the observed record. *Weather and Climate Extremes,* **11**: 17–27.

Elsner, J. B., Kossin, J. P. and Jagger, T. H. 2008. The increasing intensity of the strongest tropical cyclones. *Nature,* **455**: 92–95.

Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vie, J.-C., Akçakaya, H. R., Angulo, A., DeVantier, L. M., Gutsche, A., Turak, E., Cao, L., Donner, S. D., Katariya, V., Bernard, R., Holland, R. A., Hughes, A. F., O'Hanlon, S. E., Garnett, S. T., Şekercioğlu, Ç. H. and Mace, G. M. 2013. Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS One,* **8**: e65427.

Fox, J., Weisberg, S., Friendly, M., Hong, J., Andersen, R., Firth, D., Taylor, S. and R Core Team. 2018. Package 'effects', Effect Displays for Linear, Generalized Linear, and Other Models, version 4.0-1.

Gallego, M. C., Trigo, R. M., Vaquero, J. M., Brunet, M., García, J. A., Sigró, J. and Valente, M. A. 2011. Trends in frequency indices of daily precipitation over the Iberian Peninsula during the last century. *Journal of Geophysical Research - Atmospheres,* **116**: D02109.

Gath, H. C. 2018. Conservation Management of the Endangered Mauritius Parakeet *Psittacula echo*. PhD Dissertation. London, UK: University College London.

Geraci, M. 2018. Package 'lqmm', Linear Quantile Mixed Models, version 1.5.4.

Hammers, M., Richardson, D. S., Burke, T. and Komdeur, J. 2012. Age-Dependent Terminal Declines in Reproductive Output in a Wild Bird. *PLoS One,* **7**: e40413.

Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M.-S., Keatley, M. R., Woodward, C. A., Williamson, G., Duke, N. C. and Bowman, D. M. J. S. 2018. Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change,* **8**: 579–587.

Hawkins, E., Anderson, B., Diffenbaugh, N., Mahlstein, I., Betts, R., Hegerl, G., Joshi, M., Knutti, R., McNeall, D., Solomon, S., Sutton, R., Syktus, J. and Vecchi, G. 2014. Uncertainties in the timing of unprecedented climates. *Nature,* **511**: E3–E5.

Heller, N. E. and Zavaleta, E. S. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation,* **142**: 14–32.

Ho, C.-H., Kim, J.-H., Jeong, J.-H., Kim, H.-S. and Chen, D. 2006. Variation of tropical cyclone activity in the South Indian Ocean: El Niño-Southern Oscillation and Madden-Julian Oscillation effects. *Journal of Geophysical Research - Atmospheres,* **111**: D22101.

Hulme, P. E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology,* **42**: 784–794.

Hurrell, J. W. and Trenberth, K. E. 2010. Chapter 2. Climate Change. In *Effects of Climate Change on Birds* (eds: Møller, A. P., Fiedler, W. and Berthold, P.), pp. 9–29. Oxford, UK: Oxford University Press.

IPCC. 2014. Climate change 2014: Impacts, adaptation, and vulnerability. Fifth Assessment Report. Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Jentsch, A. and Beierkuhnlein, C. 2008. Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. *Comptes Rendus Geoscience,* **340**: 621–628.

Jones, C. G. 1987. The larger land-birds of Mauritius. In *Studies of Mascarene Island Birds* (ed: Diamond, A. W.), pp. 208–300. Cambridge, UK: Cambridge University Press.

Jones, C. G. and Duffy, K. 1993. Conservation management of the echo parakeet *Psittacula eques echo*. *Dodo,* **29**: 126–148.

Jones, C. G., Malham, J., Reuleaux, A., Richards, H., Raisin, C., Tollington, S., Zuel, N., Chowrimootoo, A. and Tatayah, V. 2013. Echo Parakeet *Psittacula eques*. In *The Birds of Africa: Volume VIII. The Malagasy Region* (eds: Safford, R. and Hawkins, F.), pp. 517–522. London, UK: Christopher Helm.

Jones, C. G. and Owadally, A. 1988. The life histories and conservation of the Mauritius kestrel *Falco punctatus*, pink pigeon *Columba mayeri*, and echo parakeet *Psittacula eques*. *Proceedings of the Royal Society of Arts and Sciences of Mauritius,* **5**: 79–129.

Jury, M. R., Pathack, B. and Parker, B. 1999. Climatic Determinants and Statistical Prediction of Tropical Cyclone Days in the Southwest Indian Ocean. *Journal of Climate,* **12**: 1738–1746.

Klein Tank, A. M. G., Zwiers, F. W. and Zhang, X. 2009. Guidelines on analysis of extremes in a changing climate in support of informed decisions for adaptation. Geneva, Switzerland: World Meteorological Organization.

Knapp, K. R., Kruk, M. C., Levinson, D. H., Diamond, H. J. and Neumann, C. J. 2010. The International Best Track Archive for Climate Stewardship (IBTrACS): Unifying Tropical Cyclone Data. *Bulletin of the American Meteorological Society,* **91**: 363–376.

Kossin, J. P., Olander, T. L. and Knapp, K. R. 2013. Trend analysis with a new global record of tropical cyclone intensity. *Journal of Climate,* **26**: 9960–9976.

Kundu, S., Faulkes, C. G., Greenwood, A. G., Jones, C. G., Kaiser, P., Lyne, O. D., Black, S. A., Chowrimootoo, A. and Groombridge, J. J. 2012. Tracking Viral Evolution during a Disease Outbreak: the Rapid and Complete Selective Sweep of a Circovirus in the Endangered Echo Parakeet. *Journal of Virology,* **86**: 5221–5229.

Kuznetsova, A., Brockhoff, P. B. and Bojesen, R. H. 2018. Package 'lmerTest', Tests in Linear Mixed Effects Models, version 3.0-1.

Martínez-Abraín, A. and Oro, D. 2013. Preventing the development of dogmatic approaches in conservation biology: A review. *Biological Conservation,* **159**: 539–547.

McKee, T. B., Doesken, N. J. and Kleist, J. 1993. The relationship of drought frequency and duration to time scales. In *8th Conference on Applied Climatology*. pp. 179–184. Anaheim, California.

McLeod, A. I. 2011. Package 'Kendall', Kendall rank correlation and Mann-Kendall trend test, version 2.2.

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., Sanchez, J. J., Kaiser, L. R., Stender, Y. O., Anderson, J. M., Ambrosino, C. M., Fernandez-Silva, I., Giuseffi, L. M. and Giambelluca, T. W. 2013. The projected timing of climate departure from recent variability. *Nature,* **502**: 183–187.

Moritz, C. and Agudo, R. 2013. The future of species under climate change: Resilience or decline? *Science,* **341**: 504–508.

Muthige, M. S., Malherbe, J., Englebrecht, F. A., Grab, S., Beraki, A., Maisha, T. R. and Van der Merwe, J. 2018. Projected changes in tropical cyclones over the South West Indian Ocean under different extents of global warming. *Environmental Research Letters,* **13**: 065019.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution,* **4**: 133–142.

Nicoll, M. A. C. 2004. The ecology and management of a re-introduced population of the Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Nicoll, M. A. C., Nevoux, M., Jones, C. G., Ratcliffe, N., Ruhomaun, K., Tatayah, V. and Norris, K. 2017. Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology,* **23**: 550–565.

Öberg, M., Arlt, D., Pärt, T., Laugen, A. T., Eggers, S. and Low, M. 2015. Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecology and Evolution,* **5**: 345–356.

Ortega, S., Sánchez-Macouzet, O., Urrutia, A., Rodríguez, C. and Drummond, H. 2017. Age-related parental care in a long-lived bird: implications for offspring development. *Behavioral Ecology and Sociobiology,* **71**: 132.

Parmesan, C., Root, T. L. and Willig, M. R. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society,* **81**: 443–450.

Powell, M. J. D. 2009. The BOBYQA algorithm for bound constrained optimization without derivatives. Cambridge, UK: Centre for Mathematical Sciences, University of Cambridge.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Republic of Mauritius. 2010. Second national communication of the Republic of Mauritius under the United Nations Framework Convention on Climate Change (UNFCCC). Vacoas, Mauritius: Mauritius Meteorological Services.

Republic of Mauritius. 2016. Third National Communication: Report to the United Nations Framework Convention on Climate Change. Port Louis, Mauritius.

Robb, G. N., McDonald, R. A., Chamberlain, D. E. and Bearhop, S. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment,* **6**: 476–484.

Rodrigues, A. S. L., Brooks, T. M., Butchart, S. H. M., Chanson, J., Cox, N., Hoffmann, M. and Stuart, S. N. 2014. Spatially Explicit Trends in the Global Conservation Status of Vertebrates. *PLoS One,* **9**: e113934.

Ruffino, L., Salo, P., Koivisto, E., Banks, P. B. and Korpimäki, E. 2014. Reproductive responses of birds to experimental food supplementation: a meta-analysis. *Frontiers in Zoology,* **11**: 80.

Safford, R. and Hawkins, F. 2013. *The Birds of Africa: Volume VIII. The Malagasy Region*. London, UK: Christopher Helm.

Schoech, S. J. and Hahn, T. P. 2007. Food supplementation and timing of reproduction: does the responsiveness to supplementary information vary with latitude? *Journal of Ornithology,* **148**: S625–S632.

Senapathi, D., Underwood, F., Black, E., Nicoll, M. A. C. and Norris, K. 2010. Evidence for long-term regional changes in precipitation on the East Coast Mountains in Mauritius. *International Journal of Climatology,* **30**: 1164–1177.

Shepherd, J. M., Grundstein, A. and Mote, T. L. 2007. Quantifying the contribution of tropical cyclones to extreme rainfall along the coastal southeastern United States. *Geophysical Research Letters,* **34**: L23810.

Smith, K. W. and Smith, L. 2013. The effect of supplementary feeding in early spring on the breeding performance of the Great Spotted Woodpecker *Dendrocopos major*. *Bird Study,* **60**: 169–175.

Staub, C. G., Stevens, F. R. and Waylen, P. R. 2014. The geography of rainfall in Mauritius: Modelling the relationship between annual and monthly rainfall and landscape characteristics on a small volcanic island. *Applied Geography,* **54**: 222–234.

Stein, B. A., Staudt, A., Cross, M. S., Dubois, N. S., Enquist, C., Griffis, R., Hansen, L. J., Hellmann, J. J., Lawler, J. J., Nelson, E. J. and Pairis, A. 2013. Preparing for and managing change: climate adaptation for biodiversity and ecosystems. *Frontiers in Ecology and the Environment,* **11**: 502–510.

Strauss, S. Y., Lau, J. A. and Carroll, S. P. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters,* **9**: 357–374.

Tatayah, R. V. V., Malham, J., Haverson, M. J., Reuleaux, A. and Van de Wetering, J. 2007. Design and provision of nest boxes for echo parakeets *Psittacula eques* in Black River Gorges National Park, Mauritius. *Conservation Evidence,* **4**: 16–19.

Thorsen, M., Shorten, R., Buchanan, G., Williams, S., Jones, V., Swinnerton, K., de Ravel, F., Webb, J., Lam, R. and Schellander, H. 1997. Echo parakeet (*Psittacula eques*) management report 1997. Unpublished report. Vacoas, Mauritius: Mauritian Wildlife Foundation and National Parks and Conservation Service.

Tollington, S., Greenwood, A., Jones, C. G., Hoeck, P., Chowrimootoo, A., Smith, D., Richards, H., Tatayah, V. and Groombridge, J. J. 2015. Detailed monitoring of a small but recovering population reveals sublethal effects of disease and unexpected interactions with supplemental feeding. *Journal of Animal Ecology,* **84**: 969–977.

Tollington, S., Jones, C. G., Greenwood, A., Tatayah, V., Raisin, C., Burke, T., Dawson, D. A. and Groombridge, J. J. 2013. Long-term, fine-scale temporal patterns of genetic diversity in the restored Mauritius parakeet reveal genetic impacts of management and associated demographic effects on reintroduction programmes. *Biological Conservation,* **161**: 28–38.

Williams, J. W., Jackson, S. T. and Kutzbach, J. E. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America,* **104**: 5738–5742.

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffman, A. A. and Langham, G. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology,* **6**: 2621–2626.

WMO. 2012. Standardized Precipitation Index User Guide. Geneva, Switzerland: World Meteorological Organization.

Young, G. 1987. Notes on the nesting behaviour of the echo parakeet *Psittacula eques echo*. *Dodo,* **24**: 102–111.

Zuur, A. F., Ieno, E. N. and Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution,* **1**: 3–14.

5.7 Appendix

Table A5.1. Candidate base models for fledgling production in echo parakeet breeding attempts. All models include female identity and year as random effects. *N* = 533 clutches (2005/2006-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
FED + Age + SF × Outbreak	8	-796.939	1610.153	0.000	0.610	0.122	0.127
FED + Age + SF + Outbreak	7	-799.410	1613.034	2.881	0.144	0.111	0.117
FED + Age + SF	6	-800.808	1613.776	3.623	0.100	0.103	0.115
FED + Age + SF + Nest	7	-800.450	1615.114	4.961	0.051	0.105	0.115
FED + Age + SF + Subpop	7	-800.633	1615.480	5.327	0.042	0.104	0.116
FED + Age + SF + Elevation	7	-800.807	1615.828	5.675	0.036	0.103	0.115
FED × Subpop + Age + SF	8	-800.500	1617.275	7.122	0.017	0.105	0.116
Null	3	-819.518	1645.082	34.929	0.000	0.000	0.078

Table A5.2. Analysis of climate impacts on fledgling production in echo parakeet breeding attempts. Only the base model and those more parsimonious are shown. Base model: FED + Age + SF × Outbreak. All models include female identity and year as random effects. *N* = 533 clutches (2005/2006-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base + Mean Tmax	0.160	9	-795.330	1609.005	0.000	0.098	0.128	0.133
Base + Raindays	-0.054	9	-795.711	1609.766	0.761	0.067	0.127	0.132
Base	-	8	-796.939	1610.153	1.148	0.055	0.122	0.127

Table A5.3. Candidate base models for egg survival in echo parakeet breeding attempts. All models include female identity and year as random effects. *N* = 533 clutches (2005/2006-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
FED + Age + SF × Outbreak	8	-667.565	1351.404	0.000	0.713	0.067	0.201
FED × Subpop + Age + SF	8	-669.194	1354.662	3.258	0.140	0.064	0.204
FED + Age + SF + Subpop	7	-671.068	1356.349	4.945	0.060	0.059	0.199
FED + Age + SF	6	-672.721	1357.602	6.198	0.032	0.053	0.197
FED + Age + SF + Outbreak	7	-672.022	1358.258	6.854	0.023	0.058	0.192
FED + Age + SF + Elevation	7	-672.174	1358.562	7.158	0.020	0.055	0.197
FED + Age + SF + Nest	7	-672.704	1359.622	8.218	0.012	0.053	0.196
Null	3	-684.928	1375.902	24.498	0.000	0.000	0.188

Table A5.4. Analysis of impacts on egg survival in echo parakeet breeding attempts from incubation (Inc) and brood phase climate indices. Only the base model and those more parsimonious are shown. Base model: FED + Age + SF × Outbreak. All models include female identity and year as random effects. N = 533 clutches (2005/2006-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base + Brood Cyclone × Age	-	10	-663.869	1348.158	0.000	0.099	0.077	0.217
Base + Brood Mean Tmax	0.329	9	-665.588	1349.521	1.363	0.050	0.072	0.208
Base + Brood Mean Tmax^2	0.0193/0.175	10	-664.638	1349.697	1.539	0.046	0.076	0.214
Base + Inc Raindays90 × Age	-	10	-664.843	1350.108	1.950	0.037	0.075	0.212
Base + Brood Cyclone × SF	-	10	-664.874	1350.169	2.011	0.036	0.073	0.207
Base + Brood Max Dry Spell × Age	-	10	-664.963	1350.348	2.190	0.033	0.076	0.201
Base + Brood Mean Tmax^2 × SF	-	12	-662.982	1350.564	2.406	0.030	0.079	0.216
Base + Inc Max Rain Spell	-0.125	9	-666.228	1350.800	2.642	0.027	0.071	0.204
Base + Brood Mean Tmax^2 × Age	-	12	-663.106	1350.813	2.655	0.026	0.079	0.217
Base + Brood Mean Tmax × SF	-	10	-665.227	1350.875	2.717	0.026	0.074	0.209
Base + Inc Max Dry Spell^2	0.801/0.103	10	-665.240	1350.902	2.744	0.025	0.074	0.194
Base + Inc Max Dry Spell^2 × SF	-	12	-663.307	1351.214	3.056	0.022	0.080	0.199
Base + Brood Cyclone	-0.360	9	-666.455	1351.254	3.096	0.021	0.071	0.205
Base + Inc Mean Tmax^2 × Age	-	12	-663.354	1351.309	3.151	0.021	0.082	0.202
Base	-	8	-667.565	1351.404	3.246	0.020	0.067	0.201

Table A5.5. Candidate base models for clutch size in echo parakeet breeding attempts. All models include female identity and year as random effects. N = 533 clutches (2005/2006-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
FED + Age + SF + Elevation	8	-440.208	896.692	0.000	0.610	0.144	0.380
FED + Age + SF	7	-442.594	899.401	2.709	0.157	0.111	0.366
FED + Age + SF + Subpop	8	-441.734	899.743	3.051	0.133	0.131	0.373
FED × Subpop + Age + SF	9	-441.338	901.019	4.327	0.070	0.137	0.382
FED + Age + SF + Outbreak	8	-444.028	904.330	7.638	0.013	0.112	0.368
FED + Age + SF + Nest	8	-444.186	904.647	7.955	0.011	0.111	0.367
FED + Age + SF × Outbreak	9	-443.938	906.221	9.529	0.005	0.114	0.368
Null	4	-464.128	936.332	39.640	0.000	0.000	0.357

Table A5.6. Analysis of climate impacts on clutch size in echo parakeet breeding attempts. Only the base model and those within ΔAICc<7 are shown. Base model: FED + Age + SF + Elevation. All models include female identity and year as random effects. *N* = 533 clutches (2005/2006-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base	-	8	-440.208	896.692	0.000	0.664	0.144	0.380
Base + Tmax10 Days	-0.043	9	-441.474	901.293	4.601	0.067	0.145	0.385
Base + Mean Tmax	0.051	9	-441.584	901.513	4.821	0.060	0.144	0.383
Base + Drought	-0.017	9	-442.044	902.433	5.741	0.038	0.145	0.381

Table A5.7. Candidate base models for first egg-laying date (FED) in echo parakeet breeding attempts. All models include female identity and year as random effects. *N* = 658 clutches (1997/1998-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
SF × Outbreak + Elevation + Subpop + Nest	14	-2655.945	5340.544	0.000	0.990	0.072	0.495
SF × Outbreak	11	-2664.325	5351.059	10.515	0.005	0.058	0.491
SF + Outbreak + Elevation + Subpop + Nest	11	-2664.451	5351.312	10.768	0.005	0.070	0.489
Outbreak + Elevation + Subpop + Nest	10	-2669.388	5359.116	18.572	0.000	0.054	0.492
SF + Outbreak	8	-2672.847	5361.916	21.372	0.000	0.056	0.485
SF + Elevation + Subpop + Nest	8	-2676.209	5368.640	28.096	0.000	0.051	0.502
Elevation + Subpop + Nest	7	-2680.610	5375.392	34.848	0.000	0.034	0.495
Outbreak	7	-2681.960	5378.093	37.549	0.000	0.024	0.494
SF	5	-2684.293	5378.677	38.133	0.000	0.034	0.491
Null	4	-2692.384	5392.830	52.286	0.000	0.000	0.481

Table A5.8. Analysis of climate impacts (July-September indices) on first egg-laying date (FED) in echo parakeet breeding attempts. Base model: SF × Outbreak + Elevation + Subpop + Nest. All models include female identity and year as random effects. *N* = 658 clutches (1997/1998-2013/2014). DF = degrees of freedom; ln(L) = log-likelihood.

Model	**Standardised climate index coefficient**	**DF**	**ln(L)**	**AICc**	**ΔAICc**	**AIC Weight**	**Marginal Pseudo-R^2**	**Conditional Pseudo-R^2**
Base + Rainfall^2	-5.519/2.362	16	-2650.482	5333.814	0.000	0.184	0.120	0.511
Base + Raindays90^2	-3.943/2.049	16	-2650.484	5333.817	0.003	0.184	0.106	0.513
Base + Rainfall90^2	-4.648/0.584	16	-2650.609	5334.068	0.254	0.162	0.112	0.508
Base + Drought	9.321	15	-2652.100	5334.947	1.133	0.104	0.116	0.505
Base + Raindays^2	-3.136/1.336	16	-2651.433	5335.715	1.901	0.071	0.102	0.514
Base + Mean Tmax^2	1.565/2.509	16	-2651.494	5335.836	2.022	0.067	0.090	0.511
Base + Rainfall90	-4.461	15	-2652.657	5336.062	2.248	0.060	0.112	0.496
Base + Rainfall	-4.295	15	-2652.799	5336.347	2.533	0.052	0.104	0.495
Base + Raindays90	-3.900	15	-2653.010	5336.768	2.954	0.042	0.103	0.501
Base + Raindays	-3.067	15	-2653.361	5337.470	3.656	0.030	0.089	0.501
Base + Mean Tmax	1.635	15	-2653.834	5338.415	4.601	0.018	0.074	0.504
Base + Max Rain Spell	-0.615	15	-2654.343	5339.433	5.619	0.011	0.071	0.504
Base + Max Rain Spell^2	0.584/-0.265	16	-2653.592	5340.033	6.219	0.008	0.070	0.516
Base	-	14	-2655.945	5340.544	6.730	0.006	0.072	0.495

Chapter 6

General Discussion

6.1 Overview

A premise of this thesis has been that climate change could increase risks to the conservation of species and to the continued recovery of those already threatened. As such, achievements in biodiversity conservation that have involved substantial investments could be put at risk. These ideas have been explored for species conservation in Mauritius, through the study of climate trends in areas of conservation importance and climate impacts on the breeding phenology and demography of two threatened bird populations. This study is conducted in the context of a paucity of long-term datasets on tropical species, and an important aim has been to contribute to the understanding of tropical species responses to climate change and climate variability. Such detailed datasets are needed in order to gain a detailed understanding of climate effects.

The results of Chapter 3 show that even within a small island of <2,000 km^2 the same changes in climate risks should not be assumed for all areas and populations of conservation concern. The analyses indicate that populations of globally threatened species that are separated by several kilometres are exposed to differing trends in the occurrence of climate risks associated with precipitation. Rainfall indices show increases in the Bambous Mountains since the 1960s, while droughts in the dry season appear to have become more likely on Ile aux Aigrettes since the 1950s.

In Chapter 4, the analysis of climate impacts on Mauritius kestrel breeding phenology and breeding success provides evidence that this species is synchronising its timing of breeding with a seasonal climate window. The seasonal window is defined by warming temperatures in the late winter and early spring and by the onset of the summer rainy season. The population shows phenological plasticity and tracking of changes in the climate window, which occur as late winter-early spring temperatures increase and earlier onset of the rainy season occurs in some recent years. Mauritius kestrels are thus advancing their breeding phenology and synchronising their breeding activity with a window of favourable conditions, despite the genetic legacy of a severe population bottleneck.

The results of Chapter 5 indicate that the breeding phenology of echo parakeets responds to interannual variability in late winter-early spring rainfall, and that earlier breeding tends to occur after wetter conditions. The use of supplementary food buffers the impact of interannual variability in environmental conditions, although the extent of the influence depends on age. Breeding success in older females is negatively impacted by tropical cyclones late in the breeding season. Further analysis shows that cyclones tend to occur earlier after drier conditions in late winter-early spring, showing that the time window of favourable conditions narrows in some years. However, supplementary feeding re-schedules breeding and reduces the temporal overlap of breeding attempts with cyclones.

6.2 Climate risks for species conservation

The overarching themes of this study have included the identification of climate risks in ecological contexts, and the importance of the temporal and spatial distribution of climate risks. These aspects are fundamentally relevant to the demography and life history of species and thus the future conservation of their populations.

6.2.1 True extremes and ecologically high impact weather

The analysis of climate impacts on the Mauritius kestrel and echo parakeet in this study included indices for overall conditions and extreme events. To increase the sample of extreme events in statistical analyses, thresholds were used that capture both true extremes and 'moderate extremes' (Klein Tank *et al.*, 2009; Alexander, 2016; Easterling *et al.*, 2016), e.g. the 10% highest or lowest values. The results for the Mauritius kestrel indicate that total rainfall, rather than 90th percentile rainfall or raindays, is marginally the most parsimonious index for rainfall impacts on breeding success. This result illustrates the limitations of characterising extreme events in an ecological context by using percentile thresholds to define events based on rarity. An alternative approach could involve a form of sensitivity analysis to identify the threshold associated with the greatest effect. Given that total rainfall has most support in this analysis, it is therefore the case that the notional temporal overlap of nesting attempts with the onset of the rainy season is a powerful predictor of the outcome of breeding attempts. Similarly, tropical storms and cyclones impact breeding success in echo parakeets, although this is influenced by age. In both cases, there is a contribution to negative impacts from conditions that are not true extremes.

An important limitation of the present study and many other studies into the ecological impacts of extremes, is that true extremes are, by definition, rare events, and there are usually few, if any, that are captured in the sample years of ecological datasets. Most long-term ecological datasets and studies cover decadal time scales in which true extremes are usually very infrequent. In the present study, the rarity of true extremes places limitations on how reliably their impact can be analysed in isolation from moderate extremes. Despite these limitations, it is evident from the results of this study that phenology and demography in tropical species can be modulated by the occurrence and timing of events that do not always represent true extremes, such as tropical storms. In this study, extremes of rainfall and temperature have been defined based on ecological or climatological seasons, thus their timing can in effect define seasons and their transitions from an ecological perspective. The timing of extreme events relative to the life cycle stages of an organism is an important aspect that influences impacts (reviewed by Bailey and van de Pol, 2016; Sergio *et al.*, 2018). The results of the present study contribute to our understanding of the mechanisms and pressures that influence biological seasonality in the tropics.

In a changing climate, the impacts of changes in true extremes may take longer to become apparent compared to changes in annually-occurring high impact events, which are perhaps more likely to impact phenology and demography over the shorter-term. These more frequent events could be a more influential source of selection pressures on life histories than true extremes. Climate change may start to exert a strong effect on populations and ecosystems over the coming decades as moderate extremes start to emerge from recent variability (Tan *et al.*, 2018). Biodiversity conservation thus has a challenge to meet in the short-term future from changes in moderate extremes.

The debate on how to define extreme events in ecological contexts will no doubt continue, but it may only be relevant to studies that utilise more than 50 years of ecological data. Such datasets are needed if extremes are to be defined based on extreme biological responses. However, impact-based definitions complicate the process of identifying such events, because the event itself and its impacts become conflated (McPhillips *et al.*, 2018). The impact of an extreme event on a biological system is a product of the conditions experienced and the vulnerability of the system. Impact definitions of extremes therefore risk not separating the rarity and severity of the abiotic event from the underlying susceptibility of the impacted biotic system. Defining extremes in ecological studies using rarity thresholds that are relevant to societal impacts is arguably less meaningful ecologically, but more practical from the perspective of policy-makers. Conclusions on human and ecological impacts can be drawn from the same study or climate projection. This approach could facilitate the design of climate change adaptation measures that aim to benefit both human communities and natural systems. In the present study, established meteorological definitions of extremes or high impact weather were used, and these allow analyses to be carried out to establish which climate aspects and thresholds are relevant to ecological impacts in a given species or ecosystem.

The ecological impacts of extremes and moderate extremes in weather conditions are evidently idiosyncratic, and it is difficult to generalise about impacts across species and ecosystems (van de Pol *et al.*, 2017; Greenville *et al.*, 2018; Harris *et al.*, 2018). This increases the urgency and need for detailed studies on a variety of species from different ecoregions. Some generalities should be justifiable between closely related species, and these could be applied using trait-based approaches (Foden *et al.*, 2013; Urban *et al.*, 2016). Detailed data on the biological mechanisms through which climate affects species are vital, as predictive models that ignore such mechanisms often become unreliable when extrapolating to projections of novel climates (reviewed by Urban *et al.*, 2016).

6.2.2 Local-scale trends in climate risks

This study has demonstrated the potential importance of local-scale variation in long-term climate trends, especially related to precipitation and extreme precipitation. Previous research has shown that variation in the local response of extremes to climate change is driven by climate processes at fine spatial scales (Diffenbaugh *et al.*, 2005). This variation is expected to be particularly important for very restricted-range species, whose population-level exposure to future climate risks will be most reliably inferred by studying local climate trends. Restricted-range species have been defined as those occupying a global (resident or breeding) range or extent of occurrence (EOO) of less than 50,000 km^2 (Stattersfield *et al.*, 1998; Eken *et al.*, 2004). Local-scale variation in climate trends will be less important at the population level towards this upper range limit, but is expected to be very influential on climate change vulnerability in species occupying much smaller areas. This is arguably most relevant to species endemic to topographically varied islands and mountain ranges.

Such spatial variation has implications for the future exposure of populations and sites of conservation importance to climate risks; however, this appears to have been frequently overlooked in previous research. Kittel *et al.* (2015) noted the ecological relevance of local variation in precipitation trends for montane plants in particular. Mountain ranges also show spatial variation in long-term temperature trends and these, combined with precipitation trends, influence the elevational ranges of birds (Tingley *et al.*, 2012). Attention has been drawn to the inadequacy for ecological research of climate projections that have coarse spatial and temporal resolutions (Nadeau *et al.*, 2017). Likewise, the importance of variation in microclimates has received much attention, including ambient temperatures within and outside forest (Senior *et al.*, 2017), as well as the potential for fine-scale temperature metrics to improve species distribution models (Frey *et al.*, 2016). Maclean *et al.* (2017) studied temperature trends at fine scales and identified some sources of variation. However, less focus has been given to local-scale trends in climate risks and their influence on climate change vulnerability. Urban *et al.* (2016) point out that researchers should evaluate environmental influences from the point of view of their study species. The relevant spatial resolution may be far more fine-scaled than the resolution at which predictions are currently made, with a scale of mm to ha usually being more appropriate (Urban *et al.*, 2016; Senior *et al.*, 2017).

Based on the results of the present study, it is recommended that future climate change vulnerability assessments for restricted-range species, especially in mountainous regions and topographically complex islands, incorporate analyses of local-scale trends in climate risks. However, it should be noted that the application of past trends in climate risks to species vulnerability assessments has some limitations, most notably that climate projections, particularly for precipitation, are not necessarily monotonic (Hawkins *et al.*, 2014b). Projections for some tropical regions show a change in the direction of precipitation trends, with an increase followed by a decrease, owing to the projected movements of the Inter-Tropical Convergence Zone (Hawkins *et al.*, 2014b). This could mean that in some areas past trends will not be indicative of future trends in climate risks. However, recent trends in local climate risks should be indicative of the immediate and short-term future pressures being experienced by a population.

Threatened species in Mauritius occupy very restricted ranges and this increases the relevance of local climate trends to management actions. The findings of the present study imply that different management actions will be needed for species of conservation concern present in the Bambous Mountains, BRGNP, and on IAA. Strategies to alleviate drought impacts on IAA could involve increased availability of fresh water, artificial nectar and fruit. In comparison, management in the Bambous Mountains may need to alleviate the impacts of increasing rainfall and more frequent rainfall extremes. For Mauritius kestrels, this might involve the re-design of artificial nest-boxes to increase resistance to heavy rain or responsive supplementary feeding during seasons with frequent and heavy raindays. Decreasing rainfall in the central uplands implies that the provision of supplementary food will become increasingly important for the conservation of the echo parakeet. The local-scale variation in climate trends shown in this study also implies that ecosystem-based adaptation should be implemented and adapted at the local scale for the benefit of human communities and natural systems.

6.2.3 Using management to reduce climate risks

The approach of adaptive conservation management in a changing climate has gained prominence in recent decades (Heller and Zavaleta, 2009; Stein *et al.*, 2013). The adaptation of management represents an ongoing process of change and modification based on the reassessment of needs. Adaptive management can be seen as addressing one or more of the components of climate change vulnerability, that is, exposure, sensitivity and adaptive capacity (Stein *et al.*, 2013). It is difficult to generalise about climate impacts on species (Urban *et al.*, 2016); however, case studies on species for which long-term detailed data exist provide insights and guidelines from which some generalities can be drawn, perhaps based on taxonomy or traits (Urban *et al.*, 2016). The results for the echo parakeet provide such a case study that may prompt future research or management trials in other species.

The re-scheduling of phenology through altered resource availability represents a management strategy that can be readily adapted to changing conditions. The results for the echo parakeet show that supplementary feeding can buffer the effects of environmental variability and re-schedule breeding in species at risk from changes in high impact events. However, the extent to which breeding can be re-scheduled by such intervention may place substantial limits on its potential use as climate change continues. Indeed, such management interventions will require the estimation of their capacity and therefore the limits to what they can achieve. While there is no strong evidence of a systematic trend in climate risks for the echo parakeet, any trend that emerges in the future, or any increase in interannual variability, could have negative impacts. It has been muted that supplementary food could be used to effectively re-schedule species that are at risk of trophic mismatch in a changing climate (Smith and Smith, 2013). This idea would be most relevant to temperate species; however, the present study has provided an example of re-scheduling in a tropical species at risk of adverse timing relative to abiotic conditions. While common and widespread species will be in less need of intervention to re-schedule maladaptive or constrained phenology, rare and restricted-range species are at higher risk from negative demographic effects and a worsening in status.

The echo parakeet may already show some adaptations to the impacts of climate variability. Older females, which show reduced breeding success when their nesting attempts coincide with a cyclone, lay larger clutches, thus reducing the impact of reduced egg survival on their overall breeding fitness. Younger females are at increased risk of delayed breeding in dry springs, but there is no evidence of negative impacts from cyclones in these birds. The danger is that climate variability increases beyond the range that the species is adapted to. An increasing frequency of breeding seasons that are preceded by drought conditions in late winter-early spring and in which cyclones occur in December could result in demographic changes at the population level. Without the existing provision of supplementary food, which is used by the majority of birds, the population or sections of the population might show substantial interannual fluctuations in phenology and breeding success. The underlying vulnerability of the echo parakeet to interannual climate variability may be influenced by the destruction and degradation of its habitat, although data are not available to test this. It is possible that supplementary food is buffering a vulnerable population against interannual climate variability in the context of a shortage of food resources in most years.

Supplementary food may be having effects in multiple ways, by both buffering against environmental variability and improving the nutrition of adult birds and nestlings.

6.3 Tropical animal phenology

Phenology is a profoundly important aspect of life-history strategies (Miller-Rushing *et al.*, 2010); however, our understanding of climate influences on phenology is very poor for animal species in the tropics (Charmantier and Gienapp, 2013; Pearce-Higgins and Green, 2014; Cohen *et al.*, 2018; Post *et al.*, 2018). The results of this thesis shed light on the phenological responses of tropical birds to a changing climate.

6.3.1 Seasonal climate windows

It has long been assumed that animal phenology in tropical regions is most influenced by precipitation, as opposed to temperature and other aspects of the climate, and recent meta-analyses have supported this view (Pearce-Higgins and Green, 2014; Cohen *et al.*, 2018). Evidence from phenological data supports the general expectation that endotherms are less sensitive to abiotic conditions (Cohen *et al.*, 2018), and this may be assumed to be particularly true at tropical latitudes, where temperature variability is relatively limited (Pearce-Higgins and Green, 2014). Previous research on the phenology of the Mauritius kestrel tested the impacts of precipitation, but not temperature, although there was no directional trend evident in the timing of egg-laying in the earlier dataset (Senapathi, 2009; Senapathi *et al.*, 2011). The results of the present study, utilising an extended dataset for the Mauritius kestrel, imply that the importance of temperature as a phenological cue has been underestimated for this species and probably for other tropical endotherms. If relatively small variations in tropical photoperiod can influence phenology it is plausible that temperature is also a very influential cue for many tropical animals. Its influence on endotherms may be particularly apparent when those species rely on the activity levels and abundance of ectotherms, which are likely to be more responsive to changes in temperature (Deutsch *et al.*, 2008). However, it should also be noted that Mauritius is in the higher latitudes of the tropics, and the patterns observed in this study may be less relevant in areas closer to the equator.

Systematic shifts and interannual variability in seasonal climate windows may be common mechanisms through which tropical species adapt their phenology. The results for the Mauritius kestrel suggest that it is successfully adapting its phenology to shifts and variability in a window of favourable climate conditions. Selection pressures on the timing of breeding may be acting at both ends of the seasonal window. The coincidence of the breeding season with warming temperatures, rather than the start of the dry season, implies that temperature influences selection on timing, perhaps through prey availability. Burgess *et al.* (2011) suspected that the breeding season is influenced by prey density. The timing of breeding in Mauritius kestrels could in part be a legacy of the species' lineage, and temperature may have been retained as a phenological cue from earlier in the species' evolution before its colonisation of Mauritius around 1.9-2.6 MYA (Groombridge *et al.*, 2002). However, the species' seasonality appears to represent a compromise between adjustments to contemporary patterns in seasonal temperature and rainfall. Both of these factors could affect prey availability, but the timing of breeding relative to the rainy season is probably related to its implications for hunting conditions and chick survival. The Mauritius kestrel, like many threatened island species, has suffered reductions in its population and genetic diversity (Groombridge *et al.*, 2000; Ewing *et al.*, 2008). Such impacts might be expected to limit the species' ability to adapt to shifts in climate if there were an influence of genetic diversity on plasticity. However, the results of the present study imply that the species is able to adjust its phenology to changes in temperature. Small populations, including those that have experienced population and genetic bottlenecks, may therefore retain some adaptive potential for responding to climate change.

The echo parakeet also appears to breed within a seasonal window of favourable conditions, defined by late winter-early spring rainfall and the timing of summer cyclones, although this window shows interannual variability rather than directional change. A recognition that changing seasonal windows may be a common mechanism in the phenology and demography of tropical animals may help the development of strategies to safeguard threatened species in a changing climate. These insights are very important given the projected emergence of novel climates in tropical regions this century (Williams *et al.*, 2007; Mora *et al.*, 2013; Hawkins *et al.*, 2014a). Projected warming in Mauritius could exceed the adaptive limits of the Mauritius kestrel in the coming decades. For now, it appears that phenological shifts by Mauritius kestrels represent a vital mode of adaptation to climate change in this species. This is important because phenological shifts can mitigate the need for range shifts (Socolar *et al.*, 2017), and the scope for range shifts in this species is very limited. These changes in phenology may 'buy time' before adaptive limits are exceeded and new management interventions are required. Such insights are very relevant to seasonally breeding tropical species, although many tropical species do not exhibit strong seasonality.

6.3.2 Changes in tropical seasons

Further improvements are needed in our understanding of the mechanisms that influence seasonality in tropical species, as these will ultimately assist the projection of future impacts from climate change. Species in the tropics are typically adapted to a relatively narrow range of temperature conditions, thus tropical species may be among the most vulnerable to climate change (Deutsch *et al.*, 2008; Bonebrake and Mastrandrea, 2010). The tropics harbour vast amounts of biodiversity (Barlow *et al.*, 2018), and tropical regions are projected to be among the first to emerge from recent climate variability into relatively novel climate regimes (Williams *et al.*, 2007; Mora *et al.*, 2013; Hawkins *et al.*, 2014a; Dahinden *et al.*, 2017; Mahony and Cannon, 2018). Indeed, for many parts of the tropics there are currently no climate analogues anywhere with seasonal cycles of temperature and precipitation matching projected future conditions (Dahinden *et al.*, 2017), implying that these future climates will be novel relative to all current climate regimes. Furthermore, the local warming signal is projected to emerge from interannual variability in many tropical countries by the 2030s (Mahlstein *et al.*, 2011).

Trends in rainfall seasonality in the tropics show regional variation (Feng *et al.*, 2013). Precipitation patterns in the tropics are projected to change substantially during this century, although there is inconsistency among model projections (Kent *et al.*, 2015; Chadwick *et al.*, 2016). Such changes are expected to have strong ecological effects in the tropics (Şekercioğlu *et al.*, 2012; Bonebrake, 2013), and are likely to affect phenology and alter the impacts of seasonal precipitation transitions on fitness and population dynamics. The present study incorporated recently-developed methods for identifying the onset and cessation of rainy seasons (Liebmann *et al.*, 2012; Dunning *et al.*, 2016). These methods have the potential for wide use in ecological studies at various spatial scales. The development of more objective methods to define seasons will continue to be important for impact studies relevant to human society and natural systems.

6.4 Climate change and conservation in Mauritius

The results of this study have the potential to help conservation managers in Mauritius safeguard the vertebrate biodiversity gains made in recent decades (Rodrigues *et al.*, 2014). Understanding of local-scale variation in climate trends is likely to be important for assessing the climate change vulnerability of protected areas and other important conservation sites. Management actions at the site level could be tailored to local-scale variation in past climate trends and future projections. Spatial variation in climate trends may also influence future reintroduction and population reinforcement strategies. Although Mauritius kestrels in the Bambous Mountains appear to be tracking a window of favourable conditions, rainfall is increasing in all seasons in this area. Future strategies for the Mauritius kestrel could therefore focus on increasing the population in the southwest of the island, where rainfall appears to be decreasing, as well as reintroduction of the species to other areas in which rainfall is not increasing. In the Bambous Mountains population, delays in egg-laying due to poor nest-site quality or competition with other species could be minimised by pre-season checks and maintenance of nest-boxes (M. A. C. Nicoll pers. comm.). This could alleviate potential constraints on phenological plasticity in kestrels. Ongoing efforts to establish a population of echo parakeets in the Bambous Mountains may be particularly beneficial, given the species' responses to dry season rainfall. The echo parakeet appears to show low vulnerability to climate impacts in current conditions, although future changes, such as decreasing rainfall and a shift towards earlier-occurring, stronger and more frequent cyclones, could alter this.

Projections for Mauritius suggest that mean annual temperatures will increase by 1.0-2.0°C by the 2060s and by 1.1-3.4°C by the 2090s (McSweeney *et al.*, 2010a, b). Projections for mean annual rainfall from different models vary widely, ranging from negative to positive changes over the 21st century, with more consistent projections for decreases in July-September (McSweeney *et al.*, 2010a, b). Projections also suggest that tropical cyclone frequency will initially increase with warming and then decrease (Muthige *et al.*, 2018). While global tropical cyclone frequency is projected to decline overall, the number of very strong cyclones is projected to increase (reviewed by Walsh *et al.*, 2016), and this is evident for projected changes in the vicinity of the Mascarene archipelago and Madagascar (Bacmeister *et al.*, 2018). More frequent El Niño-Southern Oscillation (ENSO) events could result in cyclones occurring more frequently in the vicinity of Mauritius (Ho *et al.*, 2006). Variability in rainfall will likely be influenced by Indian Ocean Dipole (IOD) events under projected climate change (Cai *et al.*, 2014). The frequency of extreme positive IOD events, which can lead to extreme rainfall over countries in eastern Africa, is projected to increase as the climate warms, with a doubling in frequency at 1.5°C warming relative to pre-industrial levels (Cai *et al.*, 2018). Global climate model projections imply that annual precipitation will decrease in the Mascarene region, with indications of some seasonal variation in trends (IPCC, 2007, 2014). Given uncertainties in projections of tropical precipitation changes and the challenges of downscaling projections to topographically varied oceanic islands (Zhang *et al.*, 2016), conservation managers may need to rely on analyses of recent climate trends and variability, combined with responsive strategies, to inform management. However, methods are being developed to improve the downscaling of projections to oceanic islands, as applied to the Hawaiian islands (Zhang *et al.*, 2016).

6.5 General limitations

In general, this study is limited by the availability of multiple long-term climate datasets in Mauritius. The availability of relatively long-term climate data from additional sites could have improved the robustness of analyses of impacts on the study species and could have provided more insights into local-scale variation in climate trends. A potential limitation of the analyses of breeding success is that the effects of density dependence may be incompletely understood in the study species, and this may place limitations on the results of analyses into climate impacts. However, the analyses in this study were based on previous research, and there is little evidence of negative density dependence through interference competition in the breeding success of the two species. In addition, the lack of data on prey availability for Mauritius kestrels and natural food availability for echo parakeets means that there is no direct evidence of the mechanisms by which temperature and rainfall influence the timing of breeding in the two species.

The relevance of the findings of this study to other species might be limited by the management that the focal populations receive. The data used for the Mauritius kestrel analyses were collected after the cessation of intensive management of the population. During the study period the extent of management received by the population only entailed the provision and maintenance of artificial nest-boxes. The findings for the Mauritius kestrel are therefore likely to be applicable to a range of tropical species that do not receive management. In contrast, echo parakeets have received more intensive management, including the provision of supplementary food, provision and maintenance of nest-boxes and control of predators. However, in this study the use of supplementary food by individual breeding pairs is not only controlled-for but studied for potential interactions with climate. The findings of this study for the echo parakeet are therefore most relevant to other managed populations, especially those receiving supplementary food. Some of the results for the echo parakeets are likely to be relevant to unmanaged populations as well, namely the apparent mediation of reproductive senescence by extreme weather, as well as the effects of climate on the timing of breeding and hence temporal exposure to extreme weather events.

6.6 Avenues for future research

This thesis has prompted many questions that could be pursued in future research. The present study could be taken forward through the collection and analysis of data on temporal patterns in food availability for the two study species, and how these relate to climate, and by studying the mechanisms behind climate impacts on breeding success. Plant phenology data being collected in Mauritius could be used to study the influence of fruit and flower timing and abundance on breeding phenology in echo parakeets, as well as the breeding success of those pairs not taking supplementary food. Research into climate influences on plant phenology would likely provide further insights into climate pressures on echo parakeets. Data could also be collected on gecko abundance and activity patterns to investigate influences on the timing and success of kestrel breeding attempts. Detailed behavioural observations could provide insights into the mechanisms through which rainfall and tropical cyclones negatively impact breeding success in Mauritius kestrels and echo parakeets respectively. Further research could also investigate the potential for delayed impacts from extreme natal conditions on future survival and reproduction, such has been applied to the impacts of agriculture on Mauritius kestrels (Cartwright *et al.*, 2014).

Previous research has suggested that there is very fine-scale variation in rainfall on Mauritius (Staub *et al.*, 2014), and a detailed model of spatial rainfall distribution could be applied to future studies into climate impacts. Projections of future demographic and population changes in the Mauritius kestrel and echo parakeet may be possible in the coming years using bias-corrected and downscaled climate projections as methods improve. This will also be important for other populations, including those being reintroduced to the Bambous Mountains. Additional research is needed into climate impacts on the demography and phenology of populations on IAA, and these are likely to be important lines of inquiry for the management of populations on the islet.

More broadly, further research is needed to identify which species are most influenced by seasonal climate windows in tropical regions. Seasonal windows may be most prevalent towards the subtropics, as annual temperature cycles become more pronounced, or in regions with pronounced rainy and dry seasons. Seasonal windows may be defined largely by high impact weather and its selection pressures. As with previous research, this study has demonstrated the value of long-term detailed ecological datasets. Such datasets are uncommon, and especially rare in the tropics (Brawn *et al.*, 2017), where our understanding of the ecological impacts of climate change has lagged behind that for temperate regions. The analyses and insights made possible by the long-term and detailed datasets collected on the Mauritius kestrel and echo parakeet illustrate the value of such monitoring programmes. There remains an urgent need for additional monitoring schemes on tropical species.

6.7 Conclusions

This thesis has uncovered new insights into the phenological response of tropical birds to climate change, and looked at the role of high impact weather in shaping demography and phenology. The findings from this study provide grounds for hope that some threatened species will be able to adapt to a changing climate, at least temporarily. It also provides some optimism for the use of management actions to alleviate risks from climate change. This study has shown that threatened species can demonstrate both adaptation and maladaptation to climate trends and variability, thus in the short-term climate change could cause both increases in costs and savings for conservation managers as the fortunes of populations fluctuate. Threatened species conservation under climate change may need to be responsive over short timescales, especially for species at risk from interannual climate variability.

The broad implications for other tropical species are that temperature may be a more important influence on the timing of life-history events in endotherms than previously assumed, that the timing of breeding represents an important way that tropical species respond to interannual variation in climate and thus food availability, and that the relationship between the timing of life-history events and the timing of seasonal transitions and extreme weather is an important influence on the demography of tropical species.

The importance of the temporal and spatial distribution of climate risks has been illustrated for two tropical species. In particular, an understanding of such dynamics and ecological impacts is needed for species occupying small ranges and topographically varied areas. Such developments in understanding will improve approaches to climate change vulnerability assessments and the adaptive management of threatened species. As climate models continue to improve, more accurate downscaling will result in more reliable projections of local climate trends. This will be essential for safeguarding some of the rarest and most range-restricted species.

6.8 References

Alexander, L. V. 2016. Global observed long-term changes in temperature and precipitation extremes: A review of progress and limitations in IPCC assessments and beyond. *Weather and Climate Extremes,* **11**: 4–16.

Bacmeister, J. T., Reed, K. A., Hannay, C., Lawrence, P., Bates, S., Truesdale, J. E., Rosenbloom, N. and Levy, M. 2018. Projected changes in tropical cyclone activity under future warming scenarios using a high-resolution climate model. *Climatic Change,* **146**: 547–560.

Bailey, L. D. and van de Pol, M. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology,* **85**: 85–96.

Barlow, J., França, F., Gardner, T. S., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., Guénard, B., Gontijo Leal, C., Isaac, V., Lees, A. C., Parr, C. L., Wilson, S. K., Young, P. J. and Graham, N. A. J. 2018. The future of hyperdiverse tropical ecosystems. *Nature,* **559**: 517–526.

Bonebrake, T. C. 2013. Conservation implications of adaptation to tropical climates from a historical perspective. *Journal of Biogeography,* **40**: 409–414.

Bonebrake, T. C. and Mastrandrea, M. D. 2010. Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proceedings of the National Academy of Sciences of the United States of America,* **107**: 12581–12586.

Brawn, J. D., Benson, T. J., Stager, M., Sly, N. D. and Tarwater, C. E. 2017. Impacts of changing rainfall regime on the demography of tropical birds. *Nature Climate Change,* **7**: 133–136.

Burgess, M. D., Nicoll, M. A. C., Jones, C. G. and Norris, K. 2011. Multiple environmental gradients affect spatial variation in the productivity of a tropical bird population. *Journal of Animal Ecology,* **80**: 688–695.

Cai, W., Santoso, A., Wang, G., Weller, E., Wu, L., Ashok, K., Masumoto, Y. and Yamagata, T. 2014. Increased frequency of extreme Indian Ocean Diploe events due to greenhouse warming. *Nature,* **510**: 234–258.

Cai, W., Wang, G., Gan, B., Wu, L., Santoso, A., Lin, X., Chen, Z., Jia, F. and Yamagata, T. 2018. Stabilised frequency of extreme positive Indian Ocean Dipole under 1.5 °C warming. *Nature Communications,* **9**: 1419.

Cartwright, S. J., Nicoll, M. A. C., Jones, C. G., Tatayah, V. and Norris, K. 2014. Anthropogenic natal environmental effects on life histories in a wild bird population. *Current Biology,* **24**: 536–540.

Chadwick, R., Good, P., Martin, G. and Rowell, D. P. 2016. Large rainfall changes consistently projected over substantial areas of tropical land. *Nature Climate Change,* **6**: 177–181.

Charmantier, A. and Gienapp, P. 2013. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications,* **7**: 15–28.

Cohen, J. M., Lajeunesse, M. J. and Rohr, J. R. 2018. A global synthesis of animal phenological responses to climate change. *Nature Climate Change,* **8**: 224–228.

Dahinden, F., Fischer, E. M. and Knutti, R. 2017. Future local climate unlike currently observed anywhere. *Environmental Research Letters,* **12**: 084004.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. and Martin, P. R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America,* **105**: 6668–6672.

Diffenbaugh, N. S., Pal, J. S., Trapp, R. J. and Giorgi, F. 2005. Fine-scale processes regulate the response of extreme events to global climate change. *Proceedings of the National Academy of Sciences of the United States of America,* **102**: 15774–15778.

Dunning, C. M., Black, E. C. L. and Allan, R. P. 2016. The onset and cessation of seasonal rainfall over Africa. *Journal of Geophysical Research - Atmospheres,* **121**: 11405–11424.

Easterling, D. R., Kunkel, K. E., Wehner, M. F. and Sun, L. 2016. Detection and attribution of climate extremes in the observed record. *Weather and Climate Extremes,* **11**: 17–27.

Eken, G., Bennun, L., Brooks, T. M., Darwall, W., Fishpool, L. D. C., Foster, M., Knox, D., Langhammer, P., Matiku, P., Radford, E., Salaman, P., Sechrest, W., Smith, M. L., Spector, S. and Tordoff, A. 2004. Key Biodiversity Areas as Site Conservation Targets. *BioScience,* **54**: 1110–1118.

Ewing, S. R., Nager, R. G., Nicoll, M. A. C., Aumjaud, A., Jones, C. G. and Keller, L. F. 2008. Inbreeding and loss of genetic variation in a reintroduced population of Mauritius Kestrel. *Conservation Biology,* **22**: 395–404.

Feng, X., Porporato, A. and Rodriguez-Iturbe, I. 2013. Changes in rainfall seasonality in the tropics. *Nature Climate Change,* **3**: 811–815.

Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vie, J.-C., Akçakaya, H. R., Angulo, A., DeVantier, L. M., Gutsche, A., Turak, E., Cao, L., Donner, S. D., Katariya, V., Bernard, R., Holland, R. A., Hughes, A. F., O'Hanlon, S. E., Garnett, S. T., Şekercioğlu, Ç. H. and Mace, G. M. 2013. Identifying the world's most climate change vulnerable species: A systematic trait-based assessment of all birds, amphibians and corals. *PLoS One,* **8**: e65427.

Frey, S. J. K., Hadley, A. S. and Betts, M. G. 2016. Microclimate predicts within-season distribution dynamics of montane forest birds. *Diversity and Distributions,* **22**: 944–959.

Greenville, A. C., Burns, E., Dickman, C. R., Keith, D. A., Lindenmayer, D. B., Morgan, J. W., Heinze, D., Mansergh, I., Gillespie, G. R., Einoder, L., Fisher, A., Russell-Smith, J., Metcalfe, D. J., Green, P. T., Hoffman, A. A. and Wardle, G. M. 2018. Biodiversity responds to increasing climatic extremes in a biome-specific manner. *Science of the Total Environment,* **634**: 382–393.

Groombridge, J. J., Jones, C. G., Bayes, M. K., van Zyl, A. J., Carrillo, J., Nichols, R. A. and Bruford, M. W. 2002. A molecular phylogeny of African kestrels with reference to divergence across the Indian Ocean. *Molecular Phylogenetics and Evolution,* **25**: 267–277.

Groombridge, J. J., Jones, C. G., Bruford, M. W. and Nichols, R. A. 2000. 'Ghost' alleles of the Mauritius kestrel. *Nature,* **403**: 616.

Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M.-S., Keatley, M. R., Woodward, C. A., Williamson, G., Duke, N. C. and Bowman, D. M. J. S. 2018. Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change,* **8**: 579–587.

Hawkins, E., Anderson, B., Diffenbaugh, N., Mahlstein, I., Betts, R., Hegerl, G., Joshi, M., Knutti, R., McNeall, D., Solomon, S., Sutton, R., Syktus, J. and Vecchi, G. 2014a. Uncertainties in the timing of unprecedented climates. *Nature,* **511**: E3–E5.

Hawkins, E., Joshi, M. and Frame, D. 2014b. Wetter then drier in some tropical areas. *Nature Climate Change,* **4**: 646–647.

Heller, N. E. and Zavaleta, E. S. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation,* **142**: 14–32.

Ho, C.-H., Kim, J.-H., Jeong, J.-H., Kim, H.-S. and Chen, D. 2006. Variation of tropical cyclone activity in the South Indian Ocean: El Niño-Southern Oscillation and Madden-Julian Oscillation effects. *Journal of Geophysical Research - Atmospheres,* **111**: D22101.

IPCC. 2007. Climate Change 2007. Fourth Assessment Report (AR4). Geneva, Switzerland: Intergovernmental Panel on Climate Change.

IPCC. 2014. Climate change 2014: Synthesis report. Fifth Assessment Synthesis Report. Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Kent, C., Chadwick, R. and Rowell, D. P. 2015. Understanding uncertainties in future projections of seasonal tropical precipitation. *Journal of Climate,* **28**: 4390–4413.

Kittel, T. G. F., Williams, M. W., Chowanski, K., Hartman, M., Ackerman, T., Losleben, M. and Blanken, P. D. 2015. Contrasting long-term alpine and subalpine precipitation trends in a mid-latitude North American mountain system, Colorado Front Range, USA. *Plant Ecology & Diversity,* **8**: 607–624.

Klein Tank, A. M. G., Zwiers, F. W. and Zhang, X. 2009. Guidelines on analysis of extremes in a changing climate in support of informed decisions for adaptation. Geneva, Switzerland: World Meteorological Organization.

Liebmann, B., Blade, I., Kiladis, G. N., Carvalho, L. M. V., Senay, G. B., Allured, D., Leroux, S. and Funk, C. 2012. Seasonality of African Precipitation from 1996 to 2009. *Journal of Climate,* **25**: 4304–4322.

Maclean, I. M. D., Suggitt, A. J., Wilson, R. J., Duffy, J. P. and Bennie, J. J. 2017. Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Global Change Biology,* **23**: 256–268.

Mahlstein, I., Knutti, R., Solomon, S. and Portmann, R. W. 2011. Early onset of significant local warming in low latitude countries. *Environmental Research Letters,* **6**: 034009.

Mahony, C. R. and Cannon, A. J. 2018. Wetter summers can intensify departures from natural variability in a warming climate. *Nature Communications,* **9**: 783.

McPhillips, L. E., Chang, H., Chester, M. V., Depietri, Y., Friedman, E., Grimm, N. B., Kominoski, J. S., McPhearson, T., Méndez-Lázaro, P., Rosi, E. J. and Shiva, J. S. 2018. Defining Extreme Events: A Cross-Disciplinary Review. *Earth's Future,* **6**: 441–455.

McSweeney, C., New, M. and Lizcano, G. 2010a. The UNDP Climate Change Country Profiles: Improving the Accessibility of Observed and Projected Climate Information for Studies of Climate Change in Developing Countries. *Bulletin of the American Meteorological Society,* **91**: 157–166.

McSweeney, C., New, M. and Lizcano, G. 2010b. UNDP Climate Change Country Profiles: Mauritius. Available from: https://www.geog.ox.ac.uk/.

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. and Post, E. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society of London, Series B,* **365**: 3177–3186.

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., Sanchez, J. J., Kaiser, L. R., Stender, Y. O., Anderson, J. M., Ambrosino, C. M., Fernandez-Silva, I., Giuseffi, L. M. and Giambelluca, T. W. 2013. The projected timing of climate departure from recent variability. *Nature,* **502**: 183–187.

Muthige, M. S., Malherbe, J., Englebrecht, F. A., Grab, S., Beraki, A., Maisha, T. R. and Van der Merwe, J. 2018. Projected changes in tropical cyclones over the South West Indian Ocean under different extents of global warming. *Environmental Research Letters,* **13**: 065019.

Nadeau, C. P., Urban, M. C. and Bridle, J. R. 2017. Coarse climate change projections for species living in a fine-scaled world. *Global Change Biology,* **23**: 12–24.

Pearce-Higgins, J. W. and Green, R. E. 2014. *Birds and Climate Change: Impacts and Conservation Responses*. Cambridge, UK: Cambridge University Press.

Post, E., Steinman, B. A. and Mann, M. E. 2018. Acceleration of phenological advance and warming with latitude over the past century. *Scientific Reports,* **8**: 3927.

Rodrigues, A. S. L., Brooks, T. M., Butchart, S. H. M., Chanson, J., Cox, N., Hoffmann, M. and Stuart, S. N. 2014. Spatially Explicit Trends in the Global Conservation Status of Vertebrates. *PLoS One,* **9**: e113934.

Şekercioğlu, Ç. H., Primack, R. B. and Wormworth, J. 2012. The effects of climate change on tropical birds. *Biological Conservation,* **148**: 1–18.

Senapathi, D., Nicoll, M. A. C., Teplitsky, C., Jones, C. G. and Norris, K. 2011. Climate change and the risks associated with delayed breeding in a tropical wild bird population. *Proceedings of the Royal Society of London, Series B,* **278**: 3184–3190.

Senapathi, G. D. 2009. Assessing the effect of changing climatic conditions in Mauritius on the population dynamics of the endemic Mauritius Kestrel (*Falco punctatus*). PhD Thesis. Reading, UK: University of Reading.

Senior, R. A., Hill, J. K., González del Pliego, P., Goode, L. K. and Edwards, D. P. 2017. A pantropical analysis of the impacts of forest degradation and conversion on local temperature. *Ecology and Evolution,* **7**: 7897–7908.

Sergio, F., Blas, J. and Hiraldo, F. 2018. Animal responses to natural disturbance and climate extremes: a review. *Global and Planetary Change,* **161**: 28–40.

Smith, K. W. and Smith, L. 2013. The effect of supplementary feeding in early spring on the breeding performance of the Great Spotted Woodpecker *Dendrocopos major*. *Bird Study,* **60**: 169–175.

Socolar, J. B., Epanchin, P. N., Beissinger, S. R. and Tingley, M. W. 2017. Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences of the United States of America,* **114**: 12976–12981.

Stattersfield, A. J., Crosby, M. J., Long, A. J. and Wege, D. C. 1998. *Endemic Bird Areas of the world: priorities for biodiversity conservation*. Cambridge, UK: BirdLife International.

Staub, C. G., Stevens, F. R. and Waylen, P. R. 2014. The geography of rainfall in Mauritius: Modelling the relationship between annual and monthly rainfall and landscape characteristics on a small volcanic island. *Applied Geography,* **54**: 222–234.

Stein, B. A., Staudt, A., Cross, M. S., Dubois, N. S., Enquist, C., Griffis, R., Hansen, L. J., Hellmann, J. J., Lawler, J. J., Nelson, E. J. and Pairis, A. 2013. Preparing for and managing change: climate adaptation for biodiversity and ecosystems. *Frontiers in Ecology and the Environment,* **11**: 502–510.

Tan, X., Gan, T. Y. and Horton, D. E. 2018. Projected timing of perceivable changes in climate extremes for terrestrial and marine ecosystems. *Global Change Biology,* **24**: 4696–4708.

Tingley, M. W., Koo, M. S., Moritz, C., Rush, A. C. and Beissinger, S. R. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology,* **18**: 3279–3290.

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., Schmitz, A., Zollner, P. A. and Travis, J. M. J. 2016. Improving the forecast for biodiversity under climate change. *Science,* **353**: aad8466.

van de Pol, M., Jenouvrier, S., Cornelissen, J. H. C. and Visser, M. E. 2017. Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Philosophical Transactions of the Royal Society of London, Series B,* **372**: 20160134.

Walsh, K. J. E., McBride, J. L., Klotzbach, P. J., Balachandran, S., Camargo, S. J., Holland, G., Knutson, T. R., Kossin, J. P., Lee, T.-c., Sobel, A. and Sugi, M. 2016. Tropical cyclones and climate change. *Wiley Interdisciplinary Reviews-Climate Change,* **7**: 65–89.

Williams, J. W., Jackson, S. T. and Kutzbach, J. E. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America,* **104**: 5738–5742.

Zhang, C., Wang, Y., Hamilton, K. and Lauer, A. 2016. Dynamical Downscaling of the Climate for the Hawaiian Islands. Part II: Projection for the Late Twenty-First Century. *Journal of Climate,* **29**: 8333–8354.