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Threats to migratory birds, and actions for their conservation

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Abstract

Migratory species undertake some of the most extreme feats of endurance known in the animal kingdom. Despite many species migrating across continents, oceans and hemispheres, most cannot survive everywhere. Migrants are highly dependent on strategically located breeding and feeding sites for survival and reproduction. Indeed, many species are constrained in time and space by seasonal resource availability, thus forming migratory bottlenecks. Threats operating in such bottlenecks can impact the population as a whole, and can impact survival and reproduction at later migratory stages. In fact, migratory species worldwide are declining at greater rates than non-migratory species. Many migratory species are at risk of extinction if no conservation action is taken.

Pinpointing where and when threats occur, and understanding how they impact population dynamics of migratory species is complex. Few tools are available for diagnosing declines, and even fewer for prioritising conservation actions in migratory species. As a result, our understanding of how to conserve migratory species is remarkably poor. In my thesis, I tackle these fundamental gaps in our knowledge by 1) developing and testing a method to distinguish local from remote drivers of population growth rate in migratory species, 2) mapping critical habitat, and 3) prioritising conservation actions at local and international scales. I use the migratory shorebirds of the East-Asian Australasian Flyway as a case study. The East-Asian Australasian Flyway supports 60 species migrating across 23 political jurisdictions, many of which are in significant decline.

In **Chapter 1,** I introduce my thesis by outlining key topics surrounding the conservation of migrants, linking them to my case study. In **Chapter 2**, I distinguish between local and remote drivers of population growth in migrants, using (i) count data from a single site within a migratory flyway, and (ii) a list of potential stopover sites. Indeed, for migratory species with large distributions, count data, mark-recapture studies or tagging records from across the entire geographic distribution are rare. Monitoring data are typically only available for one or a few sites. Newly available remote sensing data offer an opportunity to investigate how conditions in other parts of migratory cycle affect population growth rate at a monitored site. Analysing count data from Moreton Bay, Australia, I show that it is possible to identify effects of climatic conditions throughout the flyway on the population growth rate of migratory shorebirds as measured at a non-breeding site. My results also show that declines are occurring consistently

across all study species, but that there are some clear differences in temperature and rainfall impacts on population growth rate.

Information about the distribution and status of habitat is crucial when devising conservation plans for migratory species, yet very little is known about the distribution, extent and protection of the intertidal habitats used by migratory shorebirds. In **Chapter 3**, using freely available satellite imagery, I produce the first map of intertidal habitats in Australia. I find that levels of protection vary greatly between states, with some states primary under terrestrial protection, others primarily under marine protection, and some under both. Overall, 39% of intertidal habitats are protected in Australia. Shorebirds are declining despite high levels of protection in Australia, suggesting that better management within protected areas could be important

Management of disturbance in the intertidal zone is one of the key conservation actions that can be taken for shorebirds in Australia. Active management only occurs within protected areas, where managers must decide where and when to carry out enforcement given limited budgets. In **Chapter 4**, I develop a novel method of prioritising enforcement for wildlife management at the local scale, which accounts for diminishing returns on investment from repeatedly enforcing at the same site and show that robust management decisions can be made despite limited data on effectiveness of management.

Protected areas are one of the most widely used conservation tools. However, setting conservation priorities at the international scale can be complex, particularly given limited data on migratory connectivity. Currently, conservation priorities for migrants are usually based on the number of birds using a site, with little consideration for migratory connectivity due to limited data. **Chapter 5**, I develop a multi-species prioritisation for 250 sites using tracking data to estimate migratory connectivity empirically, discovering that sites that are highly connected are more critical for maintaining migratory populations than sites simply supporting large numbers of birds.

I synthesise my thesis in **Chapter 6**, by placing my research in the broader context of conservation planning for migratory species, acknowledging the limitations of my methods, and suggesting improvements and future directions. Ultimately, my PhD has delivered practical solutions for the management of migrants, and theoretical advances in conservation planning in dynamic migratory networks. Limited data is often cited as a primary barrier to

conserving migratory species; however, conservation decisions can and should be made despite uncertainty, if we are to prevent one of the most spectacular phenomena on earth from disappearing.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Dhanjal-Adams K. L., Hanson J. O., Murray N. J., Phinn S. R., Wingate V. R, Mustin K., Lee J. R., Allan J. R., Oliver J. L., Studds C. E., Clemens R. S., Roelfsema C. M., Fuller R. A. (2016) Distribution and protection of intertidal habitats in Australia, *Emu*, DOI: 10.1071/MU15046

Dhanjal-Adams K. L., Mustin K., Possingham H., Fuller R.A. (2016) Optimizing disturbance management for wildlife protection: the enforcement allocation problem, *Journal of Applied Ecology*, DOI: 10.1111/1365-2664.12606

Dhanjal-Adams K. L., Travis J.M.J, Mustin K. (in revision) The amplitude and colour of temporal environmental variability interact with population demography to determine the establishment success of an invasive species introduction, *Oikos*

Clemens R. S., Hansen B. D., Rogers D., Gosbell K., Minton C., Straw P., Bamford M., Woehler E. J., Milton D., Weston M., Venables B., Weller D., Purnell C., Hassell C., Rutherford B., Onton K., Herrod A., Choi C.-Y. , **Dhanjal-Adams K. L.,** Skilleter G., Fuller R. A. (2016) Continental-scale decreases in shorebird populations in Australia, *Emu*, DOI:10.1071/MU15056

Reports:

Dhanjal-Adams K. L. and Fuller, R.A. (2015) The efficacy of shorebird disturbance management in Moreton Bay, Australia. Report to the Queensland Department of Environment and Heritage Protection.

Fuller, R.A. and **Dhanjal-Adams, K.L.** (2012) Monitoring seabirds in the Great Barrier Reef: a power analysis, Report to Queensland Parks and Wildlife Service.

Fuller, R.A. and **Dhanjal- Adams, K.L.** (2012) A proposal for assessing the impacts of climate change on breeding seabirds of the Great Barrier Reef, Report to Queensland Parks and Wildlife Service.

Conference abstracts:

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Dhanjal-Adams *et al.* (2015) Optimizing disturbance management for wildlife protection. *Student Conference for Conservation Science*. Brisbane, Australia.

Dhanjal-Adams *et al.* (2015) Setting priorities in dynamic migratory networks. *Student Conference on Conservation Science*. Brisbane, Australia. **Second prize**

Dhanjal-Adams *et al.* (2014) Optimizing enforcement: disturbance management for migratory shorebirds. *Ecological Society of Australia*. Alice Springs, Australia.

Dhanjal-Adams *et al.* (2014) Optimizing enforcement: disturbance management for migratory shorebirds. *Australian Wader Study Group*. Darwin, Australia.

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Incorporated in Chapter 3

Contributor	Statement of contribution
Dhanjal-Adams K. L. (Candidate)	Designed protected area analysis (50%) Compiled and manually tidied up remote sensing data (100%) Carried out accuracy assessment (100%) Wrote and edited manuscript (70%)
Hanson J. O.	Designed mapping project (30%) Designed remote sensing analysis (60%) Carried out remote sensing analysis (30%) Wrote and edited manuscript (2.5%)
Murray N. J.	Designed mapping project (30%) Designed remote sensing analysis (30%) Designed accuracy assessment (20%) Wrote and edited manuscript (2.5%)
Phinn S. R.	Designed accuracy assessment (20%) Wrote and edited manuscript (2.5%)
Wingate V. R.	Designed accuracy assessment (40%) Wrote and edited manuscript (2.5%)
Mustin K.	Designed mapping project (20%) Designed remote sensing analysis (10%) Carried out remote sensing analysis (20%) Wrote and edited manuscript (2.5%)
Lee J. R.	Carried out remote sensing analysis (20%) Wrote and edited manuscript (2.5%)
Allan J. R.	Carried out remote sensing analysis (20%) Wrote and edited manuscript (2.5%)

Cappadonna J. L.	Carried out remote sensing analysis (10%) Wrote and edited manuscript (2.5%)
Studds C. E.	Tide modelling (50%) Wrote and edited manuscript (2.5%)
Clemens R. S.	Tide modelling (50%) Wrote and edited manuscript (2.5%)
Roelfsema C. M.	Designed accuracy assessment (20%) Wrote and edited manuscript (2.5%)
Fuller R. A.	Designed mapping project (20%) Designed protected area analysis (50%) Wrote and edited manuscript (2.5%)

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Dhanjal-Adams K. L. (Candidate)	Designed study (50%) Created models (100%) Analysed and interpreted data (100%) Wrote the paper (70%)
Mustin K.	Designed study (10%) Wrote and edited manuscript (15%)
Possingham H.P.	Designed study (20%) Wrote and edited manuscript (5%)
Fuller R.A.	Designed study (20%) Wrote and edited manuscript (10%)

Contributions by others to the thesis

My PhD thesis is composed of four manuscripts with the following status: Chapters 2 and 5 are under final preparation for submission. Chapters 3 and 4 have been accepted for publication. I use the plural first-person pronoun "we" in Chapters 2-5 as per their publication format. In Chapters 1 and 6, I use the singular first-person pronoun "I" as I am describing my own views of the research as a whole.

Chapter 2 Dhanjal-Adams K.L., Fuller R.A., Murray N.J., Studds C.E., Wilson H.B. and Kendall B.E. (In preparation) Distinguishing local and remote drivers of change in migratory bird population growth rates

KLDA, RAF, CES, HBW and BEK designed the study, NJM compiled remote sensing data, CES assisted with writing scripts. KLDA performed analyses and wrote manuscript. All authors discussed results and edited the manuscript.

Chapter 5 Dhanjal-Adams K.L, Klaassen M., Nicol S.C., Possingham H.P.P, Chadès I. and Fuller R.A. (submitted) Setting conservation priorities in migratory networks.

KLDA created models, ran analysis, interpreted results, created figures and wrote the manuscript. All authors designed the study, discussed the results and edited the manuscript.

Statement of parts of the thesis submitted to qualify for the award of another degree

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List of Abbreviations

AIC	Akaike Information Criterion
BIC	Bayesian Information Criterion
CRI	Credible Intervals
EAAF	East Asian-Australasian Flyway
EPBC	Environment Protection and Biodiversity Conservation
GIS	Geographic Information System
IUCN	International Union for Conservation of Nature
MNDWI	Modified Normalized Difference Water Index
NA	Not Available
NDWI	Normalized Difference Water Index
NOAA	National Oceanic and Atmospheric Administration
QWSG	Queensland Wader Study Group
VWSG	Victorian Wader Study Group
WLS	Weighted Least Squares
WMC	World migratory Convention

"Migratory birds bind up the corners of this increasingly fragmented globe – uniting the poles and the tropics, forests and deserts, wilderness and cities. A planet that sustains them will sustain us; their fate is our fate"

– Scott Weidensaul, Living on the Wind

Chapter 1

Introduction

1 Introduction

Through all aspects of their life cycles animals must interact with, and adapt to, an environment that is heterogeneous in time and space. Seasonal variations in temperature, rainfall and nutrients drive movements of organisms in search of feeding and breeding conditions. Seasonal algal blooms form in summer (Platt *et al.*, 2003), jellyfish journey diurnally up and down the water column to feed (Kaartvedt *et al.*, 2007) and pelicans aggregate around ephemeral waterholes to breed in the Australian outback (Reid, 2009). Biological populations must therefore be dynamic to survive in a dynamic environment – and none more so than migratory species.

1.1 The migratory phenomenon

Migration has classically been defined as the "predictable seasonal movement of individuals between breeding grounds and wintering grounds" (Colwell, 2010), however migration can also be unpredictable, with some species displaying nomadic or eruptive behaviour (Chan, 2001). Species which undertake migrations often travel large distances over a wide range of habitats, making them vulnerable to threats occurring over their entire range. Many reports warn of recent declines in migratory species, and they might be particularly vulnerable to certain forms of habitat loss because of their specialised lifestyle often leading them to travel across international borders (Dulvy *et al.*, 2008; Wilcove & Wikelski, 2008; Wilson *et al.*, 2011).

The development of new tracking technologies has led to increased knowledge of how migratory species as varied as insects (Chapman *et al.*, 2015), crustaceans (Adamczewska & Morris, 2001), fish (Steinhausen, 2007), birds (Hedenström, 2010), reptiles (Southwood & Avens, 2010) and mammals (Braithwaite *et al.*, 2015) exploit seasonal changes in resources (Grothues, 2009; Jellyman, 2009; Hebblewhite & Haydon, 2010). Greater and greater migratory distances are being recorded for a variety of species. For instance, bluefin tuna (*Thunnus orientalis*) have been found to migrate over 2000 kilometres yearly, both across the Pacific and Atlantic oceans (Block *et al.*, 2005; Block *et al.*, 2011) while some crocodiles (*Crocodylus porosus*) can travel up to 30 kilometres daily (Read *et al.*, 2007). The longest migration recorded to date is that of the Arctic tern (*Sterna paradisaea*) travelling some 80,000

kilometres annually (Egevang *et al.*, 2010) while the fastest is that of the Great Snipe (*Gallinago media*) which can travel at a speed of 27 metres per second (= 97.2 km.h^{-1}) during non-stop flights of 4100-6800 kilometres between central Africa and Northern Europe (Klaassen *et al.*, 2011). Studies are also becoming increasingly comprehensive: Block *et al*. (2011) deployed 4,306 tags on 23 species of marine predator in the North East Pacific over a period of nine years. Such studies have yielded a wealth of information on how tagged individuals move between breeding, staging and wintering grounds, increasing our knowledge of migratory connectivity (Hebblewhite & Haydon, 2010). However, there is still a lack of knowledge, and therefore understanding, of how movement tracking data can be linked to behaviour or population dynamics. This is further complicated by statistical uncertainty in most tracking studies whose sample sizes are too small due to expensive equipment (Hebblewhite & Haydon, 2010). However, despite this uncertainty, it is undeniable that migratory species are highly adaptable, experiencing a greater range of habitats, environmental fluctuations and physiological changes than most non-migrants.

1.2 Migratory species track pulses in resource availability

Typically, migration is perceived as a long-distance, endurance activity; yet there are a variety of migratory behaviours ranging from long-distance, to repetitive short-distance movements, which can take place over generations (Adamczewska & Morris, 2001; Steinhausen, 2007; Hedenström, 2010; Southwood & Avens, 2010; Braithwaite *et al.*, 2015; Chapman *et al.*, 2015). Insects, crustaceans and reptiles fall into the latter category due to short life-cycles or physiological constraints (Adamczewska & Morris, 2001; Southwood & Avens, 2010; Chapman et al., 2015). Indeed, many insects such as monarch butterflies (*Danaus plexippus*) migrate over multiple generations (Chapman et al., 2015), while ectothermic reptile migrations are small-scale and dependent on temperature, thus reserved for warmer seasons (Southwood & Avens, 2010). Different types of migration therefore have different energetic requirements, and resource availability is a major factor limiting all migratory species, regardless of strategy (Blem, 1990).

Migratory movements are timed to coincide with peaks in food abundance before, during or after migration. All migrants are capable of substantially increasing their mass to meet energy

demands (Blem, 1990). Where and when weight is gained is critical in determining individual survival. Income breeders for instance migrate to resource-abundant breeding grounds so both themselves and their offspring can exploit food pulses. Capital breeders on the other hand store fat before migration, to arrive in the breeding grounds fit enough to breed. American redstart (*Setophaga ruticilla*) migration, for example, coincides with peak abundance of prey in the breeding grounds (Langin *et al.*, 2006). Christmas Island red crab (*Gecarcoidea natalis*) migration, on the other hand, coincides with monsoonal rain. This minimises dehydration, maximises food availability during migration, and ensures animals arrive at coastal breeding grounds able to fight for breeding territories (Greenaway & Linton, 1995; Adamczewska & Morris, 2001).

Interrupted or reduced feeding, whether for income or capital breeding migratory species, can prevent the weight-gain necessary to complete migration and/or breeding. The timings (i.e. phenologies) of migration and resource pulses are increasingly mismatched due to climate change (Both & Visser, 2001). For instance, the migratory pied flycatcher (*Ficedula hypoleuca*) has not been able to advance its spring arrival date in response to increasing temperatures in breeding grounds, but has compensated by advancing its egg-laying date, resulting in a decreased breeding success (Both & Visser, 2001). Many migratory species are also showing adaptations to environmental changes. For instance, capital breeding loggerhead sea turtles (*Caretta caretta*) are breeding earlier and earlier and in higher latitudes (Mazaris *et al.*, 2013). Similarly, 20 migratory bird species in the UK have advanced both arrival and departure dates by an average of 8 days (Cotton, 2003). Changes in migration phenology in response to climate change are therefore dependent on species-specific cues for migration. Indeed, some species are reliant on environmental cues to trigger migration, enabling them to adapt; while others are reliant on non-environmental cues such as day length to trigger migration, making them less adaptable (Both & Visser, 2001). Given their mobile lifestyle which tracks pusles in reseaource availability, we might expect migrants to be more robust to change than non-migrants, so why are they declining more rapidly than non-migrants?

1.3 Declines in migratory species

Analyses of bird population trends across Europe (Sanderson *et al.*, 2006) and North America (Robbins *et al.*, 1989) have found that migrants have suffered more severe and sustained declines than non-migrants. Similar trends have been reported over many taxa (Dulvy *et al.*, 2008; Wilcove & Wikelski, 2008; Wilson *et al.*, 2011) and have been a conservation issue for decades (Burke, 1984; Myers *et al.*, 1987; Weston *et al.*, 1997). The decline of the passenger pigeon (*Ectopistes migratorius*) for instance was already observed to be occurring at an alarming rate in the late 1800s, leading to unsuccessful legislation aimed at reducing losses in numbers. The species finally became extinct in 1914 (Halliday, 1980). Another species deemed in severe danger in the late 1800s in North America was the bison (*Bison bison*), with only 300 individuals left in the wild in 1891 (Larter *et al.*, 2000). Currently the species is restricted to national parks where herds number in the hundreds or tens of hundreds (Wilcove & Wikelski, 2008). Despite many efforts, the species is still listed as near threatened on the IUCN Redlist (Gates & Aune, 2008). The passenger pigeon and bison are both examples of how conservation practices have aimed to reverse observed declines, not anticipate them. This is both true of migrants and non-migrants, underlining how most conservation practices fail to consider migrants as different to non-migrants (Martin *et al.*, 2007; Klaassen *et al.*, 2008). Migrants have been decreasing at a greater rate than non-migrants (Dulvy *et al.*, 2008; Wilcove & Wikelski, 2008; Wilson *et al.*, 2011) because many conservation practices fail to account for the fact that, unlike non-migratory species, migratory species 1) move within a network of connected sites and, as a result, 2) face spatially and temporally dynamic threats.

1.4 Migratory connectivity

Events occurring in one location of a migratory network can affect the overall population of a species (Webster *et al.*, 2002; Martin *et al.*, 2007; Pressey *et al.*, 2007; Buehler & Piersma, 2008). Indeed, it is not uncommon for a significant proportion of a population to aggregate in a single location to breed or feed. For example, the entire African straw-coloured fruit bat (*Eidolon helvum*) population congregates in Kasanka National Park between October and December each year to take advantage of the fruit pulse (Richter & Cumming, 2008). Similarly many bird and sea mammal species aggregate into breeding colonies in remote areas (Tickell

& Pinder, 1975; Birkhead, 1978; Sobey & Kenworthy, 1979; Harris *et al.*, 1983; Shaughnessy & Goldsworthy, 1990; Allen *et al.*, 1995). Any severe impacts at this stage of migration can have important repercussions elsewhere in the migratory network, and this phenomenon is known as a migratory bottleneck.

Schematically, a migratory network can be represented with each node as a site/region and each arrow as the movement/connectivity between each site (Fig. 1.1). A migratory bottleneck is a site through which the entire population must pass during migration, as seen for the Yellow Sea node in Fig 1.1 during southward migration (black arrows). When a population decline is observed, this complex connectivity can make it difficult to pinpoint exactly what part of the network has failed (Dulvy *et al.*, 2008; Wilcove & Wikelski, 2008; Wilson *et al.*, 2011). Incorporating connectivity is therefore crucial for effective conservation of migrants (Cabeza, 2003; van Teeffelen *et al.*, 2006; Martin *et al.*, 2007; Klaassen *et al.*, 2008; Beger *et al.*, 2010; Sheehy *et al.*, 2010; Hermoso *et al.*, 2012a; Hermoso *et al.*, 2012b; Linke *et al.*, 2012; Iwamura *et al.*, 2013; Langhans *et al.*, 2014; Runge *et al.*, 2014a; Nicol *et al.*, 2015).

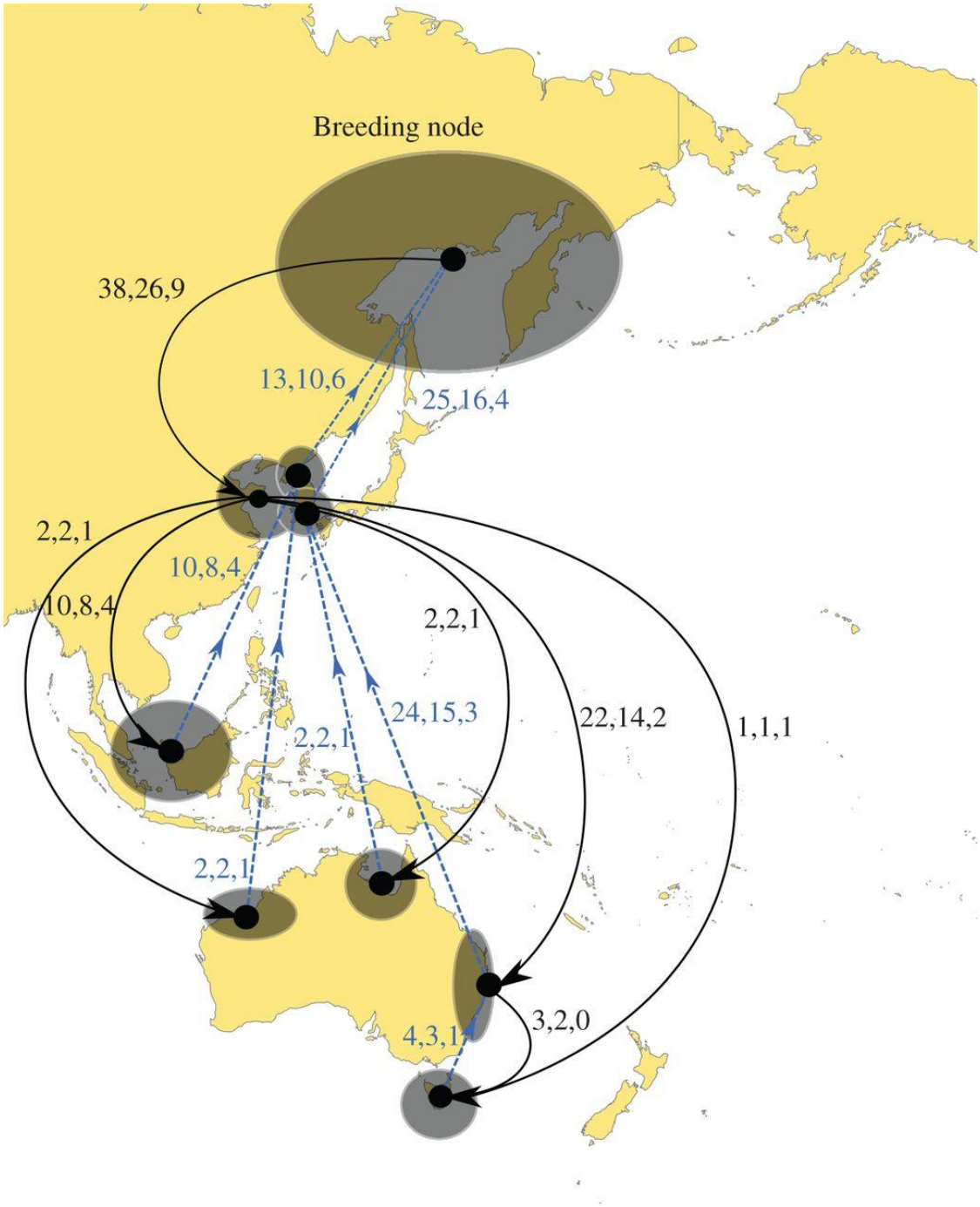

Figure 1.1 *Network representation of the migratory flyway of the eastern curlew. Shaded nodes represent the key staging, breeding and non-breeding nodes used by the curlew. Southward migration is depicted by the solid black arrows, and northward migration is depicted using dashed blue lines. Flows through the nodes decrease as the habitat of each node inundated by sea level rise increases. Numbers adjacent to lines show the maximum flows (×10^3) through the network under sea level rise scenarios of 0, 1 and 2 m, respectively. In each year, managers can counteract habitat loss at a single non-breeding node, preventing the loss of population flow through that node. Figure taken from Nicol* et al. *(2015)*

1.5 Dynamic threats within a migratory network

Because migratory species are highly mobile, they experience a wide range of environmental conditions. It is not uncommon for conditions in one migratory stage to impact survival or reproduction at a later migratory stage (Norris, 2005; Norris & Taylor, 2006; Bauer *et al.*, 2008; Studds *et al.*, 2008; Harrison *et al.*, 2011; Catry *et al.*, 2013). Indeed, carry-over effects are common within migratory systems. For instance, non-breeding season habitat quality has been found to correlate with arrival condition of male American redstarts in breeding habitat (Marra *et al.*, 1998). Similarly, conditions during the non-breeding season impact weight gain in female elk (*Cervus elaphus*), and therefore their ability to conceive and carry a pregnancy to term (Cook *et al.*, 2004). When carry-over effects negatively impact population viability, they can be threatening. For migrants in particular, such threats can occur over a great number of geographic regions, be patchy or variable, and often inconsistent in how they impact the ecology of the affected species. Much is dependent on where in the migratory path the threat takes place, and many threats can come and go over time. Saiga antelope (*Saiga tatarica*) were once threatened by climatic extremes for example, but are currently threatened by disturbance events (Singh & Milner-Gulland, 2011). The monarch butterfly (*Danaus plexippus*) migrates over several generations, and deforestation is a threatening process in Mexico only, while declines in the common milkweed (*Asclepias syriaca*) due to agricultural intensification are threatening in the USA (Bartel *et al.*, 2010; Brower *et al.*, 2012; Flockhart *et al.*, 2015). Also, the same threat might impact a migrant species quite differently depending on where it occurs in the migratory pathway (Webster *et al.*, 2002; Buehler & Piersma, 2008; Taylor & Norris, 2010). Mortality in black-throated blue warblers (*Dendroica caerulescens*) is 15 times greater during migration than at either breeding or wintering grounds (Sillett & Holmes, 2002). This is because migration results in sustained physical activity; for example the red knot (*Caldis canutus*) can lose 0.77% of its body mass per hour during flights of many thousands of kilometres (Piersma *et al.*, 2005; Hedenström, 2010). Migrants therefore pay a high energetic price when travelling, often making them more vulnerable to threats occurring in staging sites than anywhere else in the migratory network.

1.6 Conservation planning for migratory species

Broadly speaking, migratory species can be divided into two groups. The first consists of species with small numbers of distinct breeding, staging or wintering sites, with few connections, while the second consists of species with substantial breeding and wintering ranges connected by numerous yet diffuse migratory routes (Wilcove & Wikelski, 2008). The first group can be more severely impacted by local threats due to a greater number of bottlenecks in the migratory network than the second group. Paradoxically, the first presents an easier conservation problem to solve than the second, because all nodes and connections within the migratory network can be identified in addition to the threats affecting them. If there is a known method of remediating a threat, then the species can be conserved. For example, humpback whales (*Megaptera novaeangliae*), whose migratory route follows the coast of South East Queensland (Australia) have been increasing annually at rate of 10% since whaling was banned in 1962 (Paterson *et al.*, 1994). Most species however fall into the second group, where no one site is critical to the survival of the species, yet declines might still be occurring over its entire range, as seen with the cerulean warbler (*Dendroica Cerulea*) (Wilcove & Wikelski, 2008). Such species are therefore difficult to conserve because of the quasi-impossibility of protecting such a widespread species over its entire range; and the lack of knowledge regarding migratory connectivity and its impacts on threat distribution in the migratory pathway.

Such information can however make a vast difference in how a migratory species is managed, determining whether a conservation effort will be successful or unsuccessful. In a planning exercise, Martin et al. (2007) found that maximising the number of protected American redstarts in a wintering range could potentially result in the loss of subpopulations within the breeding range if migratory connectivity was not considered. Other studies such as Klaassen et al. (2008) and Sheehy et al. (2011a) have also demonstrated that including connectivity in the conservation planning process results in better conservation outcomes. Singh and Milner-Gulland (2011) take this a step further by considering how protected areas should be distributed to help protect Saiga antelope (*Saiga tatarica*) from the dynamic threat of climate change. However, these studies only consider habitat acquisition as a means of preventing declines, a method that is not always appropriate because managers must often conserve multiple species, with very different distributions in time and space (Wilson *et al.*, 2007; Redford *et al.*, 2011).

Additionally, climate change is not the only dynamic threat faced by migratory species. Disturbance (Rogers *et al.*, 2006), poaching (Maingi *et al.*, 2012), hunting (Halliday, 1980; Larter *et al.*, 2000), deforestation (Brower *et al.*, 2012), urbanisation (LeDee *et al.*, 2008), invasive species (Dowding & Murphy, 2001) and agricultural intensification (Brower *et al.*, 2012) all threaten migratory species. Such threats come and go through time, and their relative importance can be expected to change in years to come. How often they impact migrants is also dependent on where they occur in the migratory pathway.

Conservation planning is a method of optimally allocating a finite amount of resources to conservation, through a series of weighted actions (Margules & Pressey, 2000; Sarkar *et al.*, 2006; Wilson *et al.*, 2007). For migratory species, such actions should therefore move beyond classical approaches which aim to identify protected areas (Moilanen *et al.*, 2009), to newer approaches which include a range of possible conservation actions accounting for location, cost, probability of success given social and biological factors (Wilson *et al.*, 2007; McCarthy *et al.*, 2008; Joseph *et al.*, 2009; Moilanen *et al.*, 2009; Beger *et al.*, 2010) in addition to connectivity (Cabeza, 2003; van Teeffelen *et al.*, 2006; Martin *et al.*, 2007; Klaassen *et al.*, 2008; Sheehy *et al.*, 2011a) and threat dynamics (Singh & Milner-Gulland, 2011).

1.7 Migratory Shorebirds

At the end of the arctic summer, millions of shorebirds leave their breeding grounds in the northern hemisphere to start their annual migration south. Following eight broad flyways, 215 species from the order *Charadriiformes* migrate to their non-breeding grounds in the southern hemisphere (Colwell, 2010). Within the East Asian-Australasian Flyway, 60 species journey from North-Eastern Russia and Alaska, to the South-Western Pacific, where they spend the non-breeding season feeding in the subtropical wetlands of South-East Asia, Australia, New Zealand and many Pacific Islands, before returning to breed the following summer. Most migrate in several steps (Warnock, 2010), briefly stopping along the way to feed on intertidal mudflats in South East Asia and Indonesia (Fig. 1.1). A few species however, such as bar-tailed godwits (*Limosa lapponica baueri*), cross the Pacific Ocean in an astounding 11,000 km non-stop flight from Alaska to New Zealand (Gillings *et al.*, 2009). In total, the shorebirds of the

East Asian-Australasian flyway traverse 23 different countries and three continents in both hemispheres (Bamford *et al.*, 2008).

Long-distance migrations are energetically demanding, and shorebirds have developed a range of physiological adaptations enabling them to complete such journeys. Prior to migration, shorebirds are able to increase their energy stores over very short periods through rapid weight gain, drastic shrinkage of certain organs and an increase in the size of flight muscles (Colwell, 2010; Hedenström, 2010). During flight, energy consumption can remain relatively low and energy is burned straight from organs if needed (Piersma *et al.*, 2005; Hedenström, 2010). Re-fuelling before, during and after migration is therefore essential in ensuring survival of the species. The effects of interrupted re-fuelling can differ depending on where they occur within the migratory network, and whether the site they occur at forms a bottleneck. Most shorebird species would not be able to complete their migration if it were not for staging sites at which they stop to refuel for the next leg of their migration (Myers *et al.*, 2000; Rogers *et al.*, 2010).

International collaborations are therefore necessary to protect these species and Australia has developed bilateral Migratory Bird Agreements with China (CAMBA), Japan (JAMBA) and the Republic of Korea (ROKAMBA). Through these treaties, countries are bound to protecting the birds that migrate between them. Various international agreements such as the Ramsar Convention on Wetlands, the Convention on Migratory Species and the Convention on Biological Diversity also protect shorebirds. Despite this protection, current conservation strategies seem to be failing (Bamford *et al.*, 2008; Kirby *et al.*, 2008; Rogers *et al.*, 2010; Zockler *et al.*, 2010). There is accumulating evidence that shorebirds have recently been experiencing severe declines (Reid & Park, 2003; Rogers & Gosbell, 2006; Close, 2008; Nebel *et al.*, 2008; Creed & Bailey, 2009; Paton *et al.*, 2009; Rogers *et al.*, 2011; Wilson *et al.*, 2011; Cooper *et al.*, 2012; Minton *et al.*, 2012; Clemens *et al.*, in press). Though the exact cause of these declines remains largely unknown (Rogers *et al.*, 2010; Wilson *et al.*, 2011), there is accumulating evidence that loss of intertidal habitat (Murray *et al.*, 2014), hunting (Kirby *et al.*, 2008; Colwell, 2010; Zockler *et al.*, 2010; Gallo-Cajaio *et al.*, in press) and disturbance (Rogers *et al.*, 2006; Burton, 2007) may be important threatening processes occurring within the East Asian-Australasian Flyway.

However, disentangling the impacts of these threatening processes on population dynamics is no easy feat. To date, few studies have investigated how environmental variability might

influence shorebird abundance in the EAAF (Boyd *et al.*, 2005; Nebel *et al.*, 2008; Conklin & Battley, 2012), and none has done so systematically throughout the migratory cycle. Similarly, few studies have investigated how intertidal habitat loss might affect population dynamics in the EAAF (Iwamura *et al.*, 2013; Iwamura *et al.*, 2014; Nicol *et al.*, 2015), largely due to a lack of data on the distribution of intertidal habitats in the EAAF. Currently data only exist for part of East Asia (Murray *et al.*, 2012; Murray *et al.*, 2014), and are urgently needed for the rest of the flyway.

Conservation planning for migratory shorebirds in the EAAF requires methods that can simultaneously account for connectivity (Cabeza, 2003; van Teeffelen *et al.*, 2006; Martin *et al.*, 2007; Klaassen *et al.*, 2008; Beger *et al.*, 2010; Hermoso *et al.*, 2012a; Hermoso *et al.*, 2012b; Linke *et al.*, 2012; Iwamura *et al.*, 2013; Langhans *et al.*, 2014; Runge *et al.*, 2014a; Nicol *et al.*, 2015) and uncertainty (McDonald-Madden *et al.*, 2008; Wintle *et al.*, 2010; Keith *et al.*, 2011; McDonald-Madden *et al.*, 2011). Finding local, national and international solutions for managing migratory shorebirds is no trivial pursuit. Time is running out for shorebirds given the severity of their declines (Reid & Park, 2003; Rogers & Gosbell, 2006; Close, 2008; Nebel *et al.*, 2008; Creed & Bailey, 2009; Paton *et al.*, 2009; Rogers *et al.*, 2011; Wilson *et al.*, 2011; Cooper *et al.*, 2012; Minton *et al.*, 2012; Clemens *et al.*, in press), and developing cost-effective and internationally-implementable conservation plans is urgently required to ensure population persistence into the future.

1.8 Thesis Aims

This thesis aims to improve the conservation status of migratory shorebirds in the EAAF and migrants more broadly, by developing methods and theory to inform management. To do so, I use a combination of approaches, including state-space modelling, correlative statistics, remote sensing, habitat protection mapping, cost-effectiveness analysis, conservation planning and linear programming. Specifically, the proposed research will:

- Develop and test a method of identifying and quantifying drivers of changes in population growth rate of seven species of shorebird in the EAAF, using limited data (**Chapter 2**)

- Determine the distribution, extent and protection of a primary shorebird habitat in Australia: intertidal habitat (**Chapter 3**)
- Determine how to prioritise management at the local scale, given diminishing returns on investment (**Chapter 4**)
- Determine how prioritise sites at the international scale, given limited understanding of migratory connectivity (**Chapter 5**)

1.9 Thesis overview

Our understanding of how to conserve migratory species is remarkably poor. Pinpointing where and when threats occur, and understanding how they impact migratory population dynamics is essential to achieve conservation. Few tools are available for identifying drivers of population growth rate, and even fewer for prioritising conservation actions. In my thesis, I tackle these fundamental gaps in our knowledge by developing and testing a method to distinguish local from remote drivers of population growth in migratory species (**Chapter 2**), mapping critical habitat (**Chapter 3**), and prioritising conservation actions at local and international scales (**Chapter 4 and 5**). Taken as an ensemble, my thesis highlights the importance of considering threats and planning for conservation at multiple scales. Though migratory species might travel internationally, they are highly reliant on a small number of geographically isolated sites for feeding or breeding, and very often, spend a majority of their time in one or a few such sites during the non-breeding season. Furthermore, my thesis demonstrates that solutions can be found despite uncertainty, and that policy priorities now need to shift from a site-quality based conservation approach, to a spatially-explicit conservation approach (**Chapter 5**) to secure the future of one of the world's most spectacular migratory flyways.

Chapter 2

Distinguishing local and remote drivers of change in migratory bird population growth rates

2 Distinguishing local and remote drivers of change in migratory bird population growth rates

2.1 Abstract

The effects of environmental conditions on population dynamics of migratory species are difficult to discern. Data are challenging to collect on mobile species, and are often restricted to a fraction of their migratory cycle. Using count data from a single site in a global migratory flyway, in combination with remotely sensed environmental data from across the flyway, our research aims to diagnose correlates of changing abundance in migratory shorebird populations. We used a combination of N-mixture models and weighted least square regressions to estimate the association between variation in the annual population growth rate of seven shorebird species in Moreton Bay, Australia, and anomalies in rainfall and temperature at migratory stopover sites across the East Asian-Australasian Flyway. We found that species were influenced by different environmental variables at different stages of the migratory cycle. Rainfall at all migratory stages influenced population growth rate for eastern curlew, red knot, great knot and lesser sand plover; while for temperature, this was only the case for red knot and grey-tailed tattler in the breeding grounds. Bar-tailed godwit and curlew sandpiper were not strongly influenced by any climatic variable at any migratory stage. Despite these varying effects, many species were declining. There is therefore potential for other factors to be driving changes in population growth rate of these species, including intertidal habitat loss, hunting, land use change, pollution, nutrification and sea-level rise. We have shown that it is possible to diagnose remote impacts on local population changes for a migratory species using only: (i) monitoring data from a single site within a migratory flyway; and (ii) measures of environmental conditions at known migratory stopover sites. Our methods are therefore highly transferable to other migratory systems with limited data, but also provide an important first step in understanding drivers of variation in annual growth rates in one of the world's least well studied, yet most highly threatened, migratory flyways.

2.2 Introduction

Drivers of population change are notoriously difficult to pinpoint for migratory species, because they are impacted by geographically and temporally isolated threats throughout the migratory cycle (Webster *et al.*, 2002; Norris & Taylor, 2006). Furthermore, many migrants exhibit dynamic range sizes, whereby at certain periods during the migratory cycle they can be restricted to a single location, such as a critical breeding or feeding site, because conditions throughout the rest of their range are unfavourable (Runge *et al.*, 2014b). Sometimes an entire population may depend on a single region to complete migration successfully (Baker *et al.*, 2004; Rogers *et al.*, 2010). Threats occurring in such bottlenecks can impact the entire population, with disproportionately large effects on population growth rate (Iwamura *et al.*, 2013). Thus, understanding where and when such bottlenecks occur in the migratory cycle is critical, because threats operating within bottlenecks can impact survival and fecundity at later migratory stages (Webster *et al.*, 2002; Harrison *et al.*, 2011).

However, migratory bottlenecks remain unknown for many species, making it particularly difficult to understand how populations are influenced by conditions at different stages of the migratory cycle (Webster *et al.*, 2002; Bauer *et al.*, 2008; Bull *et al.*, 2013). Novel tracking devices are offering new insights into migratory movements (Grothues, 2009; Jellyman, 2009; Hebblewhite & Haydon, 2010; Block *et al.*, 2011; Wilson *et al.*, 2015), yet sample sizes remain small, either due to the overall cost of implementing such methods (Hebblewhite & Haydon, 2010), or because many tags are still too large to deploy on smaller species (however see Hallworth and Marra, 2015). Furthermore, monitoring or count data often only exist for a fraction of the migratory range of a species (Amano *et al.*, 2010) and are highly biased in space and time (Clemens *et al.*, 2012). Newly developed remote sensing techniques therefore offer a fresh opportunity to utilise time-series remote sensing data to increase our understanding of environmental conditions and land use change throughout the entire range of a migratory species. This offers a fresh opportunity to use archived satellite imagery to increase our understanding of how environmental conditions and land use change throughout the entire range of a migratory species can impact population growth rate (Robinson *et al.*, 2009b; Dodge *et al.*, 2014; Pettorelli *et al.*, 2014).

In the East Asian Australasian Flyway, shorebirds undertake seasonal migrations between breeding grounds in the Arctic and non-breeding grounds in South East Asia, Australia and

New Zealand. Many species are declining across their range (Reid & Park, 2003; Rogers & Gosbell, 2006; Close, 2008; Nebel *et al.*, 2008; Creed & Bailey, 2009; Paton *et al.*, 2009; Rogers *et al.*, 2011; Wilson *et al.*, 2011; Cooper *et al.*, 2012; Minton *et al.*, 2012; Clemens *et al.*, in press), and loss of intertidal habitat is thought to be a primary driver (Clemens *et al.*, in press). Indeed, intertidal habitat in the Yellow Sea has declined by 28% since the 1980s (Murray *et al.*, 2014). Furthermore, population declines appear to be faster in shorebird species that rely heavily on the Yellow Sea during migration (Studds *et al.*, in prep). However, these data are not temporally or spatially resolved at a fine enough scale to explain annual fluctuations in population growth rate. Remotely sensed rainfall and temperature data on the other hand are available at a fine spatial and temporal scale, enabling us to investigate how conditions throughout the migratory cycle can affect seasonal variability in population growth rate.

Sub-optimal climatic conditions occurring at specific migratory stages can negatively impact the entire population through a variety of mechanisms, depending on their location within the migratory network (Iwamura *et al.*, 2013). These potentially include reduced feeding rates (Baker *et al.*, 2004), reduced fitness (Tulp *et al.*, 2009), delayed migration (Beaumont *et al.*, 2006; Conklin & Battley, 2012), reduced competitiveness (Piersma & Lindstrom, 2004), reduced fecundity (Piersma & Lindstrom, 2004) and reduced survival (Tulp *et al.*, 2009). Environmental conditions in one migratory stage can therefore create bottlenecks to population growth in shorebirds. As a result, shorebird population dynamics have been highlighted as potential indicators of climate change (Piersma & Lindstrom, 2004). In effect, any changes in conditions at an individual stopover site are likely to impact the migratory species as a whole, particularly when stopover sites are small in number and geographically isolated (Warnock, 2010; Iwamura *et al.*, 2013).

Here, we use a combination of N-mixture models and weighted least squares regressions to tease apart the effects of climatic conditions throughout the migratory cycle on population growth rate of seven species of migratory shorebird, using count data from a single non-breeding site: Moreton Bay (Australia).

2.3 Methods

The aim of our research was to distinguish between local and remote drivers of change in migratory populations. In the next sections, we outline our methods by: (i) describing the study system, (ii) defining the count data used, (iii) explaining the choice of environmental covariates, (iv) mathematically formulating an N-mixture model, (v) discussing the assumptions of this modelling approach, and (vi) associating population growth rate with environmental covariates using weighted least squares regressions.

2.3.1 Study system

Migratory shorebirds in the EAAF are experiencing significant localised declines (Reid & Park, 2003; Rogers & Gosbell, 2006; Close, 2008; Nebel *et al.*, 2008; Creed & Bailey, 2009; Paton *et al.*, 2009; Amano *et al.*, 2010; Colwell, 2010; Rogers *et al.*, 2011; Wilson *et al.*, 2011; Cooper *et al.*, 2012; Dawes, 2012; Minton *et al.*, 2012; Clemens *et al.*, in press). In Moreton Bay in particular, between the years of 1993 and 2008, seven species of migratory shorebird showed population declines of 43 -79%, while populations of resident species (i.e. those that stay in Australia year-round) showed no directional change (Wilson *et al.*, 2011). Recent analyses of shorebird trends in Australia have revealed that abundance of many species cannot be readily explained by conditions within Australia, hinting that international threats could be the primary cause of declines (Clemens *et al.*, in press). The EAAF is now considered to be the flyway with the largest number of threatened shorebird species (International Wader Study Group, 2003; Amano *et al.*, 2010). However, the causes of these declines remain poorly understood. In fact, the EAAF is considered to be the shorebird flyway with the least information on shorebird conservation status, and therefore in most urgent need of conservation evaluation and action (International Wader Study Group, 2003; Amano *et al.*, 2010).

Little is known about what might be driving changes in population growth rate, though research from other flyways has demonstrated that migratory shorebird populations respond strongly to changes in environmental conditions via changes in survival, fecundity or migration timing (Boyd & Piersma, 2001; Butler *et al.*, 2001; Schekkerman *et al.*, 2003; Piersma & Lindstrom, 2004; Gill *et al.*, 2007; Skagen *et al.*, 2008; Smith *et al.*, 2010; Sutherland *et al.*, 2012; Hipfner & Elner, 2013). Yet the effects of climatic variability on shorebirds are poorly understood

within the EAAF (however see Boyd *et al.* (2005); Nebel *et al.* (2008); Conklin and Battley (2012)). Our research therefore aims to unravel some of these processes within a migratory network for seven migratory shorebird species whose migratory routes are most understood (Iwamura *et al.*, 2013) : Bar-tailed godwit (*Limosa lapponica baueri*), curlew sandpiper (*Calidris ferruginea*), eastern curlew (*Numenius madagascariensis*), great knot (*Calidris tenuirostris*), grey-tailed tattler (*Tringa brevipes*), lesser sand plover (*Charadrius mongolus*) and red knot (*Calidris canutus*).

2.3.2 Count data

To estimate population growth rate in Moreton Bay, we used count data collected by the Queensland Wader Study Group (QWSG) between 1992 and 2012 across 40 sites (Milton & Driscoll, 2006). Specifically, count data were used from the stationary non-breeding season between the months of December and February each year, when shorebirds are extremely unlikely to undertake migratory movements because they undergo their annual primary moult (Marchant & Higgins, 1993; Higgins & Davies, 1996). Due to the variation in observer effort inherent in volunteer-collected data, sites were not all systematically surveyed each month. However, when surveyed, counts occurred simultaneously once a month within two hours of the high tide (Zharikov & Milton, 2009). Indeed, as the tide comes in, birds are forced from their feeding sites on intertidal mudflats, into nearby roosting sites where they are concentrated in high numbers, and easier to count. Local weather conditions, including tide height and wind strength were recorded for every count by QWSG, and used as covariates for detection probability in our N-mixture model.

2.3.3 Climatic variables

To distinguish between local and remote effects, we measured climatic conditions throughout the entire migratory cycle: non-breeding, north migration stopover, breeding and south migration stopover (Appendix S.2.1). For each of these migratory stages, we identified and digitised all internationally important stopover sites (250 sites in total) according to Bamford *et al*. (2008). We then determined the timing of migration through each of these migratory

stages (Appendix S.2.1) based on a literature review (Driscoll & Ueta, 2002; Barter & Riegen, 2004; Beaumont *et al.*, 2006; Higgins *et al.*, 2006; Tomkovich & Soloviev, 2006; Branson *et al.*, 2010; Rogers *et al.*, 2010; Battley *et al.*, 2012) and extracted rainfall and temperature variables within a 15km buffer around all sites to reflect the likely extent of local scale bird movements (Coleman & Milton, 2012). In addition, we extracted inland rainfall within a 150km buffer of Moreton Bay for the non-breeding season, to test whether inland rainfall influenced annual population growth rates. We used inland rainfall during the period birds remain in the non-breeding grounds (Appendix S.2.1) both for the current year, and the previous year. Finally, we calculated mean conditions over all sites used at a given migratory stage, for each climatic variable, for each of these migratory stages, for each species. We used data from the non-breeding season, north migration season, breeding season and south migration season prior to the count (t-1), in addition to data during the non-breeding season during the count (t).

2.3.3.1 *Temperature*

We used global 5 degree monthly gridded air temperature anomaly data freely available from the National Oceanic and Atmospheric Administration (NOAA; http://www.esrl.noaa.gov/psd/data/gridded/data.crutem3.html). Temperature differed greatly between different migratory stages. By using pre-calculated anomaly data (calculated as the difference from the long term mean temperature), we were able to compare between migratory stages, and capture extreme conditions which had the potential to drive changes in population growth rate. Indeed, temperature has commonly been used to predict shorebird distribution and occurrence (Butler *et al.*, 2001; Buehler *et al.*, 2010; Suryan *et al.*, 2012; Sutherland *et al.*, 2012). Temperature has been used as a proxy for intertidal benthic prey availability and abundance (Piersma & Lindstrom, 2004), whereby relatively cold conditions resulted in decreased productivity, while hot conditions resulted in algal blooms, which are known to be particularly prevalent in some Asian stopover sites (Keesing *et al.*, 2011). Both of these extremes can reduce survival during migration, and impact breeding success through decreased fitness upon arrival in the breeding grounds and ability to produce nuptial plumage to attract a mate (Boyd & Piersma, 2001; Piersma & Lindstrom, 2004; Boyd *et al.*, 2005; Gill *et al.*, 2007; Conklin & Battley, 2012; Sutherland *et al.*, 2012; Hipfner & Elner, 2013). Within the breeding

grounds, temperature can be used to predict snow melt and therefore nesting habitat availability and timing of breeding (Smith *et al.*, 2010), food availability and chick growth (Schekkerman *et al.*, 2003; Piersma & Lindstrom, 2004).

2.3.3.2 Rainfall

We used global 2.5 degree monthly rainfall anomaly data freely available from (NOAA; http://www.esrl.noaa.gov/psd/data/gridded/data.gpcp.html). Again, we used pre-calculated anomaly data for rainfall to compare between migratory stages, and capture extreme conditions which had the potential to drive changes in population growth rate. Indeed, shorebirds have been found to respond strongly to water availability, as they rely heavily on ephemeral wetlands for suitable feeding and roosting habitat at non-breeding and stopover sites (Gill *et al.*, 2007; Nebel *et al.*, 2008; Skagen *et al.*, 2008). Within the breeding grounds, high rainfall has been shown to negatively impact shorebird fecundity and chick growth and survival, by reducing arthropod abundance (Boyd & Piersma, 2001; Schekkerman *et al.*, 2003; Piersma & Lindstrom, 2004; Sutherland *et al.*, 2012).

2.3.4 Zero-inflated N-mixture model

Shorebird counts were carried out at $\mathrm{i} = \{1, \dots, R\}$ spatially distinct roost sites over $t = \{1, \dots, K\}$ independent non-breeding seasons (or years) with $j = \{1, \dots, N\}$ counts per season. Thus counts $y_{i,j,t}$ can be viewed as realisations of a binomial random variable indexing the unobserved true number $N_{i,t}$ of individuals (i.e. abundance) observed with a detection probability $p_{i,j,t}$, such that:

$$y_{i,j,t} \sim Binomial(N_{i,t}, p_{i,j,t}) \quad (1)$$

The number of individuals available for sampling $N_{i,t}$ at a given site *i* and non-breeding season *t* was based on a Poisson distribution such that:

$$N_{i,t} \sim Poisson\,(\lambda_{i,t}) \quad (2)$$

where $\lambda_{i,t}$ is the mean abundance per sample unit (i.e. per site and year). The Poisson distribution is customary when describing a random spatial point pattern (Dail & Madsen, 2011). Thus covariates specific to year *t* and site *i* can then be incorporated into $\lambda_{i,t}$ using a logarithmic transformation as seen in equation 3:

$$\log(\lambda_{i,t}) = \alpha_i + \beta t + \varepsilon_{i,t} \quad (3)$$

where α represents a random intercept for each site, β the slope parameter to show the abundance trend over time, and ε the error rate. ε is a site-specific and year-specific random effect which accounts for unobserved sources of variation in abundance among sites over time. Similarly, detection probability can also vary in response to covariates in a similar manner based on a linear logistic model (because $0 \leq p \leq 1$) such that:

$$\text{logit}(p_{i,j,t}) = \mu_{i,j,t} + \sum_{n=1}^{N} \sigma_n x_{i,j,t,n} \quad (4)$$

We therefore account for extra-Poisson dispersion in both abundance and detection. For equations 3 and 4 we use un-informative priors where α, β, ε and μ the random intercept are each drawn from a Normal distribution of mean 0 and precision of 0.001 (where $precision = 1/variance$). For equation 4, σ is the slope parameter for each of the *n* detection covariates *x* (i.e. tide height and wind strength) at each site *i*,for each count *j* during non-breeding season *t* and is drawn from a uniform distribution of -30 to -20 (this is determined from running multiple simulations: we start small and increase the range of the distribution until the parameter is no longer bounded).

For all species, count data were zero-inflated. By this, we mean there were many counts where no birds were observed, because none were present. Indeed, shorebird form large flocks, and are easy to detect when present. We therefore used a Bernoulli distribution with a probability ψ for each year *t* such that:

$$z_{i,t} \sim Bernoulli(\psi_t) \quad (5)$$

$$\psi_t \sim Uniform(0,1) \quad (6)$$

where z for each site i during each non-breeding season t is either 0 or 1, thus the Poisson distribution is only used for $\lambda_{i,t}$ when $z_{i,t} = 1$ as seen in equation 2.

$$N_{i,t} \sim Poisson\left(\lambda_{i,t} * z_{i,t}\right) \quad (7)$$

Models were run using JAGS 3.3.0 (Plummer, 2012) in R version 3.1.1 (R Development Core Team, 2011) with packages R2jags (Su & Yajima, 2012) and R2WinBUGS (Jeon *et al.*, 2013). We ran three Markov chains in parallel using the packages snow (Tierney *et al.*, 2008) and dclone (Sólymos, 2010) and drew 10,000 samples from multiple model iterations within each chain. Number of iterations varied between species, so Gelman-Rubin diagnostics were used to estimate model convergence when R≈1 (Gelman & Rubin, 1991; Kéry & Schaub, 2012). Finally, covariates were only considered significant when the 95% credible interval (CRI) generated from the posterior distribution did not overlap with zero (Gelman & Hill, 2006).

2.3.5 N-mixture model assumptions

Covariates in the N-mixture model run in JAGS do not allow for covariate values which are missing (NA). For the tide covariate, we replaced any NAs with the highest value for that particular month as all counts within a month are assumed to have been carried out during the highest tide. For wind strength however, we replaced any NAs with the average value the month to reflect general weather conditions while counts were conducted.

Additionally, N-mixture models can account for false positives in detection probability *p*, but not false negatives. We therefore assumed that for large flocks of birds, misidentification and double counts were negligible due to the distinctive identifying features of our study species and the experience of QWSG counters.

The approach assumes the population is closed to immigration, emigration, recruitment and mortality, and so we used counts from the non-breeding season, between December and February when the birds within Moreton Bay make only minimal migratory movements (Coleman & Milton, 2012). However, birds are known to move between sites from one count to the next (Coleman & Milton, 2012), violating the closure assumption. We therefore tested our model using a conditional autoregressive model to account for spatial auto-correlation. The model did not fit the data, potentially because bird movements were not restricted to

neighbouring roosts, but to the entire study region. We therefore did not include the autoregressive model in our analyses, but accounted for spatial and temporal autocorrelation using site and year random effects. The model therefore assumed that abundance was estimated at each site independently, and that birds present at a two sites during the same monthly count, were classified as false positives. We therefore underestimate detection probability p and overestimate abundance *N*: Our model does not yield perfect estimates of abundance, but does however yield a reliable estimate of population growth rate.

2.3.6 Testing the effects of climatic variables on population growth rate

The aim of the present study was to estimate the influence of environmental covariates on changes in abundance for seven shorebird species. To do so, we correlated yearly changes in abundance (i.e. population growth rate) with climatic variables using weighted least squares (WLS) regressions. Thus, the standard errors estimated from the N-mixture models could be used to weigh the WLS regression, where weight is equal to $1/se^2$. To estimate population growth rate we used the following equation:

$$G_t = \frac{\sum_{i=1}^{S} N_{i,t}}{\sum_{i=1}^{S} N_{i,t-1}} \qquad (8)$$

, where growth rate *G* for non-breeding season *t* was dependent on abundance *N* across all sites $i \in \{1, 2, \ldots, R\}$ from the current non-breeding season *t* and the previous *t-1*. Growth rate was log transformed and all variables centred and scaled and then tested for collinearity. We estimated that if the variance inflation factor (VIF) was under the critical value of 10 (Appendix S.2.3), collinearity was not a problem (Dormann *et al.*, 2013). We then used the package MuMIn version 1.13.4 (Barton, 2015) in R version 3.1.1 (R Development Core Team, 2011) to search for the best combination of climatic predictors (including quadratic terms) of population growth rate using Bayesian Information Criterion (BIC). BIC prioritises models with fewer covariates and is considered to be better suited to exploratory statistics than Akaike Information Criterion (Shmueli, 2010). We also separated the analysis into different stages: Non-Breeding (t-1), North migration, Breeding, South Migration and Non-Breeding. We then used MuMIn to investigate all possible combinations of rainfall and temperature variables on each migratory phase, including quadratic terms. For Non-Breeding seasons, we also included

a linear and quadratic term for inland rainfall. There were therefore a maximum of two variables with quadratic terms for each migratory stage, except during the non-breeding season where there were a maximum of three with quadratic terms. Covariates from different migratory stages were never included in the same model. MuMIn ranked all possible models for each migratory stage against each other, using ΔBIC to estimate the relative weight w of each model i such that $w_i = \frac{e^{-0.5\ \Delta\mathrm{BICi}}}{\sum_{r=1}^{R} e^{-0.5\ \Delta\mathrm{BICr}}}$. Finally, we use adjusted R^2 to report effect sizes (Burnham & Anderson, 2002; Lumley, 2012).

2.4 Results

The N-mixture models revealed that species varied greatly in rates of decline (β) and that detection probability p was influenced by tide height and wind strength (Table 2.1). Population growth rate G in Moreton Bay, calculated from N-mixture abundance estimates (Fig. 2.1), was associated differently with rainfall and temperature anomaly variables for different species, and during different migratory stages (Fig. 2.2).

2.4.1 Zero-inflated N-mixture model results

Our abundance estimates revealed that curlew sandpiper and eastern curlew were significantly declining by β = 4.8% and 3.8% respectively between 1992 and 2012 (Table 2.1). In agreement with a downward population trend (Appendix S.2.2), population growth rate G was more often below the stable rate of 1, than above (Fig. 2.1) All other species except Bar-tailed godwit and great knot appeared to be declining, but not significantly (Table 2.1). High tide height negatively influenced detection probability across all species, whereas wind strength increased detection probability for bar-tailed godwit and eastern curlew, suggesting these species are more likely to concentrate in specific roosts under high wind conditions.

Table 2.1 *Population trend estimates for seven shorebird species in Moreton Bay between 1992 and 2012 including slope parameters for detection probability covariates (high tide height and wind strength). * signifies that 25-75% of parameter estimates do not overlap 0 and ** signifies that 2.5-97.5% (95% CRI) of parameter estimates do not overlap 0.*

	Slope (β)	**SE**	**Tide (x_{tide})**	**SE**	**Wind Strength (x_{wind})**	**SE**
Bar-tailed godwit	0.0059	0.0071	**-1.22 ****	**0.22**	**0.9 ****	**0.28**
Curlew sandpiper	**-0.048 ****	**0.017**	**-0.88 ****	**0.25**	0.21	0.29
Eastern curlew	**-0.038 ****	**0.007**	**-0.86 ****	**0.13**	**0.61 ****	**0.17**
Great knot	0.00013	0.015	**-1.28 ****	**0.22**	0.32	0.29
Grey-tailed tattler	-0.011	0.014	**-0.72 ****	**0.25**	0.029	0.35
Lesser sand plover	-0.019 *****	0.014	**-5.31 ****	**2.17**	1.49 *****	1.05
Red knot	-0.043	0.043	**-2.48 ****	**0.41**	0.64 *****	0.55

2.4.2 Effects of climate variables on population growth rate G

By fitting environmental variables to population growth rate, it was possible to estimate the contribution of each of these variables to yearly changes in abundance, as opposed to the overall population trend. Growth rate in essence "de-trends" the data, thus the average population growth rate G oscillated around 1; the stable population (Fig 2.1). However, $G < 1$ regularly occured in the growth rate time series (Fig 2.1), explaining why many species were declining (see β in Table 2.1, Fig 2.1 and Appendix S.2.3).

Three environmental variables had a variance inflation factor above 10 (Appendix S.2.3), yet dropping one might cause another variable in the model to appear more important than it truly was (Baguley, 2012). For this reason, we chose not to remove these variables. We therefore report full models in Appendix S.2.4 while bearing in mind some variables had a variance inflation factor greater than 10 (Appendix S.2.3). Furthermore, these variables were not weighed strongly according to BIC and therefore did not strongly influence our results (Fig. 2.2).

More specifically, BIC weights highlighted that different species are influenced by different climatic variables at different migratory stages (Fig. 2.2, Appendix S.2.4 and Appendix S.2.5). No variable strongly influnced the dynamics of bar-tailed godwit (Fig. 2.2a) and curlew sandpiper (Fig. 2.2b) and the intercept-only model had relatively strong support (Appendix S.2.4). For eastern curlew (Fig. 2.2c), a negative quadratic relationship between north migration rainfall and population growth rate represented over 90% of all model BIC weights (Appendices S.2.4 and S.2.5). For great knot (Fig. 2.2d), a positive linear relationship between south migration rainfall and population growth rate represented 60% of all model BIC weights (Appendices S.2.4 and S.2.5). For grey-tailed tattler (Fig. 2.2e), a positive quadratic relationship between breeding temperature and population growth rate represented 50% of all model BIC weights, and a negative linear relationship between breeding rainfall and population growth rate represented 30% of all model BIC weights (Appendices S.2.4 and S.2.5). For lesser sand plover, a positive linear relationship between south migration rainfall and population growth rate weighed 30% of all model BIC weights (Appendices S.2.4 and S.2.5). And finally for red knot, a negative quadratic relationship between breeding rainfall and population growth rate represented over 75% of all model BIC weights, and a positive linear relationship between breeding temperature and population growth rate represented 80% of all model BIC weights (Appendices S.2.4 and S.2.5). Overall, there were no consistent trends across species for particular migratory stages or particular environmental variables.

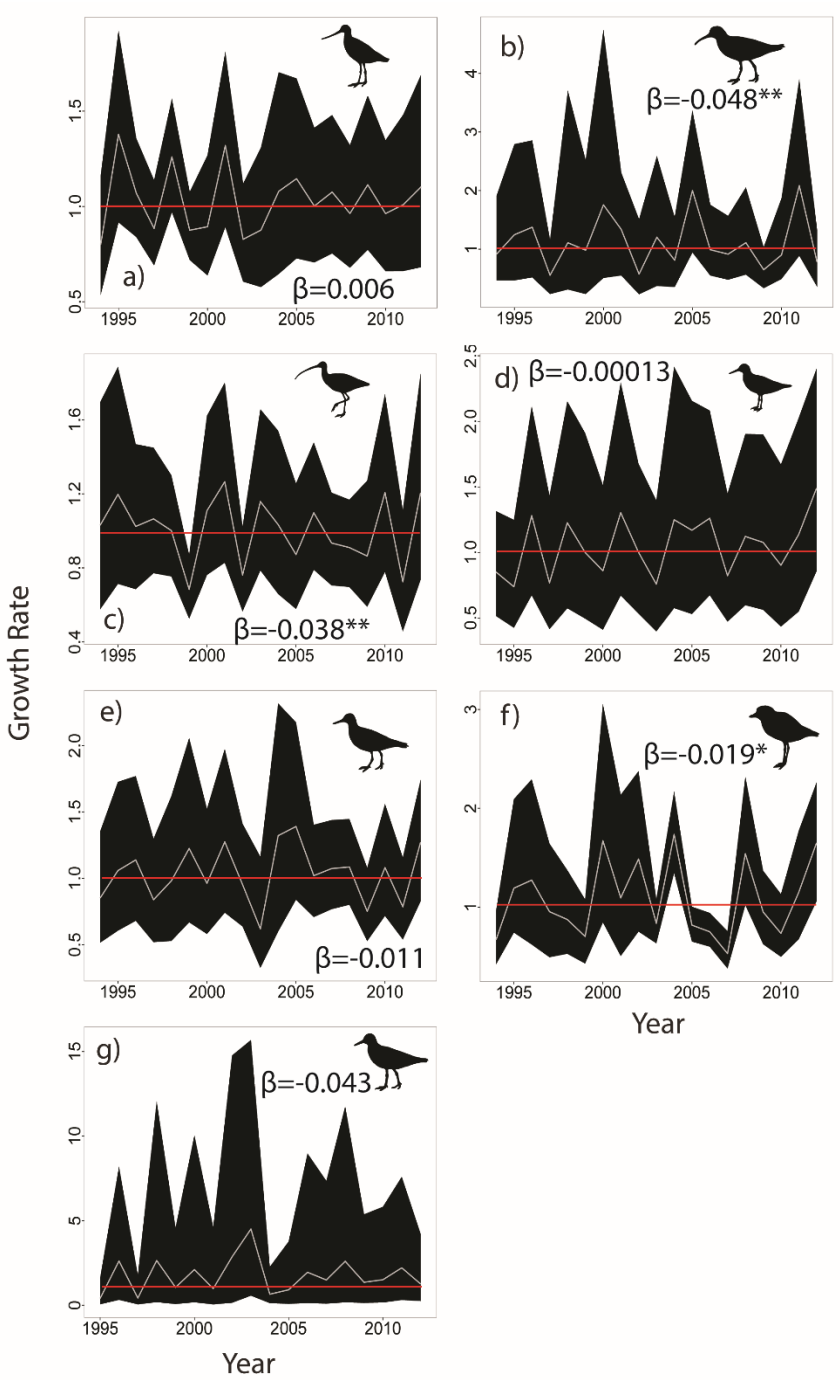

Figure 2.1 *From top to bottom, left to right, growth rate G between 1992-1993 and 2011-2012 of a) bar-tailed godwit (*Limosa lapponica*), b) curlew sandpiper (*Calidris ferruginea*), c) eastern curlew* (Numenius Madagascariensis*), d) great knot (*Calidris tenuirostris*), e) grey-tailed tattler (*Tringa brevipes*), f) lesser sand plover (*Charadrius mongolus*) and g) red knot (*Calidris canutus*). The white line represents the mean estimate of growth rate, and the black shading represents the 95% estimates of confidence intervals.*

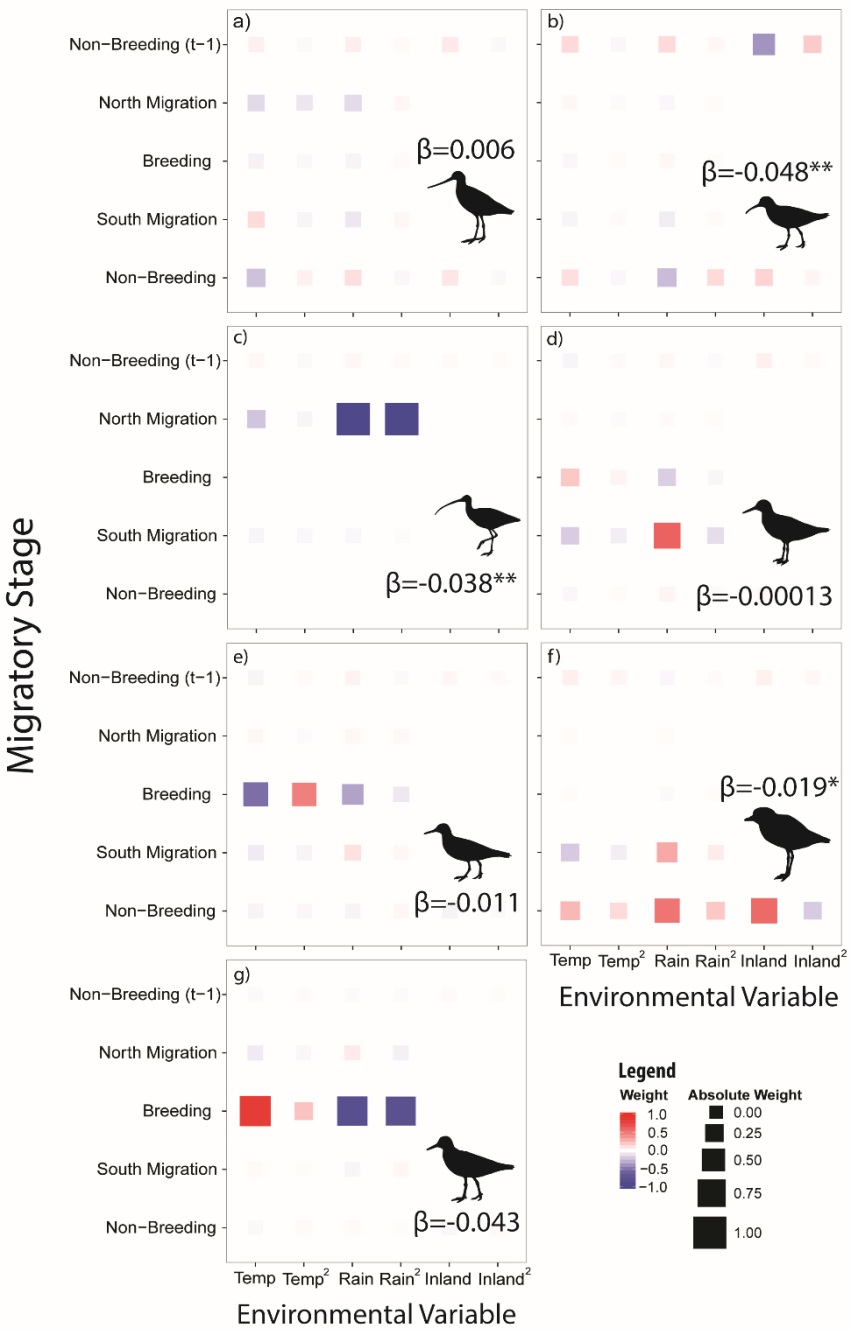

Figure 2.2 *Overall Bayesian information criterion (BIC) weights of different environmental variables at different migratory stages, from top to bottom, left to right, for of a) bar-tailed godwit (*Limosa lapponica*), b) curlew sandpiper (*Calidris ferruginea*), c) eastern curlew* (Numenius Madagascariensis*), d) great knot (*Calidris tenuirostris*), e) grey-tailed tattler (*Tringa brevipes*), f) lesser sand plover (*Charadrius mongolus*) and g) red knot (*Calidris canutus*). Blue is used to represent negative slope parameters, red for positive. Larger and darker scares represent stronger BIC weights.*

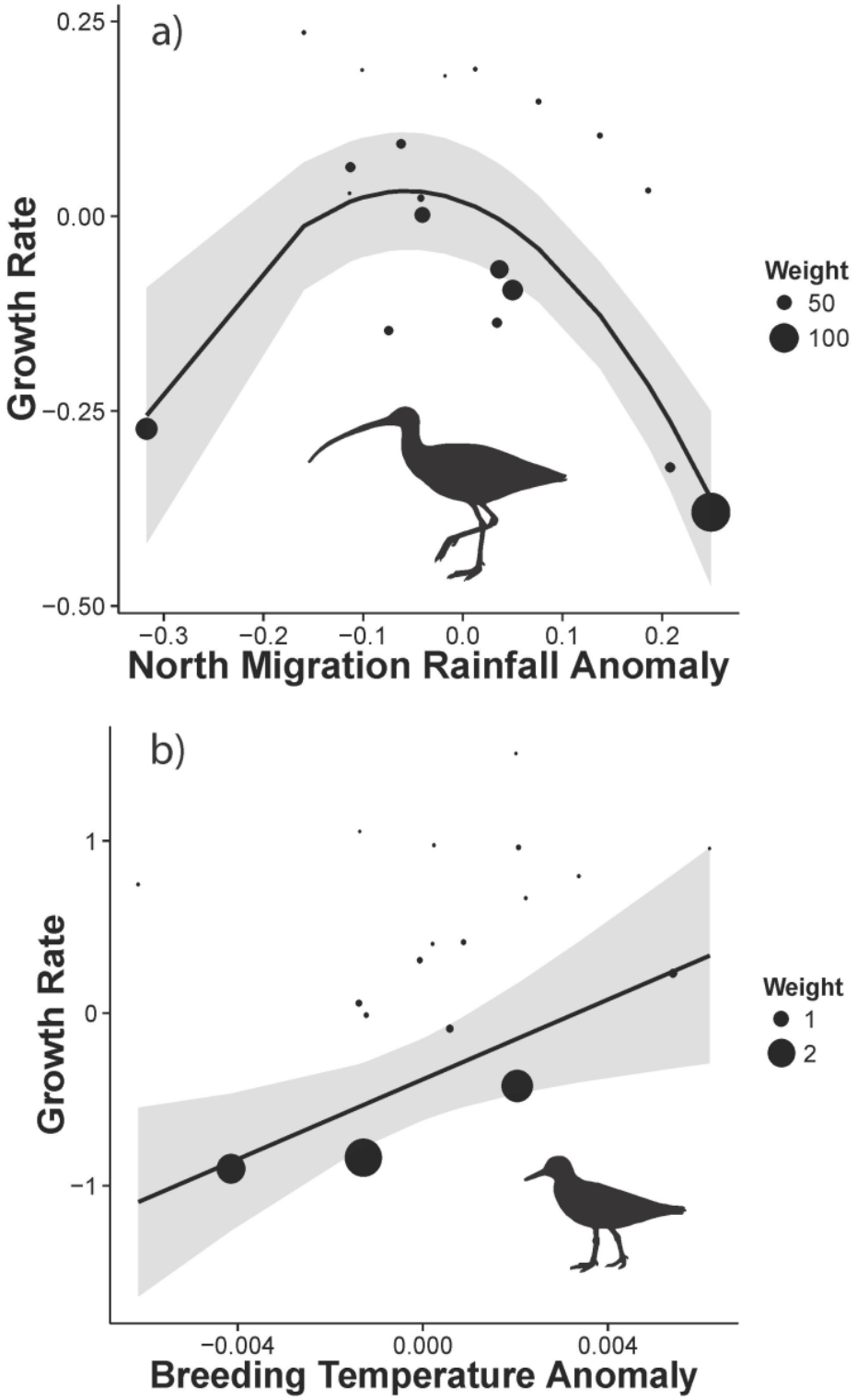

Figure 2.3 *Examples of weighted least squares regressions for a) eastern curlew and b) red knot.*

2.5 Discussion

With limited data, understanding the effects of environmental conditions on population dynamics can be difficult. In this study, we demonstrated that it is possible to utilise count data from a single site within a migratory flyway spanning more than 250 sites, to potentially identify remote factors influencing changes in population growth rate. Given migratory behaviour has generally been believed to be driven by climate-driven resource availability (Piersma & Lindstrom, 2004), in this study we analysed the relationship between two environmental variables, temperature and rainfall, on seven species of migratory shorebird from the East Asian-Australasian Flyway. We discovered that no environmental variable at any migratory stage consistently impacted population growth rates across species. This is interesting, given all species studied had previously been reported as declining from 0.8 % to 9.1% annually in Moreton Bay (Wilson *et al.*, 2011). We therefore anticipated that population growth rate might be driven by similar processes for all species. However, when testing the effects of environmental variables on population growth rate, we found that no single environmental variable at any migratory stage consistently affected all species simultaneously.

More specifically, BIC weights suggest that eastern curlew are most heavily influenced by rainfall anomalies during northward migration, grey-tailed tattler and red knot by temperature and rainfall anomalies during the breeding season, great knot by rainfall anomalies during southward migration and finally lesser sand plover by rainfall anomalies during the non-breeding season (Fig. 2.2). Rainfall is therefore important at all migratory phases for many shorebird species, and negative anomalies most likely reduce the availability of ephemeral wetlands for feeding and roosting. Species however respond differently to positive rainfall anomalies. For great knot and lesser sand plover, positive rainfall anomalies were on average positively correlated with population growth rate, most likely because of the creation of additional roosting habitat (Rogers *et al.*, 2006). For eastern curlew however, positive rainfall anomalies were on average correlated with reduced population growth rate, perhaps because anomalously high rainfall can result in excessive sedimentation (Ren & Shi, 1986) and nutrient enrichment (Huang *et al.*, 2014) of tidal flats, potentially altering sediment structure and causing algal blooms (Liu *et al.*, 2013), which in turn can disrupt feeding during migration. A similar effect was observed for red knot in the breeding grounds whereby both positive and

negative rainfall anomalies were on average negatively correlated with population growth rate, most likely because both can reduce arthropod abundance (Rehfisch et al., 2004).

In contrast to rainfall, temperature only influenced birds on the breeding grounds. In the arctic breeding grounds, temperature strongly influences timing of snow melt and productivity (Geering *et al.*, 2007). The relationship between temperature anomalies and population growth rate was however different for grey-tailed tattler and red knot (Fig. 2.2). Indeed, for grey-tailed tattler, both negative and positive rainfall anomalies were on average associated with positive population growth rate. This may be because grey-tailed tattler s breed along rivers (Geering *et al.*, 2007), which melt sooner than other arctic habitats, giving them a competitive edge over other arctic breeding shorebirds. Positive temperature anomalies on the other hand on average benefitted both red knot and grey-tailed tattler, possibly because they allow chicks to forage longer and increase survival (Tjorve *et al.*, 2007).

Compared to previous studies of shorebird abundance in Moreton Bay, our estimates of population declines were less severe (Wilson *et al.*, 2011). These differences are methodological; previous population trends were estimated using the average number of birds per site to overcome incomplete count data and fit linear models. Here, incomplete and variable count data were used to parameterise detection probability, thus accounting for variable observer effort over time and across sites. This high variability increased the credible intervals in this analysis, explaining why fewer population trends were significant (i.e. 2.5-97.5% (95% CRI) of parameter estimates did not overlap zero). Furthermore, larger 95% credible intervals flattened the trends, reducing the slope estimate β. Lastly, the present analysis used more recent data, suggesting an increase in species such as great knot, lesser sand plover and grey-tailed tattler since 2009, when the previous analysis was carried out.

One advantage of N-mixture models is that covariates can be fit to detection probability to improve abundance estimates. We found that detection probability was negatively correlated with tide height, while positively correlated with wind strength. Detection likely decreased when tide height was very high because king tides inundate most roost sites making them unavailable to birds. This would suggest that counts may achieve higher detectability if they are not performed during king tides. Detection also likely increased during strong wind conditions because birds were more likely to concentrate in roost sites to shelter. Therefore performing counts more consistently at fewer sites which are less likely to inundate during king

tides and which shelter birds from high wind conditions, has the potential to improve detectability and therefore the precision of these types of analyses.

Our results show that environmental conditions correlate with population growth rate for several shorebird species in the EAAF. However, climatic conditions are likely not the only factors influencing changes in shorebird population growth rate. In fact, for species such as bar-tailed godwit and curlew sandpiper, no environmental variable at any migratory stage strongly outweighed another (Fig. 2.2). Though bar-tailed godwit numbers were relatively stable, curlew sandpiper was decreasing significantly by 4.8% (Table 2.1). In light of these declines, curlew sandpiper and eastern curlew have recently been listed as nationally threatened in Australia (http://www.environment.gov.au/epbc/about/epbc-act-lists). Yet temperature and rainfall variables in no way explain yearly variations in population growth rate of curlew sandpiper (Fig. 2.2). curlew sandpiper and eastern curlew do however have in common a strong reliance on the Yellow Sea during migration stopover (Bamford *et al.*, 2008), where intertidal habitat (a primary feeding habitat for these species) has declined by 65% over the last five decades (Murray *et al.*, 2014). In fact, of all species considered in this analysis, only bar-tailed godwit and grey-tailed tattler did not rely heavily on the Yellow Sea during migration (Bamford *et al.*, 2008). There is therefore a potential multiplicative effect of climatic variability and intertidal habitat loss on population growth rate for many of these species.

Most likely, combinations of factors are driving the declines we are observing in migratory shorebirds (Wilson *et al.*, 2011). Hunting, pollution, sea-level rise, diseases, land-use change and disturbance have all been identified as threats to shorebirds (Sutherland *et al.*, 2012). However the purpose of the present study was not to test all possible drivers of declines, (primarily because the necessary data on habitat loss are not available at a fine enough spatial and temporal resolution across the flyway), but to determine whether it was feasible to use data from a single site within a global migratory flyway, to distinguish between local and remote drivers of population growth. We show that this is indeed possible, using very limited data comprising (i) count data from a single site, (ii) remotely sensed environmental data, and (iii) a list of potential stopover sites. Our research also provides a much needed first step in understanding how conditions across 250 stopover sites can influence the population dynamics of a suite of migratory shorebird species in the EAAF, one of the least studied migratory shorebird flyways (Amano *et al.*, 2010).

The methods we outline here can be used to quantify the contributions of different threats at different migratory stages to population growth rate of any migratory species with limited data. These types of analyses could potentially enable us to improve our understanding of migratory connectivity and better evaluate the effectiveness of local conservation actions at a global scale. Ultimately, such information could be used to prioritise and coordinate global conservation actions.

2.6 Acknowledgements

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Chapter 3

Distribution and protection of intertidal habitats in Australia

3 Distribution and protection of intertidal habitats in Australia

3.1 Abstract

Shorebirds have declined severely across the East Asian-Australasian Flyway. Many species rely on intertidal habitats for foraging, yet the distribution and conservation status of these habitats across Australia remain poorly understood. Here, we utilised freely available satellite imagery to produce the first map of intertidal habitats across Australia. We estimated a minimum intertidal area of 9856 km^2, with Queensland and Western Australia supporting the largest areas. Thirty-nine percent of intertidal habitats were protected in Australia, with some primarily within marine protected areas (e.g. Queensland) and others within terrestrial protected areas (e.g. Victoria). In fact, three percent of all intertidal habitats were protected both by marine and terrestrial protected areas. To achieve conservation targets, protected area boundaries must align more accurately with intertidal habitats. Shorebirds use intertidal areas to forage and supratidal areas to roost, so a coordinated management approach is required to account for movement of birds between terrestrial and marine habitats. Ultimately, shorebird declines are occurring despite high levels of habitat protection in Australia. There is a need for a concerted effort both nationally and internationally to map and understand how intertidal habitats are changing and how habitat conservation can be implemented more effectively.

3.2 Introduction

Migratory shorebird populations are declining rapidly across continental Australia (Clemens *et al.*, in press), and also locally in many places including Tasmania (Reid & Park, 2003; Cooper *et al.*, 2012), South Australia (Close, 2008; Paton *et al.*, 2009), Victoria (Rogers & Gosbell, 2006; Minton *et al.*, 2012), the east of the country (Nebel *et al.*, 2008; Wilson *et al.*, 2011) and in Western Australia (Creed & Bailey, 2009; Rogers *et al.*, 2011). Based on the severity of their declines and a high likelihood that threatening processes are continuing, both eastern curlew *Numenius madagascariensis* and curlew sandpiper *Calidris ferruginea* were recently up-listed to Critically Endangered under the Environment Protection and Biodiversity Conservation Act

1999 (EPBC Act; Department of the Environment, 2015a, b). At a broader scale, similar declines have also been reported across the East Asian-Australasian Flyway (EAAF; Amano *et al.*, 2010). This is particularly troubling as not only does the EAAF have the greatest number of threatened species and the largest number of shorebird populations among the world's flyways, it also has the least information on conservation status (International Wader Study Group, 2003; Amano *et al.*, 2010; Wilson *et al.*, 2011). Therefore, the EAAF is arguably the flyway in greatest need of conservation evaluation and action (Amano *et al.*, 2010).

The majority of migratory shorebirds rely on intertidal habitats for foraging (Galbraith *et al.*, 2002), defined here as the area between the high and low waterline (Murray *et al.*, 2012). Long distance migrations are so energetically demanding (Blem, 1990) that shorebirds must feed rapidly and store fat reserves before, during and after migration to ensure survival and reproduction (Drent & Piersma, 1990). Relative to other habitat types, intertidal habitats are limited to a narrow strip along the coastline, leaving the species these habitats support vulnerable to extinction (Purvis *et al.*, 2000; Lee & Jetz, 2011). For migratory shorebirds, the likelihood that a particular site will sustain large numbers of birds is strongly correlated with the area of available intertidal habitat, a key factor influencing the availability of benthic prey organisms (Evans & Dugan, 1983; Galbraith *et al.*, 2002). Loss of intertidal habitats could reduce the carrying capacity of a site, decreasing the number of birds in an area and increasing the risk of local extinctions (Sutherland & Anderson, 1993; Sheehy *et al.*, 2011a; Iwamura *et al.*, 2013)

Currently, migratory shorebirds are considered a matter of national environmental significance under the EPBC Act, owing to their inclusion in bilateral migratory bird agreements with China, Japan, and the Republic of Korea. Any development or activity likely to cause significant impact must be assessed under the EPBC Act (Deptartment of the Environment, 2013), where the concept of 'important habitats' plays a crucial role in protecting shorebirds from significant impacts. Important habitats in Australia for migratory shorebirds under the EPBC Act include those recognised as nationally or internationally important, based on criteria adopted under the Ramsar Convention on Wetlands (1971). According to this convention, wetland habitats should be considered internationally important if they regularly support: 1% of the individuals in a population or a minimum of 20000 individuals of all species combined. Nationally important habitats can be defined using a similar approach if they regularly support:

0.1% of the flyway population of a single species, 2000 migratory shorebirds, or 15 migratory shorebird species (Clemens *et al.*, 2010). However, with no formal evaluation of the distribution and protection of intertidal habitats in Australia, it remains difficult to assess how well such criteria are performing.

Mapping the occurrence and protection of intertidal habitats is critical given their restricted distribution and importance to migratory shorebirds. Indeed, formal evaluation of the distribution and extent of intertidal habitats will provide valuable data to help assess the impact of alternative coastal development plans on shorebird populations. Conserving intertidal habitats requires an understanding of habitat distribution, as well as extent and current levels of protection by both marine and terrestrial protected areas. However, mapping intertidal habitats can be complicated using any form of field survey, airborne, or satellite remote sensing, as the waterline is highly dynamic, inundating the habitat once or twice per day and exposing it to a varying extent. Although many habitats have been effectively mapped in Australia, the distribution and status of intertidal habitats at a national scale, aside from mangroves and saltmarsh, remain unknown below a resolution of 10 km^2 (http://www.ozcoasts.gov.au/nrm_rpt/habitat_extent.jsp). Recent advances in the availability of satellite image archives and multi-temporal image analysis techniques have led to the development of a method for mapping the distribution of intertidal habitats at continental scales (Murray *et al.*, 2012). This has paved the way for a regional status assessment of tidal flat habitats in the Yellow Sea (Murray *et al.*, 2014; Murray *et al.*, 2015). Murray *et al.* (2014) demonstrated that intertidal habitats in the Yellow Sea have declined by 65% in the last five decades, and by 28% since the 1980s. However, there is little information on the extent of intertidal habitats outside the Yellow Sea. Here, we use the methodology developed by Murray *et al.* (2012) to create the first map of intertidal habitats for Australia, and assess the extent to which intertidal habitats are protected by marine and terrestrial protected areas. This mapping (i) enables a better understanding of the distribution and protection of intertidal habitats in Australia, (ii) forms an exemplar for the development of continent wide tidal flat maps in other parts of the world, and finally (iii) helps identify critical shorebird habitat at a national scale.

3.3 Methods

The method we used to map the extent and distribution of intertidal habitats in Australia was based on a continental-scale mapping project conducted across Asia by Murray *et al.* (2012;

2014). We first obtained the complete metadata of the freely available Landsat Archive from USGS Earth Explorer (http://earthexplorer.usgs.gov). We constrained our analysis to the years spanning 1999 and 2014, to maximise coverage and permit the identification of images acquired at low tidal elevations (Appendix S.3.1). We identified all Landsat images that intersected the Australian coastline. Using the Tide Model Driver (TMD) MATLAB toolbox for tide modelling, we estimated the tidal elevation at the time of image acquisition with the Indian Ocean, Tasmania, and Northern Australia tide models available from the Oregon State University suite of tide models (Egbert & Erofeeva, 2002; Padman & Erofeeva, 2005). Images acquired within the upper and lower 10% of the tidal range were downloaded and visually reviewed before being selected for the final remote sensing analysis. For Landsat images not available via Earth Explorer, due to extensive cloud cover or other problems, we obtained the ortho-corrected Landsat Archive images from Geoscience Australia and the Department of Environmental Resource Management (Filmer *et al.*, 2010). Image pre-processing, sorting and pairing for intertidal mapping, followed the procedure in Murray *et al.* (2012).

The final image set consisted of 99 pairs of Landsat scenes over 79 path-row footprints of 185-km × 170-km each, with 170 Enhanced Thematic Mapper Plus (ETM+), and 28 Landsat Thematic Mapper (TM) satellite images (Appendix S.3.1). The mean difference in acquisition time between high and low tide image pairs was 1.49 ±1.18 years. The Normalised Differenced Water Index (NDWI; McFeeters, 1996) and, where possible, the Modified Normalised Differenced Water Index (MNDWI; Xu, 2006) were calculated for each pixel to maximise the likelihood of differentiating between water and non-water areas, irrespective of the substrate or benthos (McFeeters, 1996; Xu, 2006). Each image was then classified into a binary land/water image by manually assigning a threshold that most effectively identified the waterline in each image. Images were discarded if a suitable threshold could not be found that consistently identified the waterline throughout the image. The classified high and low tide images in each pair were then differenced, resulting in a delineation of intertidal habitats as the difference between the two input images (Murray *et al.*, 2012). For further detail on the NDWI differencing method refer to Murray *et al.* (2012).

The intertidal areas identified from all Landsat images were merged to create the first estimate of the intertidal habitat distribution across Australia at a 30m resolution (full dataset can be found in Dhanjal-Adams *et al.*, 2015). Post-processing was necessary to remove incorrectly

classified pixels (Murray *et al.*, 2012; Murray *et al.*, 2014). False positive classification errors occurred both landward and seaward in many images. In part, these were due to seasonal changes in water presence, such as flooding and inland ephemeral wetlands inland appearing in one image but not the other, but most errors occurred when ocean was classified as intertidal. Such errors resulted from cloud cover, water turbidity, algal blooms and whitewash from waves being classified as land, thus affecting the classification output. Such limitations are inherent in delimiting tidal flat and open water features, but are easily corrected during post-processing (McFeeters, 1996; Ryu *et al.*, 2002; Xu, 2006; Liu *et al.*, 2012).

We completed an accuracy assessment on the final intertidal habitat map to measure classification error, by comparing the mapped data set with a reference set using a confusion matrix (Congalton & Green, 2008; Roelfsema & Phinn, 2013). Using stratified random sampling, we generated 204 sample locations within 10 km of the coastline and within intertidal habitats. Each point was assessed by an independent reviewer and labelled as belonging to one of the two classes ("intertidal" or "other") to create a reference data set based on a combination of ground-truth information, including low tide Landsat imagery, Google Earth imagery and ESRI World imagery. For each point, the mapped data were extracted from the intertidal habitat map created in this study. Then, using the mapped data and the reference data set, we populated a confusion matrix (Appendix S.3.2) and quantified the map category, user's and producer's accuracy, as well as the map overall accuracy (Congalton and Green 2008).

User's accuracy represents the probability that a pixel on the map is correctly classified as intertidal. Producer's accuracy represents a measure of omission error, i.e. the probability a pixel was missed by the classification (Congalton & Green, 2008). Individual user's accuracy for the intertidal class was 100% and for the "other" class was 91.2% (Appendix S.3.2), i.e. all the pixels in the intertidal class were intertidal, but some pixels in the "other" class were also intertidal. The producer's accuracy for the intertidal class was 91.9%, and for the "other" class was 100% (Appendix S.3.2), i.e. some intertidal habitats were found in the ocean class, while no ocean was found in the intertidal class. This resulted in an overall accuracy of 95.6%, which is well above the commonly cited acceptable Landsat scale mapping accuracy level of 85% (Congalton & Green, 2008; Foody, 2009). These small errors highlight false negative classification errors, where not all intertidal habitats were picked up during the mapping process. These errors were, in part, due to striping on Landsat ETM+ imagery as a result of a

sensor malfunction after May 2003, causing some images to miss 22% data. We applied the standard approach used to minimise striping by merging 15 years of classification maps together (Markham *et al.*, 2004). False negative classification errors (omission errors) were also, in part, due to the image selection process. To maximise the number of images used in the analysis with the aim of maximising coverage, we used images taken within 10% of the high and low tide, not the highest or lowest possible tides. Therefore, small strips of intertidal habitats were missing on the landward and seaward sides of the correctly mapped intertidal habitats. Although we used highly accurate tide models, errors were likely to remain in the tide predictions due to tidal variation across the extent of each Landsat image, as well as variability in timing of Landsat imagery. By combining multiple images, these errors were again minimised. For further discussion of errors associated with this remote sensing method, refer to Murray *et al.* (2012).

Finally, to determine the level of protection of mapped intertidal habitat, we acquired data from the Collaborative Australian Protected Area Database (CAPAD) for 2014 (http://www.environment.gov.au/land/nrs/science/capad/2014) and estimated the area of intertidal habitats protected by marine protected areas, terrestrial protected areas, or both.

3.4 Results

Our map of the intertidal habitats of Australia achieved 91% coverage of the Australian coastline with an overall classification accuracy of 95.6% at a 30m resolution (Table 3.1; Appendix S.3.2). However, 9% of the coastline remained un-mapped particularly in Western Australia (Fig. 3.1). Roebuck Bay for example, an internationally and nationally important shorebird site was not mapped due to a lack of good quality images of the area.

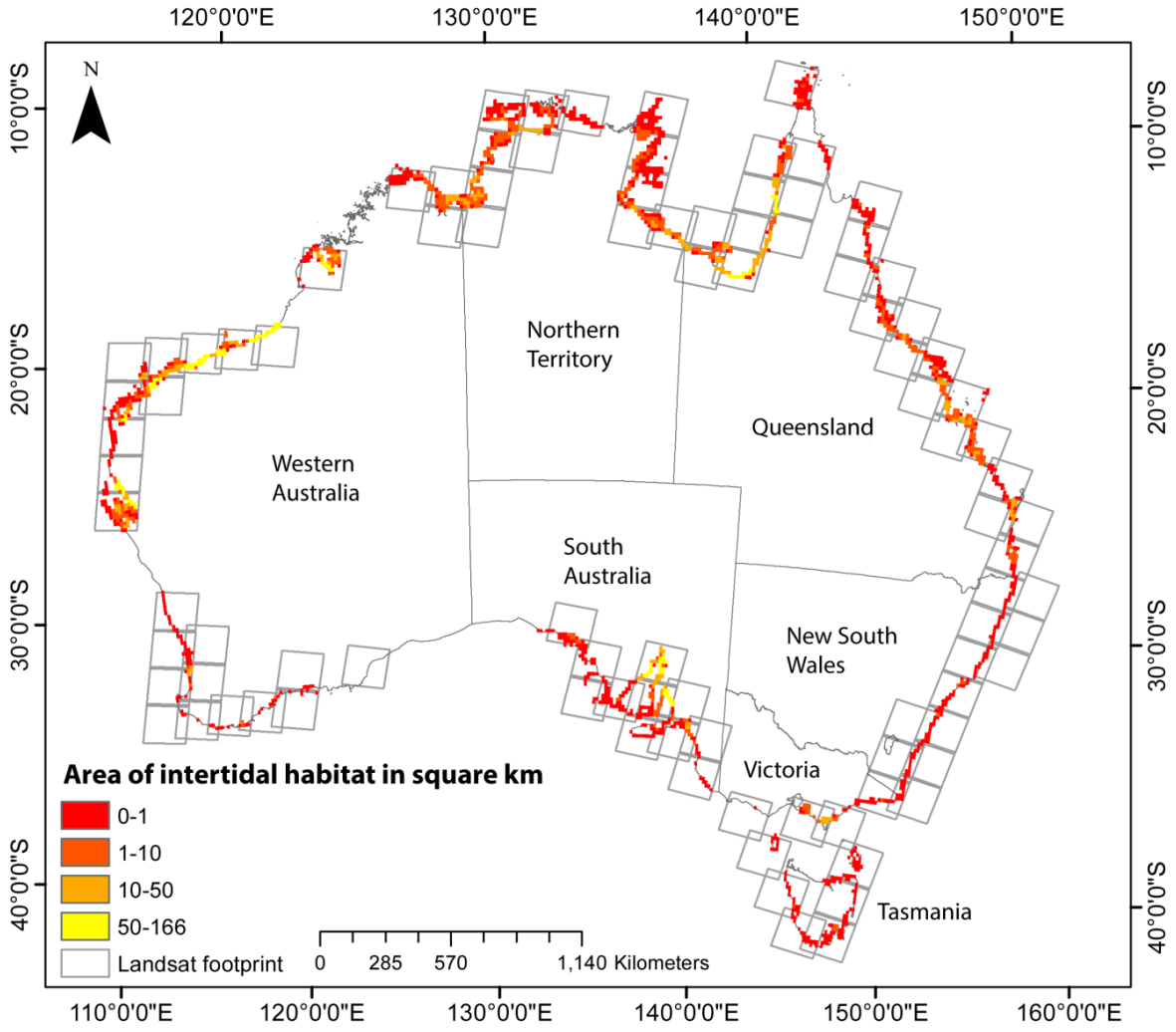

Figure 3.1 *Net area of intertidal habitats across Australia mapped at a 14 km grid resolution.*

We identified a minimum total of 9856 km^2 of intertidal habitat across Australia (Figs. 3.1 and 3.2; Table 3.1). The states with the largest areas of intertidal habitat were, in decreasing order, Queensland, Western Australia, Northern Territory and South Australia with >0.2 km^2 per mapped kilometre of coastline (Table 3.1; Fig. 3.1). Intertidal habitats were largely concentrated in estuaries, embayed coastlines and areas protected by coral reefs (Figs. 3.1 and 3.2).

Intertidal habitats were generally very well covered by protected areas, with 39% of all intertidal habitats across Australia overlapping marine and / or terrestrial protected areas (Table

3.1; Fig. 3.2). The Northern Territory had the lowest level of protection at 6% and Victoria the highest at 80% (Table 3.1). There was marked variation in whether intertidal habitats were primarily represented in marine or terrestrial protected areas. For example, of the protected intertidal habitat in Queensland, 96% occurred exclusively within marine protected areas. Yet in Victoria, only terrestrial protected areas covered intertidal habitat (Table 3.1; Fig. 3.2). Furthermore, 3% of protected intertidal habitats in Australia were covered by both marine and terrestrial protected areas, with up to 11% overlap between marine and terrestrial protected areas in South Australia (Table 3.1; Fig. 3.2).

Table 3.1 *Distribution and protection of mapped intertidal habitats in Australia.*

STATE	Mapped coastline in km (Percentage of total coastline)	Total Intertidal Habitat in km^2	Area of intertidal habitat per km of coastline mapped (km^2)	Total PA in km^2 (Percentage of Total Intertidal Habitat)	Marine PA in km^2 (Percentage of Total PA)	Terrestrial PA in km^2 (Percentage of Total PA)	Marine and Terrestrial PA in km^2 (Percentage of Total PA)
NSW	3793 (100)	95.6	0.03	47.6 (49.7)	30.8 (64.9)	20.0 (42)	3.3 (6.9)
NT	10384 (96.68)	2235.1	0.22	129.5 (5.8)	24.3 (18.8)	105.2 (81.2)	0 (0)
QLD	11235 (97.54)	2682.1	0.24	1608.6 (60)	1535.6 (95.5)	95.2 (5.9)	22.2 (1.4)
SA	4709 (99.99)	925.8	0.20	616.1 (66.5)	595.7 (96.7)	85.5 (13.9)	65.2 (10.6)
TAS	4235 (87.10)	91.8	0.02	47.5 (51.7)	8.2 (17.3)	39.3 (82.7)	0 (0)
VIC	2404 (99.99)	231.7	0.10	185.6 (80.1)	0 (0)	185.6 (100)	0 (0)
WA	15611 (80.15)	3593.4	0.23	1226.1 (34.1)	670.9 (54.7)	566.4 (46.2)	11.3 (0.9)
AUSTRALIA	**52372 (91.08)**	**9855.6**	**0.19**	**3860.9 (39.2)**	**2865.7 (74.2)**	**1097.2 (28.4)**	**101.9 (2.6)**

3.5 Discussion

We present the first high spatial resolution map of intertidal habitats in Australia, determining that intertidal habitats have a minimum total area in Australia of 9856 km^2 (Table 3.1; Figs. 3.1 and 3.2). About 39% of the total extent of intertidal habitat is covered by protected areas (Fig. 3.2; Table 3.1), suggesting these habitats are well represented within the Australian protected area network. This information is crucial for assessing how Australia's coastal protected area networks are contributing towards global targets such as Aichi Target 11, laid out under Goal C of the Strategic Plan for Biodiversity (https://www.cbd.int/sp/) suggesting that 10% of coastal and marine environments be protected by 2020.

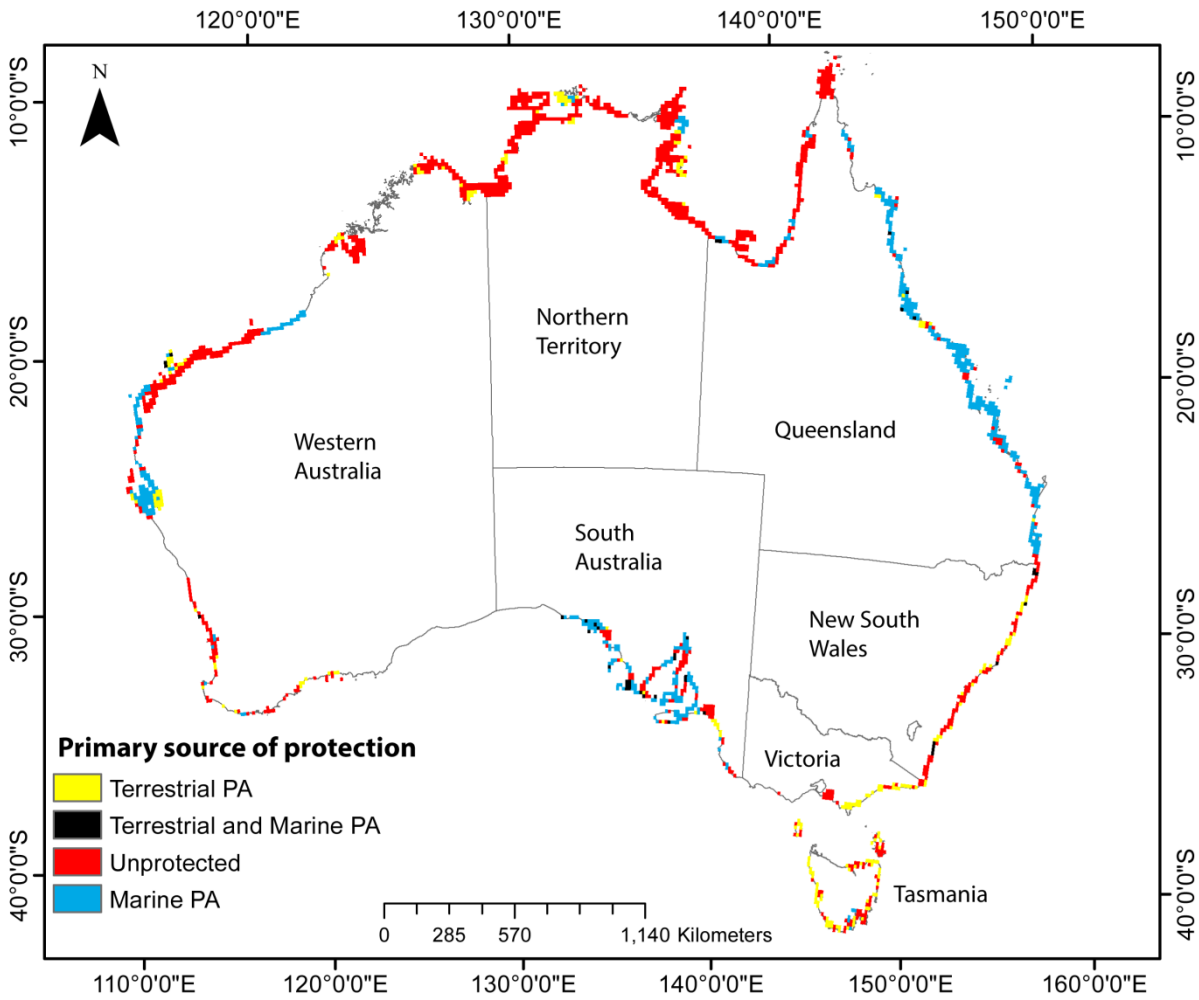

Figure 3.2 *Primary source of protection of intertidal habitats across Australia mapped at a 14 km grid resolution.*

We discovered large differences in the extent to which intertidal habitats are protected among states, with some states protecting over 60% of their intertidal area (Victoria, South Australia and Queensland), and others less than 6% (Northern Territory; Table 3.1; Fig. 3.2). The lowest levels of protection however occurred in the Northern Territory, where some of the largest numbers of shorebirds (Chatto, 2003; Clemens *et al.*, in press) and largest areas of intertidal habitats (0.22 km^2 / km mapped coastline; Table 3.1) have been observed. The Northern Territory is currently aiming to increase the exploitation of energy and mineral resources (Northern Territory Government, 2013), and low levels of protection could be detrimental to already declining shorebird populations if development is not planned strategically. Variations between states probably highlight differences in protected area designation and management, potentially as a result of the socio-political context. Queensland, for instance, has particularly high levels of protection as a result of the Great Barrier Reef being designated as a UNESCO world heritage site. However, it is unclear how such designations can benefit shorebirds when they are not specifically targeted at shorebird management.

In addition, some intertidal habitats were primarily managed as part of a marine protected area, while others as part of a terrestrial protected area (Table 3.1; Fig. 3.2). There is a clear potential for such differences to lead to inadequate management, as terrestrial protected areas might not always prioritise their marine environments and marine parks might underplay the importance of supratidal habitats that function as shorebird breeding or roost sites (Department of Environment Water and Natural Resources, 2014; Department of National Parks Recreation Sport and Racing, 2014; Department of Parks and Wildlife, 2014; Department of Primary Industries Parks Water and Environment, 2014; Office of Environment and Heritage, 2014; Parks and Wildlife Commission of the Northern Territory, 2014; Parks Victoria, 2014). Furthermore, some intertidal habitats are managed under both marine and terrestrial protected area designations (Table 3.1; Fig. 3.2). In Australia, this occurs for 3% of all protected intertidal habitats. In South Australia in particular, where there are large areas of intertidal habitats (0.20 km^2 per km of coastline mapped; Table 3.1), 10% of protected intertidal habitats are under the jurisdiction of both terrestrial and marine protected areas. Such overlap could lead to confusion, with neither management agency taking full responsibility for the conservation of intertidal habitats and the shorebirds reliant on them. Alternatively, overlap has the potential to lead to better protection when both agencies manage intertidal habitats together. Indeed, shorebirds move between intertidal habitats to forage and inland wetlands to roost, so combined

management of terrestrial and marine environments will be critical for ensuring healthy shorebird populations. There is a strong need for sustained collaboration between terrestrial and marine protected area managers, as well as other stakeholders, to ensure that protected area boundaries align more sensibly with intertidal habitats to benefit shorebirds. Accurate, spatially comprehensive maps derived from satellite imagery such as ours are therefore important for identifying habitat, delineating protected area boundaries, and facilitating targeted management of migratory shorebirds in intertidal habitats.

Shorebirds congregate in large numbers in roost sites, which can be readily identified as important habitat under the EPBC Act, but disperse during feeding. Densities while foraging in intertidal areas are typically far lower, making it more difficult to delineate important habitat, because the birds rarely concentrate in sufficiently large numbers to trigger the criteria. Such conservation criteria are therefore often inappropriate for protecting intertidal habitats from developments, despite their importance to shorebirds. In such cases, determination of important habitat could usefully occur at a broader scale, for example with all intertidal habitats within an important estuarine system being classified as important habitat. Not all shorebirds rely on intertidal habitats, and such criteria also apply to supra-tidal habitats, including saltworks and ephemeral wetlands, which are critically important for shorebirds in Australia. Intertidal habitat usage both inside and outside of protected areas needs to be formally assessed for all nationally important shorebird species, as not all intertidal habitats are used equally by different species. Finally, greater understanding of how protected areas are designated and regulated, and how these vary between states is an important step towards coordinating management at the national scale.

Ultimately, protection of intertidal habitats across Australia remains essential to the long-term conservation of EAAF shorebird species. However, shorebirds are declining across Australia despite the apparent high level of protection of intertidal habitats (Clemens *et al.*, in press). There is mounting evidence that these declines are driven by loss of intertidal habitats from migratory stopover sites outside Australia, such as the Yellow Sea (Moores *et al.*, 2008; MacKinnon *et al.*, 2012a; Ma *et al.*, 2014; Murray *et al.*, 2014). Any threat impacting such restricted habitats, particularly in stopover sites, is likely to have a disproportionate effect on abundance (Sutherland & Anderson, 1993; Sheehy *et al.*, 2011a; Iwamura *et al.*, 2013). Mapping of the Yellow Sea, for example, has already revealed declines of 65% in extent of

tidal flats in the last five decades (Murray *et al.*, 2014). It remains unclear to what degree these changes in habitat availability are being mirrored throughout the flyway. Mapping of intertidal habitats is urgently needed across the entire flyway to inform coordinated protection of shorebirds and to identify population bottlenecks during migration. Well-managed and well-connected intertidal habitats across the flyway are essential if we are to prevent further migratory shorebird extinctions within our lifetimes.

3.6 Acknowledgements

We thank Tony Gill and staff from the Joint Remote Sensing Research Program for their time, expertise, and access to data and computer processing systems. Landsat data are freely available from the U.S. Geological Survey and pre-processed and ortho-rectified Landsat images were provided by Geoscience Australia and the Department for Environmental Resource Management. We also thank Amelie Corriveau, Maggie McKeown and Madeleine Stigner for their involvement in the mapping component of the project. This project was supported by an Australian Research Council Linkage Grant LP150101059, co-funded by the Burnett-Mary Regional Group, the Queensland Department of Environment and Heritage Protection, and the Queensland Wader Study Group. Additional support was provided by Birds Queensland, the Australian Government's National Environmental Science Programme's Threatened Species Recovery Hub, and the CSIRO Climate Adaptation Flagship.

Chapter 4

Optimizing disturbance management for wildlife protection

4 Optimizing disturbance management for wildlife protection

4.1 Abstract

To ensure public compliance with regulations designed to protect wildlife, many protected areas need to be patrolled. However, there have been few attempts to determine how to deploy enforcement effort to get the best return on investment. This is particularly complex where repeated enforcement visits may result in diminishing returns on investment. Straightforward quantitative methods to solve such problems are not available to conservation practitioners. We use structured decision-making to find the most cost-effective allocation of patrol effort among sites with a limited budget. We use the case study of declining migratory shorebirds in Moreton Bay, Australia, to determine where and when Marine Park personnel could reduce disturbance using two different scenarios: (i) where a fixed subset of sites is chosen for management each year, and (ii) where different sites are visited during each patrol. The goal is to maximize the number of undisturbed birds for a given budget. We discovered that by prioritizing enforcement based on cost-effectiveness, it is possible to avoid inefficient allocation of resources. Indeed, 90% of the maximum possible benefit can be achieved with only 25% of the total available budget. Visiting a range of enforcement sites at varying rates yields a greater return on investment than visiting only a fixed number of sites. Assuming an exponential reduction in disturbance from enforcement, the greatest benefit can be achieved by patrolling many sites a small number of times. Assuming a linear reduction in disturbance from enforcement, repeatedly patrolling a small number of sites where return on investment is high, is best. If we prioritize sites where wildlife is disturbed most often, or where abundance is greatest, we will not achieve an optimal solution. The choice of patrol location and frequency is not a trivial problem, and prudent investment can substantially improve conservation outcomes. Our research demonstrates a straightforward objective method for allocating enforcement effort while accounting for diminishing returns on investment over multiple visits to the same sites. Our method is transferable to many other enforcement problems, and provides solutions that are cost-effective and easily communicable to managers.

4.2 Introduction

Effective enforcement is often needed to ensure that protected areas achieve successful conservation outcomes (Rowcliffe *et al.*, 2004; Gibson *et al.*, 2005; Keane *et al.*, 2008; Plumptre *et al.*, 2014). Reductions in enforcement levels have repeatedly been shown to result in increases in illegal activities harmful to wildlife, both in marine (Walmsley & White, 2003; Floeter *et al.*, 2006) and terrestrial environments (Jachmann & Billiouw, 1997; Hilborn *et al.*, 2006; de Merode *et al.*, 2007). Enforcement techniques such as fines, sanctions and patrols can be effective in dealing with illegal activities (Kahler & Gore, 2012), and the efficacy of enforcement improves when the probability of detecting illegal activities increases (Leader-Williams & Milner-Gulland, 1993). Managers therefore often target enforcement where threats are predicted to occur (Campbell & Hofer, 1995), with less regard for cost, or for the expected benefit to biodiversity. However equipment, training and salaries for enforcement patrols over large areas can be expensive and budgetary constraints often limit the quality or quantity of enforcement (Keane *et al.*, 2008). Given that the effectiveness of repeated enforcement in a single location can decrease over time as perpetrators desist or transfer their activities elsewhere, and therefore that continued enforcement once threats have been mitigated can result in misspent funds, it follows that there exists an optimal number of visits which ensures cost-effective resource allocation for diminishing returns on investment (Jachmann, 2008).

Structured decision-making enables managers to allocate resources among actions in a transparent and rational manner (Possingham *et al.*, 2001; Naidoo *et al.*, 2006; McDonald-Madden *et al.*, 2008; Shwiff *et al.*, 2013) and can therefore be used to determine cost-effective enforcement options. Most enforcement allocation studies have assessed the budgetary requirements for reducing illegal activities to a level that does not significantly impact conservation objectives (Leader-Williams *et al.*, 1990; Jachmann & Billiouw, 1997; Jachmann, 2008). However, there have been few attempts to determine how enforcement effort might be optimally allocated over both time and space. When optimized, targeted enforcement actions reduce patrol effort and hence cost, while continuing to achieve conservation targets (Hofer *et al.*, 2000; Linkie *et al.*, 2010; Plumptre *et al.*, 2014), or deliver greater conservation outcomes for the same budget. However, many optimization methods are data hungry or require complex models (Hofer *et al.*, 2000; Linkie *et al.*, 2010; Plumptre *et al.*, 2014), meaning that easily

accessible and reproducible methods to prioritize enforcement based on limited data are not yet easily reproducible or accessible to managers.

Here, we outline a simple method to allocate enforcement among sites subject to disturbance through recreational use, using data readily available to managers: number of infractions, average number of target species observed during patrols, and enforcement cost. We apply a structured decision-making framework to the problem of allocating patrol effort within a protected area with the aim of maximizing benefits to wildlife. We use enforcement of disturbance management for migratory shorebirds in Moreton Bay Marine Park, Australia, as a case study. We explore two enforcement strategies, first where a fixed set of sites is patrolled throughout a season, and second where different sites are visited during each patrol. The method we develop is transferable to other systems and is general enough to be modified for management of a wide range of threats, not just disturbance. For small data sets, this optimization can be solved using non-specialist software such as Microsoft Excel by simply comparing all possible scenarios, although larger problems will require more specialist software and programming.

4.3 Materials and methods

We use enforcement of shorebird disturbance patrols in Moreton Bay as our study system. In the following sections we describe a method of allocating enforcement effort between sites by: (i) defining our study system, (ii) determining the benefits of enforcement, (iii) outlining enforcement cost, (iv) mathematically formulating and solving the enforcement allocation problem and (v) carrying out a sensitivity analysis.

4.3.1 Study System

Moreton Bay Marine Park, Australia, is situated at 27.25˚ S 153.25˚ E and covers an area of 3400 km² (Fig. 4.1), providing internationally-important feeding and roosting habitat for migratory shorebirds. The Park is managed as a multi-use Marine Protected Area by the Department of Environment Heritage Protection (EHP) and the Department of National Parks, Recreation, Sport and Racing (NPRSR). Queensland Parks and Wildlife Service (QPWS) is

the business unit responsible for the day-to-day management of the marine park, regulating vessel size, speed, anchoring, bait gathering, crabbing, spear fishing, line fishing, trawling, netting, tourism, personal water crafts, vehicles on beaches, dog walking and other forms of recreation on the foreshore (Queensland Government, 2005).

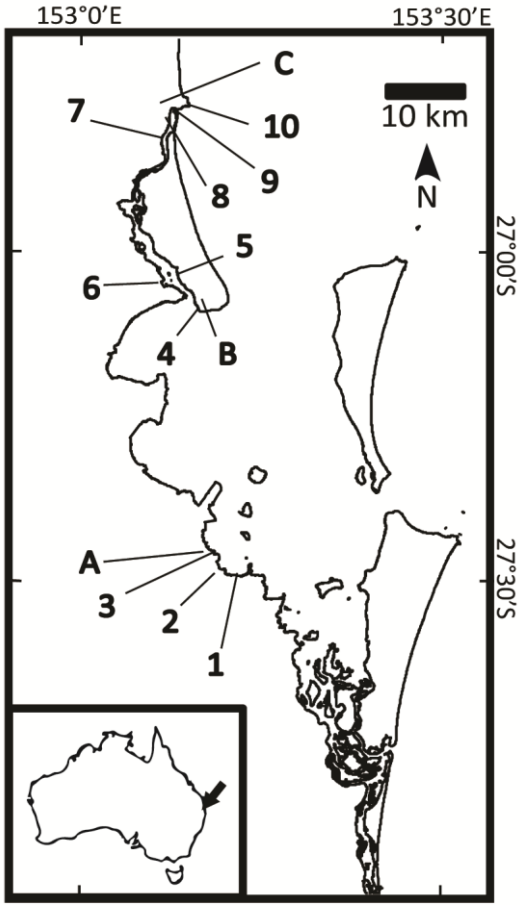

Figure 4.1 *Study area: Moreton Bay in south-east Queensland, Australia. A, B and C represent patrol bases where patrols originate: A=Manly, B=Bribie Island and C=Caloundra. Numbers 1 to 10 represent the potential patrol sites where 1=Wellington point, 2=Thorneside, 3=Manly Harbour, 4=Buckley's Hole, 5=Kakadu Beach, 6=Toorbul, 7=Bell's Creek, 8=Caloundra Sandbank, 9=Caloundra Bar and 10=Wickham Point.*

Some of the human activities occurring in the park are known to cause disturbance to shorebirds, defined here as "the response of birds to a stimulus such as the presence of a person" (Weston *et al.*, 2012a). Indeed, penalties apply for violations of the following provisions under the 1997 *Marine Parks (Moreton Bay) Zoning Plan*: (1) "a person must not disturb shorebirds or their habitats", (2) "dogs must be controlled when near shorebirds", and (3) "vehicles must

be driven away from/around feeding or roosting shorebirds". Furthermore, migratory shorebirds are protected in Moreton Bay by state law (1992 *Queensland Nature Conservation act*), national law (1999 *Environment Protection and Biodiversity Conservation Act (EPCB Act)*) and international law (1971 *Ramsar Convention*, 1979 *Bonn Convention*, 1974 *Japan-Australia Migratory Bird Agreement*, 1986 *China-Australia Migratory Bird Agreement* and 2007 *Republic of Korea-Australia Migratory Bird Agreement*).

Repeated disturbance to shorebirds can prevent individuals from gaining the necessary weight to complete migration. For many species, pre-migration lipid reserves must reach roughly 50% of total body mass before departure (Blem, 1990). Shorebirds feed in the intertidal zone and roost during high tide, when large numbers concentrate in to a small area: disturbances at roost sites can therefore impact all roosting individuals simultaneously. Indeed, shorebirds are highly responsive to anthropogenic stimuli and thus are readily disturbed (Glover *et al.*, 2011). Short-term disturbance includes increased levels of stress and behavioural changes (Landys *et al.*, 2006). Long-term disturbance includes chronic avoidance of disturbed habitat and abandonment of otherwise suitable habitat as individuals move to less disturbed areas (Nudds & Bryant, 2000), increasing density and therefore competition between individuals at undisturbed sites (Dolman & Sutherland, 1997; Van Gils *et al.*, 2005).

With a multitude of factors for QPWS to manage in addition to shorebirds, funding and time allocated to shorebird disturbance enforcement are limited, yet the abundance of some migratory shorebird species has decreased by almost 80% in Moreton Bay between 1995 and 2009 (Wilson *et al.*, 2011). Though many other factors may be driving declines in migratory shorebird numbers, anthropogenic disturbance represents an immediate and manageable impact on shorebirds which should be minimized where possible. Furthermore, the human population surrounding Moreton Bay has been estimated to increase from 4.5 million people in 2011, to 7.1 million by 2036 (Queensland Government, 2013). Migratory shorebirds are therefore likely to be under increasing pressure from anthropogenic disturbances and in urgent need of cost-effective enforcement strategies. Indeed, simple and implementable solutions exist for reducing disturbance to shorebirds, such as education (Antos *et al.*, 2006), establishing a local culture of compliance (Williams *et al.* 2009), keeping dogs on leashes (Williams *et al.*, 2009) and limiting access to important feeding or roosting areas (Weston *et al.*, 2012b).

4.3.2 Enforcement benefit

Cost-effective decision-making requires a measurable benefit. We therefore quantified the benefit of enforcement as the number of birds freed from disturbance by enforcement patrols. To do so, we used volunteer-collected data on shorebird numbers and disturbance rates in Moreton Bay. It is important to note however that volunteer-monitored data is not always available, and that different data may be more appropriate elsewhere, such as data collected during patrols on numbers of infractions and/or average abundances of target species.

We collated data from systematic bird count surveys conducted by volunteers from the Queensland Wader Study Group (QWSG; Milton & Driscoll, 2006). About 40 sites were counted simultaneously by QWSG observers each month, with counts carried out within two hours of the high tide to include roosting individuals (Zharikov & Milton, 2009). Disturbances were systematically recorded from 2009 onwards. We therefore use data on disturbance rates at roost sites between 2009 and 2012, and bird numbers between 1992 and 2012, both during the months of December through to February when shorebirds are most abundant in Moreton Bay (Wilson *et al.*, 2011). We selected all 10 sites experiencing forms of disturbance that could be enforced under the regulations outlined above. For each site we calculated the average number of disturbances observed during a bird count. We also assumed that all counts were carried out with equal detection error, and used the average numbers of birds present in the roost for 19 shorebird species (Appendix S.4.1).

4.3.3 Enforcement cost

Cost-effective decision-making requires information about management costs. We estimated a ranger's salary at $2414.70 fortnightly (search term "ranger" on the smartjobs website of the Queensland Government, 2014). Assuming 38 hours' work per week (as per http://www.fairwork.gov.au/about-us/policies-and-guides/fact-sheets/minimum-workplace-entitlements/maximum-weekly-hours), hourly salaries were estimated at $31.77. We used the maximum possible salary so as not to underestimate the budget. We assumed that patrols were always carried out by two rangers and that staff on-costs were 25% (Ban *et al.*, 2011). Assuming a 2.6-L engine we estimated vehicle costs at $0.75 per kilometre (Australian Government, 2014). Using Google maps (https://maps.google.com.au/), we estimated the

distance by road from the main marine parks office to each management site, in addition to travel time. Finally, we assumed enforcement was always carried out with teams of two staff members working for two hours at each site, thus:

$$C_i = N \times S \times 1.25 \times (T_i + E) + P \times D_i \quad (1)$$

where C_i is the cost of patrolling site i, N is the number of rangers, S is the hourly salary of one ranger, $T_i$is the time spent travelling to site i and E is the time spent enforcing each site, P is the price per kilometre of travel and D_i is the distance in kilometres to each site i from the ranger base (Appendix S.4.1).

4.3.4 Optimising enforcement

We optimized the enforcement visits over three different scenarios (Fig. 4.2): scenario 1 where patrol effort was fixed for all sites for the entire season, and where birds benefitted from a fractional reduction in disturbance rate as a result of enforcement at each site; scenario 2 where patrol effort could vary across sites during the season, and where birds benefitted from an exponential reduction in disturbance as a result of enforcement at each site; and scenario 3 where patrol effort could vary across sites during the season, and where birds benefitted from a linear reduction in disturbance as a result of enforcement at each site. Scenario 2 therefore represents a scenario where enforcement is highly effective in the beginning, but less so at the end; while scenario 3 represents a scenario where enforcement is not effective immediately, but increases in effectiveness incrementally through repeated visits. There is no constraint on the number of sites being patrolled. We also assumed that disturbance from enforcement was minimal, as patrols were land-based, and shorebirds were present on the foreshore.

To optimise enforcement, it is therefore necessary to determine firstly (i) which scenario best fits the case study, (ii) what the available budget is, (iii) what the maximum number of enforcement visits possible at a site is, (iv) how much disturbance is likely to be reduced by, (v) how many target species are present on average at a site, (vi) and how much disturbance occurs at each site. Once these data are available, the problem is therefore to determine where a site should be patrol given these factors, and how often using equations 2, 3 or 4.

The details of each scenario, and the algorithms used to implement them are provided in the following sections. All optimizations were implemented in Microsoft Excel (Appendix S.4.4) and Matlab 2014a by comparing all possible solutions (Mathworks, 2014).

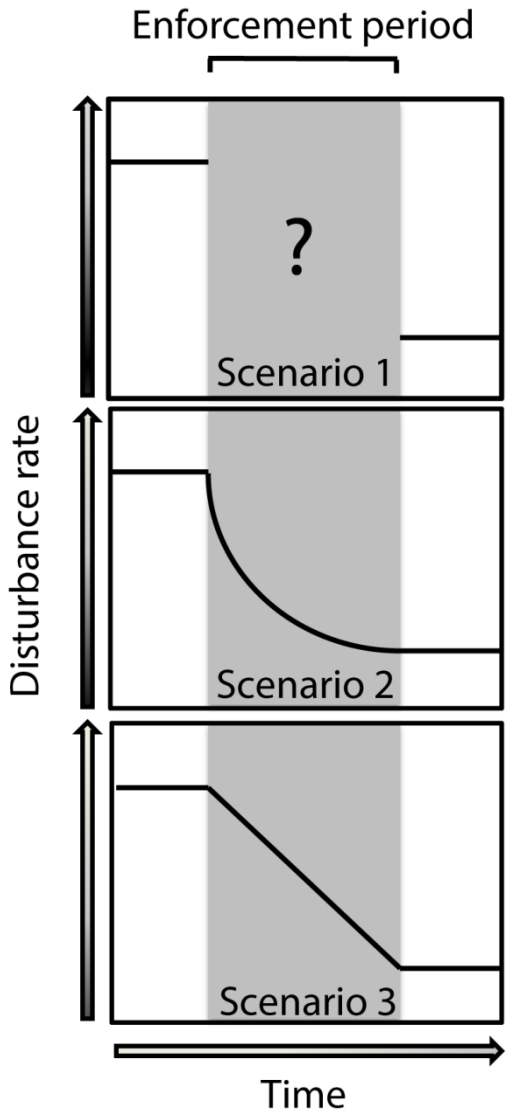

Figure 4.2 *Comparison among disturbance reduction scenarios. The period of enforcement is represented by the grey shading. In scenario 1, we assume no knowledge of the shape of the relationship between enforcement effort and disturbance rate, simply that a site can either be patrolled five times, or not (equation 2); and that a fractional reduction in disturbance occurs if the site is patrolled. For scenarios 2 and 3 (equations 3 and 4), we assume that sites can be patrolled a different number of times and that the benefit depends on the number of visits. We assume an exponential decrease in disturbance from repeated enforcement visits in scenario 2, and a linear decrease in scenario 3.*

4.3.4.1 *Fixed patrol effort over time, fixed disturbance reduction*

In this scenario it is assumed that: (i) each site can be either managed or unmanaged for the entire season each year, (ii) that the benefit of managing sites is dependent on the number of birds present at that site before management, (iii) that the benefit of managing sites is dependent on the level of disturbance prior to management and (iv) that birds do not move between sites as a result of disturbance.

Our objective was to maximize the number of birds being freed from disturbance through enforcement in Moreton Bay, and our control variable was whether or not a site was managed in that year, such that:

$$Max \sum_{i=1}^{M} x_i \sum_{j=1}^{N} d_{i,j,0}\gamma_{i,j}N_{i,j}w_j \quad subject\ to \sum_{i=1}^{M} x_i C_i \leq B, \qquad (2)$$

where $x_i \in \{0,1\}$ represents the decision whether or not to manage site i, $d_{i,j,0}$ is the number of disturbances at site i experienced by species j before management, $\gamma_{i,j}$ is the fractional reduction in disturbance at site i for species j due to management, $N_{i,j}$ is the number of birds of species j at site i, and w_j represents the relative importance given to species j. Throughout our case study we assume all species have an equal importance of 1, but the weight can be modified for other studies (to represent, for example, a conservation status). We also assume that initial disturbance rate $d_{i,j,0}$ is constant for all species, and that $\gamma_{i,j}$ the fractional reduction in disturbance is identical for all species across all sites.

4.3.4.2 *Different sites patrolled over time, exponential disturbance reduction from multiple visits*

In this scenario it is assumed that: (i) each site can be visited a number of times over the season each year such that $V_i \in \{0, \dots, V_{max}\}$, (ii) the benefit of visiting sites multiple times is proportional to the number of birds present at that site, (iii) the benefit of visiting sites increases logarithmically with the number of visits and (iv) that birds do not move between sites as a result of disturbance.

Our objective was to maximize the number of birds being freed from disturbance through enforcement in Moreton Bay, and our control variable was the number of visits to each site, such that:

$$Max\ \sum_{i=1}^{M}\sum_{j=1}^{N} d_{i,j,0}\gamma_{i,j}(1-e^{\frac{-6.9}{V_{max}}V_i})N_{i,j}w_j \quad subject\ to\ \sum_{i=1}^{M} V_iC_i \leq B, \qquad (3)$$

where $V_i \in \{0, \dots, V_{max}\}$ represents the number of visits to site *i*, $d_{i,j,0}$ is the number of disturbances at site *i* experienced by species *j* before management, $\gamma_{i,j}$ is the fractional reduction in disturbance at site *i* for species *j* due to enforcement, $N_{i,j}$ is the number of birds of species *j* at site *i*, and w_j represents the relative importance given to species *j*. Because we expect the amount of disturbance being enforced to increase to 99.9% of $\gamma_{i,j}$ over V_{max} visits we have $\gamma_{i,j}(1-e^{-\frac{-\ln(1-0.999)}{V_{max}}V_i})$, thus $\ln(0.001) = -6.9$ in equation 3.

4.3.4.3 Different sites patrolled over time, linear disturbance reduction from multiple visits

In this scenario it is assumed that: (i) each site can be visited a number of times over the season each year such that $V_i \in \{0, \dots, V_{max}\}$, (ii) the benefit of visiting sites multiple times is linearly proportional to the number of birds present at that site as well as (iii) the number of visits and (iv) that birds do not move between sites as a result of disturbance.

Our objective was to maximize the number of birds being freed from disturbance through enforcement in Moreton Bay, and our control variable was the number of visits to each site, such that:

$$Max \sum_{i=1}^{M}\sum_{j=1}^{N} d_{i,j,0}\ (Max\ \left[1, \frac{\gamma_{i,j}}{V_{max}}V_i\right])N_{i,j}w_j \quad subject\ to\ \sum_{i=1}^{M} V_iC_i \leq B, \qquad (4)$$

where $V_i \in \{0, \dots, V_{max}\}$ represents the number of visits to site *i*, $d_{i,j,0}$ is the number of disturbances at site *i* experienced by species *j* before management, $\gamma_{i,j}$ is the fractional reduction in disturbance at site *i* for species *j* due to enforcement, $N_{i,j}$ is the number of birds of species *j* at site *i*, and w_j represents the relative importance given to species *j*.

4.3.5 Sensitivity analysis

We compared prioritising sites according to scenario 1 with prioritizing sites by ranking them based only on cost, number of birds, number of disturbances or score (calculated using the average rank for cost, number of birds and number of disturbances). To control for variability in travel costs, and to determine whether conclusions were robust, all optimization scenarios were run with three separate starting points for patrols: two randomly selected locations within 1 km of a roost to determine whether proximity influenced the prioritization (Caloundra and Bribie), in addition to the current patrol base location (Manly) as seen in Fig. 4.1. We also tested two disturbance reduction scenarios, one where disturbance was reduced by 20% due to management, one where disturbance was reduced by 80%, thus $\gamma_{i,j} \in \{0.2,0.8\}$. The 20% reduction represents the observed reduction rate from our case study (Appendix S.4.2). The 80% reduction represents an extreme case, where management is highly effective, and is used to explore model behaviour. These two scenarios therefore illustrate how prioritizations can differ according to efficiency. Finally, for all simulations, $V_{max}$was set to 5, because WQPS patrol each shorebird site on average once a month, between the months of November and March.

4.4 Results

It is possible to achieve 90% of the total benefit to shorebirds, within a budget of $1000 AUD using the Manly patrol base, $2500 with Bribie and $2700 with Caloundra (Fig. 4.3; Appendix S.4.3). Additional budget beyond this did not significantly increase management benefit along the efficiency frontier (which can be defined as the greatest benefit for a given budget, and is represented by the lines in Fig. 4.3 and Appendix S.4.3).

Scenarios 2 and 3 represent exponential and linear disturbance reductions respectively. Across all three patrol stations (Manly, Caloundra and Bribie), these two scenarios produced more cost-effective solutions for smaller budgets than scenario 1, the fractional disturbance reduction (Figs. 4.3; Appendix S.4.3). Indeed, scenarios 2 and 3 allowed combinations of single enforcement visits at multiple sites, unlike scenario 1 which assumed five visits to the same site. Overall, at low budgets, the optimal solution was to repeatedly visit the most cost-effective site, and the cost of repeatedly carrying out enforcement did not outweigh the high benefit

(Appendix S.4.4). However, with an increasing budget, the optimal solution included an increasing number of visits to additional sites complementing those already being visited (Appendix S.4.4). Overall, the greatest benefit could be achieved by carrying out enforcement at sites with a large number of birds experiencing a large number of disturbances (Appendix S.4.5). Either metric (cost, number of birds or number of disturbances) in isolation delivered less efficient outcomes (Table 4.1; Appendix S.4.5). Cost-effective sites are therefore not intuitive and benefit can be increased by including information on all factors impacting the system, including the number of birds present, the disturbance rate, and the cost of enforcement (Appendix S.4.5).

By ranking sites according to the number of times they were selected as part of the optimal solution for every dollar spent, we found that the results across scenarios were surprisingly similar (Fig. 4.4; Table 4.2; Appendices S.4.6, S.4.7 and S.4.8). However, there was a marked difference between scenario 1 and scenarios 2 and 3. Indeed, some sites which were selected in scenarios 2 and 3 were not selected as part of the optimal solution for scenario 1. This is because scenarios 2 and 3 allow multiple sites to be patrolled, and scenario 1 does not. In addition, we found that all scenarios were identical for both disturbance reduction scenarios ($\gamma_{i,j} \in \{0.2,0.8\}$). Uncertainty in the effectiveness of enforcement, over repeated visits, as a strategy to reduce disturbance did not therefore impact the optimal solution.

Table 4.1 *Relative ranking of sites according to cost-effectiveness (scenario 1), cost, number of birds, number of disturbances and score across sites for patrol stations M=Manly, C=Caloundra and B=Bribie. A rank of 1 represents a high enforcement priority (i.e. highly cost-effective, cheap to manage, bird abundant or highly disturbed) while a rank of 10 represents a low enforcement priority (i.e less cost-effective, expensive to manage, small numbers of birds or small numbers of disturbances). The rank of the scoring system was calculated using the average of the rank of cost, number of birds and number of disturbances.*

Site code	Cost-Effectiveness			Management Cost			Number of Birds			Number of Disturbances			Scoring System		
	M	C	B	M	C	B	M	C	B	M	C	B	M	C	B
Manly Harbour	1	1	1	1	8	8	1	1	1	1	1	1	1	1	3
Kakadu Beach	2	2	2	6	7	2	3	3	3	4	4	4	4/5	3/4/5	2
Thorneside	3	5	5	2	9	9	6	6	6	2	2	2	2	6	5/6
Buckley’s Hole	4	3	3	5	6	1	4	4	4	3	3	3	3	2	1
Toorbul	5	4	4	4	5	3	2	2	2	7	7	7	4/5	3/4/5	4
Wellington Point	6	7	6	3	10	10	5	5	5	8	8	8	6	10	8/9
Caloundra Bar	7	6	7	7	1	4	7	7	7	6	6	6	7	3/4/5	5/6
Bell’s Creek	8	9	9	10	4	7	9	9	9	9	9	9	10	9	10
Sandbank Caloundra	9	8	9	8	2	5	8	8	8	10	10	10	9	8	8/9
Wickham Point	10	10	10	9	3	6	10	10	10	5	5	5	8	7	7

Table 4.2 *Frequency at which sites are selected as part of an optimal solutions for every dollar spent, where the budget is limited to $4,000 for all scenarios and Manly is the patrol base.*

	20% disturbance reduction			80% disturbance reduction		
Site	Scenario 1	Scenario 2	Scenario 3	Scenario 1	Scenario 2	Scenario 3
Manly Harbour	3139	13 300	17 419	3139	13 300	17 419
Thorneside	1280	3965	4239	1280	3965	4239
Kakadu Beach	751	4569	7950	751	4569	7950
Wellington Point	140	522	0	140	522	0
Buckley's Hole	40	3008	0	40	3008	0
Bell's Creek	0	0	0	0	0	0
Caloundra Bar	0	0	0	0	0	0
Sandbank Caloundra	0	0	0	0	0	0
Toorbul	0	1887	0	0	1887	0
Wickham Point	0	0	0	0	0	0

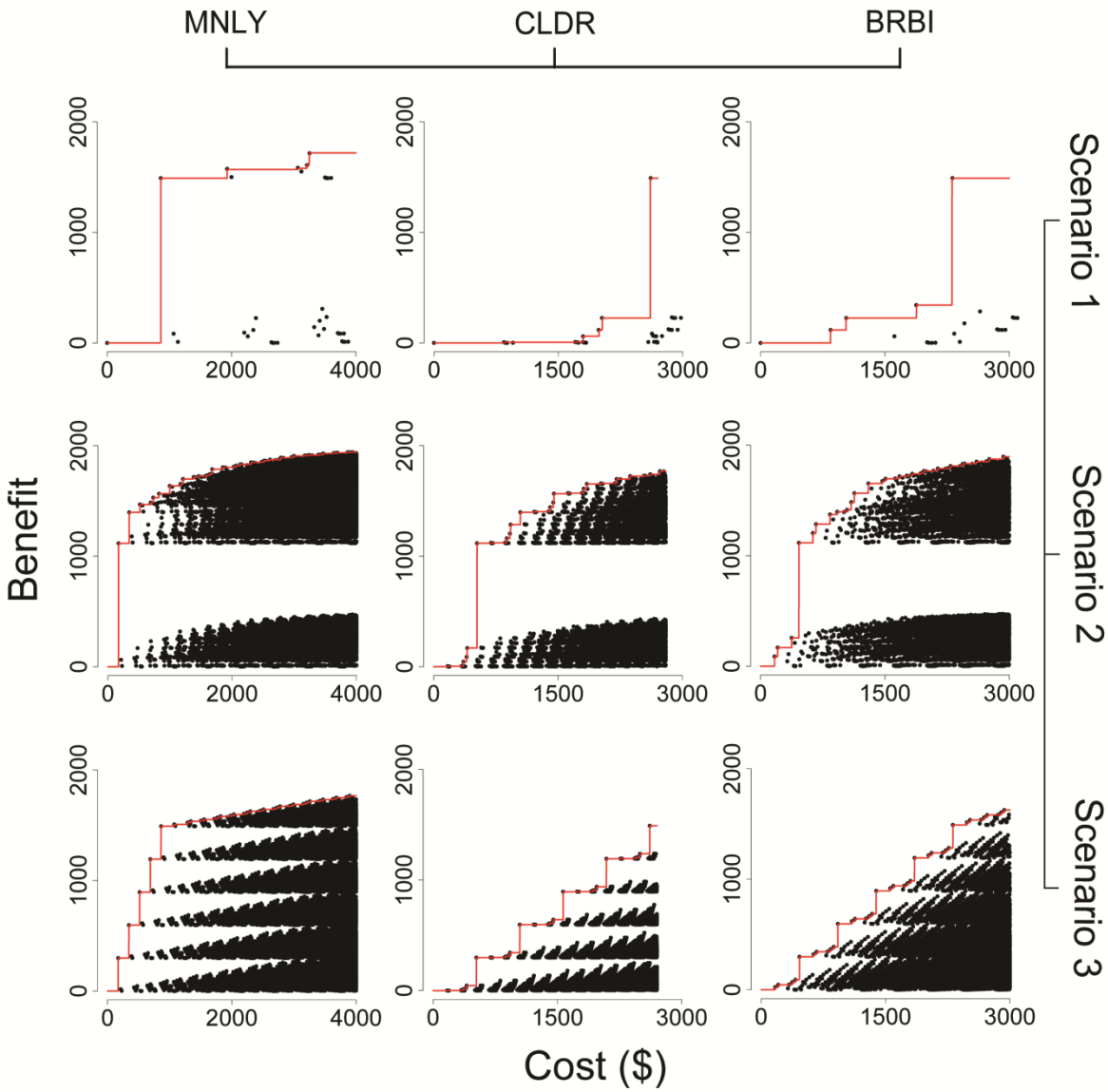

Figure 4.3. *Trade-offs between the cost of enforcing patrols and the benefit to shorebirds of reducing disturbance by 20%. Benefit is measured as the number of birds released from disturbance as a result of enforcement. Scenario 1 where birds benefitted from a fixed disturbance reduction of as a result of enforcement at each site; scenario 2 where patrol effort could vary across sites and where birds benefitted from an exponential reduction in disturbance; and scenario 3 where patrol effort could vary across sites and where birds benefitted from a linear reduction in disturbance. For each scenario, we plotted trade-off curves for three different patrol stations where rangers could be based: MNLY=Manly, CLDR=Caloundra and BRBI=Bribie. Lines indicate the optimal solution.*

4.5 Discussion

Using structured decision-making, we discover simple rules of thumb that can be used to prioritize enforcement effort across a landscape, while accounting for both diminishing returns on investment and uncertainty in management outcomes. Indeed, in our case study, it was possible to achieve 90% of the maximum possible benefit with a relatively small budget by repeatedly reducing shorebird disturbance at the most cost-effective sites (Fig. 4.3; Appendix S.4.3). However, with an increasing budget, the optimal solution was complemented by an increasing number of enforcement visits to an increasing number of less cost-effective sites (Appendix S.4.4). Crucially, basing enforcement activity solely on the amount of disturbance, or the number of birds present, yielded very inefficient outcomes (Table 4.1; Appendix S.4.5).

We observed a large number of sub-optimal solutions under medium to large budgets, many of which provided negligible benefits, thus increasing the probability of poor investment in enforcement (Fig. 4.3; Appendix S.4.3). These results are unusual: past research has found a strong positive correlation between benefits and costs, with the relative variability of cost greater than that of benefit (Ferraro, 2003). Here, we observe highly variable benefits, because there is a high level of variability in shorebird numbers and disturbance rates among sites. This is a common enforcement scenario. In addition, we find no correlation between benefit and cost because benefit is calculated using bird numbers and level of disturbance while cost is calculated using duration of enforcement, travel time and travel distance.

Interestingly, by ranking the number of times sites were selected as part of the optimal solution for every dollar spent, it was possible to observe that scenarios 2 (exponential) and 3 (linear) were very similar, relative to scenario 1 (proportional; Table 4.2, Appendices S.4.6 and S.4.7). Visiting a range of enforcement sites at varying rates yielded a greater return on investment than visiting only a fixed number of sites. Single visits to less cost-effective sites can therefore be used to complement more cost-effective solutions (Appendix S.4.4). S2).

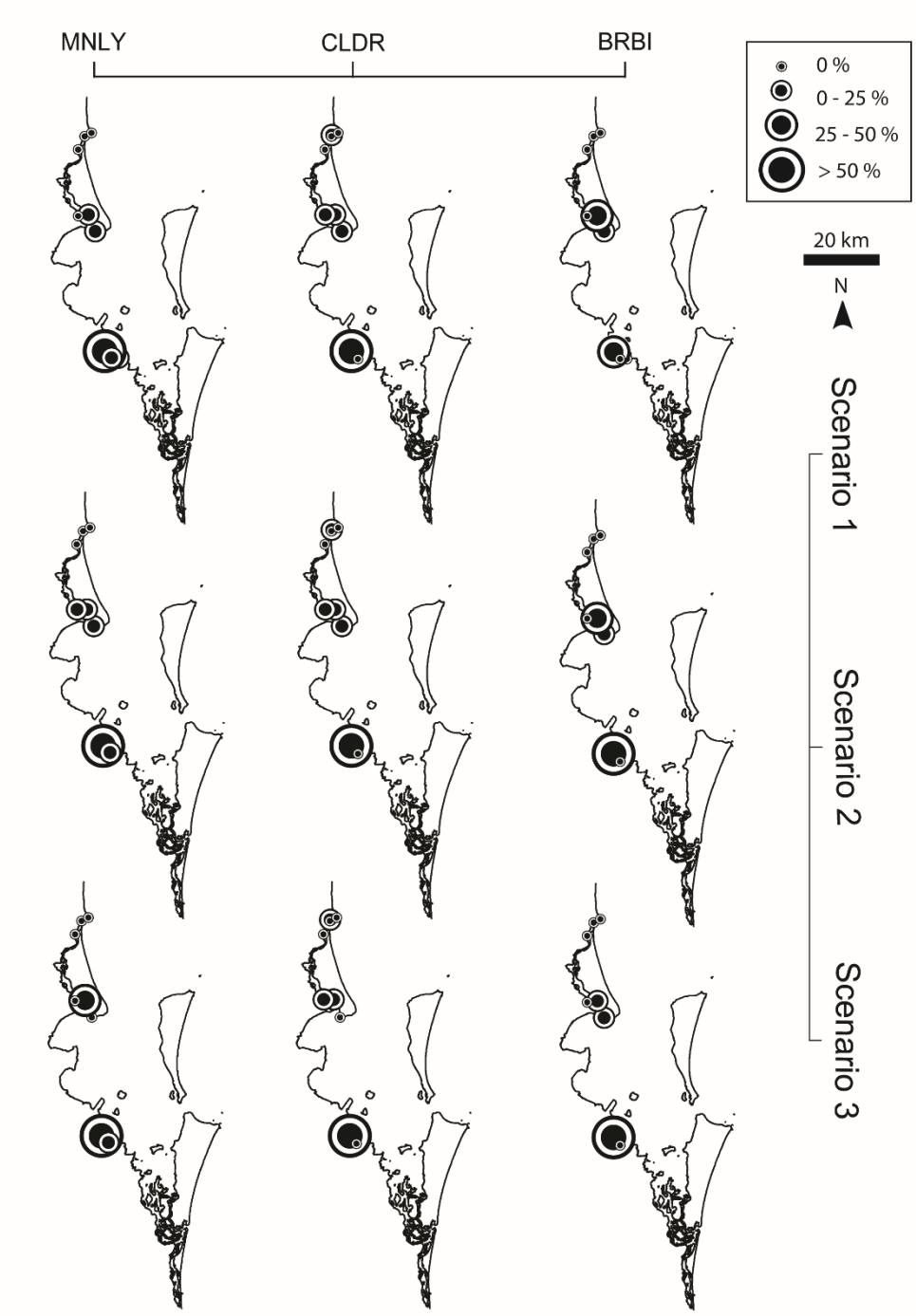

Figure 4.4 *The frequency at which sites are selected as part of an optimal solution for every dollar spent, expressed as a percentage, for each scenario at each patrol station for a disturbance reduction of 20%. The budget is limited for all scenarios to $0–4000 for patrol station Manly (MNLY), $0–2700 for patrol station Caloundra (CLDR) and $0–3000 for patrol station Bribie (BRBI). The differences in budget reflect the number of solutions: the number of solutions under $2700 at Caloundra is the same as the number of solutions under $3000 at Bribie, and $4000 at Manly.*

For example in Table 4.2, for scenario 1 it is more beneficial to visit Thorneside more often than Kakadu Beach, while for scenarios 2 and 3 it is more beneficial to visit Kakadu Beach more often than Thorneside. This is because Kakadu Beach is more expensive than Thorneside, but offers a greater benefit, achieving a greater return on investment under variable visitation rates. Furthermore, scenario 2 assumes an exponential decrease in disturbance rate, where enforcement is highly effective in the beginning, but less so at the end. The benefit of managing once for scenario 2 is therefore much greater than for scenario 3, where enforcement effectiveness increases incrementally. Assuming diminishing returns on investment in scenario 2, it is more beneficial to patrol many sites a small number of times. For scenario 3 on the other hand, it is more important to find the sites with the greatest return on investment and repeatedly patrol them.

When comparing 20% and 80% disturbance reduction scenarios, the optimal solutions remained identical for each scenario (Table 4.2, Appendices S.4.6 and S.4.7). Uncertainty in the effectiveness of enforcement at reducing disturbance over repeated visits did not impact the optimal solution found for each of these scenarios. It is therefore possible to identify robust solutions within a given budget despite uncertainty. These findings echo previous work indicating that management actions can be less sensitive to uncertainty than management outcomes (McCarthy *et al.*, 2003). Indeed, acting despite uncertainty is more likely to deliver better outcomes than not acting at all (McDonald-Madden *et al.*, 2011).

Failing to account for both cost and benefit together can result in misspent funds, particularly with small budgets. For instance, there are a number of enforcement sites such as Thorneside that are highly cost-effective to enforce (patrol station Caloundra and Bribie in Table 4.1), yet also relatively expensive to visit. The benefit of carrying out enforcement at these sites therefore made the higher cost worthwhile. Similarly, there are a number of enforcement sites such as Caloundra Bar which are cheap to patrol (patrol station Caloundra in Table 4.1), yet are not cost-effective to enforce because of the low possible benefit. The intricacies of such trade-offs cannot be reflected by scoring sites based solely on cost, bird number or disturbance number (Table 4.1). Cost-effectiveness analysis therefore offers a simple, transparent and rational manner of allocating patrol effort between sites which cannot be achieved by ranking sites based on scores for particular criteria (Joseph *et al.*, 2009) Furthermore, it enables an optimal solution to be found amongst thousands of possible combinations of site visits.

We observed a logarithmic increase in the benefit of the optimal solution for every dollar spent (Fig. 4.3; Appendix S.4.3). A small increase in spending therefore resulted in a large increase in benefit under small budgets (Fig. 4.3; Appendix S.4.3). Our methods, which aimed at maximizing the number of birds being freed from disturbance through enforcement, yielded highly cost-effective solutions. Therefore, the greatest benefit could be achieved by carrying out enforcement at sites with a large number of birds experiencing disturbances (Table 4.1; Appendix S.4.5). If enforcement was carried out at sites with few birds experiencing high levels of disturbance, the overall shorebird population would not benefit from the reduction in disturbance from enforcement at that site. These simple rules of thumb are highly transferable to other enforcement scenarios, whereby the most cost-effective sites for enforcement are the cheapest sites with the greatest number of target species in combination with the greatest number of illegal wildlife activities.

The methods we develop here could easily complement an adaptive management framework (Chadès *et al.*, 2012), whereby priorities are set using our methods, illegal activities are then monitored and enforcement is evaluated so that priorities can be reset for the following season using the same method. Indeed, it is not unreasonable to expect illegal wildlife activities to become displaced and change in response to the enforcement itself, such that a continually evolving arms race is needed to keep up with the changing pattern of disturbance, and to ensure previously undisturbed sites do not become disturbed (Keane *et al.*, 2008). In some cases, target species might also change behaviour in response to the changing impact of wildlife activities. Our methods could further be modified to allow for multiple sites to be visited per patrol by solving the travelling salesman problem (Larrañaga *et al.*, 1999), finding the shortest route between a set of sites. By modifying this problem to minimize cost and maximize benefit simultaneously, and by adding a decision variable to limit the number of sites patrolled, it would be possible to determine the optimal route through the most cost-effective sites.

It is worth bearing in mind that enforcement is not always the most cost-effective solution for achieving long-term conservation goals, nor is it the only tool available to conservation practitioners (Steinmetz *et al.*, 2014). In our case study for instance, the sparse availability of options for dog-walking (Cutt *et al.*, 2008) means that dog owners might take the risk of exercising dogs on the foreshore contrary to regulations. Better dog-walking facilities, such as dog off-leash areas that are situated away from threatened wildlife, are not only likely to benefit

dog-walkers in urban areas (Cutt *et al.*, 2008), but also shorebirds. In addition, the lack of awareness that shorebirds are present on beaches (Antos *et al.*, 2006) and of how migration and feeding ecology are impacted by disturbances might be important in shaping dog-walkers' attitudes towards disturbing shorebirds (Williams *et al.*, 2009). Raising awareness and better infrastructure could therefore complement enforcement in a variety of management scenarios.

The goal of our research was to propose a simple and objective method of allocating enforcement effort over space and time, which accounted for both diminishing returns on investment and uncertainty in enforcement outcome. We find that as a general rule of thumb, the most cost-effective sites for enforcement are the cheapest sites with the greatest number of target species in combination with the greatest number of illegal wildlife activities. By using cost-effectiveness analyses our methods are easily transferable to other case studies, transparent and therefore easily communicable to managers.

4.6 Acknowledgments

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Chapter 5

Setting conservation priorities in migratory networks

5 Setting conservation priorities in migratory networks

5.1 Abstract

Conserving migratory species requires protecting intact chains of habitat along the pathways they travel. Despite recent improvements in animal telemetry, migratory pathways remain poorly resolved at a population level for the vast majority of species, hampering conservation prioritisation. In the face of these data limitations, we develop a novel approach to spatial prioritization based on a model of potential connectivity, derived from empirical data on distances travelled between sites while on migration. Applying this approach to migratory shorebirds using the East Asian-Australasian Flyway, we find that prioritising protection of sites supporting high numbers of animals may perform as poorly as randomly selecting sites. The conservation value of a site depends on both its capacity to support migratory animals and its position within the migratory pathway, with the loss of crucial sites leading to partial or total population crashes. We suggest that conservation strategies should consider the spatial arrangement of sites as well as focusing on conserving sites that support large populations of migrants.

5.2 Introduction

Conservation plans often assume that species are static in time and space (Pressey *et al.*, 2007), yet many species undertake seasonal, cyclic or dispersive movements throughout their lifecycles, and none more so than migratory species. Migratory journeys take animals across continents and oceans, to exploit ephemeral pulses in resource availability (Alerstam *et al.*, 2003) or to avoid inhospitable conditions (Runge *et al.*, 2014b). For instance, many migratory species time their breeding or migration to coincide with peaks in food abundance to maximise their chances of survival, as well as that of their offspring (Langin *et al.*, 2006). Many individuals can concentrate at a smaller number of sites during a migratory journey, and in some cases the entire population may congregate in a single location (Richter & Cumming, 2008). Habitat degradation at such bottleneck sites can result in disproportionately large decreases in abundance and survival of a migratory species (Iwamura *et al.*, 2013; Piersma *et*

al., 2016). Migratory species therefore depend on chains of intact connected sites to complete their migratory cycle, and the loss of sites can result in a broken chain and population declines. Conservation plans that account for connectivity repeatedly outperform plans that do not (Sheehy *et al.*, 2011b; Hermoso *et al.*, 2012a; Linke *et al.*, 2012; Iwamura *et al.*, 2014; Runge *et al.*, 2014a; Nicol *et al.*, 2015), yet more than 90% of the world's migratory birds are inadequately protected across their annual cycle (Runge *et al.*, 2015).

Recent advances in animal telemetry have revolutionised the study of migratory pathways, with lightweight devices accurately able to track migrations over thousands of kilometres (Block *et al.*, 2011), and the development of expansive citizen science networks that report sightings of individually marked animals (Sullivan *et al.*, 2014; Secretariate of the Pacific Community, 2016). Such methods are beginning to show promise for describing migratory pathways in a comprehensive manner to permit formal spatial prioritisation, yet presently our knowledge is very patchy, with many migrants having never been formally studied, and with only sparse data from those that have. Despite the increasing sophistication of the technology, tracking animal movements remains rather difficult and expensive, and animals are often only tagged or banded in a small number of locations (e.g. Block *et al.*, 2011), limiting inference at a population level (Lisovski *et al.*, in press). Re-sightings or re-captures are often needed to track animals that have been colour tagged or fitted with geolocators, causing bias toward areas with many observers (e.g. Minton *et al.*, 2006). Though the resulting data are important for mapping connectivity, it is unclear how well they represent population level connectivity patterns. With many migratory animals in severe decline (Wilcove & Wikelski, 2008), methods that make best use of the data that are available will be crucial in setting appropriate conservation priorities in migratory networks.

Here, we use available telemetry data to parameterise a model of migratory connectivity for migratory species and the optimal spatial distribution of investment in habitat protection for seven migratory shorebird species in the East-Asian Australasian Flyway (EAAF). We use tracking data to estimate the frequency of migratory movements of different distances, and calculate the potential for animal movements between any two sites in the migratory network. We estimate the effect of habitat loss at sites on overall population flow through the migratory network, and use prioritisation to allocate investment in protection of sites that minimises population loss. We compare our spatially-explicit approach with a prioritisation of sites

supporting large numbers of individuals, revealing that abundance can be misleading when setting conservation priorities in migratory networks.

5.3 Methods

To model potential connectivity between all sites within a migratory network, we use a maximum-flow approach. In the following sections, we describe how we: (a) formulated the maximum-flow problem, (b) tailored it to migratory species (c) prioritised sites for conservation, and (d) applied our approach to migratory shorebirds in the EAAF.

5.3.1 Formulating the maximum-flow problem

Migratory networks can be conceptualised using graph theory (Goldberg & Tarjan, 1988; Wilson & Watkins, 1990; Goldberg *et al.*, 1991). Let *G* (*V*, *E*) be a directed graph or network, defined by a set of nodes *V* and edges *E*. Nodes represent important migratory habitat (i.e. discrete habitat patches used for breeding, non-breeding or staging). An edge (u, v) represents movement between nodes *u* and *v*. Each edge (u, v) in *E* has a capacity c_{uv}, the maximum number of animals that can migrate along edge (u, v). Let *G* have a source node *s* and sink node *t* in *V* which represent the start and end of the migratory cycle (respectively the breeding and non-breeding grounds, for example). Every node *u* in *V* other than *s* and *t* can have multiple edges entering and exiting *u*.

The objective of the maximum-flow problem is to maximise the flow between source node *s* and sink node *t*, without exceeding the edge capacities. For migratory species, maximum flow can measure how local changes to node capacity will affect population level migratory connectivity (Urban & Keitt, 2001; Minor & Urban, 2007; Iwamura *et al.*, 2013). Representing the flow between edges (u, v) in *E* with x_{uv}, we can formulate the maximum-flow problem as:

$$Maximize\ f(x) = \sum_{(u,v)\in E(s)} x_{uv},$$

$$Subject\ to: \quad \sum_{\{v:\,(u,v)\in E\}} x_{uv} - \sum_{\{v:\,(v,u)\in E\}} x_{vu} = 0 \qquad \forall u \in V\{s,t\},$$

$$0 \le x_{uv} \le c_{uv} \qquad \forall (u,v) \in E.$$

The first constraint ensures that the number of birds entering and exiting a node must be the same. The second constraint ensures that the number of birds migrating along each edge cannot exceed the edge capacity. The maximum-flow problem is a linear programming problem which we solve using Gurobi 6.0.0 (Gurobi Optimization, 2012).

5.3.2 Defining a migratory network using tracking data

The strength of the migratory connection between all pairs of nodes depends on (i) the abundance of migrants at each node, (ii) the direction of travel between the nodes, and (iii) the probability of an animal travelling between any given pair of nodes. Tracking data can be used to estimate the probability density distribution for migratory movements between nodes using the function "density" in R (R Core Team, 2015). Density distributions measure the likelihood that an animal can travel a given distance, trading off over-fitting that produces multiple peaks, and over-extrapolating, that produces flat distributions with similar probabilities for all distances. A good fit (*adjust = 2* in the *density* function in R) was found by manual iteration. The density distribution gives the probability P_{uv} of migration along edge (u,v) according to distance (Fig. 5.1), and is used to parameterise edge weights w_{uv}:

$$w_{uv} = P_{uv} N_v A_{uv},$$

where N_v represents the proportion of the population using node v and $A_{uv} = |\cos(\phi_{uv})|$ represents the absolute cosine of the azimuth angle ϕ between nodes u and v in radians. A_{uv} weights northerly or southerly nodes more heavily than easterly or westerly nodes, specifically for species which undertake North-South migrations, to prevent them from "zigzagging" northward and southward. For species which do not undertake directional migrations, A_{uv} can be set to 1. w_{uv} weights nodes with many migrants and within likely travel distances more heavily than nodes supporting few migrants that are within an unlikely travel distance. These assumptions approximate the observed pattern of migratory journeys; it is likely that migratory routes with larger carrying capacities and with stopover nodes within preferential migratory distances will support a larger proportion of the population.

We use w to determine the proportion of each species population migrating between each set of nodes. w_{uv} is used to parameterise the capacity c_{uv}, or number of animals moving along each

edge (u,v) in E, such that $c_{uv} = x_u\,(w_{uv} / \sum_{\{v:\,(u,v)\in E\}} w_{uv})$, where x_u represents the number of animals which has flowed into node u. The capacity calculation is initiated from start node s where x_s is equal to the known population size of the species. Finally, we determine the proportion of the population migrating through each graph *G (V, E)* as per the maximum flow problem formulation above.

Our methods allow migratory animals to go anywhere in the network, although the majority of the population utilises edges with the greatest capacity going in the correct direction, with few individuals utilising unlikely edges. These methods allocate similar numbers of animals to migratory routes with similar capacities. In contrast, a greedy approach could allocate all animals to one route, but none to a minutely poorer route (e.g. Dijkstra, 1959).

5.3.3 Prioritising nodes for conservation

Our objective was to protect nodes that maximise expected migratory population flow. We use a reverse-greedy approach for the prioritisation, sequentially removing nodes least likely to deliver our objective. In practice, this approach usually delivers similar results to more complex optimal algorithms (Pressey *et al.*, 1997; Polasky *et al.*, 2000).

We used three prioritisation strategies, based on: (i) flow, (ii) maximum count and (iii) random allocation. For the population flow and maximum count strategies, we iteratively removed the node that contributed least to the prioritisation criteria (i.e. population flow or maximum count) through the network until no nodes remained (the approach of Conklin *et al.*, 2014). For the random prioritisation strategy, we iteratively removed nodes from the network at random, and repeated this process 1000 times. We compared these strategies by estimating how well they maintained population flow through the migratory network.

5.3.4 Migratory shorebird case study

We constructed directional graphs representing migration for seven EAAF shorebird species: bar-tailed godwit (*Limosa lapponica baueri*), eastern curlew (*Numenius madagascariensis*), great knot (*Calidris tenuirostris*), grey-tailed tattler (*Tringa brevipes*), red knot (*Calidris canutus*), ruddy turnstone (*Arenaria interpres*) and sanderling (*Calidris alba*). These species

(i) have been tracked, albeit in small numbers, (ii) have mapped breeding, stopover and non-breeding sites which can be used as nodes within a maximum flow framework, (iii) have an estimate of overall population size, and (iv) are known to migrate directionally northward and southward (Alerstam *et al.*, 2001). Each species took different north and south migratory routes, using a distinct suite of stopover nodes Bamford *et al.* (2008).

We used a literature review and geolocator data provided by the Victorian and Queensland Wader Study Groups to parameterise migration through the network of sites. We acquired tracks from sixteen migrating bar-tailed godwits (Battley *et al.*, 2012), nine eastern curlews (Driscoll & Ueta, 2002), four great knots (Victorian Wader Study Group), three grey-tailed tattlers (Queensland Wader Study group http://waders.org.au/studying-waders/banding-shorebirds/satellite-transmitters-and-geolocators/), three red knots (Victorian Wader Study Group), forty-eight ruddy turnstones (Minton *et al.*, 2010; Minton *et al.*, 2011) and thirteen sanderlings (Victorian Wader Study Group http://www.waderstudygroup.org/article/1839/).

5.4 Results

The density distribution of recorded flight lengths varied between species (Fig. 5.1). Some were very narrow (eastern curlew, grey-tailed tattler and sanderling) and others broad (bar-tailed godwit and red knot). For species with narrow distributions, the probability density distribution generally peaked and receded before 5,000 km (eastern curlew, great knot, grey-tailed tattler and sanderling). Species with broader distributions varied more substantially. For instance, bar-tailed godwits had a similar probability of migrating between 5,000 and 10,000 km, but were unlikely to migrate less than 5,000 km. In contrast, red knots and ruddy turnstones were most likely to migrate less than 5,000 km, although birds were still capable of making long-distance (>10,000 km) flights with a small probability. These probability

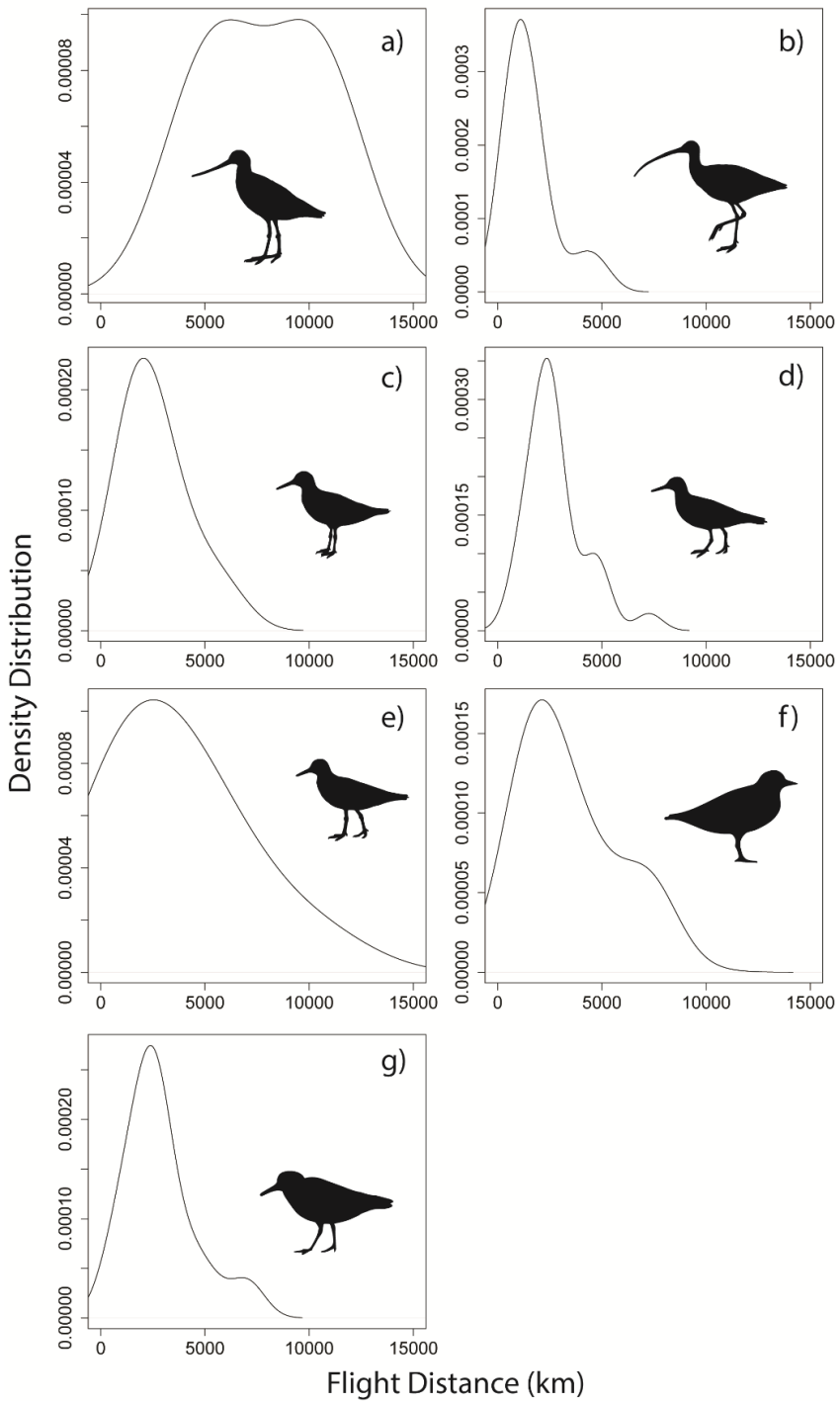

Figure 5.1 *Density distribution of tracking data for a) bar-tailed godwit (Limosa lapponica), b) eastern curlew (Numenius madagascariensis), c) great knot (Calidris tenuirostris), d) grey-tailed tattler (Tringa brevipes), e) red knot (Calidris canutus), f) ruddy turnstone (Arenaria interpres) and g) sanderling (Calidris alba).*

distributions drove the structure of network connectivity for each species, and therefore the outcomes of the prioritisation strategies.

As expected, the flow prioritisation strategy outperformed the maximum count prioritisation strategy for all species, which generally outperformed the random prioritisation strategy (Fig. 5.2). However, there were some marked differences among species. The difference between the strategies reduced as nodes/sites were removed for some species (great knot and red knot), but remained large for others (bar-tailed godwit, eastern curlew, grey-tailed tattler and ruddy turnstone). Surprisingly, selecting the sites supporting the greatest number of birds was no better at retaining population flow than selecting sites at random for two species (great knot and sanderling; Fig. 5.2).

Some species (bar-tailed godwit) lost population flow slowly as sites were progressively lost (Figs. 5.2 and Appendix S.5.1), while in contrast, populations of other species crashed when the number of sites crossed a critical threshold, around 50% of the sites (e.g. great knot and sanderling). These differences among species may be associated with variation in migratory network structure. Some species used many sites during migration (bar-tailed godwit, 53 sites; ruddy turnstone, 69), while others used few (great knot, 33; red knot, 30; sanderling, 35). The importance of network structure in maintaining populations of birds was apparent when spatially comparing site rankings between the maximum count and flow prioritisation strategies (Appendices S.5.2 and S.5.3). The rank of most sites did not shift markedly between the maximum count and the flow prioritisations (circles in Appendices S.5.2 and S.5.3), however some greatly increased in rank (downward facing triangles in Figs S.5.2 and S.5.3) while others decreased (upward facing triangles in Appendices S.5.2 and S.5.3). Sites that increased in rank were removed later in the flow prioritisation than the maximum count prioritisation, and vice versa. Sites that were not well connected, or that supported birds during only southward or northward migration were removed earlier in the flow prioritisation than the maximum count prioritisation, despite being able to support large numbers of birds (Appendices S.5.2, S.5.3 and S.5.4). A few key sites were therefore fundamental in driving the efficiency of the flow prioritisation strategy. This trend is likely reflected in multi-species prioritisations, as a small number of sites are internationally important for many species, while most are only internationally important for a few (Appendix S.5.5).

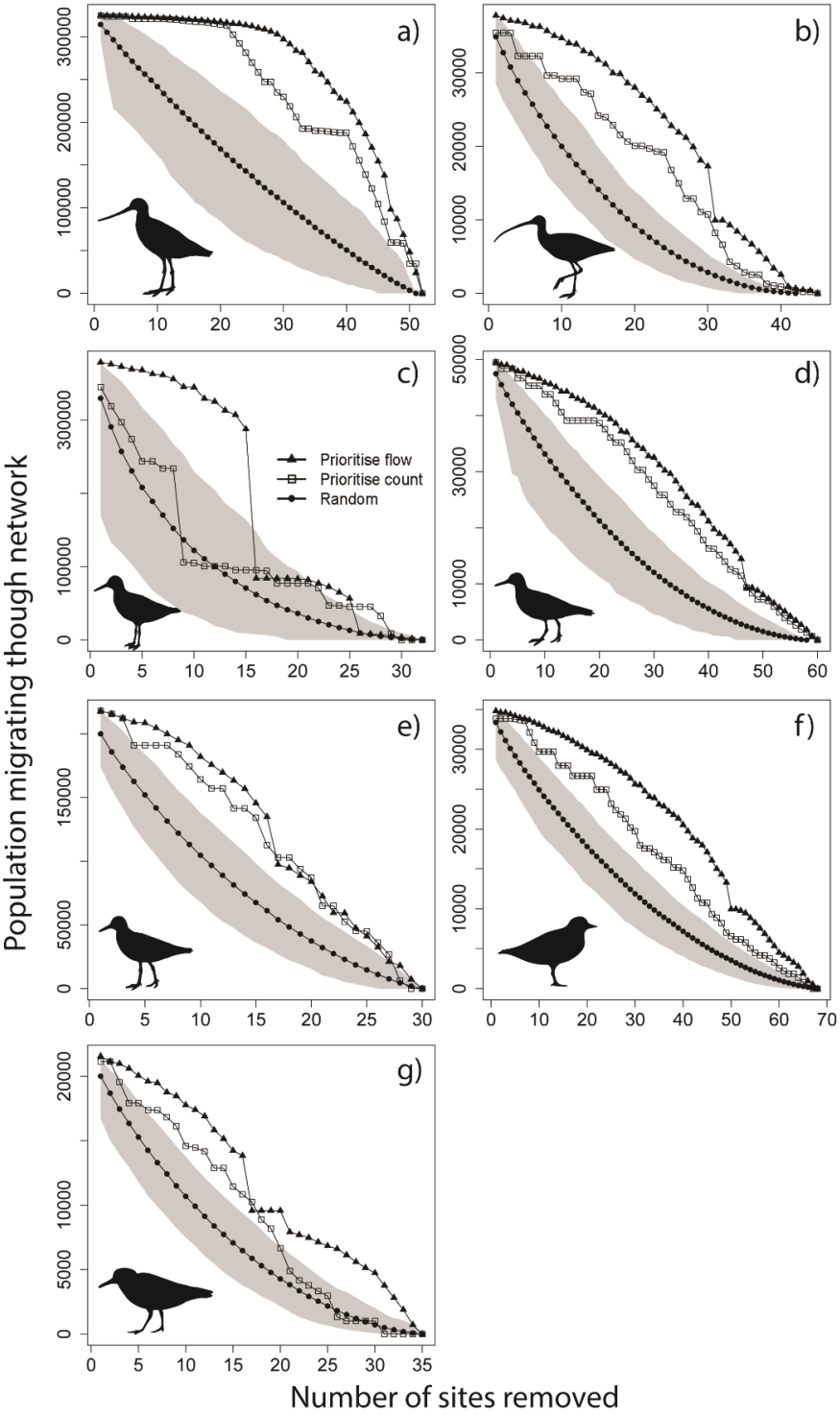

Figure 5.2 *Loss of population flow as nodes are removed: according to (i) the flow prioritisation strategy, (ii) the maximum count prioritisation strategy, and (iii) the random prioritisation strategy (+- 95% quantiles), for a) bar-tailed godwit, b) eastern curlew, c) great knot, d) grey-tailed tattler, e) red knot, f) ruddy turnstone and g) sanderling..*

5.5 Discussion

Despite telemetry devices becoming smaller, cheaper and more accurate, and the availability of tracking data increasing rapidly, much remains unknown about species' migratory routes, making conservation planning challenging. Here, we have shown that limited tracking data can be used to parameterise a simple model of migratory connectivity to aid decision-making for migratory species. We show that prioritising sites with the largest counts of individuals is not as efficient as prioritising using migratory connectivity, and in some cases, maximum count strategies can perform as poorly as randomly selecting sites (Fig. 5.2).

These relationships can vary depending on species-specific network structure. For the EAAF migratory shorebirds, the flow maximisation strategy is more effective for some species (e.g. bar-tailed godwit and great knot), than for others (Appendices 5.2 and S.5.1). The distribution of migration distances for these species hints at the mechanisms involved. For example, bar-tailed godwits can fly long distances and have many sites available to them (53). The effect of removing one site on population flow is low. The cumulative effect of removing sites remains incremental until the population suddenly declines rapidly. This decline occurs once stopover sites are no longer available and non-breeding sites begin to be removed (Appendix S.5.2). Beyond that point, the population declines stepwise as non-breeding sites are removed until no birds remain (Fig. 5.2 and Appendix S.5.1). No site strongly outweighs another in terms of its contribution to population flow, however, a critical mass of sites is required to maintain the flyway.

In contrast, the migration of great knots depends on a few key sites, and crashes rapidly as these are lost (Appendix S.5.1). This is partly because great knots prefer to fly shorter distances than bar-tailed godwits (Fig. 5.1) and are dependent on stopover sites to complete both their northward and southward migration (Yang *et al.*, 2011; Ma *et al.*, 2013; Choi *et al.*, 2015). Furthermore, they have relatively few sites available (33). Losing stopover habitat, which birds can exploit during both north and south migration, and that are highly connected to non-breeding sites, results in rapid population declines. Unlike bar-tailed godwits, where non-breeding habitats were prioritised (Appendix S.5.4a), for great knots the flow maximisation strategy prioritises non-breeding and stopover habitat alike (Appendix S.5.4c). Non-breeding and stopover habitats are prioritised for all species except bar-tailed godwit (Appendix S.5.4).

Site prioritisation is highly dependent on the pattern of migratory connectivity among sites, which is impossible to determine comprehensively given the sparse data currently available. Additional tracking data would refine modelled connectivity estimates, however, more biologically realistic results could be achieved by developing mechanistic (e.g. population growth, density-dependence) and eco-physiological models (e.g. energetics, starvation risk, predation risk) of the migration itself (Taylor & Norris, 2007; Bauer *et al.*, 2008; Taylor & Norris, 2010; Bauer & Klaassen, 2013). The approach we develop here is therefore not intended to replace such models, but to provide insight for large samples of sites when data are limited. Indeed, mechanistic approaches are data hungry, computationally complex, and limited in their spatial accuracy. In the face of ongoing population declines and data paucity, estimates of connectivity patterns that make best use of existing data are urgently needed to inform coordinated protection for migratory species. Our research tackles this major hurdle of conservation planning by demonstrating how to use limited tracking data to develop estimates of population connectivity to improve conservation outcomes. Indeed, we show that prioritising sites for conservation based on connectivity and abundance simultaneously, maintains larger populations than assessments based solely on abundance. This research highlights that for many species, a migratory network is more than the sum of its parts. Loss of some sites can lead to partial or even total population crashes. Some species are especially vulnerable when migratory connectivity is not taken into account, and clear thinking on this issue is needed to avoid making poor protection decisions. Managing sites that support large numbers of individuals will not always deliver the most efficient conservation outcomes.

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Chapter 6

General Discussion

6 General Discussion

6.1 Outline

Declines are apparent in many migratory species across the globe (Brower & Malcolm, 1991; Wilcove & Wikelski, 2008; Harris *et al.*, 2009), and this spectacular global phenomenon is in danger of disappearing altogether, if conservation activities are not planned more strategically (Bowlin *et al.*, 2010). Despite legislation and international collaborations specifically designed to protect migratory species (Kirby *et al.*, 2008), there is a large gap between aspirations and achievements, no doubt owing at least in part to a very limited scientific foundation on which to base decisions. The study of migration has largely been dominated thus far by trying to understand and describe the phenomenon itself (Faaborg *et al.*, 2010), while methods for conserving migratory species are only in the early stages of development (Runge *et al.*, 2014a). This thesis is focused around reducing this gap, using the migratory shorebirds of the East Asian Australasian Flyway (EAAF) as a case study. My thesis aims to (i) increase our understanding of how threatening processes throughout the migratory cycle can influence population growth rate, (ii) increase our understanding of habitat availability, protection and management during the non-breeding season, (iii) design optimal management strategies at the local scale, and finally (iv) investigate how conservation action can be prioritised at the international level when migratory connectivity is uncertain.

Below, I outline the core achievements of each chapter. I then synthesise the thesis and discuss it in the context of current research, before outlining the assumptions and limitations not previously addressed within each chapter. Finally, I suggest avenues for future research.

6.2 Identifying drivers of change in migratory species

Environmental conditions vary in time and space (Ruokolainen *et al.*, 2009). Understanding how these influence temporally and spatially mobile species can be complex. For migrants in particular, tracking data are limited and spatially biased (Block *et al.*, 2005), leading to uncertainty in migratory connectivity. Unravelling how environmental conditions in one part

of the flyway can impact population growth rate in another part (Norris & Taylor, 2006), can be difficult with limited data. In **Chapter 2**, I use count data from a single Ramsar site in a migratory flyway, in combination with remote sensing data from 250 sites across the flyway, to find environmental correlates of changing abundance in migratory shorebird populations. This chapter contributes two main advances to the conservation of shorebirds, and migratory species more broadly. Firstly, it develops a methodological framework for using limited data to make inferences about drivers of population growth rate that are geographically separated from where their effects on populations are measured. Second, it provides much needed insight into population responses to environmental conditions throughout the entire EAAF for seven shorebird species. Indeed the EAAF is greatly understudied in relation to other flyways (Amano *et al.*, 2010). Interestingly, though different species are influenced by different environmental conditions throughout migration, these variations only explain in part the the variable growth rates we are observing in bird numbers. Most likely, combinations of factors are driving the variations we are observing in migratory shorebirds (Wilson *et al.*, 2011).

6.3 Mapping the extent and protection of important habitat

Australia is a major non-breeding terminus for migratory shorebirds in the EAAF. Yet the extent, distribution and protection of intertidal habitat, one of the most critical habitats for migratory shorebirds, remain poorly understood. In **Chapter 3**, I produce the first map of intertidal habitats in Australia using freely available satellite imagery. The primary contribution of this chapter is in the form of data, which are freely available on http://doi.pangaea.de/10.1594/PANGAEA.845726 as a GIS layer. This chapter also brings to light how inconsistently this habitat is dealt with in the planning process. Though levels of protection are high across Australia (39.2%), they vary greatly among states, with some states protecting as little as 6% (the Northern Territory). In fact, marine and terrestrial protected areas overlap in the intertidal zone in some states (10% of protected areas in South Australia) potentially leading to confusion if neither management agency takes full responsibility for the conservation of intertidal habitats and the shorebirds reliant on them. This said, shorebirds move between intertidal habitats as a food resource, and supratidal wetlands as roosting habitat, and so joined up management of the terrestrial and marine environment will be critical for ensuring healthy shorebird populations.

6.4 Optimal allocation of management effort

Within protected areas, one of the most effective tools available to managers is enforcement (Rowcliffe *et al.*, 2004; Gibson *et al.*, 2005; Keane *et al.*, 2008; Plumptre *et al.*, 2014).. However, determining where and when to carry to enforcement is no trivial question, particularly given diminishing returns on investment. Indeed, the more a site is patrolled, the fewer infractions will be committed at that site. There is therefore a trade-off between the benefit of enforcing and the cost of carrying out enforcement. In **Chapter 4**, I develop and test a method of allocating disturbance enforcement effort among shorebird roosts within a protected area, given limited data and funds. The contribution of this chapter is a novel formulation of a cost-benefit analysis to account for diminishing returns on investment, which is easily transferrable to other case studies in protected area management. Importantly, this chapter demonstrates that prioritizing enforcement sites based on greatest disturbance to wildlife, or greatest abundance of target species alone, will not yield an optimal solution. Furthermore, visiting a range of enforcement sites at varying rates yields a greater return on investment than visiting only a fixed number of sites. Assuming a high reduction in disturbance from enforcement, the greatest benefit can be achieved by patrolling many sites a small number of times. Assuming a small reduction in disturbance from enforcement, repeatedly patrolling the most cost-effective sites yields the greatest benefit. The choice of patrol location and frequency is not a trivial problem, and prudent investment can substantially improve conservation outcomes.

6.5 Prioritising conservation for migrants internationally

Protected areas are one of the most widely used conservation tools used today. However, setting conservation priorities to designate protected areas for migratory species that cross international borders can be complex, particularly given limited data on migratory connectivity. Currently, conservation priorities for migratory species are often set based on number of animals utilising a site (Kirby *et al.*, 2008; Samraoui & Samraoui, 2013; Conklin *et al.*, 2014), with little consideration for migratory connectivity as a result of limited data. In **Chapter 5**, I

develop a spatial prioritisation among 250 internationally important shorebird wetlands (or nodes), using tracking data as a proxy for migratory connectivity. I show that nodes which are highly connected are more likely to maintain migratory populations than nodes supporting large numbers of birds. The contribution of this chapter is primarily to demonstrate explicitly how tracking data can be incorporated into migratory models to form a better picture of population-level movements, and overcome some of the geographic biases inherent in tracking data. The results also suggest that conservation paradigms need to move beyond an approach which prioritises birds according to numbers (Bamford *et al.*, 2008; Conklin *et al.*, 2014), to also considering migratory connectivity (Cabeza, 2003; van Teeffelen *et al.*, 2006; Martin *et al.*, 2007; Klaassen *et al.*, 2008; Sheehy *et al.*, 2011a; Iwamura *et al.*, 2014; Nicol *et al.*, 2015).

6.6 Synthesis

All too often, efforts to conserve migratory species can be paralysed by uncertainty, typically arising from poor or no information about migratory connectivity (Martin *et al*. 2007). My thesis has made a contribution toward resolving this, in part by reducing uncertainty through new empirical data and analysis (Chapters 2 and 3), and in part by developing models that make the best use of the data that are available to find efficient planning solutions given the uncertainty (Chapters 4 and 5). This extends an emerging body of literature in conservation science that focuses on making the most efficient use of information we already have (Ferraro & Simpson, 2002; Naidoo *et al.*, 2006; Arponen *et al.*, 2010; Urban *et al.*, 2012; Shwiff *et al.*, 2013; Plumptre *et al.*, 2014), carefully assessing the value of collecting new information (Oostenbrink *et al.*, 2008; Runge *et al.*, 2011; Williams *et al.*, 2011; Maxwell *et al.*, 2015), and conservation decision-making under uncertainty (McDonald-Madden *et al.*, 2008; Wilson *et al.*, 2009; Carwardine *et al.*, 2010; Wintle *et al.*, 2010; Keith *et al.*, 2011; McDonald-Madden *et al.*, 2011; Nicol *et al.*, 2015).

My thesis has taken a multi-scalar approach, tackling the issue of conserving migratory species from local management interventions through to trans-national designation of protected area networks. A clear narrative thread running throughout my chapters is that even though migrants travel thousands of kilometres each year visiting sites that are widely dispersed, the amount of habitat they actually rely on is often very small (Chapters 2-5). This is a recipe for extreme

vulnerability to some forms of environmental change (Kaitala *et al.*, 1996; Walther *et al.*, 2002; Crick, 2004; Piersma & Lindstrom, 2004; Chambers *et al.*, 2005; Robinson *et al.*, 2009a; Warnock, 2010; Chambers *et al.*, 2011). Understanding migratory connectivity and finding ways to integrate this information into conservation planning is essential both for maintaining healthy populations of migratory species across their global range, and to place local management issues in a broader context. For example, if the decline in a population at a particular site is being driven by remote threats, management action taken locally might be redundant, or at least have a lesser impact that the same management action taken at a site where the population is actually being limited.

6.7 Assumptions and limitations

6.7.1 Estimating abundance and drivers of change in abundance

As already highlighted in **Chapter 2**, N-mixture models, though considered one of the best methods for estimating abundance (Dail & Madsen, 2011), assume a closed population. In our case study, birds can move between sites, violating the closure assumption. These methods therefore underestimate detection probability and overestimate abundance: Our model does not yield reliable estimates of abundance, however it does yield a reliable estimate of population growth rate, assuming proportional overestimation of abundance is the same each year. Therefore, if it is reasonable to assume that shorebird movement between sites does not vary substantially between years, we can assume that the estimates of population growth rate are robust. To our knowledge only one study has investigated local-scale shorebird movements in Moreton Bay. Coleman and Milton (2012) found that multiple re-sightings of individual birds were made at the same locations both within and between seasons, suggesting that is not unreasonable to assume that birds move as much between sites from one year to the next.

We used these estimates of population growth rate in a weighted least squares regression to investigate the relative influence of different environmental variables. An underlying assumption of this method is that weights (as an inverse of the variance of yearly growth rate) represent yearly differences in measurement error. However, there may be other sources of error in the model (random error, misclassification error). We therefore assume that species are

not misidentified, which is probably reasonable given that most shorebirds roost in the open and can be readily identified with training of the kind QWSG counters undergo.

6.7.2 Mapping intertidal habitats

In **Chapter 3**, I compiled remotely sensed tidal flat data to create the first map of intertidal habitat in Australia. The remote sensing approach used, which aims to differentiate low and high tide Landsat images, has associated uncertainties related to tidal elevation, image availability, waterline delineation and observer error.

Tidal elevation determines the amount of the maximum possible extent of intertidal habitat that is exposed or underwater on any one occasion. Images must therefore be taken at the highest and lowest astronomical tides to avoid underestimating intertidal habitat area. Pre-selection of images for analysis requires an estimate of past tide height at a national level. We used the Tide Model Driver (TMD) MATLAB toolbox to estimate tide height using the Indian Ocean, Tasmania and Northern Australia tide models available from the Oregon State University (Egbert & Erofeeva, 2002; Padman & Erofeeva, 2005). Tidal elevation predictions were made at the mid-point of the coastline of each Landsat footprint, 5km offshore (Murray *et al.*, 2012). Tide height will naturally vary across an area the size of a Landsat footprint, resulting in under- or over-exposure of tidal flats in the image. The tide prediction location was therefore kept consistent across all Landsat footprints so that the degree of underestimation or overestimation was kept constant over time. Furthermore, we restricted our image selection to those from the upper and lower 10% of the tidal range for each Landsat footprint. To further prevent an underestimation of intertidal habitat, we merged multiple estimates of intertidal habitat for each Landsat footprint, when available.

Due to the high/low tide constraint for selecting images, the number of images available for image differentiation was low; this number was further reduced due to the large amount of cloud in the image. Therefore high and low tide images were not always acquired in close succession meaning tidal flights might have changed from one image to the next due to seasonal changes in sedimentation. Here too, by merging multiple years together we aimed to capture seasonal variations in intertidal habitat cover and compensate for the small number of available images.

This remote sensing procedure requires waterline delineation between in both low and high tide images so they may be differentiated. This is a manual step carried out by the remote sensing analyst to identify the threshold which delineates the waterline. A standard methodology was developed so that all analyses carried out the same procedures, minimising variation between observers as per Murray *et al.* (2012).

I carried out an accuracy assessment on the final intertidal habitat map to measure classification error, by comparing a mapped data set with a reference set, using a confusion matrix (Congalton and Green 2008; Roelfsema and Phinn 2013). Using stratified random sampling, I generated 204 sample locations within 10 km of the coastline and within the intertidal class as per the methods of Congalton and Green (2008). I then independently labelled each sample point as tidal flat or other, based on all available Landsat bands of the low-tide images used in the analysis, Google Earth imagery and ESRI World imagery. This revealed an accuracy of 95.6%. Many classification errors occurred consistently on the landward side, where small strips of intertidal habitat were not correctly classified due to the methodological limitation requiring the selection of images within 10% of the high tide, rather than the highest possible tide. However, this was not deemed problematic as the overall accuracy far exceeded 85%, the normally acceptable threshold (Congalton and Green 2008).

6.7.3 Optimal disturbance management for wildlife protection

In **Chapter 4**, I investigate how to optimally allocate patrol effort to account for diminishing returns on investment. One of the main barriers to implementing such an approach on the ground is a lack of understanding of the effectiveness of enforcement. Indeed, it is extremely difficult to determine how well enforcement reduces disturbance events. I conducted fieldwork to collect data on numbers of infractions before and after patrols by Moreton Bay Marine Park rangers, however patrols were carried out only five times at four sites. The sample size was therefore small and it was not statistically possible to determine whether management caused a reduction in disturbance, or whether another factor was at play, such as rainfall or tide height. On average, however, there were 20% fewer disturbances after management. To account for this in our modelling, we devised several different management scenarios and different disturbance reduction scenarios to investigate how disturbance might vary in response to

enforcement. Furthermore, by investigating multiple scenarios, we make our results more applicable to other studies.

Furthermore, in this research, I assume that only one site is patrolled at a time, or in other words, that rangers carry out enforcement at a site and then return to base camp. Patrols are often time consuming, and it is not unreasonable to assume only one site is patrolled at a time. In our case study for instance, Marine Park personnel patrol each site for an extended period, observing public behaviour, intervening in the case an infraction is committed and carrying out public outreach. However, to allow for multiple sites to be visited per patrol, it would be possible to use an approach such as the travelling salesman problem (Larrañaga *et al.*, 1999), to find the shortest route between a set of sites. By modifying this problem to minimise cost and maximise benefit simultaneously, and by adding a decision variable to limit the number of sites patrolled, it would be possible to determine the optimal route through multiple sites.

Finally, the true aim of managing disturbance to shorebirds is to maintain a viable population. To determine how shorebirds benefit from disturbance reduction, it would be necessary to model feedbacks. For instance, it would be possible to model population responses to disturbance using an eco-physiological model to assess the impacts of reduced feeding as a result of disturbance. It would therefore be possible to test different management options within a population viability analysis (PVA) to determine which offered the best benefit. However such models are complicated and can be lengthy to parameterise and implement (Joseph *et al.*, 2009). Furthermore the necessary data for parameterising such a model are not yet available for the study system we used, and accumulated error arising from multiple parameters would render the results unusable.

6.7.4 Maximum flow

In **Chapter 5**, I use linear programming to solve the maximum flow problem for migratory networks. One of the primary limitations with this approach is that it is impossible to evaluate whether I have correctly estimated connectivity at the population level. Direct validation of the model via field observation is almost impossible to obtain without an enormous tracking exercise, and this illustrates clearly the limitation of relying on the incremental accumulation of field data. At the present rate of progress, it will be decades before we have sufficient directly

observed tracking data to validate connectivity models. One interesting approach might be to build a priori predictions of the possible routes a specific group of newly tagged individuals will take. This could lead to field data updating a connectivity model incrementally over time, although one would need to determine some method of allowing the model to learn.

Other information could help too. Indeed, weather conditions are important predictors of migratory pathways (Kranstauber *et al.*, 2015), and in particular wind which can facilitate birds flight, causing individuals to fly different distances during north and south migration. Better data on the quality of stopover nodes (e.g. benthic food availability), could also greatly improve our connectivity estimates, as could formal eco-physiological models (e.g. energetics, starvation risk, predation risk) of the migration itself (Taylor & Norris, 2007; Bauer *et al.*, 2008; Taylor & Norris, 2010). Density-dependence is another important factor governing usage of nodes, and might cause the relative importance of nodes to change as a decline continues. To some degree, my methods account for adaptability by using potential connectivity to parameterise models. An interesting extension of my research would be to incorporate a population model in the breeding node (e.g. Ricker, 1954), so that potential connectivity calculations for the network could be recalculated when nodes are lost, to allocate all the remaining post-breeding population through the updated network. This however could assume an unrealistically adaptable population unless density dependence and carrying capacity estimates at stopover and non-breeding nodes could also be incorporated, in addition to the trade-offs of making single vs multiple migratory flights. Another extension of my research, particularly when tracking data are available for more species, would be a multi-species prioritisation.

6.8 Future directions

Declines in migratory shorebirds in the East Asian Australasian Flyway are likely driven by suite of factors including habitat loss, hunting, environmental variability, pollution, disturbance and disease (MacKinnon *et al.*, 2012b; Sutherland *et al.*, 2012; Murray *et al.*, 2014). Disentangling these effects is a major challenge for conservation, especially given data are not readily available for many of these factors (Faaborg *et al.*, 2010). In reality, data will likely never be available comprehensively from across the flyway, owing to the huge cost of

systematically conducting surveys at the international scale. Even if these data are collected, past data will not be available to hind-cast and determine whether these have influenced overall population declines, unless we are able to remotely sense them (e.g. Chapter 2). Conservation scientists are therefore faced with a dilemma: to spend funds on increasing certainty, or devising management plans with uncertain outcomes. Both hold a certain amount of risk. On one hand, species could be monitored to extinction. On the other, the wrong management action could be taken, failing to avert extinction. Much of my thesis has therefore focused on making the most efficient use of information we already have (Chapters 2, 3 and 5) and determining how to make conservation decisions under uncertainty (Chapters 4 and 5).

In the East Asian Australasian Flyway, where declines have been widely reported, uncertainty surrounding the need to act has largely been removed (Reid & Park, 2003; Rogers & Gosbell, 2006; Close, 2008; Nebel *et al.*, 2008; Creed & Bailey, 2009; Paton *et al.*, 2009; Rogers *et al.*, 2011; Wilson *et al.*, 2011; Cooper *et al.*, 2012; Minton *et al.*, 2012; Clemens *et al.*, in press). However, there is now substantial uncertainty about *how* to act. The challenge therefore lies in determining which actions are most likely to mitigate future declines given these uncertainties. More specifically, (i) how effectively can threats be mitigated through management, (ii) how do populations respond to mitigation actions, and (iii) how well can we detect population responses and evaluate the efficacy of conservation actions? As discussed in the limitations section, under uncertainty, scenario testing can be used determine whether a management actions will be beneficial (e.g. Chapter 4). Very often, the same management action will consistently perform better than others (McCarthy *et al.*, 2008; McDonald-Madden *et al.*, 2008; Keith *et al.*, 2011; McDonald-Madden *et al.*, 2011). This is intuitive given that certain threats, such as disease or predation are difficult to mitigate through management, while others such as habitat loss or hunting can be mitigated through habitat protection or catch quotas. However, there are trade-offs between implementing these different conservation mitigation actions, suggesting that the exploration of these trade-offs will be a fruitful avenue for future research.

Understanding the trade-offs between different management strategies is however not an end in itself, but a first step towards averting declines. International collaboration is required to ensure these conservation strategies are implementable. A series of international agreements is currently in place (1971 *Ramsar Convention*, 1979 *Bonn Convention*, 1974 *Japan-Australia Migratory Bird Agreement*, 1986 *China-Australia Migratory Bird Agreement* and 2007

Republic of Korea-Australia Migratory Bird Agreement), as well as the East Asian-Australasian Flyway Partnership, to protect migratory shorebirds (Gallo-Cajaio *et al.*, in press). This range of binding and non-binding agreements between countries forms a potentially strong mechanism for coordinating conservation action across the 26 countries within the flyway. Such coordinated efforts have previously proven effective in maintaining healthy populations of migratory species. The parties of the Nauru Agreement (PNA) for instance have collaboratively managed sustainable populations of highly migratory tuna fisheries throughout the pacific region. To do so, PNA banned boats that fished in the high seas, from fishing within any of their joined economic zones – thus managing migratory fisheries beyond their political jurisdiction (Lodge, 1992). Unfortunately shorebirds do not hold the same economic sway as tuna fisheries. With so many geographically, politically and economically distant countries across the flyway, conservation is prioritised differently from country to country (Dallimer & Strange, 2015). In fact, when considering the trade-offs between economic development and conservation, it is of course not surprising that many choose economic development. Offsetting policy is therefore an important avenue for future research (Bull *et al.*, 2013; Barton *et al.*, 2015), allowing countries and NGOs with a vested interest in maintaining healthy populations in their own countries, to act beyond their political boundaries by financially offsetting development internationally, at key migratory nodes (e.g. Chapter 5), by improving or creating new habitat.

6.9 Concluding remarks

Ultimately, my thesis has fit but a small piece in a much wider and as yet unsolved conservation puzzle. It has highlighted the fact that even though migrants may travel the globe, they remain reliant on small, strategically-located habitat patches (Chapters 2 and 5). My thesis has demonstrated that identifying these habitats (Chapters 3 and 5), and identifying management actions for maintaining healthy populations within these habitats (Chapter 4) is invaluable for conserving migratory species. Furthermore, it has demonstrated that policy priorities now need to shift from a site-quality based conservation approach, to a spatially-explicit conservation approach (Chapter 5) to secure the future of one of the world' most spectacular migratory flyways.

Chapter 7

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7 References

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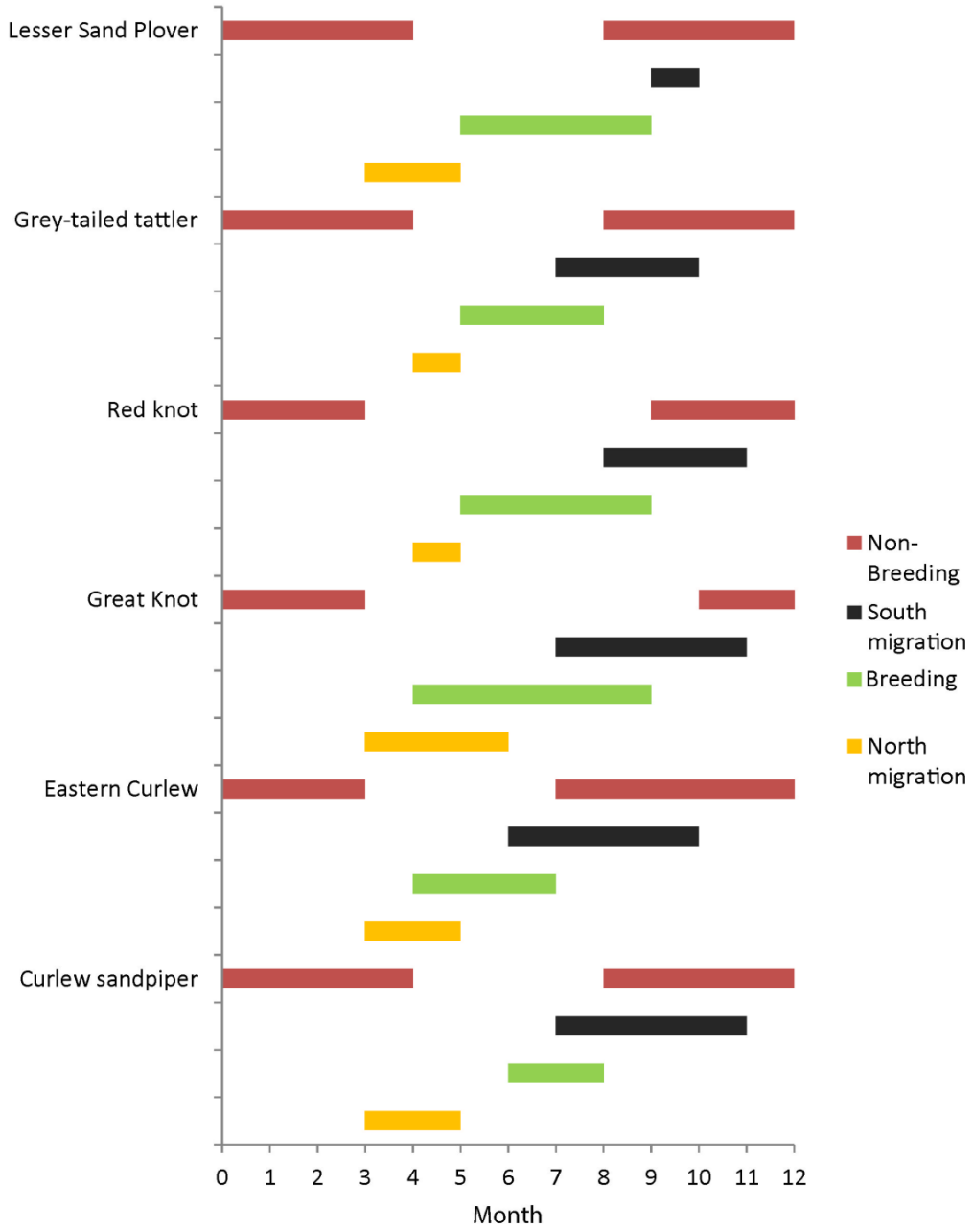
Chapter 8

Appendices

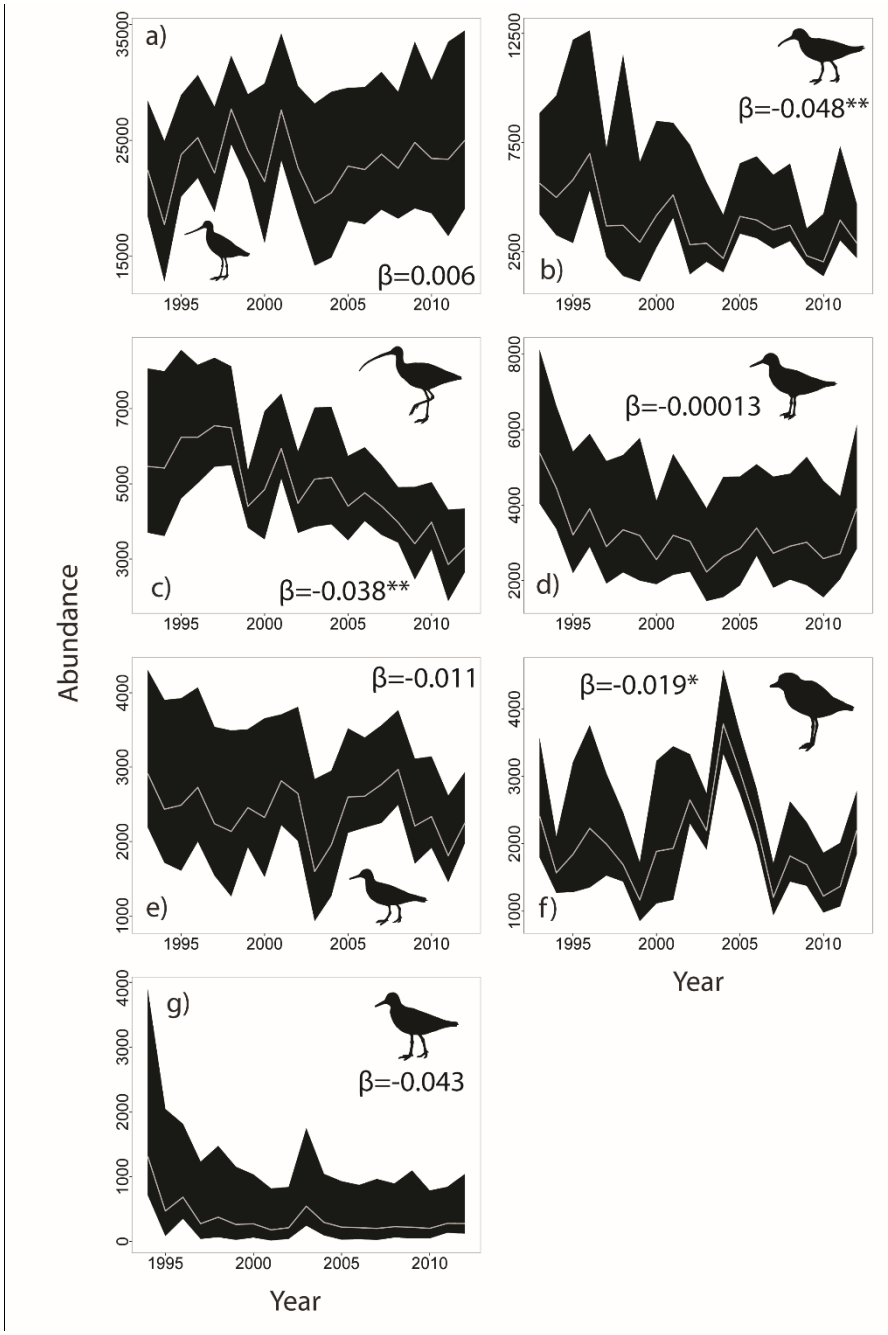
8 Appendices

8.1 Appendix S.2.1



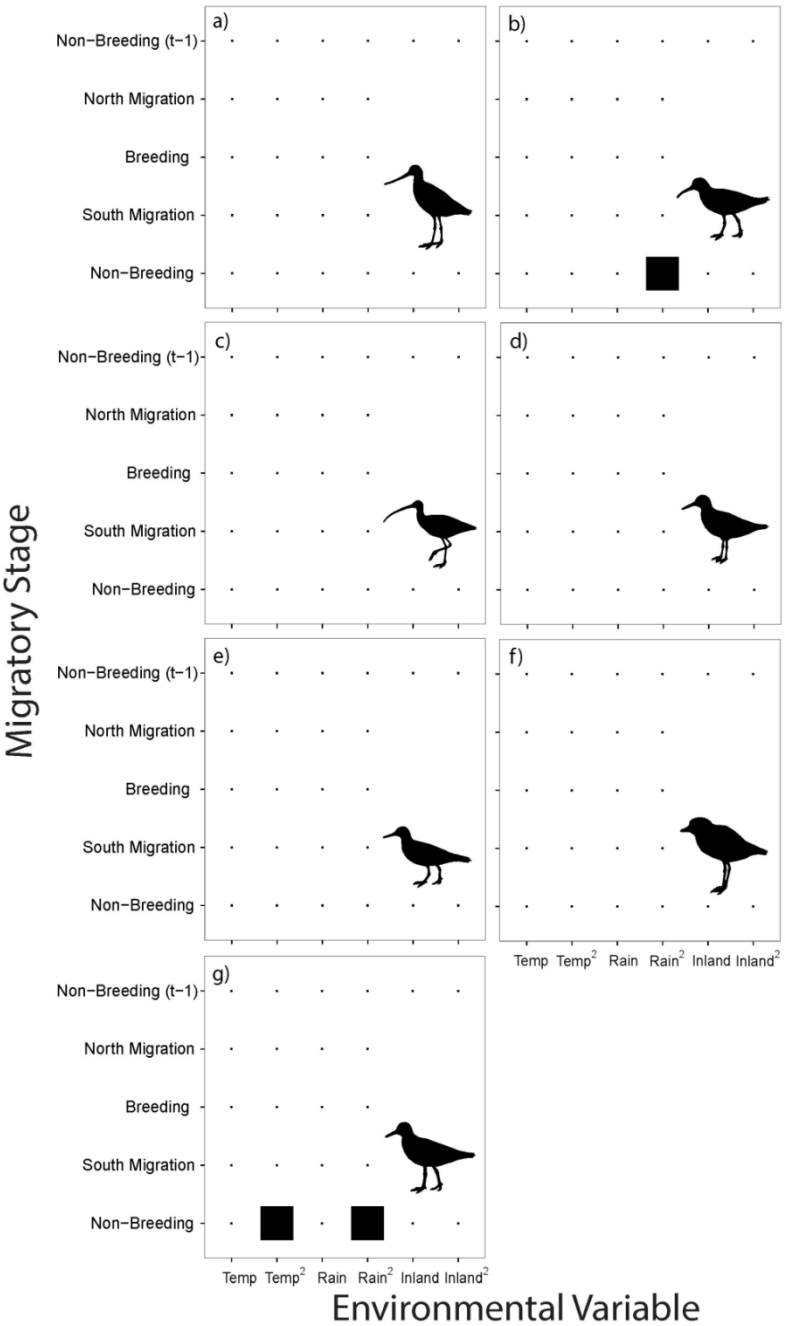
Detail of migratory timing for curlew sandpiper, eastern curlew, great knot, red knot, grey-tailed tattler and lesser sand plover based on literature review.

8.2 Appendix S.2.2



From top to bottom, left to right, total abundance between 1992 and 2012 of a) bar-tailed godwit (Limosa lapponica), b) curlew sandpiper (Calidris ferruginea), c) eastern curlew (Numenius Madagascariensis), d) great knot (Calidris tenuirostris), e) grey-tailed tattler (Tringa brevipes), f) lesser sand plover (Charadrius mongolus) and g) red knot (Calidris canutus). The white line represents the mean estimate of abundance, and the black shading represents the 97.5% estimates of confidence intervals.

8.3 Appendix S.2.3



From top to bottom, left to right, multi-collinearity of environmental variables for a) bar-tailed godwit (Limosa lapponica), b) curlew sandpiper (Calidris ferruginea), c) eastern curlew (Numenius Madagascariensis), d) great knot (Calidris tenuirostris), e) grey-tailed tattler (Tringa brevipes), f) lesser sand plover (Charadrius mongolus) and g) red knot (Calidris canutus). Large squares represent variables with a variance inflation factor greater than 10.

8.4 Appendix S.2.4

Details of all models tested for all species ranked according to BIC. Models with 6<ΔBIC are shaded in grey.

Bar-tailed godwit

Model	K	logLik	BIC	ΔBIC	w	adjR^2
Temp $_{NB}$	3	9.92	-11.01	0.00	0.10	-0.10
NULL	2	8.40	-10.92	0.09	0.09	0.00
Rain $_{NM}$	3	9.55	-10.27	0.74	0.07	-0.08
Temp $_{NM}$ + Temp $_{NM}^2$	4	10.95	-10.12	0.89	0.06	-0.17
Temp $_{SM}$	3	9.43	-10.02	0.99	0.06	-0.07
Rain $_{INLAND\ (t-1)}$	3	8.98	-9.14	1.88	0.04	-0.04
Rain $_{NB}$	3	8.85	-8.86	2.15	0.03	-0.03
Rain $_{NB}$ + Temp $_{NB}$	4	10.20	-8.62	2.40	0.03	-0.12
Rain $_{SM}$	3	8.72	-8.61	2.40	0.03	-0.02
Temp $_{NB}$ + Temp $_{NB}^2$	4	10.18	-8.58	2.43	0.03	-0.12
Rain $_{B}$	3	8.66	-8.48	2.53	0.03	-0.02
Temp $_{NM}$	3	8.57	-8.30	2.71	0.02	-0.01
Rain $_{INLAND}$ + Temp $_{NB}$	4	9.98	-8.18	2.83	0.02	-0.11
Rain $_{SM}$ + Temp $_{SM}$	4	9.94	-8.11	2.91	0.02	-0.11
Temp $_{B}$	3	8.45	-8.06	2.95	0.02	0.00
Rain $_{NB\ (t-1)}$	3	8.43	-8.03	2.98	0.02	0.00
Temp $_{NB\ (t-1)}$	3	8.43	-8.02	2.99	0.02	0.00
Rain $_{INLAND}$	3	8.41	-7.98	3.03	0.02	0.00
Rain $_{NM}$ + Temp $_{NM}$ + Temp $_{NM}^2$	5	11.30	-7.87	3.14	0.02	-0.19
Temp $_{SM}$ + Temp $_{SM}^2$	4	9.72	-7.65	3.36	0.02	-0.09
Rain $_{NM}$ + Rain $_{NM}^2$	4	9.68	-7.59	3.42	0.02	-0.09
Rain $_{NM}$ + Temp $_{NM}$	4	9.55	-7.33	3.68	0.02	-0.08
Rain $_{SM}$ + Temp $_{SM}$ + Temp $_{SM}^2$	5	10.91	-7.10	3.92	0.01	-0.16
Temp $_{B}$ + Temp $_{B}^2$	4	9.31	-6.85	4.16	0.01	-0.06
Rain $_{SM}$ + Rain $_{SM}^2$	4	9.31	-6.85	4.16	0.01	-0.06
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$	4	9.05	-6.33	4.68	0.01	-0.05
Rain $_{NM}$ + Rain $_{NM}^2$ + Temp $_{NM}$ + Temp $_{NM}^2$	6	12.00	-6.32	4.69	0.01	-0.22
Rain $_{INLAND\ (t-1)}$ + Temp $_{NB\ (t-1)}$	4	9.03	-6.28	4.73	0.01	-0.05
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$	4	9.01	-6.25	4.76	0.01	-0.04
Rain $_{NB}$ + Rain $_{NB}^2$	4	8.95	-6.12	4.89	0.01	-0.04
Rain $_{INLAND}$ + Rain $_{NB}$	4	8.91	-6.05	4.96	0.01	-0.04
Rain $_{NB}$ + Temp $_{NB}$ + Temp $_{NB}^2$	5	10.37	-6.01	5.00	0.01	-0.13
Rain $_{NB}$ + Rain $_{NB}^2$ + Temp $_{NB}$	5	10.22	-5.72	5.29	0.01	-0.12
Rain $_{INLAND}$ + Rain $_{NB}$ + Temp $_{NB}$	5	10.20	-5.69	5.33	0.01	-0.12
Rain $_{INLAND}$ + Temp $_{NB}$ + Temp $_{NB}^2$	5	10.19	-5.66	5.35	0.01	-0.12
Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$	4	8.71	-5.65	5.37	0.01	-0.02
Rain $_{B}$ + Rain $_{B}^2$	4	8.68	-5.58	5.43	0.01	-0.02
Rain $_{B}$ + Temp $_{B}$	4	8.66	-5.54	5.47	0.01	-0.02
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$	5	10.04	-5.35	5.66	0.01	-0.11
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Temp $_{NB}$	5	10.02	-5.32	5.69	0.01	-0.11
Rain $_{INLAND}$ + Rain $_{INLAND}^2$	4	8.50	-5.23	5.78	0.01	-0.01

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	4	8.46	-5.15	5.86	0.01	0.00
$Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	4	8.45	-5.13	5.88	0.01	0.00
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM}$	5	9.75	-4.78	6.23	0.00	-0.09
$Rain_{B} + Temp_{B} + Temp_{B}^2$	5	9.55	-4.38	6.63	0.00	-0.08
$Rain_{SM} + Rain_{SM}^2 + Temp_{SM} + Temp_{SM}^2$	6	11.00	-4.33	6.68	0.00	-0.17
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	5	9.34	-3.96	7.06	0.00	-0.07
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	5	9.11	-3.50	7.51	0.00	-0.05
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)}$	5	9.09	-3.45	7.56	0.00	-0.05
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	9.07	-3.42	7.59	0.00	-0.05
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB}$	5	9.04	-3.36	7.65	0.00	-0.05
$Rain_{INLAND\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	9.04	-3.35	7.66	0.00	-0.05
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2$	5	9.01	-3.30	7.71	0.00	-0.04
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	6	10.41	-3.15	7.86	0.00	-0.13
$Rain_{INLAND} + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	6	10.37	-3.06	7.95	0.00	-0.13
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB}$	6	10.26	-2.86	8.15	0.00	-0.13
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	8.78	-2.83	8.18	0.00	-0.03
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB} + Temp_{NB}^2$	6	10.23	-2.80	8.21	0.00	-0.12
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	6	10.23	-2.79	8.22	0.00	-0.12
$Rain_{B} + Rain_{B}^2 + Temp_{B}$	5	8.68	-2.64	8.37	0.00	-0.02
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	8.48	-2.24	8.77	0.00	-0.01
$Rain_{B} + Rain_{B}^2 + Temp_{B} + Temp_{B}^2$	6	9.58	-1.49	9.52	0.00	-0.08
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	6	9.45	-1.23	9.78	0.00	-0.07
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	6	9.35	-1.03	9.98	0.00	-0.07
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	6	9.16	-0.66	10.36	0.00	-0.05
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2$	6	9.16	-0.65	10.36	0.00	-0.05
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	9.13	-0.60	10.41	0.00	-0.05
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	9.11	-0.56	10.45	0.00	-0.05
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	9.08	-0.49	10.52	0.00	-0.05
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	7	10.42	-0.23	10.78	0.00	-0.14
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	7	10.41	-0.22	10.79	0.00	-0.13
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	7	10.28	0.05	11.06	0.00	-0.13
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	9.52	1.58	12.59	0.00	-0.08
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	7	9.46	1.68	12.69	0.00	-0.07
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	9.19	2.23	13.24	0.00	-0.06
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	8	10.50	2.57	13.58	0.00	-0.14
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	8	9.52	4.51	15.52	0.00	-0.08

Curlew sandpiper

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Rain_{INLAND\ (t-1)}$	3	-6.13	21.09	0.00	0.12	0.36
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2$	4	-4.69	21.16	0.07	0.11	0.55
$Rain_{NB}$	3	-6.83	22.49	1.40	0.06	0.25
$Rain_{NB} + Rain_{NB}^2$	4	-5.36	22.50	1.41	0.06	0.46
NULL	2	-8.34	22.58	1.48	0.06	0.00
$Rain_{INLAND}$	3	-7.32	23.48	2.39	0.04	0.17
$Rain_{SM}$	3	-7.33	23.50	2.41	0.04	0.17
$Rain_{INLAND\ (t-1)} + Temp_{NB\ (t-1)}$	4	-6.03	23.83	2.74	0.03	0.37
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)}$	4	-6.07	23.93	2.83	0.03	0.36
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	-4.69	24.11	3.01	0.03	0.55
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)}$	5	-4.69	24.11	3.01	0.03	0.55
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2$	5	-4.83	24.38	3.29	0.02	0.53
$Temp_{NB\ (t-1)}$	3	-7.81	24.45	3.36	0.02	0.09
$Rain_{INLAND} + Rain_{NB}$	4	-6.41	24.59	3.50	0.02	0.32
$Rain_{NB\ (t-1)}$	3	-7.93	24.70	3.60	0.02	0.07
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	5	-5.10	24.93	3.83	0.02	0.50
$Rain_{NB} + Temp_{NB}$	4	-6.59	24.96	3.86	0.02	0.29
$Temp_{SM}$	3	-8.19	25.22	4.13	0.01	0.03
$Rain_{B}$	3	-8.24	25.31	4.21	0.01	0.02
$Temp_{NB}$	3	-8.27	25.37	4.27	0.01	0.01
$Temp_{NM}$	3	-8.29	25.40	4.31	0.01	0.01
$Rain_{INLAND} + Temp_{NB}$	4	-6.82	25.41	4.32	0.01	0.25
$Temp_{B}$	3	-8.33	25.49	4.39	0.01	0.00
$Rain_{INLAND} + Rain_{INLAND}^2$	4	-6.87	25.52	4.43	0.01	0.25
$Rain_{NM}$	3	-8.34	25.52	4.43	0.01	0.00
$Rain_{SM} + Temp_{SM}$	4	-6.92	25.61	4.52	0.01	0.24
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	4	-7.25	26.28	5.18	0.01	0.19
$Rain_{SM} + Rain_{SM}^2$	4	-7.29	26.36	5.27	0.01	0.18
$Rain_{INLAND} + Rain_{NB} + Temp_{NB}$	5	-5.83	26.37	5.28	0.01	0.40
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	5	-5.86	26.44	5.35	0.01	0.39
$Rain_{INLAND\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	-5.87	26.46	5.37	0.01	0.39
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	5	-5.92	26.57	5.48	0.01	0.39
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	6	-4.52	26.71	5.62	0.01	0.57
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB}$	5	-6.01	26.74	5.65	0.01	0.37
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2$	6	-4.58	26.83	5.73	0.01	0.56
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	-4.68	27.03	5.94	0.01	0.55
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	6	-4.69	27.04	5.95	0.01	0.55
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	6	-4.69	27.05	5.96	0.01	0.55
$Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	4	-7.68	27.14	6.05	0.01	0.12
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	6	-4.78	27.23	6.13	0.01	0.54

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	5	-6.39	27.50	6.41	0.00	0.32
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	4	-7.87	27.51	6.42	0.00	0.08
$Temp_{NB} + Temp_{NB}^2$	4	-7.91	27.60	6.51	0.00	0.08
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB}$	5	-6.48	27.69	6.60	0.00	0.30
$Temp_{SM} + Temp_{SM}^2$	4	-8.05	27.87	6.78	0.00	0.05
$Rain_{INLAND} + Temp_{NB} + Temp_{NB}^2$	5	-6.58	27.88	6.79	0.00	0.29
$Temp_{NM} + Temp_{NM}^2$	4	-8.11	28.00	6.90	0.00	0.04
$Rain_{SM} + Temp_{SM} + Temp_{SM}^2$	5	-6.71	28.15	7.06	0.00	0.27
$Temp_{B} + Temp_{B}^2$	4	-8.19	28.15	7.06	0.00	0.03
$Rain_{B} + Rain_{B}^2$	4	-8.21	28.20	7.11	0.00	0.02
$Rain_{NM} + Rain_{NM}^2$	4	-8.23	28.23	7.14	0.00	0.02
$Rain_{B} + Temp_{B}$	4	-8.23	28.25	7.15	0.00	0.02
$Rain_{NM} + Temp_{NM}$	4	-8.28	28.35	7.25	0.00	0.01
$Rain_{SM} + Rain_{SM}^2 + Temp_{SM}$	5	-6.89	28.51	7.41	0.00	0.24
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB}$	6	-5.55	28.77	7.67	0.00	0.44
$Rain_{INLAND} + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	6	-5.73	29.12	8.03	0.00	0.41
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	7	-4.26	29.14	8.05	0.00	0.60
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	-7.22	29.16	8.07	0.00	0.19
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	-7.24	29.19	8.10	0.00	0.19
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	6	-5.76	29.19	8.10	0.00	0.41
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	-5.83	29.33	8.24	0.00	0.40
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	7	-4.51	29.63	8.53	0.00	0.57
$Rain_{B} + Temp_{B} + Temp_{B}^2$	5	-7.46	29.64	8.55	0.00	0.15
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	-4.68	29.98	8.88	0.00	0.55
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	7	-4.69	29.99	8.89	0.00	0.55
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB} + Temp_{NB}^2$	6	-6.26	30.18	9.09	0.00	0.34
$Rain_{NM} + Temp_{NM} + Temp_{NM}^2$	5	-8.11	30.94	9.85	0.00	0.04
$Rain_{B} + Rain_{B}^2 + Temp_{B}$	5	-8.17	31.06	9.97	0.00	0.03
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM}$	5	-8.18	31.08	9.99	0.00	0.03
$Rain_{SM} + Rain_{SM}^2 + Temp_{SM} + Temp_{SM}^2$	6	-6.71	31.09	9.99	0.00	0.27
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	8	-3.96	31.47	10.38	0.00	0.63
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	7	-5.46	31.53	10.44	0.00	0.45
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	-7.22	32.10	11.01	0.00	0.19
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	-5.76	32.12	11.03	0.00	0.41
$Rain_{B} + Rain_{B}^2 + Temp_{B} + Temp_{B}^2$	6	-7.30	32.26	11.16	0.00	0.18
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	8	-4.68	32.92	11.82	0.00	0.55
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM} + Temp_{NM}^2$	6	-8.05	33.77	12.68	0.00	0.05

Eastern curlew

Model	K	logLik	BIC	ΔBIC	w	adjR^2
Rain $_{NM}$ + Rain $_{NM}^2$	4	13.70	-15.62	0.00	0.73	-2.38
Rain $_{NM}$ + Rain $_{NM}^2$ + Temp $_{NM}$	5	13.71	-12.69	2.93	0.17	-2.38
Rain $_{NM}$ + Rain $_{NM}^2$ + Temp $_{NM}$ + Temp $_{NM}^2$	6	13.71	-9.75	5.87	0.04	-2.38
Rain $_{SM}$ + Temp $_{SM}$ + Temp $_{SM}^2$	5	11.22	-7.71	7.91	0.01	-2.07
Temp $_{SM}$ + Temp $_{SM}^2$	4	9.47	-7.17	8.45	0.01	-1.79
Rain $_{SM}$ + Temp $_{SM}$	4	8.99	-6.20	9.42	0.01	-1.71
Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$	4	8.54	-5.29	10.32	0.00	-1.62
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$ + Temp $_{SM}^2$	6	11.33	-4.99	10.63	0.00	-2.08
Temp $_{SM}$	3	6.78	-4.73	10.89	0.00	-1.26
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$	5	9.60	-4.48	11.14	0.00	-1.82
Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$	5	9.51	-4.31	11.31	0.00	-1.80
Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	6	10.94	-4.21	11.41	0.00	-2.03
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	8	13.63	-3.70	11.92	0.00	-2.37
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$	5	9.12	-3.52	12.10	0.00	-1.73
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$	6	10.55	-3.44	12.18	0.00	-1.97
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$	7	12.00	-3.39	12.23	0.00	-2.18
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$	6	10.46	-3.25	12.37	0.00	-1.95
Temp $_{NM}$ + Temp $_{NM}^2$	4	7.48	-3.19	12.43	0.00	-1.41
Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	5	8.60	-2.49	13.13	0.00	-1.64
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	7	11.53	-2.45	13.17	0.00	-2.11
Rain $_{NB\ (t-1)}$	3	5.33	-1.83	13.79	0.00	-0.90
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	6	9.61	-1.55	14.07	0.00	-1.82
Rain $_{SM}$	3	5.17	-1.51	14.11	0.00	-0.86
Temp $_{NM}$	3	5.05	-1.26	14.36	0.00	-0.82
Rain $_{NM}$ + Temp $_{NM}$ + Temp $_{NM}^2$	5	7.56	-0.39	15.23	0.00	-1.43
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	7	10.47	-0.32	15.30	0.00	-1.96
Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$	4	5.99	-0.20	15.42	0.00	-1.07
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$	4	5.96	-0.15	15.47	0.00	-1.06
Temp $_{B}$ + Temp $_{B}^2$	4	5.90	-0.03	15.59	0.00	-1.05
Rain $_{B}$	3	4.38	0.08	15.70	0.00	-0.63
Rain $_{SM}$ + Rain $_{SM}^2$	4	5.71	0.37	15.99	0.00	-1.00
Temp $_{B}$	3	4.18	0.47	16.09	0.00	-0.58
Rain $_{NM}$ + Temp $_{NM}$	4	5.46	0.86	16.48	0.00	-0.93
Temp $_{NB\ (t-1)}$	3	3.93	0.97	16.58	0.00	-0.50
NULL	2	2.43	1.02	16.64	0.00	0.00
Rain $_{NM}$	3	3.68	1.48	17.10	0.00	-0.42
Rain $_{B}$ + Temp $_{B}$	4	5.15	1.48	17.10	0.00	-0.85
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Rain $_{NB\ (t-1)}$	5	6.62	1.49	17.11	0.00	-1.22

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	5	6.58	1.57	17.19	0.00	-1.21
$Rain_{B} + Temp_{B} + Temp_{B}^2$	5	6.49	1.74	17.36	0.00	-1.19
$Rain_{INLAND}$	3	3.26	2.31	17.93	0.00	-0.29
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	6	7.60	2.46	18.08	0.00	-1.44
$Rain_{INLAND} + Rain_{INLAND}^2$	4	4.51	2.76	18.38	0.00	-0.67
$Rain_{NB}$	3	3.02	2.79	18.41	0.00	-0.21
$Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	4	4.43	2.92	18.54	0.00	-0.65
$Rain_{B} + Rain_{B}^2$	4	4.41	2.95	18.57	0.00	-0.64
$Rain_{INLAND\ (t-1)} + Temp_{NB\ (t-1)}$	4	4.21	3.37	18.99	0.00	-0.58
$Rain_{INLAND\ (t-1)}$	3	2.64	3.55	19.17	0.00	-0.07
$Temp_{NB}$	3	2.44	3.96	19.58	0.00	0.00
$Temp_{NB} + Temp_{NB}^2$	4	3.79	4.21	19.83	0.00	-0.46
$Rain_{B} + Rain_{B}^2 + Temp_{B}$	5	5.15	4.43	20.04	0.00	-0.85
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	5.05	4.62	20.24	0.00	-0.83
$Rain_{B} + Rain_{B}^2 + Temp_{B} + Temp_{B}^2$	6	6.51	4.64	20.26	0.00	-1.20
$Rain_{INLAND} + Rain_{NB}$	4	3.54	4.71	20.32	0.00	-0.38
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB}$	5	4.96	4.81	20.43	0.00	-0.80
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2$	4	3.38	5.02	20.64	0.00	-0.33
$Rain_{INLAND} + Temp_{NB}$	4	3.32	5.15	20.77	0.00	-0.30
$Rain_{NB} + Rain_{NB}^2$	4	3.25	5.28	20.90	0.00	-0.28
$Rain_{INLAND\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	4.63	5.47	21.09	0.00	-0.71
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB}$	5	4.51	5.70	21.32	0.00	-0.67
$Rain_{NB} + Temp_{NB}$	4	3.03	5.73	21.35	0.00	-0.21
$Rain_{INLAND} + Temp_{NB} + Temp_{NB}^2$	5	4.48	5.77	21.39	0.00	-0.66
$Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	5	4.19	6.34	21.96	0.00	-0.58
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB} + Temp_{NB}^2$	6	5.61	6.46	22.08	0.00	-0.97
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	5.46	6.76	22.37	0.00	-0.93
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2$	5	3.90	6.93	22.55	0.00	-0.49
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2$	6	5.09	7.48	23.10	0.00	-0.84
$Rain_{INLAND} + Rain_{NB} + Temp_{NB}$	5	3.57	7.59	23.21	0.00	-0.39
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB}$	6	4.97	7.74	23.36	0.00	-0.80
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	5	3.25	8.22	23.84	0.00	-0.28
$Rain_{INLAND} + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	6	4.64	8.39	24.00	0.00	-0.71
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	7	5.94	8.74	24.35	0.00	-1.06
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	6	4.39	8.89	24.51	0.00	-0.64
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	6	4.04	9.59	25.21	0.00	-0.53
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	7	5.09	10.42	26.04	0.00	-0.84
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	8	6.40	10.76	26.37	0.00	-1.17
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	7	4.67	11.27	26.89	0.00	-0.72

Great knot

Model	K	logLik	BIC	ΔBIC	w	adjR^2
Rain $_{SM}$	3	6.42	-4.00	0.00	0.35	-1.49
Rain $_{B}$ + Temp $_{B}$	4	6.68	-1.58	2.42	0.10	-1.56
Rain $_{SM}$ + Temp $_{SM}$	4	6.52	-1.26	2.74	0.09	-1.52
Rain $_{SM}$ + Rain $_{SM}^2$	4	6.50	-1.23	2.77	0.09	-1.52
Rain $_{SM}$ + Temp $_{SM}$ + Temp $_{SM}^2$	5	7.32	0.08	4.08	0.05	-1.73
Temp $_{B}$	3	4.04	0.75	4.75	0.03	-0.76
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$	5	6.73	1.27	5.26	0.02	-1.58
Rain $_{B}$ + Rain $_{B}^2$ + Temp $_{B}$	5	6.71	1.30	5.29	0.02	-1.57
Rain $_{B}$ + Temp $_{B}$ + Temp $_{B}^2$	5	6.71	1.30	5.29	0.02	-1.57
NULL	2	2.08	1.72	5.72	0.02	0.00
Rain $_{INLAND\ (t-1)}$	3	3.50	1.84	5.83	0.02	-0.57
Rain $_{NB}$	3	3.33	2.17	6.17	0.02	-0.50
Temp $_{NB\ (t-1)}$	3	3.28	2.27	6.27	0.02	-0.48
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$ + Temp $_{SM}^2$	6	7.53	2.60	6.60	0.01	-1.78
Rain $_{B}$	3	3.03	2.77	6.77	0.01	-0.39
Temp $_{B}$ + Temp $_{B}^2$	4	4.34	3.09	7.09	0.01	-0.86
Rain $_{INLAND\ (t-1)}$ + Temp $_{NB\ (t-1)}$	4	4.05	3.68	7.67	0.01	-0.76
Rain $_{INLAND}$ + Rain $_{NB}$	4	3.87	4.05	8.04	0.01	-0.70
Temp $_{NB}$	3	2.36	4.12	8.12	0.01	-0.12
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$	4	3.79	4.19	8.19	0.01	-0.67
Rain $_{B}$ + Rain $_{B}^2$ + Temp $_{B}$ + Temp $_{B}^2$	6	6.73	4.20	8.20	0.01	-1.58
Temp $_{SM}$	3	2.31	4.21	8.21	0.01	-0.10
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$	4	3.76	4.25	8.25	0.01	-0.66
Rain $_{NM}$	3	2.28	4.28	8.28	0.01	-0.08
Rain $_{INLAND}$	3	2.25	4.34	8.34	0.01	-0.07
Rain $_{NB\ (t-1)}$	3	2.15	4.54	8.54	0.00	-0.03
Temp $_{NM}$	3	2.09	4.66	8.66	0.00	0.00
Rain $_{NB}$ + Rain $_{NB}^2$	4	3.46	4.86	8.86	0.00	-0.55
Rain $_{NB}$ + Temp $_{NB}$	4	3.39	4.99	8.99	0.00	-0.53
Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	4	3.37	5.04	9.04	0.00	-0.52
Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$	4	3.28	5.21	9.21	0.00	-0.48
Rain $_{B}$ + Rain $_{B}^2$	4	3.27	5.25	9.25	0.00	-0.48
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$	5	4.54	5.65	9.65	0.00	-0.93
Rain $_{INLAND\ (t-1)}$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	5	4.31	6.11	10.11	0.00	-0.85
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$	5	4.13	6.47	10.47	0.00	-0.79
Rain $_{INLAND}$ + Rain $_{INLAND}^2$	4	2.60	6.57	10.57	0.00	-0.22
Rain $_{INLAND}$ + Rain $_{NB}$ + Rain $_{NB}^2$	5	4.07	6.58	10.58	0.00	-0.77
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$	5	4.07	6.59	10.59	0.00	-0.77
Temp $_{SM}$ + Temp $_{SM}^2$	4	2.56	6.66	10.66	0.00	-0.20
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Rain $_{NB\ (t-1)}$	5	4.01	6.70	10.70	0.00	-0.75
Temp $_{NB}$ + Temp $_{NB}^2$	4	2.53	6.72	10.72	0.00	-0.19

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Rain_{NM} + Rain_{NM}^2$	4	2.49	6.79	10.79	0.00	-0.17
$Rain_{INLAND} + Temp_{NB}$	4	2.45	6.88	10.88	0.00	-0.15
$Temp_{NM} + Temp_{NM}^2$	4	2.44	6.89	10.89	0.00	-0.15
$Rain_{INLAND} + Rain_{NB} + Temp_{NB}$	5	3.87	6.99	10.99	0.00	-0.70
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	5	3.85	7.03	11.03	0.00	-0.69
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	5	3.81	7.11	11.11	0.00	-0.68
$Rain_{NM} + Temp_{NM}$	4	2.28	7.22	11.22	0.00	-0.08
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	4	2.15	7.47	11.47	0.00	-0.03
$Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	5	3.41	7.90	11.90	0.00	-0.53
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	3.39	7.95	11.95	0.00	-0.52
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	3.38	7.97	11.97	0.00	-0.52
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	4.81	8.04	12.04	0.00	-1.02
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	6	4.55	8.56	12.56	0.00	-0.93
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	4.39	8.88	12.88	0.00	-0.88
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2$	6	4.33	9.00	13.00	0.00	-0.86
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB}$	5	2.81	9.11	13.11	0.00	-0.30
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	6	4.25	9.17	13.16	0.00	-0.83
$Rain_{NM} + Temp_{NM} + Temp_{NM}^2$	5	2.75	9.22	13.22	0.00	-0.28
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	6	4.19	9.29	13.29	0.00	-0.81
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	6	4.18	9.30	13.30	0.00	-0.81
$Rain_{INLAND} + Temp_{NB} + Temp_{NB}^2$	5	2.65	9.42	13.41	0.00	-0.24
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB}$	6	4.07	9.53	13.53	0.00	-0.77
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	6	4.01	9.64	13.64	0.00	-0.75
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM}$	5	2.51	9.70	13.70	0.00	-0.18
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	3.92	9.82	13.82	0.00	-0.72
$Rain_{INLAND} + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	6	3.89	9.89	13.89	0.00	-0.71
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	5.14	10.32	14.32	0.00	-1.12
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	4.84	10.94	14.94	0.00	-1.03
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	7	4.59	11.43	15.42	0.00	-0.95
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	7	4.56	11.49	15.49	0.00	-0.94
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB} + Temp_{NB}^2$	6	3.06	11.54	15.54	0.00	-0.40
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	7	4.51	11.60	15.60	0.00	-0.92
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM} + Temp_{NM}^2$	6	2.98	11.71	15.71	0.00	-0.37
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	7	4.11	12.40	16.39	0.00	-0.78
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	8	5.30	12.96	16.96	0.00	-1.17
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	8	4.88	13.81	17.80	0.00	-1.04

Grey-tailed tattler

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Temp_{B} + Temp_{B}^2$	4	7.10	-2.41	0.00	0.25	-1.24
$Rain_{B} + Temp_{B} + Temp_{B}^2$	5	8.18	-1.64	0.77	0.17	-1.45
$Rain_{B}$	3	4.43	-0.03	2.39	0.08	-0.58
$Rain_{B} + Rain_{B}^2 + Temp_{B} + Temp_{B}^2$	6	8.58	0.50	2.91	0.06	-1.53
NULL	2	2.55	0.79	3.20	0.05	0.00
$Rain_{SM}$	3	3.81	1.22	3.63	0.04	-0.40
$Rain_{SM} + Temp_{SM} + Temp_{SM}^2$	5	6.38	1.95	4.37	0.03	-1.08
$Rain_{NB\ (t-1)}$	3	3.00	2.83	5.24	0.02	-0.15
$Rain_{B} + Temp_{B}$	4	4.46	2.85	5.26	0.02	-0.59
$Rain_{B} + Rain_{B}^2$	4	4.43	2.92	5.33	0.02	-0.58
$Rain_{INLAND}$	3	2.87	3.10	5.52	0.02	-0.11
$Temp_{NB\ (t-1)}$	3	2.82	3.20	5.61	0.02	-0.09
$Temp_{NM}$	3	2.75	3.33	5.74	0.01	-0.07
$Rain_{NB}$	3	2.61	3.61	6.03	0.01	-0.02
$Temp_{B}$	3	2.61	3.62	6.03	0.01	-0.02
$Rain_{NM}$	3	2.57	3.69	6.11	0.01	-0.01
$Rain_{INLAND\ (t-1)}$	3	2.56	3.71	6.12	0.01	-0.01
$Temp_{SM}$	3	2.56	3.72	6.13	0.01	0.00
$Temp_{NB}$	3	2.55	3.73	6.14	0.01	0.00
$Rain_{NM} + Rain_{NM}^2$	4	3.88	4.01	6.43	0.01	-0.43
$Rain_{SM} + Temp_{SM}$	4	3.86	4.05	6.46	0.01	-0.42
$Rain_{SM} + Rain_{SM}^2$	4	3.85	4.08	6.49	0.01	-0.42
$Rain_{SM} + Rain_{SM}^2 + Temp_{SM} + Temp_{SM}^2$	6	6.68	4.30	6.71	0.01	-1.15
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	6	6.47	4.72	7.14	0.01	-1.10
$Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	4	3.50	4.78	7.19	0.01	-0.31
$Temp_{SM} + Temp_{SM}^2$	4	3.38	5.02	7.43	0.01	-0.27
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	7	7.79	5.04	7.45	0.01	-1.38
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	4	3.20	5.38	7.79	0.01	-0.22
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)}$	4	3.14	5.50	7.91	0.00	-0.20
$Temp_{NB} + Temp_{NB}^2$	4	3.09	5.60	8.01	0.00	-0.18
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	4	3.06	5.66	8.08	0.00	-0.17
$Rain_{INLAND} + Rain_{INLAND}^2$	4	3.01	5.77	8.18	0.00	-0.15
$Rain_{B} + Rain_{B}^2 + Temp_{B}$	5	4.47	5.78	8.19	0.00	-0.60
$Rain_{INLAND} + Rain_{NB}$	4	2.87	6.03	8.44	0.00	-0.11
$Rain_{INLAND} + Temp_{NB}$	4	2.87	6.04	8.45	0.00	-0.11
$Rain_{INLAND\ (t-1)} + Temp_{NB\ (t-1)}$	4	2.82	6.14	8.55	0.00	-0.09
$Temp_{NM} + Temp_{NM}^2$	4	2.80	6.19	8.60	0.00	-0.08
$Rain_{NM} + Temp_{NM}$	4	2.76	6.25	8.66	0.00	-0.07
$Rain_{NB} + Rain_{NB}^2$	4	2.68	6.43	8.84	0.00	-0.04
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2$	4	2.67	6.44	8.85	0.00	-0.04
$Rain_{NB} + Temp_{NB}$	4	2.62	6.55	8.96	0.00	-0.02

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM}$	5	3.99	6.74	9.15	0.00	-0.46
$Rain_{SM} + Rain_{SM}^2 + Temp_{SM}$	5	3.90	6.92	9.33	0.00	-0.43
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	3.83	7.07	9.48	0.00	-0.41
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	8	8.03	7.49	9.90	0.00	-1.43
$Rain_{INLAND} + Temp_{NB} + Temp_{NB}^2$	5	3.61	7.51	9.92	0.00	-0.34
$Rain_{INLAND\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	3.51	7.71	10.12	0.00	-0.31
$Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	5	3.44	7.83	10.25	0.00	-0.29
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	5	3.24	8.24	10.65	0.00	-0.23
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	4.69	8.28	10.70	0.00	-0.66
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)}$	5	3.21	8.31	10.72	0.00	-0.22
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	3.20	8.32	10.73	0.00	-0.22
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	5	3.17	8.38	10.79	0.00	-0.21
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB}$	5	3.03	8.67	11.08	0.00	-0.16
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB}$	5	3.01	8.71	11.12	0.00	-0.15
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	2.98	8.76	11.17	0.00	-0.15
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2$	5	2.92	8.88	11.29	0.00	-0.13
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM} + Temp_{NM}^2$	6	4.36	8.95	11.36	0.00	-0.56
$Rain_{INLAND} + Rain_{NB} + Temp_{NB}$	5	2.88	8.97	11.38	0.00	-0.11
$Rain_{NM} + Temp_{NM} + Temp_{NM}^2$	5	2.80	9.12	11.53	0.00	-0.09
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	5	2.68	9.36	11.78	0.00	-0.04
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB} + Temp_{NB}^2$	6	3.93	9.80	12.21	0.00	-0.44
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	3.86	9.94	12.36	0.00	-0.42
$Rain_{INLAND} + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	6	3.79	10.10	12.51	0.00	-0.40
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	3.62	10.43	12.84	0.00	-0.35
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	6	3.34	10.99	13.40	0.00	-0.26
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	6	3.28	11.11	13.52	0.00	-0.24
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	4.73	11.15	13.56	0.00	-0.67
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	6	3.25	11.18	13.59	0.00	-0.23
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2$	6	3.06	11.56	13.97	0.00	-0.17
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB}$	6	3.03	11.61	14.02	0.00	-0.16
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	6	2.97	11.73	14.15	0.00	-0.14
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	7	4.31	12.00	14.41	0.00	-0.55
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	3.93	12.75	15.16	0.00	-0.44
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	8	5.09	13.38	15.79	0.00	-0.76
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	7	3.36	13.89	16.31	0.00	-0.27
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	7	3.06	14.49	16.90	0.00	-0.17

Lesser sand plover

Model	K	logLik	BIC	ΔBIC	w	adjR^2
Rain $_{SM}$ + Temp $_{SM}$	4	-2.93	17.64	0.00	0.10	0.74
Rain $_{SM}$	3	-4.42	17.67	0.03	0.10	0.58
Rain $_{INLAND}$ + Rain $_{NB}$ + Rain $_{NB}^2$	5	-1.49	17.71	0.07	0.10	0.88
Rain $_{INLAND}$ + Rain $_{NB}$	4	-3.02	17.82	0.18	0.09	0.73
Rain $_{INLAND}$ + Rain $_{NB}$ + Temp $_{NB}$ + Temp $_{NB}^2$	6	-0.49	18.64	1.00	0.06	0.96
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$	5	-2.05	18.82	1.17	0.06	0.83
Rain $_{INLAND}$ + Rain $_{NB}$ + Temp $_{NB}$	5	-2.18	19.08	1.44	0.05	0.82
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$ + Rain $_{NB}^2$	6	-0.85	19.37	1.73	0.04	0.93
Rain $_{SM}$ + Temp $_{SM}$ + Temp $_{SM}^2$	5	-2.44	19.60	1.96	0.04	0.79
Rain $_{INLAND}$	3	-5.64	20.11	2.47	0.03	0.42
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$ + Temp $_{NB}$ + Temp $_{NB}^2$	7	0.21	20.20	2.56	0.03	1.02
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$ + Temp $_{NB}$	6	-1.29	20.24	2.60	0.03	0.90
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$	5	-2.76	20.24	2.60	0.03	0.76
Rain $_{SM}$ + Rain $_{SM}^2$	4	-4.30	20.38	2.74	0.03	0.59
Rain $_{INLAND}$ + Rain $_{NB}$ + Rain $_{NB}^2$ + Temp $_{NB}$	6	-1.49	20.64	3.00	0.02	0.88
Rain $_{INLAND}$ + Rain $_{NB}$ + Rain $_{NB}^2$ + Temp $_{NB}$ + Temp $_{NB}^2$	7	-0.48	21.58	3.94	0.01	0.96
Rain $_{INLAND\ (t-1)}$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	5	-3.55	21.82	4.17	0.01	0.68
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$ + Temp $_{SM}^2$	6	-2.08	21.83	4.19	0.01	0.83
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$ + Rain $_{NB}^2$ + Temp $_{NB}$	7	-0.83	22.27	4.62	0.01	0.94
NULL	2	-8.34	22.56	4.92	0.01	0.00
Rain $_{INLAND}$ + Rain $_{INLAND}^2$	4	-5.44	22.66	5.02	0.01	0.45
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	6	-2.50	22.67	5.03	0.01	0.79
Rain $_{INLAND}$ + Temp $_{NB}$ + Temp $_{NB}^2$	5	-4.05	22.82	5.18	0.01	0.62
Rain $_{INLAND}$ + Temp $_{NB}$	4	-5.64	23.05	5.41	0.01	0.42
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$ + Rain $_{NB}^2$ + Temp $_{NB}$ + Temp $_{NB}^2$	8	0.24	23.08	5.44	0.01	1.02
Temp $_{SM}$	3	-7.27	23.37	5.73	0.01	0.18
Rain $_{INLAND\ (t-1)}$ + Temp $_{NB\ (t-1)}$	4	-5.88	23.53	5.89	0.01	0.39
Temp $_{SM}$ + Temp $_{SM}^2$	4	-5.94	23.66	6.02	0.01	0.38
Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	4	-5.98	23.75	6.10	0.00	0.38
Temp $_{NB\ (t-1)}$	3	-7.58	23.98	6.34	0.00	0.13
Rain $_{NB}$	3	-7.59	24.02	6.37	0.00	0.13
Rain $_{INLAND\ (t-1)}$ + Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	6	-3.29	24.25	6.61	0.00	0.71
Rain $_{INLAND\ (t-1)}$	3	-7.73	24.28	6.64	0.00	0.11
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$	4	-6.45	24.67	7.03	0.00	0.31
Rain $_{NB}$ + Rain $_{NB}^2$	4	-6.48	24.73	7.09	0.00	0.30
Rain $_{NM}$	3	-7.98	24.80	7.16	0.00	0.06
Rain $_{B}$	3	-7.99	24.82	7.18	0.00	0.06
Rain $_{INLAND\ (t-1)}$ + Rain $_{INLAND\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$	5	-5.11	24.94	7.30	0.00	0.49
Rain $_{NB\ (t-1)}$	3	-8.06	24.95	7.30	0.00	0.05

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Temp_{NM}$	3	-8.08	24.98	7.34	0.00	0.05
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	-2.29	25.19	7.55	0.00	0.81
$Temp_{B}$	3	-8.24	25.31	7.67	0.00	0.02
$Temp_{NB}$	3	-8.34	25.50	7.86	0.00	0.00
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB} + Temp_{NB}^2$	6	-3.94	25.55	7.91	0.00	0.63
$Rain_{INLAND} + Rain_{INLAND}^2 + Temp_{NB}$	5	-5.44	25.60	7.96	0.00	0.45
$Rain_{B} + Rain_{B}^2$	4	-7.01	25.80	8.16	0.00	0.22
$Temp_{NB} + Temp_{NB}^2$	4	-7.06	25.89	8.25	0.00	0.22
$Rain_{NM} + Rain_{NM}^2$	4	-7.29	26.36	8.72	0.00	0.18
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	5	-5.86	26.45	8.81	0.00	0.39
$Rain_{NB} + Temp_{NB}$	4	-7.37	26.52	8.87	0.00	0.17
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	5	-5.97	26.66	9.01	0.00	0.38
$Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	4	-7.46	26.70	9.06	0.00	0.15
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	4	-7.47	26.73	9.08	0.00	0.15
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	-3.10	26.81	9.16	0.00	0.73
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)}$	4	-7.58	26.93	9.29	0.00	0.13
$Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	5	-6.17	27.06	9.41	0.00	0.35
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	6	-4.80	27.27	9.62	0.00	0.53
$Rain_{B} + Temp_{B}$	4	-7.75	27.28	9.64	0.00	0.10
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)}$	5	-6.31	27.33	9.69	0.00	0.33
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	5	-6.35	27.42	9.78	0.00	0.32
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	7	-3.46	27.52	9.88	0.00	0.69
$Rain_{NM} + Temp_{NM}$	4	-7.94	27.66	10.01	0.00	0.07
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	6	-5.07	27.81	10.16	0.00	0.50
$Temp_{NM} + Temp_{NM}^2$	4	-8.02	27.82	10.18	0.00	0.06
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	6	-5.11	27.88	10.24	0.00	0.49
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	-6.66	28.05	10.41	0.00	0.28
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	8	-2.27	28.10	10.46	0.00	0.81
$Temp_{B} + Temp_{B}^2$	4	-8.23	28.25	10.60	0.00	0.02
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	5	-6.99	28.70	11.06	0.00	0.23
$Rain_{B} + Rain_{B}^2 + Temp_{B}$	5	-6.99	28.71	11.07	0.00	0.23
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM}$	5	-7.21	29.14	11.50	0.00	0.19
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	-5.95	29.56	11.92	0.00	0.38
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	6	-6.02	29.71	12.07	0.00	0.37
$Rain_{B} + Temp_{B} + Temp_{B}^2$	5	-7.74	30.21	12.57	0.00	0.10
$Rain_{NM} + Temp_{NM} + Temp_{NM}^2$	5	-7.92	30.56	12.92	0.00	0.07
$Rain_{B} + Rain_{B}^2 + Temp_{B} + Temp_{B}^2$	6	-6.95	31.56	13.92	0.00	0.23
$Rain_{NM} + Rain_{NM}^2 + Temp_{NM} + Temp_{NM}^2$	6	-7.19	32.06	14.41	0.00	0.19

Red knot

Model	K	logLik	BIC	ΔBIC	w	adjR^2
Rain $_{B}$ + Rain $_{B}^2$ + Temp $_{B}$	5	-13.83	42.11	0.00	0.56	0.70
Rain $_{B}$ + Rain $_{B}^2$ + Temp $_{B}$ + Temp $_{B}^2$	6	-13.45	44.25	2.14	0.19	0.71
Temp $_{B}$	3	-19.45	47.57	5.47	0.04	0.36
Rain $_{NM}$ + Rain $_{NM}^2$ + Temp $_{NM}$	5	-16.61	47.67	5.56	0.03	0.56
Rain $_{SM}$ + Rain $_{SM}^2$	4	-18.50	48.57	6.46	0.02	0.43
Rain $_{B}$ + Temp $_{B}$	4	-18.69	48.95	6.84	0.02	0.42
Rain $_{NM}$ + Rain $_{NM}^2$ + Temp $_{NM}$ + Temp $_{NM}^2$	6	-16.08	49.49	7.39	0.01	0.59
Rain $_{NM}$ + Temp $_{NM}$	4	-19.29	50.15	8.04	0.01	0.37
Temp $_{B}$ + Temp $_{B}^2$	4	-19.33	50.21	8.10	0.01	0.37
Rain $_{NM}$ + Temp $_{NM}$ + Temp $_{NM}^2$	5	-18.01	50.46	8.36	0.01	0.47
Rain $_{INLAND}$ + Rain $_{INLAND}^2$	4	-19.66	50.89	8.78	0.01	0.34
Rain $_{NM}$	3	-21.22	51.11	9.01	0.01	0.20
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$	5	-18.43	51.31	9.20	0.01	0.44
Rain $_{B}$ + Temp $_{B}$ + Temp $_{B}^2$	5	-18.57	51.59	9.49	0.00	0.43
Rain $_{B}$	3	-21.47	51.60	9.49	0.00	0.18
Temp $_{NB}$ + Temp $_{NB}^2$	4	-20.07	51.71	9.60	0.00	0.31
Rain $_{SM}$ + Rain $_{SM}^2$ + Temp $_{SM}$ + Temp $_{SM}^2$	6	-17.28	51.91	9.80	0.00	0.52
NULL	2	-23.09	51.96	9.85	0.00	0.00
Rain $_{NM}$ + Rain $_{NM}^2$	4	-20.59	52.75	10.64	0.00	0.26
Rain $_{NB}$	3	-22.10	52.86	10.76	0.00	0.11
Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	4	-20.76	53.09	10.98	0.00	0.25
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Temp $_{NB}$ + Temp $_{NB}^2$	6	-18.09	53.52	11.41	0.00	0.46
Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$	4	-20.99	53.54	11.43	0.00	0.23
Temp $_{NB\ (t-1)}$	3	-22.44	53.54	11.44	0.00	0.08
Rain $_{SM}$	3	-22.50	53.68	11.57	0.00	0.07
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$	5	-19.62	53.70	11.59	0.00	0.35
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Temp $_{NB}$	5	-19.66	53.78	11.67	0.00	0.34
Rain $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	5	-19.74	53.93	11.82	0.00	0.34
Rain $_{NB}$ + Temp $_{NB}$ + Temp $_{NB}^2$	5	-19.80	54.05	11.95	0.00	0.33
Rain $_{INLAND}$	3	-22.70	54.08	11.97	0.00	0.05
Temp $_{NB}$	3	-22.71	54.09	11.98	0.00	0.05
Rain $_{B}$ + Rain $_{B}^2$	4	-21.30	54.16	12.05	0.00	0.20
Rain $_{INLAND\ (t-1)}$	3	-22.85	54.36	12.26	0.00	0.03
Rain $_{INLAND}$ + Temp $_{NB}$ + Temp $_{NB}^2$	5	-19.99	54.43	12.33	0.00	0.32
Temp $_{NM}$	3	-23.04	54.75	12.65	0.00	0.01
Temp $_{SM}$	3	-23.08	54.82	12.71	0.00	0.00
Rain $_{NB\ (t-1)}$	3	-23.08	54.83	12.73	0.00	0.00
Rain $_{NB}$ + Rain $_{NB}^2$	4	-21.64	54.85	12.74	0.00	0.16
Rain $_{NB\ (t-1)}$ + Rain $_{NB\ (t-1)}^2$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	6	-18.85	55.05	12.94	0.00	0.41
Rain $_{INLAND}$ + Rain $_{INLAND}^2$ + Rain $_{NB}$ + Temp $_{NB}$ + Temp $_{NB}^2$	7	-17.59	55.40	13.30	0.00	0.50
Rain $_{INLAND\ (t-1)}$ + Temp $_{NB\ (t-1)}$ + Temp $_{NB\ (t-1)}^2$	5	-20.52	55.50	13.39	0.00	0.27

Model	K	logLik	BIC	ΔBIC	w	adjR^2
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2$	4	-22.01	55.59	13.48	0.00	0.12
$Rain_{NB} + Temp_{NB}$	4	-22.08	55.72	13.62	0.00	0.12
$Rain_{INLAND} + Rain_{NB}$	4	-22.09	55.75	13.64	0.00	0.11
$Temp_{SM} + Temp_{SM}^2$	4	-22.12	55.79	13.69	0.00	0.11
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	-19.40	56.14	14.03	0.00	0.36
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	-20.85	56.14	14.04	0.00	0.24
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	5	-20.86	56.18	14.07	0.00	0.24
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2$	6	-19.42	56.19	14.08	0.00	0.36
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	6	-19.43	56.20	14.09	0.00	0.36
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	6	-19.43	56.20	14.09	0.00	0.36
$Rain_{INLAND\ (t-1)} + Temp_{NB\ (t-1)}$	4	-22.39	56.35	14.24	0.00	0.08
$Rain_{SM} + Temp_{SM}$	4	-22.45	56.46	14.36	0.00	0.07
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Temp_{NB}$	6	-19.62	56.58	14.47	0.00	0.35
$Rain_{INLAND} + Temp_{NB}$	4	-22.51	56.59	14.48	0.00	0.07
$Rain_{INLAND} + Rain_{NB} + Temp_{NB} + Temp_{NB}^2$	6	-19.78	56.90	14.80	0.00	0.33
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)}$	4	-22.77	57.11	15.00	0.00	0.04
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	8	-17.03	57.19	15.08	0.00	0.53
$Temp_{NM} + Temp_{NM}^2$	4	-22.82	57.20	15.09	0.00	0.03
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Temp_{NB\ (t-1)}$	5	-21.45	57.35	15.24	0.00	0.18
$Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	5	-21.45	57.35	15.25	0.00	0.18
$Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	4	-22.94	57.43	15.32	0.00	0.02
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2$	5	-21.64	57.73	15.63	0.00	0.16
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	-18.83	57.89	15.78	0.00	0.41
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	7	-18.84	57.92	15.81	0.00	0.41
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Temp_{NB\ (t-1)}$	6	-20.49	58.31	16.21	0.00	0.27
$Rain_{SM} + Temp_{SM} + Temp_{SM}^2$	5	-21.93	58.32	16.21	0.00	0.13
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	6	-20.52	58.39	16.28	0.00	0.27
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)}$	5	-22.01	58.48	16.37	0.00	0.12
$Rain_{INLAND} + Rain_{INLAND}^2 + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	7	-19.17	58.58	16.47	0.00	0.38
$Rain_{INLAND} + Rain_{NB} + Temp_{NB}$	5	-22.08	58.61	16.50	0.00	0.12
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)} + Temp_{NB\ (t-1)}^2$	8	-17.82	58.77	16.67	0.00	0.48
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB} + Temp_{NB}^2$	7	-19.35	58.94	16.84	0.00	0.37
$Rain_{INLAND\ (t-1)} + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	5	-22.75	59.95	17.84	0.00	0.04
$Rain_{INLAND} + Rain_{NB} + Rain_{NB}^2 + Temp_{NB}$	6	-21.45	60.23	18.13	0.00	0.18
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2 + Temp_{NB\ (t-1)}$	7	-20.19	60.62	18.51	0.00	0.30
$Rain_{INLAND\ (t-1)} + Rain_{INLAND\ (t-1)}^2 + Rain_{NB\ (t-1)} + Rain_{NB\ (t-1)}^2$	6	-22.00	61.33	19.23	0.00	0.12

8.5 Appendix S.2.5

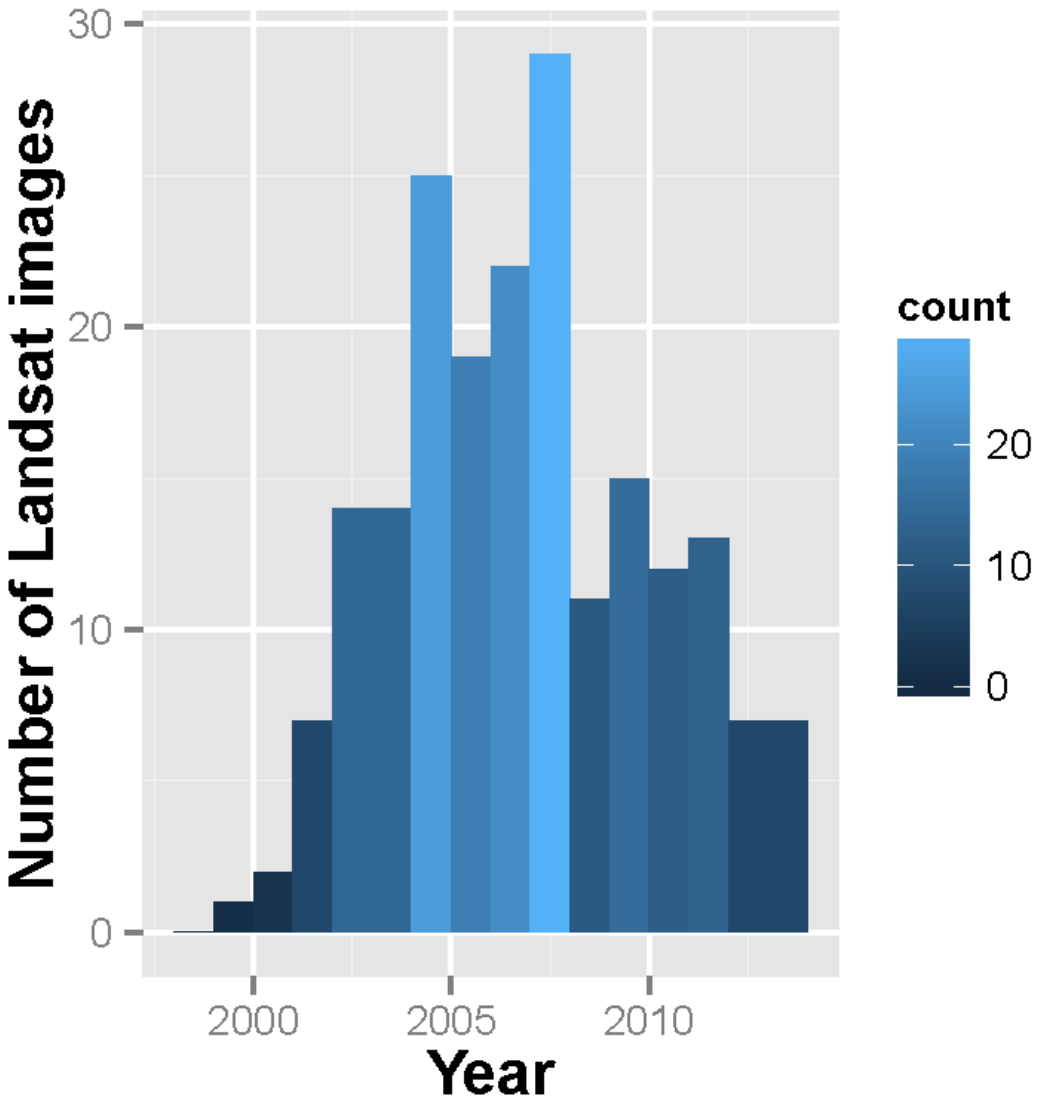
Average parameter estimates and standard errors (in brackets) for each model subset for each migratory stage and each species.

	bar-tailed godwit	curlew sandpiper	eastern curlew	great knot	grey-tailed tattler	lesser sand plover	red knot
Intercept	-0.03 (0.04)	-0.17 (0.09)	-0.05 (0.06)	-0.05 (0.06)	-0.05 (0.05)	-0.27 (0.09)	-0.47 (0.19)
Rain $_{INLAND(t-1)}$	0.14 (0.15)	-0.55 (0.31)	0.13 (0.17)	0.24 (0.2)	0.02 (0.19)	0.41 (0.29)	0.04 (0.85)
Rain $_{INLAND(t-1)}{}^{2}$	-0.08 (0.38)	0.1 (0.3)	0.49 (0.38)	0.29 (0.43)	0.16 (0.42)	0.77 (0.66)	1.58 (1.55)
Rain $_{NB(t-1)}$	0.03 (0.17)	0.74 (0.52)	0.5 (0.2)	0.07 (0.23)	0.17 (0.22)	-0.01 (0.39)	-0.69 (0.77)
Rain $_{NB(t-1)}{}^{2}$	0.41 (0.64)	0.14 (0.34)	0.99 (0.73)	-0.25 (0.89)	-0.93 (0.92)	0.68 (1.55)	-1.74 (3.78)
Temp $_{NB(t-1)}$	0.04 (0.18)	0.1 (0.3)	0.39 (0.17)	-0.27 (0.24)	-0.16 (0.24)	0.47 (0.34)	-1.21 (0.8)
Temp $_{NB(t-1)}{}^{2}$	-0.07 (0.62)	-0.32 (1.12)	-0.64 (0.7)	0.44 (0.89)	0.38 (0.98)	1.67 (0.94)	2.71 (1.89)
Intercept	-0.01 (0.05)	-0.2 (0.08)	0.02 (0.04)	-0.05 (0.06)	-0.06 (0.06)	-0.24 (0.07)	-0.09 (0.28)
Rain $_{NM}$	-0.39 (0.33)	-0.04 (0.82)	-0.47 (0.18)	0.16 (0.27)	0.01 (0.25)	0.41 (0.66)	1.61 (0.63)
Rain $_{NM}{}^{2}$	1.68 (2.83)	2.34 (5.87)	-4.22 (0.88)	0.59 (1.05)	1.76 (1.26)	3.64 (3.59)	-2.7 (1.5)
Temp $_{NM}$	-3.25 (17.73)	12.22 (46.06)	-2.05 (16.22)	0.72 (23.64)	13.12 (25.4)	17.16 (34.72)	-179.08 (81.97)
Temp $_{NM}{}^{2}$	-17301.45 (9325.44)	-11679.43 (23448.11)	-407.42 (7837.31)	-6223.73 (8348.08)	-2531.65 (7910.79)	2539.38 (11659.66)	-41834.59 (43016.98)
Intercept	-0.03 (0.04)	-0.2 (0.08)	-0.08 (0.07)	-0.04 (0.05)	-0.14 (0.09)	-0.24 (0.08)	0.1 (0.24)
Rain $_{B}$	-0.16 (0.26)	0.21 (0.45)	-0.41 (0.3)	-0.6 (0.32)	-0.49 (0.39)	-0.21 (1.01)	-4.59 (1.6)
Rain $_{B}{}^{2}$	0.16 (0.96)	0.23 (2.06)	0.17 (1.11)	-0.12 (1.01)	-0.79 (1.6)	3.06 (2.62)	-13.77 (4.83)

Temp $_{B}$	-3.68 (10.58)	-5.98 (20.71)	33.98 (20.87)	31.87 (13.94)	-22.28 (16.77)	27.01 (67.59)	179.32 (53.08)
Temp $_{B}{}^{2}$	-2147.47 (1893.36)	2833.16 (4227.31)	-14414.96 (9308.11)	1102.29 (3533.59)	11255.37 (4251.72)	1686.45 (37482.58)	10781.95 (17175.18)
Intercept	-0.03 (0.04)	-0.19 (0.08)	0 (0.06)	-0.03 (0.05)	-0.03 (0.06)	-0.16 (0.07)	-0.59 (0.18)
Rain $_{SM}$	-0.22 (0.25)	-0.95 (0.74)	-0.35 (0.24)	1.11 (0.39)	0.55 (0.35)	0.52 (0.2)	-3.14 (1.38)
Rain $_{SM}{}^{2}$	1.27 (1.96)	1.6 (7.3)	-0.7 (1.71)	-1.74 (4.27)	0.66 (1.71)	0.19 (0.38)	18.45 (6.96)
Temp $_{SM}$	44.58 (33.45)	-54.44 (85.71)	-121.12 (40.75)	-1.43 (40.6)	-3.21 (28.46)	-43.54 (31.02)	3.98 (144.42)
Temp $_{SM}{}^{2}$	-18932.01 (21716.34)	33775.31 (69204.42)	-41124.27 (21611.14)	-17560.94 (17017.16)	-18016.78 (10124.08)	-15630.15 (17561.59)	172135.21 (144998.2)
Intercept	-0.04 (0.04)	-0.19 (0.09)	-0.1 (0.06)	-0.05 (0.06)	-0.04 (0.06)	-0.15 (0.09)	-0.51 (0.18)
Rain $_{INLAND}$	0 (0.14)	0.37 (0.37)	-0.11 (0.17)	0.12 (0.21)	-0.1 (0.17)	0.81 (0.29)	-0.97 (1.05)
Rain $_{INLAND}{}^{2}$	-0.1 (0.32)	0.65 (0.93)	-0.47 (0.35)	0.28 (0.46)	-0.17 (0.37)	-0.59 (0.61)	4.26 (2.15)
Rain $_{NB}$	0.09 (0.14)	-0.48 (0.33)	0.14 (0.2)	0.21 (0.18)	-0.1 (0.26)	0.49 (0.26)	0.1 (0.92)
Rain $_{NB}{}^{2}$	-0.05 (0.35)	0.76 (0.55)	0.19 (0.5)	0.25 (0.43)	1.04 (0.77)	0.52 (0.53)	0.19 (2.17)
Temp $_{NB}$	-0.23 (0.15)	0.06 (0.34)	-0.01 (0.21)	-0.11 (0.22)	-0.03 (0.21)	0.05 (0.34)	-0.47 (1.14)
Temp $_{NB}{}^{2}$	0.25 (0.45)	-0.54 (1.4)	0.81 (0.63)	0.11 (0.73)	-1.59 (1.12)	1.05 (0.77)	5.22 (3.1)

8.6 Appendix S.3.1

Number of Landsat images between 1999 and 2014 used to produce map of intertidal habitats in Australia.



8.7 Appendix S.3.2

Confusion matrix for mapping of Australian intertidal habitats. The matrix compares 204 randomly stratified points from the reference and mapped data, in the columns and rows respectively. The proportion of correctly allocated cases indicates the overall classification accuracy.

		Reference			**User's Accuracy**
		Intertidal Flat	Other	Sum	
Mapped	Intertidal Flat	102	0	102	100.0%
	Other	9	93	102	91.2%
	Sum	111	93	204	
Producer's accuracy		91.9%	100.0%		
Overall accuracy		**95.6%**			

8.8 Appendix S.4.1

Optimization model parameter inputs: species, cost and disturbance rate

	Wellington Point	Bell's Creek	Buckley's Hole	Caloundra Bar	Kakadu Beach	Manly Harbour	Sandbank Caloundra	Thorneside	Toorbul	Wickham Point
Bar-tailed godwit* *Limosa lapponica*	145	16	247	60	1031	720	34	96	763	0
Black-tailed godwit* *Limosa limosa*	0	0	4	0	20	47	0	5	15	0
Black-winged stilt* *Himantopus himantopus*	4	8	4	0	29	30	0	43	61	2
Curlew sandpiper* *Calidris ferruginea*	0	0	20	24	14	51	10	7	12	0
Eastern curlew* *Numenius madagascariensis*	3	3	1	17	19	44	13	2	62	0
Great knot* *Calidris tenuirostris*	21	0	192	0	79	47	0	13	148	0
Greater sand plover* *Charadrius leschenaultia*	0	0	21	3	52	12	4	0	0	0

Greenshank* *Charadrius leschenaultia*	2	2	0	0	0	6	0	2	10	0
Grey-tailed tattler* *Tringa brevipes*	42	2	1	0	40	308	0	59	156	0
Lesser sand plover* *Tringa brevipes*	0	0	4	2	33	65	0	0	29	0
Pacific golden plover* *Pluvialis fulva*	2	13	0	2	1	27	7	15	1	0
Pied oystercatcher* *Haematopus longirostris*	2	2	4	0	5	105	2	5	17	2
Red knot* *Calidris canutus*	10	0	14	1	7	21	0	1	29	0
Red-capped plover* *Charadrius ruficapillus*	0	0	4	20	8	9	5	0	3	0
Red-necked stint* *Calidris ruficollis*	0	0	16	5	61	210	1	3	21	0
Ruddy turnstone* *Arenaria interpres*	1	0	1	0	1	22	0	0	0	0

Sharp-tailed sandpiper* *Calidris acuminate*	8	0	5	0	40	63	0	10	88	0
Terek sandpiper* *Xenus cinereus*	19	0	2	0	7	18	0	12	4	0
Whimbrel* *Numenius phaeopus*	29	4	1	24	1	46	14	11	120	0
Manly patrol cost	228	548	470	529	478	172	531	214	452	537
Caloundra patrol cost	538	190	397	169	405	523	172	526	360	176
Bribie patrol cost	481	422	169	402	207	463	405	467	323	413
Average number of disturbances per count	0.17	0.17	1.08	0.19	0.78	4.03	0.08	1.47	0.19	0.22

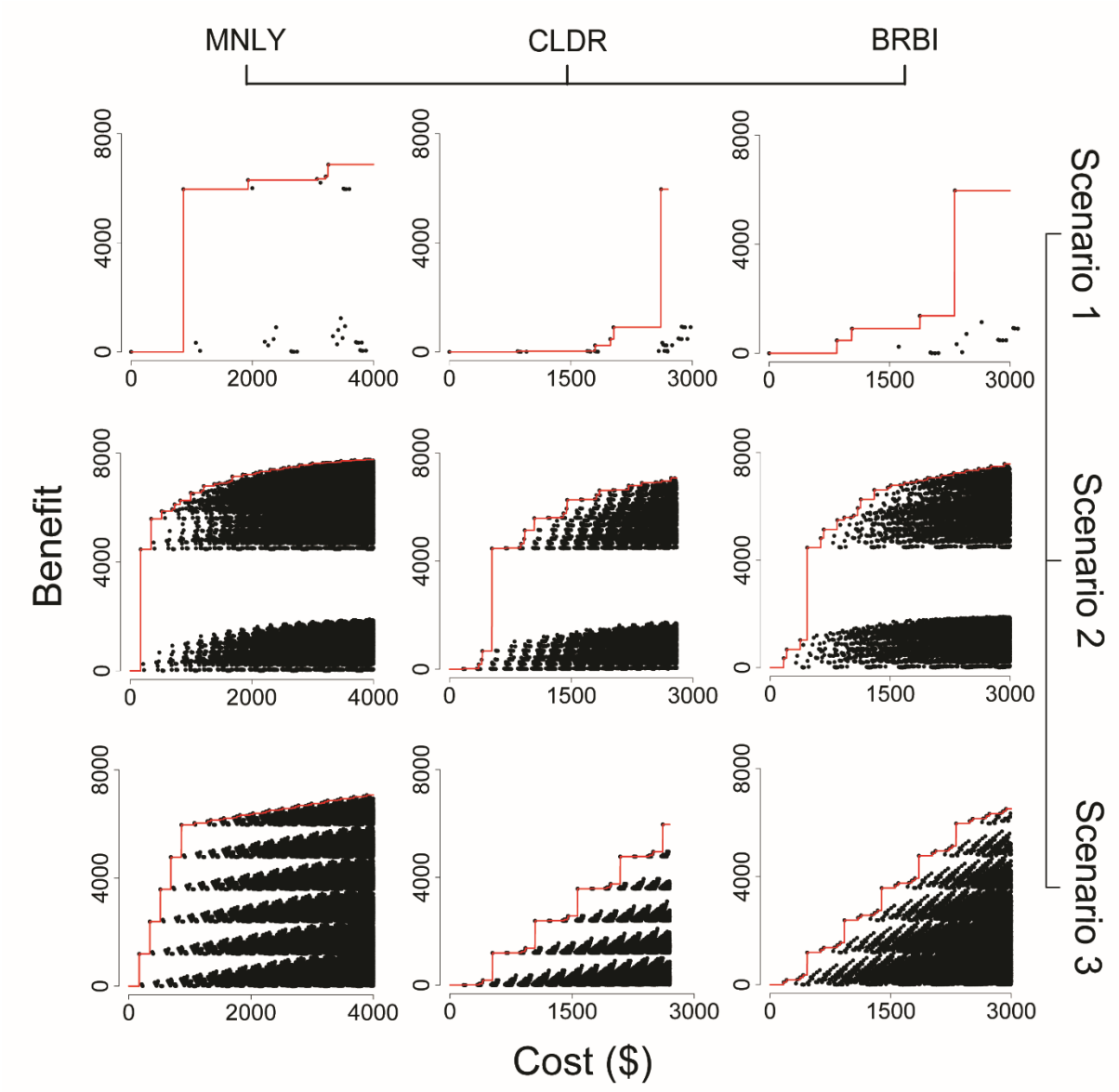
***** Bird numbers estimated from average counts by QWSG between 1992 and 2012 at different roost sites in Moreton Bay, Australia.

8.9 Appendix S.4.2

Benefit of management

To determine the benefit of management, we worked in collaboration with QWPS and visited all 4 land-based shorebird sites currently managed, before and after patrols, in addition to 4 unmanaged control sites. For each site, we timed potential disturbance events over a 3 hour period, and whether or not these events caused birds to walk away or take flight. Bird counts were carried out each half hour. All managed sites were patrolled a total of five times: Two were patrolled once a week, the other two once a month. Weather and tide conditions were recorded. Finally, we carried out paired t-tests, in addition to generalized linear models to determine whether management was impacting disturbance rates. We used the results of these analyses to parameterise γ the extent to which management reduces disturbance in our optimization algorithm. We observed on average a 20% reduction in disturbance after management had taken place 5 times at a site over our study period, thus $\gamma = 0.2$ and $V_{max} = 5$.

8.10 Appendix S.4.3



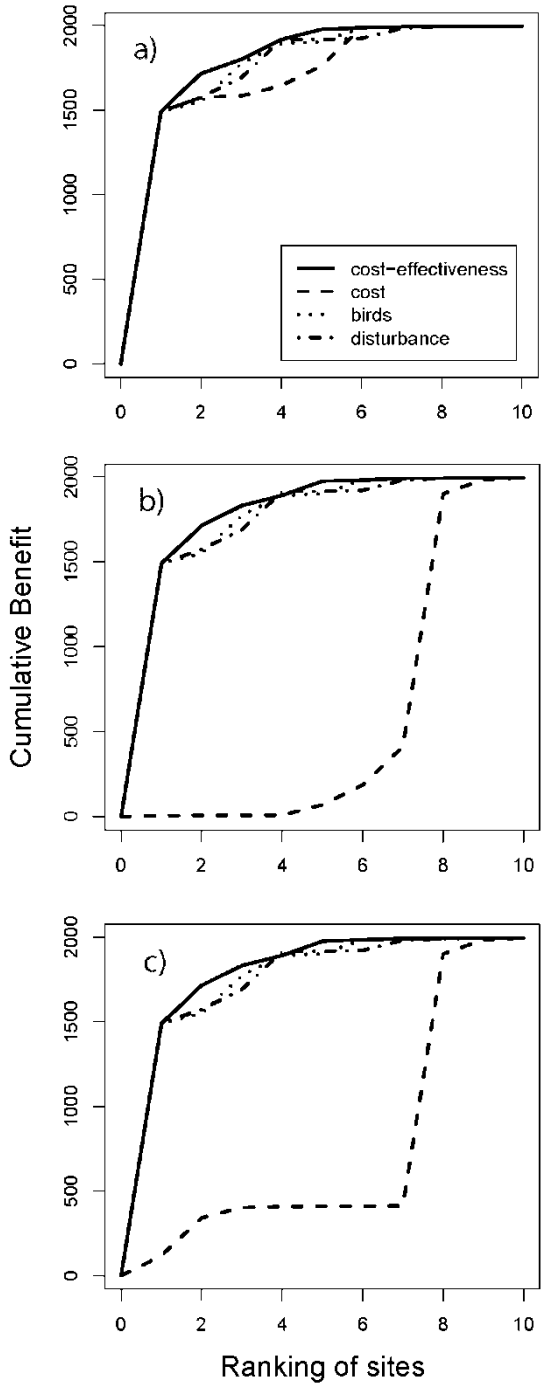
Trade-offs between the cost of enforcing patrols and the benefit to shorebirds of reducing disturbance by 80%. Scenario 1 where patrol effort was constant for all sites for the entire season, and where birds benefitted from a fixed disturbance reduction of as a result of enforcement at each site; scenario 2 where patrol effort could vary across sites during the season, and where birds benefitted from an exponential reduction in disturbance as a result of enforcement at each site; and scenario 3 where patrol effort could vary across sites during the season, and where birds benefitted from a linear reduction in disturbance as a result of enforcement at each site. For each scenario, we plotted trade off curves for three different patrol stations where rangers are based: MNLY=Manly, CLDR=Caloundra and BRBI=Bribie. Red lines indicate the optimal solution.

8.11 Appendix S.4.4

Link to google document showing how to calculate cost effectiveness

https://docs.google.com/spreadsheets/d/1KfQrdQGIBpmJOnbrn0B2T7ImRTxDivBMbbmAuo-D5Jo/edit?usp=sharing

8.12 Appendix S.4.5



Comparison between benefits (i.e. number of birds freed from disturbance in equation 1) when ranking sites according to cost-effectiveness, cost, birds number, or disturbance rate, for patrol station a) Manly, b) Caloundra and c) Bribie. Note the number of birds and disturbance rates do not vary as a function of patrol location a), b) or c).

8.13 Appendix S.4.6

Frequency at which sites are selected as part of an optimal solution for every dollar spent. The budget is limited to $2700 for all scenarios and Caloundra is the patrol base.

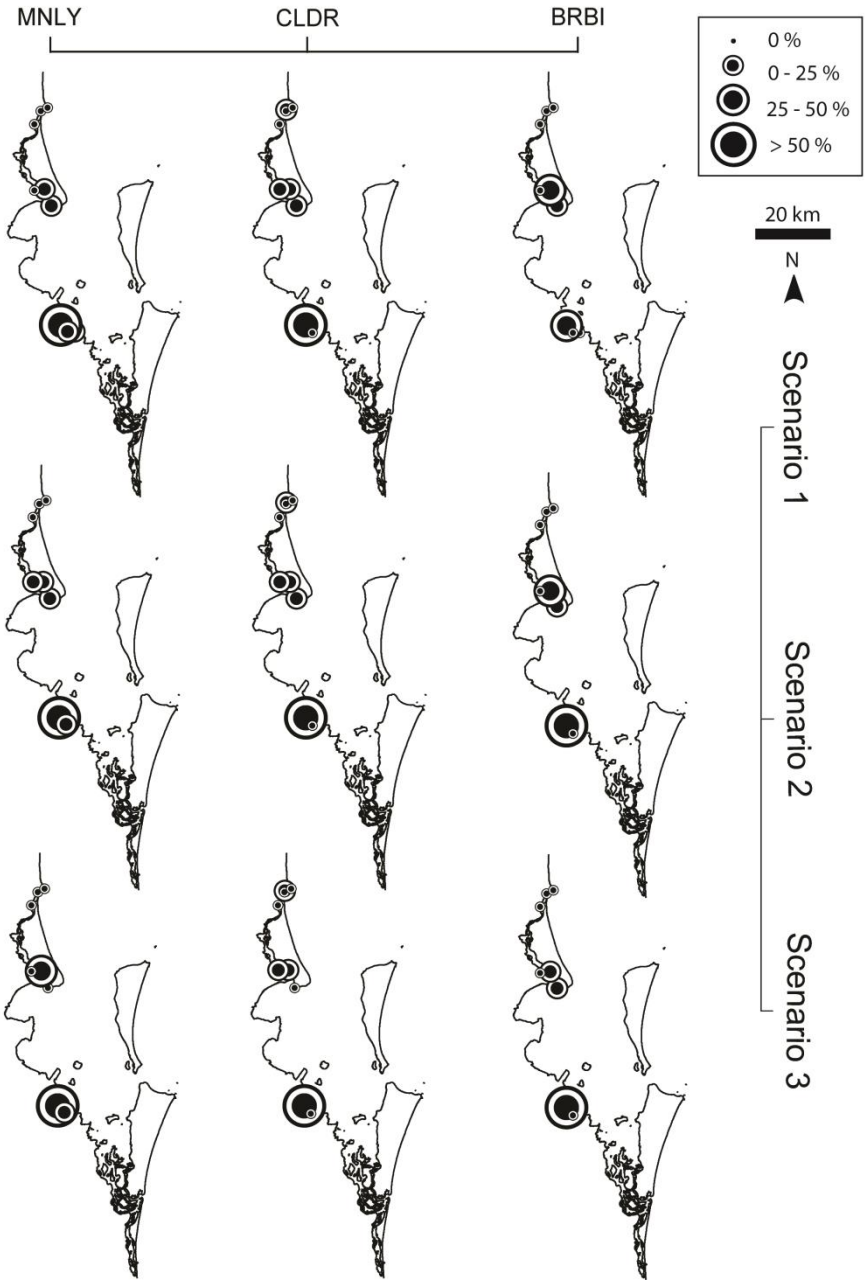
	20% disturbance reduction			80% disturbance reduction		
Sites	Scenario 1	Scenario 2	Scenario 3	Scenario 1	Scenario 2	Scenario 3
Caloundra Bar	957	1138	1066	957	1138	1066
Kakadu Beach	580	1704	588	580	1704	588
Toorbul	190	501	189	190	501	189
Sandbank Caloundra	100	0	0	100	0	0
Manly Harbour	91	4345	5662	91	4345	5662
Buckley's Hole	40	977	40	40	977	40
Bell's Creek	0	3	0	0	3	0
Thorneside	0	0	0	0	0	0
Wellington Point	0	0	0	0	0	0
Wickham Point	0	0	0	0	0	0

8.14 Appendix S.4.7

Frequency at which sites are selected as part of an optimal solution for every dollar spent. The budget is limited to $3000 for all scenarios and Bribie is the patrol base.

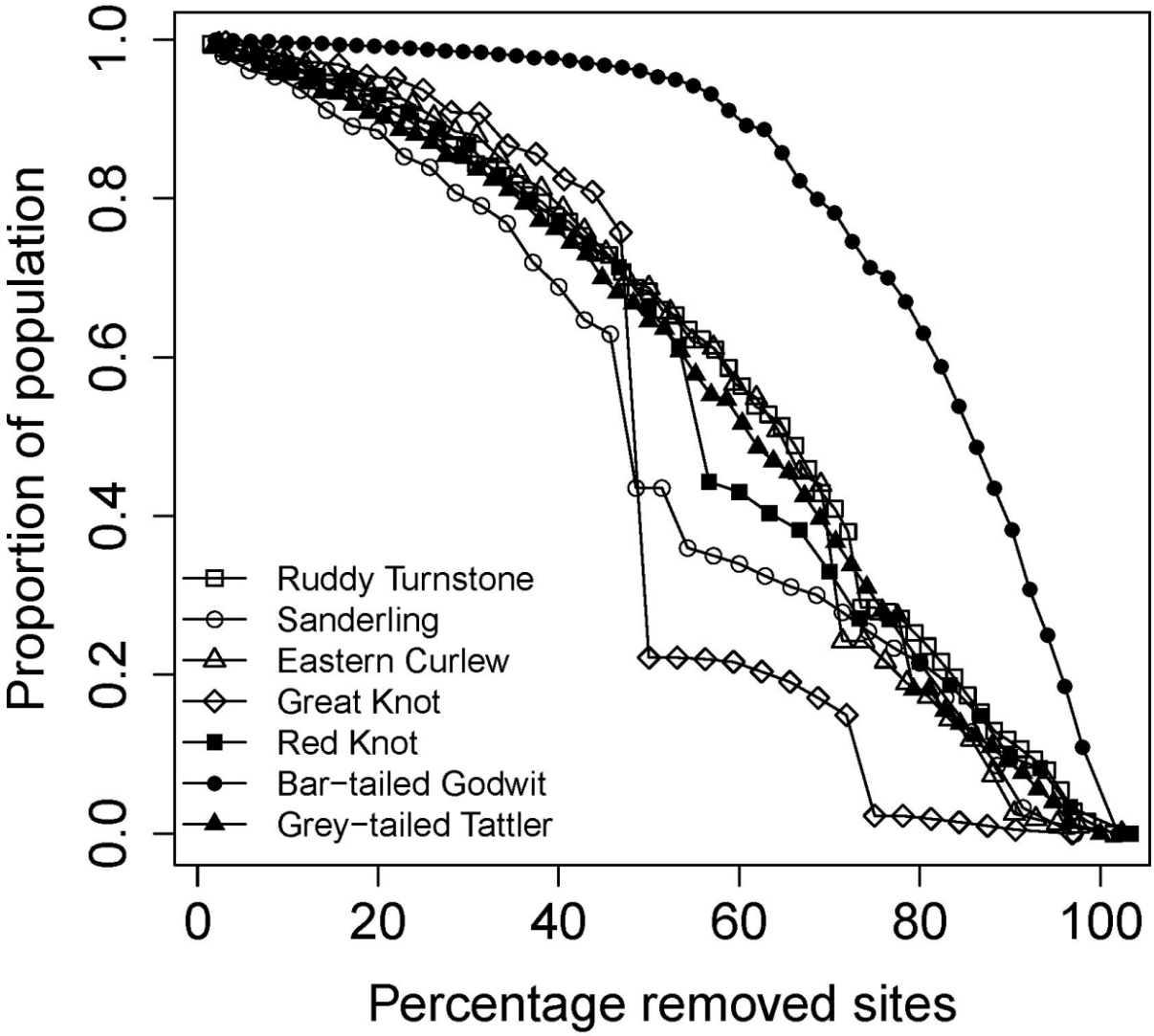
	20% disturbance reduction			80% disturbance reduction		
Sites	Scenario 1	Scenario 2	Scenario 3	Scenario 1	Scenario 2	Scenario 3
Kakadu Beach	1280	3689	2086	1280	3689	2086
Manly Harbour	691	5699	8063	691	5699	8063
Buckley's Hole	616	2724	1019	616	2724	1019
Bell's Creek	0	0	0	0	0	0
Caloundra Bar	0	0	0	0	0	0
Sandbank Caloundra	0	0	0	0	0	0
Thorneside	0	418	0	0	418	0
Toorbul	0	812	0	0	812	0
Wellington Point	0	0	0	0	0	0
Wickham Point	0	0	0	0	0	0

8.15 Appendix S.4.8



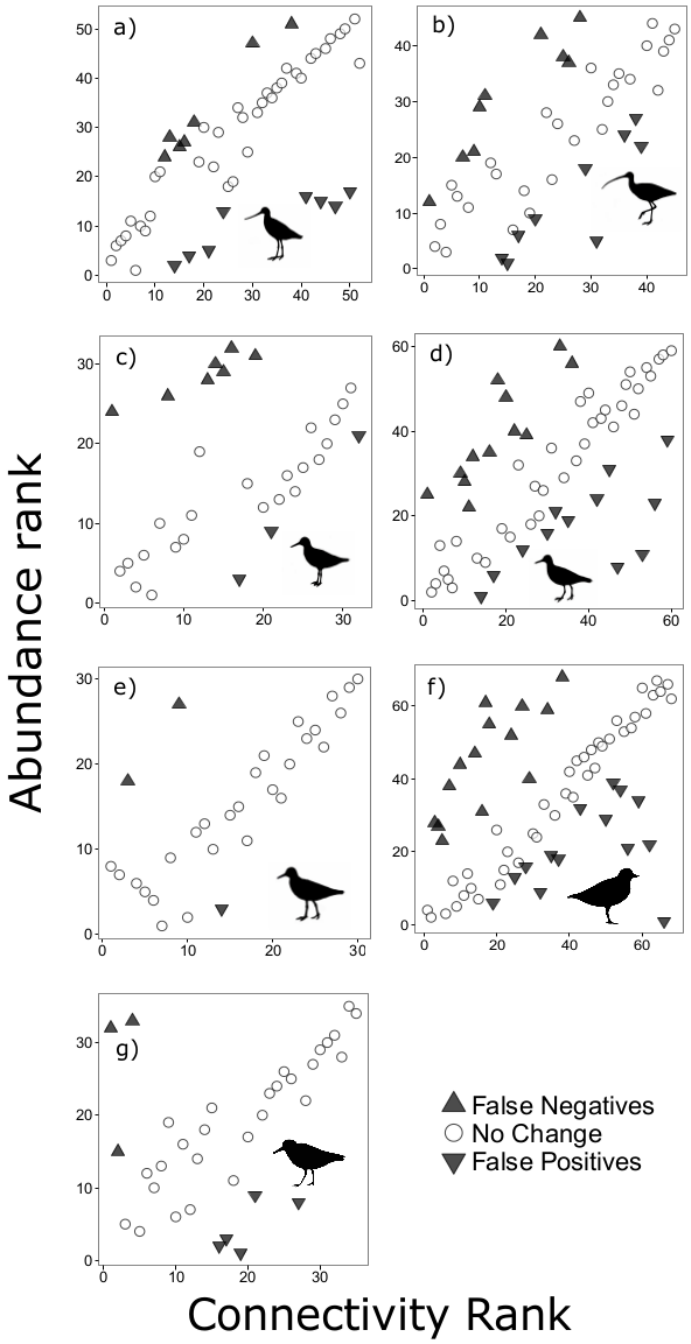
The relative frequency sites are selected as part of an optimal solution for every dollar spent, expressed as a percentage, for each scenario at each patrol station for a disturbance reduction of 80%. The budget is limited for all scenarios to $0-4000 for patrol station Manly (MNLY), $0-2700 for patrol station Caloundra (CLDR) and $0-3000 for patrol station Bribie (BRBI). The differences in budget reflect the number of solutions: the number of solutions under $2700 at Caloundra is the same as the number of solutions under $3000 found at Bribie, which is the same as the number of solutions under $4000 found at Manly.

8.16 Appendix S.5.1



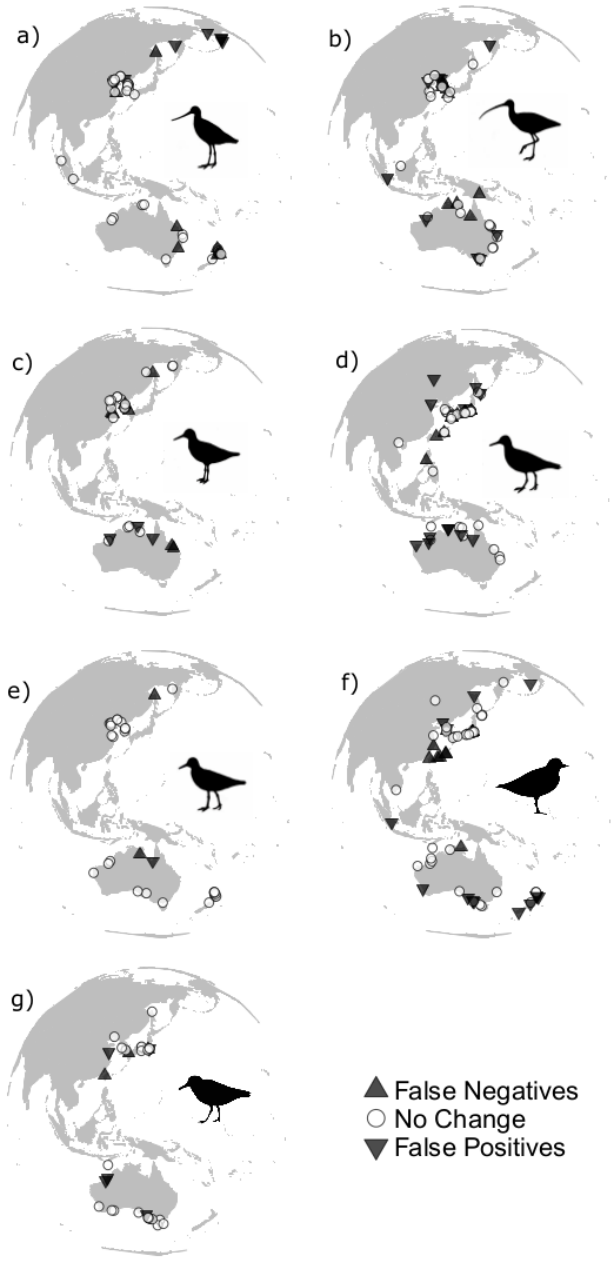
Proportional loss of population flow as nodes are removed according to the flow prioritisation strategy, for bar-tailed godwit, eastern curlew, great knot, grey-tailed tattler, red knot, ruddy turnstone and sanderling.

8.17 Appendix S.5.2



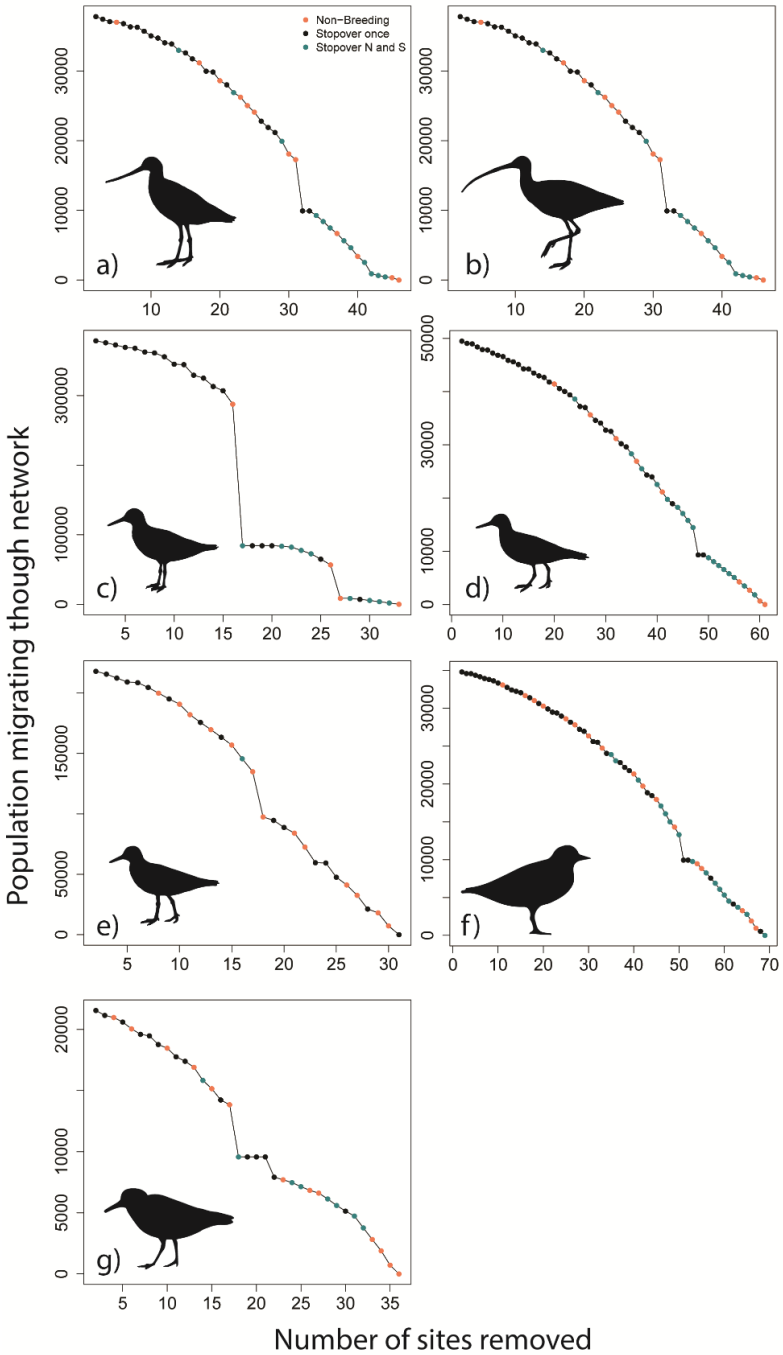
Rank change between maximum count prioritisation strategy and flow prioritisation strategy for a) bar-tailed godwit, b) eastern curlew, c) great knot, d) grey-tailed tattler, e) red knot, f) ruddy turnstone and g) sanderling. Downward facing arrows indicate false positive results, whereby nodes appear high in the count prioritisation strategy, but are in fact lowly ranked in the flow prioritisation strategy. Circles represent no a change in rank of less than 5. Finally, upward facing arrows represent false negative ranking, whereby nodes appear lowly ranked in the count prioritisation strategy, but are in fact highly ranked in the flow prioritisation strategy.

8.18 Appendix S.5.3



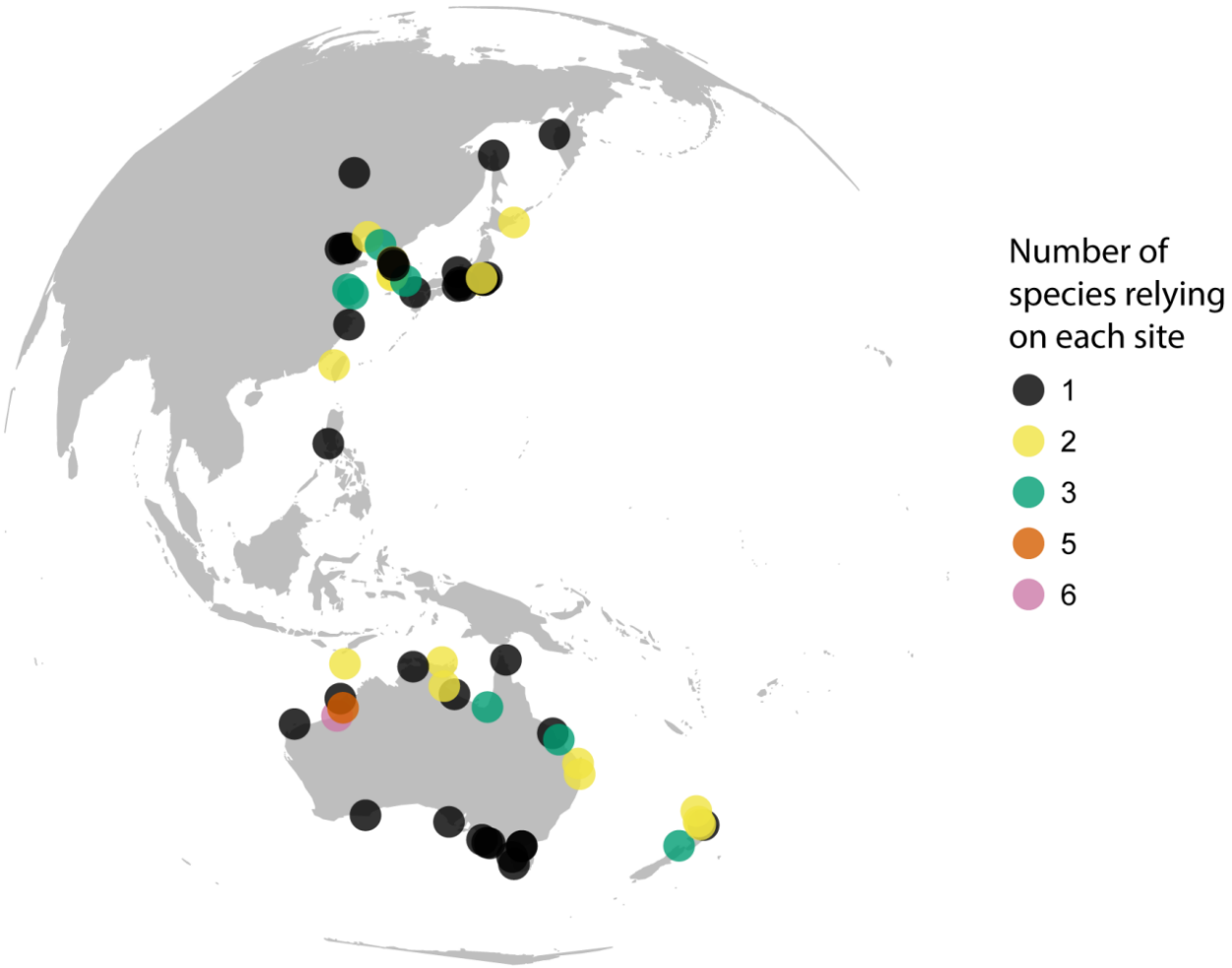
Geographical distribution of rank changes between maximum count prioritisation and flow prioritisation strategies for a) bar-tailed godwit, b) eastern curlew, c) great knot, d) grey-tailed tattler, e) red knot, f) ruddy turnstone and g) sanderling. Downward facing arrows indicate false positive results, whereby nodes appear high in the count prioritisation strategy, but are in fact lowly ranked in the flow prioritisation strategy. Circles represent no a change in rank of less than 5. Finally, upward facing arrows represent false negative ranking, whereby nodes appear lowly ranked in the count prioritisation strategy, but are in fact highly ranked in the flow prioritisation strategy.

8.19 Appendix S.5.4



Identification of sites used in the flow prioritisation strategy for a) bar-tailed godwit, b) eastern curlew, c) great knot, d) grey-tailed tattler, e) red knot, f) ruddy turnstone and g) sanderling. Orange indicated the site removed is a non-breeding site, black that the site removed is used during only north or only south migration and blue indicates that the site is used during both north and south migration.

8.20 Appendix S.5.5



Number of species using each internationally important shorebird node during migration. Most nodes are used by only one species, with only a handful used by more than three species.