CONSERVATION OF NORTH AUSTRALIAN MAGPIE GEESE *ANSERANAS SEMIPALMATA* POPULATIONS UNDER GLOBAL CHANGE

By

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Contents

Abstract

The magpie goose (*Anseranas semipalmata*) is a spectacular and unique waterbird from tropical north Australia and southern New Guinea. Due to recent human persecution, the species has been eliminated from most of its former strongholds in southern and south-eastern Australia – reduced to small conservation-dependent populations through habitat loss, exploitation and drought. Yet, genuine conservation opportunity still exists in northern Australia, in the country"s Northern Territory in particular, to maintain viable populations through evidence-based management of wetlands that support the waterbirds and mitigation of the threats posed by global change. Much has been achieved over the last 50 years to understand the ecology and life history of magpie geese, but little has been done to understand important population-level interactions with wetland habitat and the likely outcomes under climate warming, wetland loss to sea level rise, altered competitive interactions among wetland plants, increased frequency and severity of epizootics, and synergies with over-hunting. My review of pathogens and parasites likely to cause morbidity and mass mortality in magpie geese shows that bacterial diseases such as avian cholera and botulism, as well as pathogenic avian influenza viruses, pose the most serious threats. Bacterial diseases in particular are more likely to occur under warmer and wetter conditions, and geese are susceptible to these given large aggregations at favoured nesting and feeding sites. I use a metapopulation model to demonstrate that increased frequency and severity of epizootics will likely force extirpation of geese under current harvest rates across the Northern Territory. Magpie geese are also vulnerable to climate change through dependency on a favoured food plant – the water chestnut (*Eleocharis dulcis*). As a result of a two-year field programme, I was able to show how birds seasonally migrate and aggregate in response to the availability of this resource and gain body condition following predation on the root tubers of the plants. My geospatial modelling of ocean level inundation of wetlands that support *E. dulcis* show marginal habitat loss under 1.4 m of sea level rise, and large-scale losses under multi-metre sea level rise, but the current resolution of GIS data do not account for fine-scale saline water intrusion through channel or eroded levees. The population models constructed predict that magpie geese are broadly resilient to change where harvest is tightly regulated, but current harvest rates are unlikely to be sustainable. Given the importance of maintaining viable, connected subpopulations large enough to maintain genetic diversity, and because of the value of magpie geese to Aboriginal Australians as a food source, ongoing monitoring of geese population trends will be essential. Wetland management options include erecting buffers to stop or slow down saltwater intrusion resulting from sea level rise, and implementing a system to monitor annual indigenous harvest. Temporary restrictions on harvest may be necessary following mass mortality events such as epizootics or droughts. Only the careful management of wetlands that support current geese populations, and close monitoring of populations will ensure continued sustainable harvest of geese under global change. Given the cultural and biological significance of this species and the north Australian wetlands that support it, this is a conservation resource we cannot afford to squander.

Statement of Originality

This work contains no material which has been accepted for the award of any other degree or diploma in any University, or any other tertiary institution. To the best of my knowledge, this work contains no material previously published or written by any other person except where due reference has been made in the text.

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Lochran W. Traill Date

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CHAPTER ONE

1. Introduction

Anthropogenic climate change is one of the most serious challenges facing biodiversity this century (Walther et al. 2002; Colwell et al. 2008). Global change acting concomitantly with habitat loss, exploitation and other threats will drive the extirpation and extinction of numerous species over the next 90 years (Thomas et al. 2004). Fluctuations in global climate regimes are natural, as are species extinction events (Raup & Sepkoski 1984; Alroy 2008), but few of these have occurred at the rate of the current phenomena (Bradshaw et al. 2008). The response of conservation biologists to the extinction crisis will need to be adaptive and multi-disciplinary. Practitioners will require first the best available information on species or taxa of concern and habitat relations, detail on current and projected threats, and the skills to build and interpret complex (including genetic) models that project population viability under global change. These will inform the decision-making process and hopefully allow biologists to be effective in conserving - at the very least - remnant habitat and taxa.

The arrival of first aboriginal and then European people to Australia precipitated the extirpation of many native vertebrates (Bowman 2001). One of the more recent and most serious local extinction events was that of magpie geese (*Anseranas semipalmata*) across southern and south-eastern Australia (Garnett 1992). North Australian populations of the species remain relatively intact, but face habitat loss, overexploitation and perturbations through global warming. Although relatively well-studied over the last ~ 50 years, crucial aspects of the ecology of geese and their likely response to global change are not known. For example, dry season wetland aggregations of geese in response to food resources are not well understood. The loss of these wetlands to saline water intrusion through sea level rise (Eliot et al. 1999) and the ramifications for the long-term persistence of geese have not been explicitly tested. These have consequences beyond the conservation of magpie geese: as a keystone species geese play a part in the present-day composition of wetland plant communities, and the loss of these will affect waterbird communities and indeed the biodiversity of tropical Australian floodplains (see Finlayson et al. 2006).

Here I outline the ecology of magpie geese and current and projected threats to tropical populations. This provides the broad context within which the field monitoring and modelling of the impacts of global change on geese has been framed. My research programme was based in the Northern Territory (NT) of Australia; reference is made to tropical north Australia in the text when broad conservation of geese is considered.

1.2 Ecology of magpie geese

Magpie geese (hereafter geese) are endemic to Australia and New Guinea, and monotypic to the family Anseranatidae (Frith & Davies 1961; Halse et al. 1996; Nye et al. 2007). The species has remained evolutionarily constant over the past 4 million years, with recent (south Australian) fossil identification from the Pliocene Tirari formation (Worthy 2008). Further, geese are more closely related to South American screamers (Anhimidae) than the Anatidae (Livezy 1996), despite the diversity of Anatidae across Australia (Kingsford & Norman 2002; Finlayson et al. 2006). Indeed, its taxonomic status as the sole member of its Family underscores its uniqueness and intrinsic conservation value (Whitehead 1998).

Although listed as Least Concern by the World Conservation Union‟s Red List of threatened species (IUCN 2008), large, viable goose populations are now restricted to the tropical north of Australia and southern Papua (Whitehead 1998). European settlement of southern and south-eastern Australia reduced once numerous sub-tropical and temperate populations to small and isolated subpopulations dependent on intense conservation effort (Harper 1990; Nye et al. 2007). The relative abundance of north Australian geese populations, and their continued importance to Aboriginal Australians as a seasonal food source (Whitehead et al. 2000; Gorman et al. 2008), recreational hunters (Whitehead 1988) and the tourist industry (Bradshaw et al. 2007) has ensured protective management and ongoing research effort (Whitehead 1998).

One of the historically most comprehensive studies of magpie geese was undertaken at a time when birds were seen as a threat to north Australia‟s agricultural industry: Frith and Davies (1961) were tasked with research on the life history and ecology of geese in response to the challenges faced by a developing rice-growing industry. The tropical rice scheme ultimately succumbed to poor planning and logistical failures (Mollah 1982), but the ecological research conducted by these authors nevertheless formed a template for work on geese over the next forty years. Many studies have addressed different aspects of the life history and ecology of geese (see especially Whitehead 1998) and the species remains one of the better-studied waterbirds in tropical Australia.

1.2.1 Habitat and Environment

Geese are abundant across much of tropical north Australia (see Fig. 1.1), with large concentrations of birds in the NT (Nye et al. 2007). There, an estimated 2.5 – 3.5 million birds depend on subcoastal floodplains of the major river systems (Bayliss and Yeomans 1990). Coastal floodplains are geologically recent landforms; these systems formed in the recent Holocene after sea levels stabilised ~ 6 000 – 4 000 years Before Present (Nanson 1992; Mulrennan and Woodroffe 1998). The rapid rise in early Holocene sea levels allowed marine inland incursion and creation of large shallow estuaries. The mid Holocene stabilising of sea levels allowed progradation of marine sediment and the formation of dominant mangrove communities (Woodroffe et al. 1985). Vertical accretion gradually eradicated these communities and accumulation of alluvial sediment led to the formation of the extensive floodplains in their present form (Fig. 1.2), perhaps as recently as 1 000 years BP (Woodroffe 1993).

Alluvial deposition has led to the modern-day floodplain soils being among the more fertile of the region (Cowie et al. 2000). Extensive 0.5 – 1 m deep floodplain clays overlie estuarine muds which support ecologically diverse and abundant wetland vegetation communities (Finlayson et al. 2006). Frith and Davies (1961, after Kutena 1957) categorised floodplains into two major parts: the high black soils that flood only periodically and low black soils that hold water through most of the tropical dry season. Vegetation communities, dominant on high black soils, are mostly annual grasses, including *Echinochloa* and *Paspalum* species, the sedges *Cyperus* and *Fimbristylis* and some woody vegetation, especially *Barringtonia* (see Cowie et al. 2000). Low-lying black clay soils are dominated by *Eleocharis* and *Hymenachne* species and wild rice.

(*Oryza rufipogon*), as well as the aquatics from the genera *Paspalum*, *Monochoria* and *Nymphoides*. Low black soils also support patchy *Melaleuca* woodlands and forests (Brock 2001).

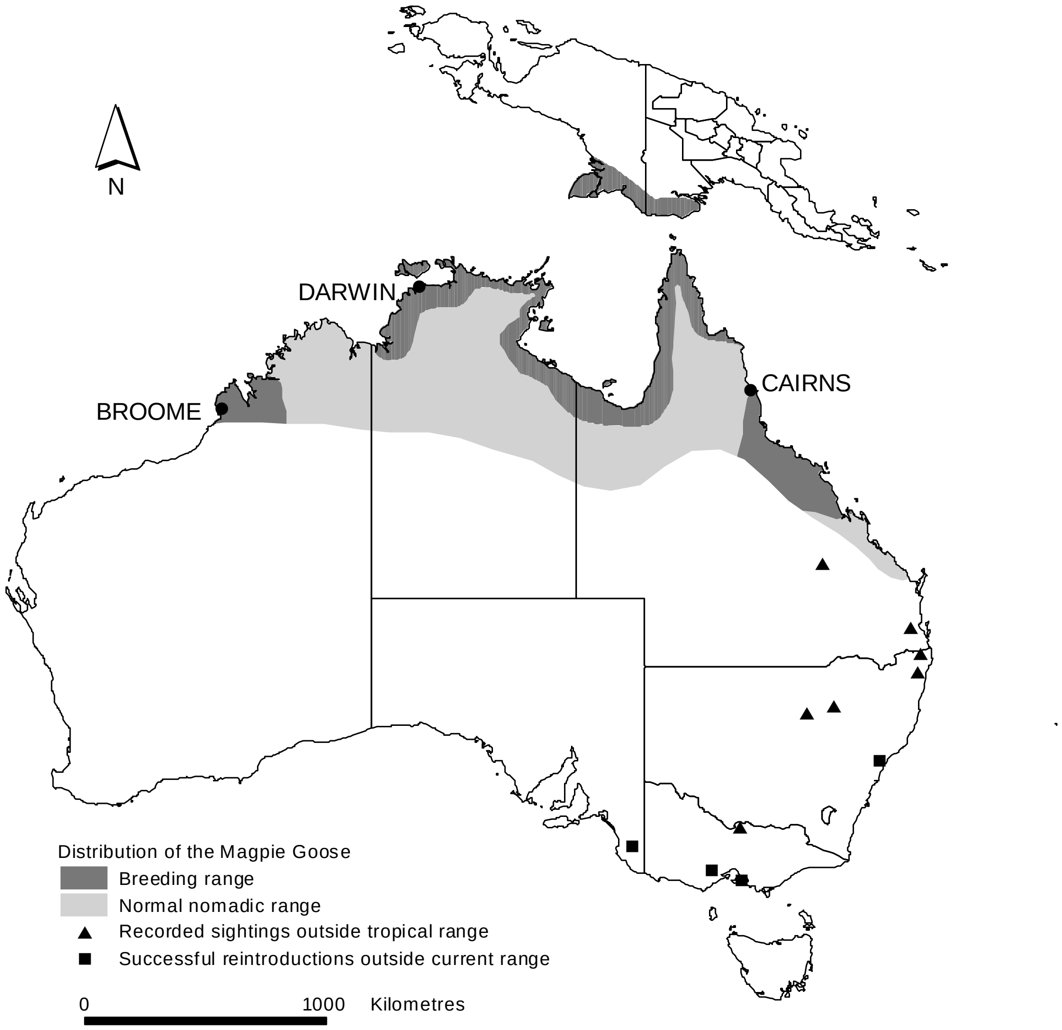


Figure 1.1 The distribution of magpie geese in Australia and Papua. Regular breeding range of the species is highlighted in dark grey and the lighter shade represents habitat (includes inland billabongs) potentially used during non-breeding periods. Extant remnant southern populations are represented using symbols.

The spatial and temporal arrangement of emergent, semi-aquatic and submerged aquatic vegetation communities are driven in part by water depth, period of inundation and salinity (Wilson et al. 1991). Introduced pasture grasses and woody weeds such as *Mimosa* spp. are invasive on many of the NT floodplains (see Lonsdale 1994) and weed-control programmes are in place on all protected areas.

The seasonal fluctuations in tropical north Australian climate are reflected in floodplain ecology, where alternating cycles of flooding and drying track monsoonal rainfall (Bayliss 1989; Cowie et al. 2000). The tropical wet-dry climate is typified by high temperatures and seasonally high humidity and precipitation, followed by dry season „drought" and high evaporation (Banfai et al. 2007). Mean annual rainfall for Jabiru in Kakadu National Park is 1 579 mm (see monthly data Fig. 1.3) and mean annual maximum temperature is 34.2°C (after www.bom.gov.au). The wet season is marked by localised depressions that bring heavy rain and cyclones (Frith & Davies 1961), and runs from beginning December through April. Destructive cyclones can also bring torrential rain, destructive winds and storm-surges along the coastline (Taylor & Tulloch 1985).

Temporal and spatial distribution of magpie geese across the NT approximately tracks cyclic floodplain inundation (Morton et al. 1990; Wilson 1997). Bayliss and Yeomans (1990) noted that the range of geese expands in the wet season as birds dispersed to breed, and contract during the dry season as birds concentrate their feeding effort on several select sites.

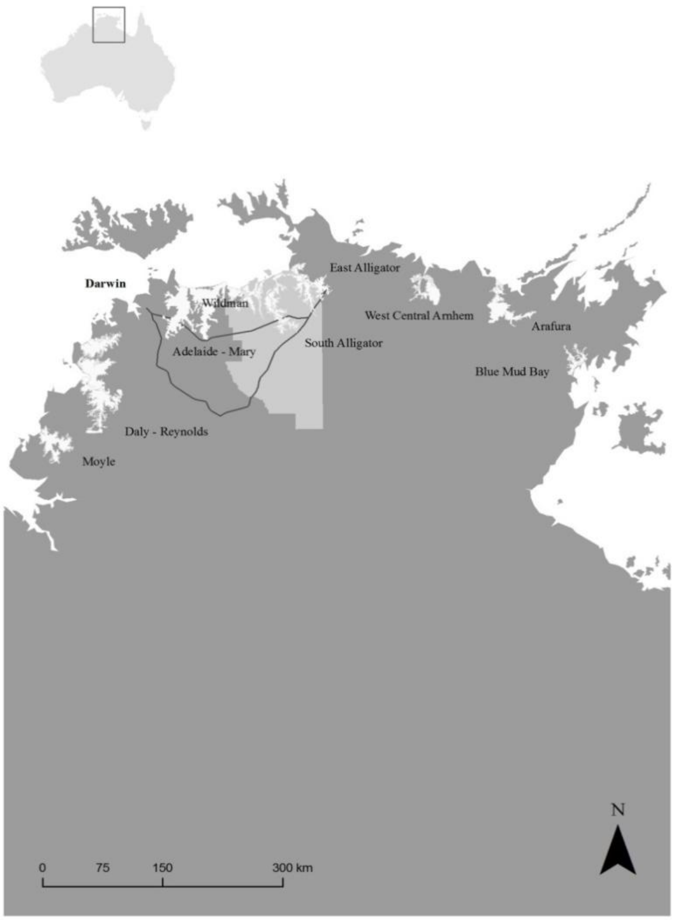


Figure 1.2 Subcoastal floodplains across the NT of Australia. Floodplains shown as white are utilised by magpie geese during wet and dry seasons. Kakadu National Park is highlighted as a light grey and main access roads to Darwin represented as dark lines.

Indeed, up to 70% of the NT population of magpie geese has been recorded on the South Alligator floodplain system during the dry period, where birds forage for nutrient-rich root tubers of the sedge plant *E. dulcis* (Whitehead 1998). Although birds tend not to venture far from water, individuals will utilise dry-land habitat if forage is available (Whitehead & Tschirner 1992).

1.2.2 Diet

Magpie geese are generalist herbivores and eat a variety of plant species and plant parts, including seeds, root tubers, grass blades and exotic fruit and root crops (Frith & Davies 1961; Whitehead & Tschirner 1992). Food is manipulated almost entirely with the bill, whilst foraging and digging is done using the bill and feet (Frith & Davies 1961).

Seasonal variation in diet corresponds to environmental change (in response to rainfall). Birds consume large amounts of grass blades and seeds following the first rains (Whitehead 1998) and up to 80% of the diet of geese in January consists of grass seeds from *Oryza*, *Echinochloa*, *Paspalum* and *Cynodon* (Frith & Davies 1961). Hatching appears to coincide with peak availability of wild rice (*O. rufipogon*) – this forms the principal food item for rapidly growing young birds (Whitehead et al. 1992). Throughout the dry season, birds grub for *Eleocharis* root tubers (Bayliss 1989). As the late-dry season progresses and these tubers become inaccessible, birds grub for other tubers, roots and nodules from senescent shoreline grasses (Whitehead & Tschirner 1992). Body condition of birds is lowest at this time and preceding the rains (Frith & Davies 1961).

1.3 Population ecology

Geese nest in large colonies during the peak of the wet season (February through March) on low-black soil swamps (Whitehead & Saalfeld 2000). Colonies can be larger than 40 km^2 and peak nest density can exceed 20 ha^{-1} (Dexter 1988). Age at sexual maturity is around 24 months for females and 36 – 48 months for males (Whitehead 1998). Wild birds can live up to 27 years (Tulloch & McKean 1983), although the average generation length is 15 years (Brook & Whitehead 2005a). Magpie geese are thought to mate for life (Frith & Davies 1961) but the evidence for this is weak (Whitehead 1998). Apparently stable polygynous trios (one male, two females) are the predominant reproductive unit (Whitehead 1999). The joint clutch can be as large as 16 eggs in a single shared nest (Whitehead 1998). Recruitment rates are not known.

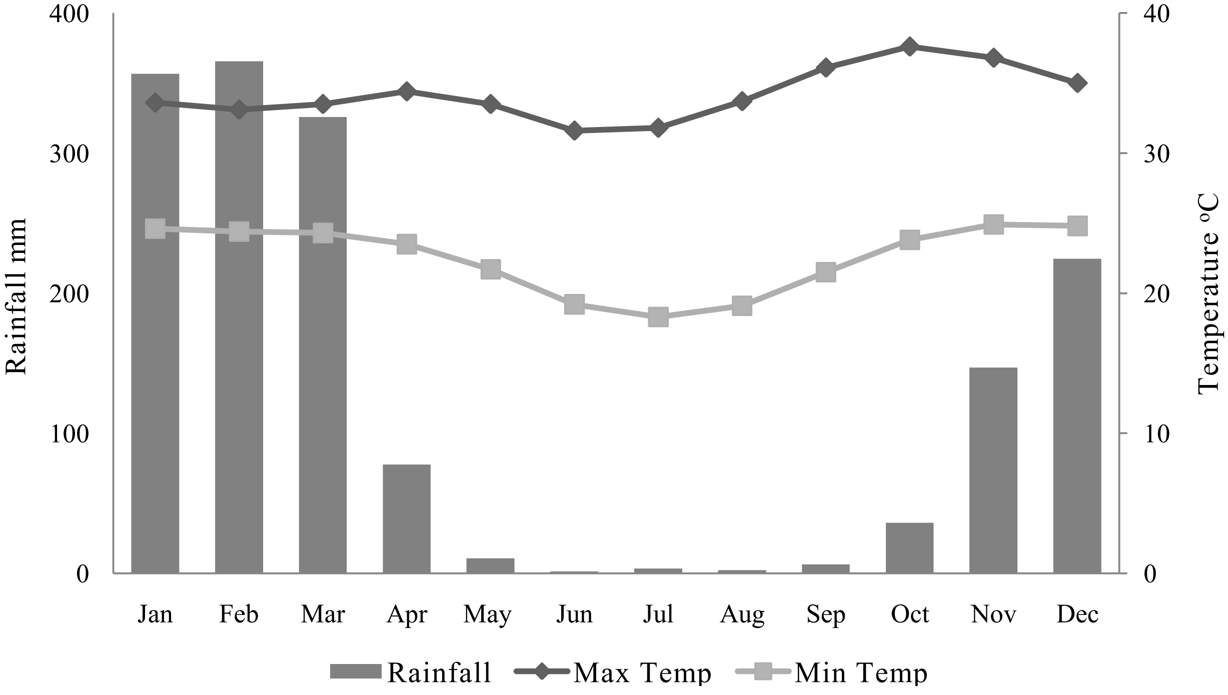


Figure 1.3 Mean monthly rainfall (mm) and minimum and maximum temperatures (°C) for Jabiru, Kakadu National Park 1971 – 2008 (http://bom.gov.au)

Age-specific survival rates of birds have not been quantified. Mortality among pre-fledged birds is considered to be high, and juvenile and adult mortality from predation and periodic starvation is thought to be common (Tulloch & McKean 1983). Non-human predators are principally water python (*Liasis fuscus*), dingoes (*Canis lupus dingo*) and some raptors which eat fledglings (Whitehead 1998). Aboriginal Australians have harvested birds and eggs for thousands of years (Whitehead et al. 2000). Current harvest by indigenous people is thought to range from ~ 50 000 to 150 000 birds yr^{-1}, and regulated recreational harvest is ~ 30 000 birds yr^{-1} (Brook & Whitehead 2005b). There is risk of under-estimate of total mortality as these figures do not account for culling by tropical fruit-growers (Lindner, D. pers. comm., Kakadu Buffalo Farm), or mortality through injury by shot (e.g., Noer et al. 2007).

There is evidence of a population-level response by geese to environmental fluctuation through seasonal rainfall (Bayliss 1989). Population regulation of geese populations is likely driven by *per capita* forage availability, especially during the dry season.

1.4 Conservation status

Magpie geese were prevalent across much of southern and south-eastern Australia prior to European settlement (Frith & Davies 1961; Harper 1990a). A recent review has attributed population decline and range retraction principally to drought, habitat loss and past overhunting (Nye et al. 2007). Other drivers include predation by introduced predators such as foxes (*Vulpes vulpes*), poisoning and the diversion of water flows for crop irrigation.

Unregulated hunting of geese was prevalent following European settlement. Birds were culled for sale at markets and eggs were also harvested (Nye et al. 2007). Wetland habitats were drained for agricultural use and urban expansion, and thus the loss of critical nesting and feeding sites (Harper 1990a). In addition, geese were very likely to have been poisoned in large numbers by crop-growers, and via toxicosis caused by the ingestion of lead shot (Harper 1990b). Remarkably, lead (as opposed to bismuth and steel) shot remains legal outside hunting reserves to this day; despite research that has linked avian mortality to spent shot (Whitehead & Tschirner 1991).

The additive and synergistic (Brook 2008) impacts of these many factors involved in population decline, as well as demographic fluctuations and catastrophic events such as drought (Caughley 1994) have driven the extirpation of southern geese populations. Indeed, no other Australian waterbird has been so thoroughly eradicated (through anthropogenic influence) from so large an area as magpie geese (Garnett 1992). Assisted reintroduction programmes have met only limited success in southern Australia and (southern) geese populations remain conservation dependent (Harper 1990a).

Northern populations of geese are relatively intact (Frith & Davies 1961; Whitehead 1998). Immediate threats are habitat loss and over-harvest (Brook & Whitehead 2005). Introduced pasture grasses and weeds outcompete favoured forage plants such as *E. dulcis* and prevent nesting (Lonsdale 1994; Rossiter et al. 2003). Notable weeds are *Mimosa pigra*, *Salvinia molesta*, *Brachiaria mutica* and *Andropogon gayanus* (Finlayson et al. 2006). Further, non-native ungulates such as water buffalo (*Bubalus bubalis*) and pigs (*Sus scrofa*) alter wetland vegetation through rooting, and buffalo swim channels facilitate salt water intrusion and the subsequent loss of forage (Corbett & Hertog 1996; Bradshaw et al. 2007). Recreational and aboriginal harvest are high but sustainable under current conditions (Brook & Whitehead 2005). Catastrophic mass mortality events through epizootic or drought are likely to lead to the extirpation of small or isolated goose populations (Wikelski et al. 2004).

Despite these threats, there is some progress in goose conservation management. The marine-listed status of magpie geese (under the Australian *Environment Protection and Biodiversity Conservation Act* 1999) allows for legal protection by Government wildlife authorities, and current effort is focused on securing wetland habitat across the NT (Whitehead et al. 1992). Non-aboriginal hunting is tightly regulated.

Global warming, however, is the biggest medium to long-term threat facing tropical magpie geese populations, and due to its interjuristicional scope, is one that conservation authorities are poorly equipped to control or manage (Hennessy et al. 2004; Finlayson et al. 2006). Altered temperature and rainfall regimes, and especially habitat loss through sea level rise, will reduce carrying capacities across tropical floodplains (Eliot et al. 1999; Winn et al. 2006). Moreover, the impacts of climate change will act additively and synergistically with current pressures on geese viability, such as harvest and invasive species, and will very likely force north Australian geese populations into smaller, more fragmented populations (Chapter 6). This range retraction and spatial disaggregation will leave geese more vulnerable to environmental and demographic stochasticity, catastrophic events such as disease outbreaks (Chapter 3) and loss of genetic diversity (Chapter 7).

Inevitably, given these interacting threats due to local and global change, the conservation management of geese will depend crucially on robust, evidence-based decision making (Burnham & Anderson 2002). It is within this context that I address the likely outcomes for geese across the NT under local and global change. I conduct exhaustive literature reviews (Chapters 2 and 3) on important aspects of the ecology of geese including habitat – population interactions and infectious disease. I contextualise the latter within the impacts of threat drivers and discuss the likely mechanisms of change. I also model the additive impacts of mortality through disease and harvest (Chapter 3). I explore the interaction between geese and dry season feeding sites (Chapter 4) through two years of intensive field-based research on the South Alligator floodplains, Kakadu. I examine dry season aggregations of birds, departure thresholds and gains in body condition. I also measure seasonal migration of geese from these feeding sites using satellite telemetry (Chapter 5) and quantify habitat selection. The use of satellite telemetry allowed fine-scale movement to be mapped, building on past research based on radio-telemetry which was of more limited spatial extent (Whitehead 1998).

Through literature review and research on habitat association, I take inference on habitat loss a step further by modelling sea level rise in the NT using digital elevation models (Chapter 6). On the basis of this GIS modelling, I make some forecasts of metapopulation persistence, using population models based in RAMAS Metapop (Akcakaya & Root 2001), to explore the additive impacts of habitat loss and harvest.

Finally, I review likely outcomes of small and isolated subpopulations, should the north Australian geese metapopulation be severely reduced under global change. I discuss the concept of minimum viable population size and relate the requirements of viable populations derived by both empirical and genetic methods (Chapter 7). I bring research together in the concluding chapter (8) and develop proposals for future research for tropical geese populations, and indeed any tropical waterbird likely to be impacted by global change in the coming decades of this century of environmental upheaval.

CHAPTER TWO

2. HOW WILL CLIMATE CHANGE AFFECT PLANT-HERBIVORE INTERACTIONS? A TROPICAL CASE STUDY.

Published as a review paper at *Emu - Austral Ornithology*, by Lochran W. Traill, Peter J. Whitehead & Barry W. Brook

Lochran Traill read all papers, and prepared the first draft manuscript (0.9). Co-authors Brook and Whitehead allocated 0.05 each by reviewing draft manuscripts and advising on general theme and outlay. Two anonymous reviewers at *Emu* provided valuable feedback.
All co-authors agree that this manuscript can be submitted as a chapter for a PhD thesis.

Abstract

We review wetland-waterfowl interactions, and outline the shifts that are likely to occur within these relationships through global change. We highlight the relative paucity of research on tropical waterfowl populations, and use an iconic tropical waterfowl - magpie geese - as a case study. We provide background on the known and hypothesised geese – wetland interactions and provide a hypothetical framework of the mechanistic changes to these relationships through climatic change, and including sea level rise, temperature increase, elevated CO_2 and altered rainfall regimes. We outline multiple competing hypotheses that can test these mechanisms in the field and laboratory, and advocate the coupling of goose population models to projected changes in key wetland habitat. These are likely to provide the backdrop to the adaptive management of tropical waterfowl in the coming decades.

2.1 Introduction

A warming global climate now stands as one of the most important, yet least understood, threats to the future of biodiversity (Hitz & Smith 2004; Parry et al. 2007). Despite the evidence for rises in atmospheric CO_2 levels, average and extreme global air and ocean temperatures, and mean sea levels (Parry et al. 2007), the mechanisms through which climate change will alter ecological processes and functioning within established communities are only beginning to be revealed (see Lim et al. 2008). Moreover, shifts in climatic parameters are not likely to be uniform across geographic regions, and the responses of organisms, communities, and the geophysical systems which shape them, are likely to be nonlinear and subject to abrupt transitions (IPCC 2007; Brook et al. 2008).

Important to ecological complexity are population-level interactions and processes such as predator - prey relations (Holling 1959b; Rosenzweig & Macarthur 1963; Berryman 1992), pathogen-vector-host relationships (Smith et al. 2006; Plowright et al. 2008b), competition (Tilman 1994) and resource partitioning (Traill 2004; Behmer & Joern 2008). Improved knowledge of these processes among populations will allow adaptive management in the face of future challenges such as climate change (IPCC 2007; Lim et al. 2008). A key ecological interaction is that between plants and herbivores (Scholes & Walker 1993; Jefferies & Rockwell 2002; Heck & Valentine 2006), and the nature and extent of these strongly determine abundances, diversity and community structure (Brathen et al. 2007; Rivers & Short 2007).

One example of an important plant-herbivore system thought to be threatened by rapid future climate change, perhaps within just the next few decades (Eliot et al. 1999; Finlayson et al. 2006), are the seasonal floodplains of tropical north Australia, and the numerous populations of geese that depend on these for food plants (Bayliss & Yeomans 1990; Whitehead et al. 1992). Current threats to these wetlands include invasive weeds (Lonsdale 1994; Rossiter et al. 2003), habitat degradation by feral vertebrates, especially pigs (*Sus scrofa*) and water-buffalo (*Bubalus bubalis*, Bradshaw et al. 2007), and the potential for overexploitation by recreational and aboriginal hunters. Saline water intrusion due to rising sea level and more frequent intense storm surges have become the focus of recent concern for tropical floodplains (Mulrennan and Woodroffe 1998; Hughes 2003) following projections of ongoing and accelerating global sea-level rise due to thermal expansion, ice cap loss and the potential for destabilisation of large polar ice sheets (Bindoff et al. 2007; Hansen 2007). Indeed, tropical Australian floodplains were highlighted in the 2007 IPCC Working Group II report as one of the most severe climate-change related threats to biodiversity in Australasia (IPCC 2007).

Here we review plant-herbivore interactions with a specific focus on wetlands and waterfowl. We discuss both the symbiotic and antagonistic relationships that can occur as a result of these interactions, based on a review of relevant field-based studies. In addition, we consider how these will respond to climate change in the tropics, using a case study of geese to explore mechanisms of change. We provide the background necessary for confronting multiple-working hypotheses with field data and thereafter, evidence-based policy and decision-making. We also provide examples on how these can be achieved.

2.2 Magpie geese

Native to Australia and New Guinea (Fig. 1.1) and the sole member of the Family Anseranatidae, geese are estimated to number up to 3.5 million individuals in Australia‟s „Top End‟ alone (Bayliss & Yeomans 1990; Whitehead et al. 1992). Once prevalent through eastern and southern Australia, geese have been restricted to their present tropical northern stronghold through the combined effects of habitat loss (mostly agricultural displacement and draining of wetlands), deliberate poisoning, predation by introduced species and overexploitation (Nye et al. 2007).

Magpie geese are dependent on extensive sub-coastal wetlands for forage and breeding sites (Frith & Davies 1961; Whitehead & Tschirner 1990). During the dry months, June through to October, geese aggregate in numbers in excess of 250 000 on shallow-water wetlands and grub for tubers of the sedge plant *E. dulcis* (Cyperaceae), gaining body condition in the process (Frith & Davies 1961; Whitehead 1998). Anecdotal evidence suggests a positive feedback loop between geese and *E. dulcis*, where despite intense seasonal predation on bulbs, *E. dulcis* plants return each year in dense swards (D. Lindner, pers. comm., Kakadu National Park).

Seasonal floodplains are utilised by geese for nesting following tropical rains, and the development of vegetation sufficient to physically support nests (Whitehead 1998). Migration is seasonally nomadic, typically between favoured forage and nesting sites (Whitehead et al. 1992). Sexual maturity is attained by 24 months in females and 36 in males, the mating system is polygynous, and breeding is co-operative with clutches ranging from five to 11 eggs (Frith & Davies 1961).

Known threats to geese in northern Australia are habitat loss to invasive species and saline water intrusion (Lonsdale 1994; Hennessy et al. 2004), wetland alteration by non-native ungulates (Bradshaw et al. 2007; Brook 2008), emerging infectious diseases (Tracey et al. 2004) and unsustainable harvest (Brook & Whitehead 2005b).

2.3 Global climate change and the tropics

Current global warming is evident from increases in average air and ocean temperatures, melting of snow and ice, and rising mean sea levels (IPCC 2007). Across tropical Australia, sea level rise is anticipated to alter coastal biomes, low-lying floodplains and mangrove systems (Hennessy et al. 2007; Hughes 2003). There will also very likely be future increases in the frequency of hot extremes and heavy precipitation events, and likely increases in the relative frequency of the most intense category 4 and 5 storms which cause substantial storm surges (Hennessy et al. 2007). By 2030, northern coastal areas of Australia will be 1 – 2°C warmer that 1990 mean values (Hennessy et al. 2004) and evaporation levels are expected to rise by 5 – 15% (Hennessy et al. 2007).

Brook (2008) considers the current warming event to pose a greater threat to biodiversity than most past climatic events in deep-time because of the pace of this change. The rapid warming of the Earth‟s atmosphere and surfaces will challenge the evolutionary adaptability of species (Visser 2008), especially since the resilience of many populations has been undermined through the combined loss of habitat, co-dependent species, and genetic variation (Spielman et al. 2004; Brook 2008). Moreover, global climate change acts in synergy with known causes of species decline (O'Grady et al. 2004), and amplified feedbacks have been demonstrated to cause extirpation of populations where no-single cause would have if acting in isolation or additively (Brook et al. 2008).

2.4 Plant-herbivore interactions

Complex interactions between plant and herbivore populations may be mutually beneficial, antagonistically one-sided, or detrimental to both communities (Crawley 1983; McNaughton 1986), and can be modelled on predator-prey theory (Holling 1959a; Rosenzweig & MacArthur 1963). The nature and strength of these relationships are spatially and temporally dynamic, and site-specific knowledge of these allows informed decisions relating to the outcomes of shifts (driven by climate change or other interacting threats) in plant or herbivore population abundance, structure and composition. Here we review the published literature for possible or known interactions between geese and *E. dulcis* sedge plants, including evidence for population-level feedbacks (either positive or negative), the temporal and spatial configurations of interactions, and evidence for herbivore dispersal triggers. An initial investigation showed a paucity of available data and published research; therefore we also selected articles on such interactions in an ecologically-similar Family, Anserinatidae. Waterfowl included were geese (tribes Anserini and Cereopsini) and swans (tribe Cygnini) from the sub-family Anserinae. We excluded other members of Superorder Galloanserae, such as ducks (Anatinae) and coots (Rallidae), because we regarded these as ecologically dissimilar to geese.

Interactions between waterfowl and foodplants include functional and numerical responses of bird populations to forage availability (Belanger & Bedard 1994), negative feedback loops where birds are the principal driver of change in plant populations (Jefferies & Rockwell 2002; Brathen et al. 2007), or positive feedbacks where waterfowl promote plant abundance (for example Prins & Nell 1990). An example of a negative feedback loop is that where the grubbing activity of Lesser snow geese (*Chen caerulescens*) caused considerable loss of graminoid vegetation on inter-tidal marshes (Jefferies & Rockwell 2002).

2.4.1The functional and numerical response

Theory on functional or numerical responses of predator populations to prey availability is based principally on the pioneering conceptual and analytical work of Buzz Holling (Holling 1959a, b). Tests on predation of pine sawflies by small mammals showed that predation rates increased with increasing prey population density (Holling 1959a, b), and that there were two principal effects, namely:

1) each predator within a population increased its consumption rate when exposed to increasingly higher prey densities (the functional response), and

2) predator densities increased as prey densities increased (numerical response).

The functional response modelled by Holling (1959b) is based on the principle of a time budget and assumes that predators spend their time on two types of activities: searching and prey handling (eating and processing). The consumption rates of predators are limited by these, and if prey is abundant, predators are still constrained in handling. Functional responses can be linear (Type I), asymptotic (Type II, and the most common) and S-shaped, or Type III (Holling 1959b; Real 1977). The numerical response predicts an increased rate of predator reproduction, and thus abundance in response to prey density. More typically in wild populations it can also represent an aggregation response of predators. Thus, herbivores, as plant predators, aggregate for periods of time in areas where food abundance is high, as has been shown in waterfowl populations (Jefferies et al. 1994; Rowcliffe et al. 1999).

Density-dependent numerical response is difficult to parameterise in highly mobile populations typical of many waterfowl. Functional type responses have been demonstrated in waterfowl (see Rowcliffe et al. 1999), although more typically, work has shown an aggregative response (Bayliss & Yeomans 1990; Bos et al. 2004). Some studies have demonstrated strong aggregative responses, for example Black Swan (*Cygnus atratus*) density was positively correlated with that of a favoured food plant (*r* = 0.95) in New Zealand (Mitchell & Wass 1996).

Ecologically, it is clear that waterfowl benefit from the seasonal availability of preferred forage (Person et al. 2003), and the loss of these food sources will alter plant-herbivore interactions to the detriment of herbivores.

2.4.2 Prey response

The numerical response of prey abundance to predation is evident through the predator-prey cycle (see Volterra 1931), whereby prey density declines, and then increases, relative to predator abundance. Herbivore-plant relationships are mixed: positive where plant („prey‟) growth is promoted or succession halted through herbivory and negative where the competitive ability of a community or species is reduced by predation pressure.

Wetland plant growth has been shown to be promoted (in response to herbivory) under some conditions, typically through nutrient loading (Gauthier et al. 1996; Post et al. 1998;

Zacheis et al. 2002), or compensation (Nolet 2004). Predation can also alter competitive interactions within wetland plant communities, to the advantage of one plant species (Bazely & Jefferies 1986), or in favour of an incumbent community by halting succession (Joenje 1985; Weisner et al. 1997). Waterfowl may also encourage vegetative growth without altering the competitive state of the waterplants (Nolet 2004). There is clearly a wide spectrum of observed responses – in some field-based studies, waterfowl had no measurable effect on the structure and biomass of favoured food plants (Beaulieu et al. 1996; Badzinski et al. 2006), whilst other authors have labelled geese as keystone species due to their ability to maintain or alter plant community structure and species composition (Olff et al. 1997).

As might be logically expected from predation, waterfowl have also been shown to negatively affect plant populations in a variety of ways. Field studies have documented substantial reductions in plant biomass in grazed or grubbed sites as opposed to protected sites (Esselink et al. 1997; Idestam-Almquist 1998; Kotanen & Jefferies 1997). Herbivory can cause decline in the net above-ground and below-ground wetland plant productivity (Cyr & Pace 1993; Gauthier et al. 1995; Bakker & Loonen 1998). Further, the impacts of waterfowl have precipitated the loss of vegetation cover, and shifts in wetland plant community structure and composition (Srivastava & Jefferies 1995; Jefferies & Rockwell 2002; McLaren & Jefferies 2004). The nature of the impact and long-term consequences for plant communities depend on the timing of herbivory, location (part of plant consumed) and amount taken (Crawley 1983), as well as duration over successive annual cycles.

2.4.3 Migration triggers

Mobile herbivore populations have a greater capacity to adapt to resource availability than sedentary species and as such, habitat switching is an effective response to the heterogeneous configuration of food-plant communities (Crawley 1983). Waterfowl may respond to plant abundance through dispersal, and there is evidence of giving-up densities or departure thresholds that are almost entirely determined by food-plant abundance. For example, Brent geese (*Branta bernicla*) were recorded to switch (food) from algal beds to salt marsh, and then to agricultural fields following resource depletion (Vickery et al. 1995), and Tundra Swan (*Cygnus columbianus*) predating on pondweed tubers migrated when these fell below 12 g per m^{-2} (Nolet & Drent 1998; Nolet et al. 2001). Migration triggers may also be seasonally influenced, such as day-length periods (Ball 1983).

2.4.4 Plant refugia

Seasonal variation in plant growth might allow temporal refuge from predation (to plants), and likewise the spatial heterogeneity of plant abundance allows for spatial refugia (Crawley 1983). The forage activity of migratory waterfowl is transient (Rowcliffe et al. 1999; Noordhuis et al. 2002), allowing subsequent plant regeneration, and indeed plants can take refuge from predation by growing tubers out-of-reach of grubbing waterfowl. For example, Santamaria et al. (2002) showed *Potamogeton pectinatus* (Potamogetonaceae) tubers escaped predation below 275 mm of soil depth. In recent times, access to cereal crops and grazing lawns has opened up a supplementary diet to many waterfowl species and thus a refuge to wetland plants (Lane et al. 1998; Fox et al. 2005; Gauthier et al. 2005).

While research on geese has not explicitly shown the type and strength of relationship between these and *E. dulcis* populations, some evidence implies a strong aggregative response of geese during the late-dry season, and a sigmoidal functional response to forage availability (Whitehead 1998). A migration threshold is apparent when geese depart from floodplains following drying (Whitehead 1998), although empirical estimates of giving-up densities have not been systematically measured. Moreover, an apparent positive (density) feedback loop between geese and *E. dulcis* has not been quantitatively verified. While it is likely that nutrient loading may benefit food plant growth, the drying and flooding of wetlands across tropical Australia forces herbivore departure and thus provides critical temporal refuge to food plants. Shifts in climatic parameters might alter these, to the detriment of geese (Eliot et al. 1999; Hughes 2003).

2.5 Mechanisms of change

We have used geese and tropical Australian coastal floodplains as a case study because of the ecological and cultural importance of World Heritage listed Kakadu National Park. Discussion here of possible mechanisms that require future adaptation in this system will allow research of these and similar tropical systems.

Across Australia‟s tropical coastal regions, the following scenarios are likely under global warming:

1) Sea level rise. A projected global rise of 0.22 – 0.44 m by 2090 is virtually certain (Bindoff et al. 2007) and multi-metre rises on a century time scale, due to accelerated ice sheet dynamics cannot be confidently ruled out (Hansen 2007).

2) Increased atmospheric CO_2 levels. Global CO_2 levels are anticipated to reach 450 – 1 000 ppm by 2100, assuming emission reduction (IPCC 2007).

3) A rise in mean atmospheric temperatures. These are projected to increase by 0.2 – 2.2°C by 2030, and 0.8 – 7.2°C by 2070, relative to 1990 levels (Hennessy et al. 2007) and with increases likely to be in the lower ranges for coastal regions (Hennessy et al. 2004).

4) An increase in rainfall is across coastal regions. Monsoonal rainfall patterns (here November through March) are unlikely to change (Hennessy et al. 2004) – although this conclusion is subject to a high degree of uncertainty regarding abrupt shifts, with some models predicting sudden instability of the Indian monsoon (Lenton et al. 2008).

5) More Category 4 and 5 cyclones (Hennessy et al. 2007). Intense tropical cyclones will cause greater inland penetration of storm surges and enhanced saline water intrusion (Hennessy et al. 2004).

6) More frequent hot days and nights (Hennessy et al. 2004; IPCC 2007).

7) Possible increased emerging infectious disease and epizootics, through vector range expansion (Rogers & Randolph 2006) and disruption due to vector-host-pathogen relationships (Brooks & Hoberg 2007; Olwoch et al. 2008).

Ostensibly, global warming will likely affect tropical (wetland) plant growth, plant community composition and structure, plant phenology, waterfowl abundance, phenology and patterns of spatial distribution and density (of plants). Heightened sea levels and saline water intrusion will alter coastal, estuarine and floodplain plant communities (Mulrennan & Woodroffe 1998; Hennessy et al. 2007). Dominant floodplain plants such as *E. dulcis*, which are adapted to the fresh-brackish water transitional zone (Cowie et al. 2000), will give way to more salt-tolerant plant communities. Storm surges will increase the risk and rate of saline water intrusion, and shifts in time-period of floodplain inundation and drying will further alter plant community composition (Finlayson et al. 2006).

The impact of increased CO_2 levels (as well as other long-lived greenhouse gases CH_4, N_2O, and O_3, linked to fossil fuel emissions or acting as precursors) on plant growth will vary, but will in general favour C_3 plants (Larson 1994; Weltzin et al. 2003). Competitive plant interactions will likely change through this factor alone (Stacey & Fellowes 2002). *E. dulcis* is resilient in this respect, being adapted to switch between C_3 and C_4 photosynthesis and so we predict that it will remain competitive under changes in CO_2 levels (Cowie et al. 2000).

Temperature rises may benefit tropical plant growth (Cowie et al. 2000). Evaporation rates are likely to increase and this will possibly favour plant communities adapted to drier or more saline conditions. Waterfowl immuno-suppression may occur through heat stress, increasing the incidence and impact of infectious diseases (Olwoch et al. 2008; Senior 2008).

Changes in season duration and day-night temperature regimes may affect geese phenology, such as dispersal dates and breeding periods (Chambers et al. 2005). Changes to seasonal dispersal will alter site-specific plant-herbivore interaction. For instance, the first arrival and last departure dates of migratory Australian waterfowl have changed in response to modest warming over the past few decades (Beaumont et al. 2006). Elevated temperatures may additionally increase the frequency and severity of bacterial disease outbreaks, such as avian cholera (Blanchong et al. 2006).

2.6 Future research

Assumed mechanisms of change in goose-wetland interactions allows the development of multiple competing hypotheses (see Burnham & Anderson 2001) that can be challenged with field data. We recommend two key areas of future research on geese in northern Australia: first the abundance of *E. dulcis* is critical to maintaining the present-day geese populations (Frith & Davies 1961; Bayliss & Yeomans 1990), and therefore any effort to determine drivers of *E. dulcis* abundance - and likely outcomes through climatic changes - will go a long way toward pre-empting the extirpation of geese. Second, competing hypotheses that determine or infer key drivers of goose abundance (principally on survival and fecundity) can be used to test the impacts of environmental shifts through global warming. These can be incorporated into predictive metapopulation models (for example Brook & Whitehead 2005b) that allow consideration of future management options, such as restriction on harvest.

We elaborate further: the key drivers of *E. dulcis* abundance (a factor of both germination success, and seedling and adult plant survival) are floodplain water salinity, timing and duration of flooding (Frith & Davies 1961), soil nutrient content, intensity and duration of predation (includes pigs and magpie geese) and competition with invasive plants (Frith & Davies 1961; Rossiter et al. 2003). Field and laboratory-based experiments can test these and determine the critical variables that influence *Eleocharis* abundance - using an information-theoretic approach based on likelihood (McCarthy 2007). Laboratory-based experiments can replicate predicted changes in water and air temperature, rainfall regimes, water salinity and rise in CO_2 levels. These will not only indicate critical environmental variables, but also life history parameters (of *E. dulcis*) sensitive to changes (such as germination or seedling success). Varying levels of root tuber predation can also be incorporated and account for a possible rise or decline in goose and feral pig abundance.

So, for example multiple competing hypotheses that test the response of *E. dulcis* can start with:

1) *E. dulcis* density ~ water salinity

2) *E. dulcis* density ~ water salinity + period of inundation

3) *E. dulcis* density ~ predation, and so on.

Field data can be collected and the above-mentioned hypotheses fitted using generalised linear models (Burnham & Anderson 2001). Some good examples of this approach in tropical Australia are Banfai et al. (2007) and Lehmann et al. (2008).

Likewise, the abundance and spatial distribution of magpie geese across northern Australia is the product of forage availability, especially *E. dulcis* during the dry season (Bayliss & Yeomans 1990), the availability of nesting sites and nest-building material (Whitehead 1998), disease and hunting pressure (Brook & Whitehead 2005b). Population models can test the resilience of magpie geese across tropical Australia to habitat loss through sea level rise (Eliot et al. 1999) by calculating percent loss of habitat under rising oceans. These can further incorporate increasing severity and probability of epizootics and increased predation by a burgeoning human population. Predictive population models can further be linked to habitat suitability maps for *E. dulcis* under climate change to test the outcomes of habitat loss (for example Keith et al. 2008). Past research suggests that saline water intrusion through sea level rise will force the extirpation of *E. dulcis* (Frith & Davies 1961; Mulrennan & Woodroffe 1998) and we speculate that this factor alone will dramatically alter the nature and extent of interaction between *E. dulcis* – geese populations (see also Eliot et al. 1999; Finlayson et al. 2006).

2.7 Conclusions

Our review of wetland-waterfowl interactions across the tropics reveals a paucity of peer-reviewed literature and relevant data for risk assessment, particularly for vulnerable regions such as northern Australia. The bias in the literature toward temperate waterfowl species may be a cultural artefact of European and north American interest in hunting of waterfowl, and the pest status of some of these species to agricultural interests (for example, Crawley & Bolen 2002). Moreover, little information is available regarding the interactions between magpie geese and their favoured wetland habitat, despite the economic and cultural importance of these to Australians (Whitehead et al. 1988; Whitehead et al. 2000).

A review of ecologically-similar temperate waterfowl shows that a number of important predator - prey relationships are possible between waterfowl and wetlands, and that these relationships can influence both the spatial and temporal configuration and densities of the respective populations (Rowcliffe et al. 1999). Inferences from these are possible for the tropics, although context-specific and field-based research is required to verify these. Importantly, ongoing and accelerating shifts in climatic and environmental variables will alter interactions (Soussana & Luscher 2007). While it might not be possible to prevent transition between ecological states, careful consideration of the plausible mechanisms of change and the likely outcomes, as we have done for geese, is needed to act as a catalyst for research and subsequent decision making (Lim et al. 2008). This process provides the relevant background needed for the development of an *a priori* set of multiple hypotheses (Burnham & Anderson 2001) – in our specific case on plant-herbivore interactions between geese and *E. dulcis*, and so allows these ideas to be challenged with field data and better-designed monitoring programmes. The hypotheses that we have outlined, and the building of more complex population models are likely to be the cornerstone of adaptive management and policy regarding geese (and other tropical waterfowl) over the next few decades.

CHAPTER THREE

3. CLIMATE CHANGE ENHANCES THE POTENTIAL IMPACT OF INFECTIOUS DISEASE AND HARVEST ON TROPICAL WATERFOWL

Published as a research paper in *Biotropica* by Lochran W. Traill, Corey J. A. Bradshaw, Hume E. Field and Barry W. Brook

Lead author Traill reviewed all literature outlined in this review, took the lead in writing all draft manuscripts, prepared all data and ran all analyses and the presentation of these (score of 0.9). Brook guided the structure of the manuscript and relevance of disease to global change and recommended models (0.05). Bradshaw gave advice on data analyses and commented on draft manuscripts (0.025) and Field commented on draft manuscripts and provided a veterinary perspective (0.025).

All co-authors agree that this manuscript can be submitted as a chapter for a PhD thesis.

Abstract

Global warming exacerbates threats to biodiversity as ecological systems shift in response to altered climatic conditions. Yet the long-term survival of populations at direct risk from climate change may also be undermined by local factors such as infectious disease or anthropogenic harvest, which leave smaller and more isolated populations increasingly vulnerable to the rapid pace of global change. We review current and future threats to an exemplar tropical waterfowl species, magpie geese, and focus on the potential synergies between infectious diseases, harvest and climate change. We outline viral, bacterial and fungal pathogens likely to cause disease in geese, and give mention to parasites. Further, we elaborate on a previously developed, spatially explicit population viability model to simulate demographic responses to hunting and novel or enhanced disease outbreaks due to climate change. With no harvest, the simulated disease epizootics only threatened metapopulation viability when both mortality rate was high and outbreaks were regular (a threshold response). However, when contemporary site-specific harvest is included as an additive impact, the response to disease severity and probability was linear. We recommend field research to test these hypotheses linking drivers of waterfowl population decline to disease-climate change interactions.

3.1 Introduction

The predicted effects of global climate change on the extinction risk of most species and ecosystems are still highly uncertain. While there is reasonable evidence to demonstrate that global warming heightens extinction risk (Nogués-Bravo et al. 2008; Sekercioglu et al. 2008; Sodhi et al. 2008), the dominant mechanisms driving demographic changes that can result in extinction due to global warming, and particularly the potential interactions between climate change and other anthropogenic stressors, are not well-quantified (Brook 2008). Recent studies have linked climate change to shifts in species abundance and range (Murray et al. 2006; Nogués-Bravo et al. 2008) and changes in phenology and behaviour, but only a few have directly attributed extinctions to climate change (Sekercioglu et al. 2008), and some have disputed particular hypothesised links (for example Lips et al. 2008).

One reason for this uncertainty is that changes in climatic parameters are not expected to be uniform across geographic regions (IPCC 2007), and the impacts of these on local environments, and species populations therein, are likely to be complex and nonlinear (Parry et al. 2007). The mechanisms of species extinction through climate change will depend on interactions between the drivers of global change and localised threats, the net effect of amplifying (positive) and attenuating (negative) feedbacks (Brook et al. 2008), and the ability (or lack thereof) of species to adapt to shifting conditions (Visser 2008).

Population persistence is intricately linked to a suite of deterministic drivers of decline and intrinsic characteristics that may be unique to the location and population (Traill et al. 2007). Drivers of extinction include habitat loss, overexploitation, invasive species (via competitive exclusion or predation) and infectious diseases (Gilpin & Soulé 1986). These may act singularly or simultaneously, and by reducing species to small and isolated populations, they leave them (populations) more vulnerable to environmental and demographic stochasticity and catastrophic events (Caughley 1994). For example, habitat loss, hunting pressure, and competition have forced once-numerous, contiguous African antelope populations in Zimbabwe into disconnected wildlife reserves, allowing a recent, single disease event nearly to eradicate them from the region (Clegg et al. 2007). Thus, a synergy of processes can combine ultimately to precipitate species extirpation (Brook et al. 2008). Synergies between local drivers of decline and climate change are difficult to anticipate, but are expected to play a pivotal role in future extinction events (Brook 2008).

Harvest and infectious diseases can interact to drive species to extinction (Smith et al. 2006; Rizkalla et al. 2007), and global warming may contribute further by facilitating the spread of existing pathogens or the emergence of new diseases (Epstein 2002; Zell 2004; Senior 2008). Although recent work has reviewed the likely impacts of global warming on biodiversity (Parry et al. 2007; Sekercioglu et al. 2008), the evidence has thus far been skewed heavily toward temperate regions (see Sodhi et al. 2007). Given that tropical regions harbour some of the greatest species richness and endemism, and tropical species tend to be more physiologically susceptible than temperate species to small changes in temperature (Deutsch et al. 2008), the threats posed by climate change will be particularly pronounced in this region (Sodhi et al. 2007).

Here we consider the impacts of climate change-enhanced infectious diseases on a wide-ranging tropical waterfowl species, the magpie goose, and simulate the changing consequences of these under alternative harvest regimes. Although not currently threatened (IUCN 2008), geese have been historically eliminated from their previously extensive southern range through the additive effects of habitat loss, hunting, toxicosis and predation (Nye et al. 2007). Research on the exemplar tropical goose population, which has been well-studied since the 1960s (Frith & Davies 1961), will be useful to gauge the potential effect of disease–climate change interactions on other tropical waterfowl species and will contribute toward pre-emptive conservation action for geese.

To achieve these objectives, we first review avian diseases affecting Anseriformes and derive or infer:

1) pathogens and parasites most likely to cause morbidity and / or mortality in geese;

2) the frequency and severity of past mass-mortality events in geese, or ecologically similar waterfowl;

3) the ecological correlates of these events, such as high temperatures and anaerobic wetland conditions; and

4) possible mechanisms of disease spread or enhancement through global change.

Second, we simulate the outcomes of epizootics in tropical geese populations under increasing frequency and severity and include harvest as a present-day threat that can potentially be managed. We discuss the implications of the disease-harvest-climate change synergy for population persistence and the sustained use of magpie geese.

3.2 Global and tropical climate change

Modern and rapid global warming is evident from a consistent increase in air and ocean temperatures, the melting of polar and montane snow and ice, and rising mean sea levels (IPCC 2007). Global mean surface temperatures have increased by 0.74°C (0.56 – 0.92°C) in the last 100 years (IPCC 2007) and the projections for mean global sea level rise by 2100 are 0.5 – 1.4 m above that of 1990 (Rahmstorf 2007), and substantially more (3 – 5 m) should the recent changes in ice sheet dynamics in Greenland and West Antarctica continue to accelerate over the next few decades (Hansen 2007). Sea levels have been altered through thermal expansion of the oceans and the exchange of water between oceans and frozen reservoirs such as glaciers, ice sheets and ice caps (Bindoff et al. 2007). These temperature and geophysical changes have been attributed primarily to the (anthropogenic) combustion of fossil fuels releasing CO_2 and other long-lived greenhouse gases (IPCC 2007). As a result, global atmospheric CO_2 concentration has risen from pre-industrial levels of ~ 280 parts per million (ppm) to 385 ppm by 2006 (IPCC 2007).

Shifts in climate are not expected to be uniform across geographic regions, and the impacts on biodiversity will be asymmetrical. For example, some biomes are projected to be worse-affected than others, including low-lying coastal wetlands, saltmarshes, mangrove systems, coral reefs, the sea-ice biome, mid-latitude Mediterranean systems and the Arctic tundra (Parry et al. 2007). As an example of a tropical system, north Australia is projected to experience sea level rise and more frequent and penetrating saline intrusions into freshwater systems due to increased storm surges (Bindoff et al. 2007), increased CO_2 concentration affecting plant growth and competitive interactions (Malhi & Grace 2000), heightened mean temperatures (0.2 – 2.2°C by

2030, and 0.8 – 7.2°C by 2070) relative to 1990, increased rainfall and more intense (but not necessarily more frequent) cyclones (Hennessy et al. 2007).

Brook (2008) argued that the current warming event poses a greater threat to biodiversity than past Quaternary events because recent anthropogenic climate change is occurring at a rate faster than would have likely occurred in the past (see also Visser 2008). Rapid shifts in environmental conditions (such as through global change) challenge the evolutionary adaptability of species (Franklin 1980), especially for those populations whose resilience has been undermined already by loss of habitat area, degradation of habitat quality, and loss of genetic variation (Spielman et al. 2004; Brook 2008). Synergies between pathogens and climatic shifts are known (Paz et al. 2007; Pascual et al. 2008), and are therefore a serious concern for the preservation of biodiversity.

3.3 Climate change and infectious diseases

Climate is an important determinant of the global range limits of infectious diseases, and regional weather patterns may play an important role in modifying the risk and severity of disease outbreaks (Epstein 2002). Shifts in rainfall or temperature favour the emergence of new diseases, or outbreaks of existing diseases; global warming has contributed toward the worldwide emergence and redistribution of infectious diseases since the 1970s (Epstein 2001). For example, Smith et al. (2006) found that disease acted concomitantly with habitat loss, hunting and competition in the extinction of 18 bird species across the world‟s biomes.

Global warming may interact with disease in a number of ways:

1) Shifts in climate can cause range expansion of disease vectors and so facilitate the invasion of the pathogens they carry (Epstein 2002). For example, global warming has been implicated in the spread of pathogenic chytrid fungi and the subsequent extirpation of endemic anurans in Costa Rica (Pounds et al. 2006, but see Lips et al. 2008);

2) Climate shifts might also weaken an individual‟s body condition, immune response and adaptive capacity through habitat loss, extreme weather events or prolonged periods of resource scarcity (Epstein 2001). These conditions can then permit the expression of disease in hosts that might otherwise have been resistant. For instance, nutritional stress enhances the risk of Hendra virus infection in Australasian flying foxes (Plowright et al. 2008a);

3) Warming can also hasten pathogen development and increase survival; growth rates of marine bacteria and fungi are correlated with temperature (Harvell et al. 2002), and increased infection rates of tropical Columbids by parasitic flagellate protozoa have been linked to warmer temperatures (Bunbury et al. 2007).

3.4 Infectious diseases and tropical waterfowl

Given these observed and hypothesised interactions, an appropriate step for proactive species conservation is the documentation of infectious diseases that do and may potentially infect populations, the measurement of their known or likely effects on mortality rates, and inference on possible mechanisms of these under climate change. Below we consider the role of infectious disease in waterfowl populations; although we include reference to epizootics in temperate regions, we only include these where there is the potential for occurrence in the tropics. We base the review below on the major taxonomic groupings of pathogens (i.e., viruses, bacteria, fungi and parasites) and summarise pathogens and parasites most likely to cause disease in our case study species.

3.4.1 Viral diseases

Viral infections have been responsible for substantial mortality in avian populations and waterfowl are epidemiologically important by acting as natural reservoirs and sources of transmission (Hess & Pare 2004; Tracey et al. 2004). Indeed, waterfowl play a potentially pivotal role in the transmission of viruses in tropical regions because of the sizes of communal aggregations on seasonal tropical floodplains (Bayliss & Yeomans 1990) and mingling of these populations with those of migratory species (Tracey et al. 2004).

Duck viral enteritis, or duck plague, is transmitted primarily through viruses shed in faeces (Hess & Pare 2004). An epizootic killed ~ 43 000 waterfowl in North America, including muscovy (*Cairina moschate*), mallards (*Anas platyrhynchos*) and black ducks (*Anas rubripes*) (Converse & Kidd 2001). Virulence in magpie geese is unknown, but Spieker et al. (1996) found that Canada geese (*Branta canadensis*) were less susceptible than duck species.

Goose parvovirus infection seriously affects goslings, with extremely high (up to 99%) mortality (Jansson et al. 2007). Prevalent in Asia, transmission may be faecal-oral, or via eggshell from sub-clinically infected geese (Hess & Pare 2004). Tropical anatids are also susceptible to infection by Newcastle disease virus (NDV), but typically do not develop disease symptoms. Velogenic NDV were however, responsible for outbreaks among farmed geese in China, accounting for 17.5% morbidity and 9.2% mortality (Wan et al. 2004). Geese may play an important role in the epidemiology of this disease by acting as a reservoir and dispersal agent (Hess & Pare 2004). Pathogenesis (of NDV) in magpie geese is unknown, and monitoring of a NT population in 2006 showed nil sero-prevalence (AQIS 2006).

Tropical waterfowl are an important reservoir and possible dispersal agent for avian influenza viruses (Tracey et al. 2004). With 65.9 % of all avian influenza virus (AIV) isolates sourced from Anatidae (Kaleta et al. 2005), global prevalence in geese ranges from 0.6 - 2.2% (Munster et al. 2007), and outbreaks are uncommon. Nonetheless, mortality from these can be high; a recent H5N1 epizootic killed 5 to 10% of a bar-headed goose (*Anser indicus*) population in western China (Chen et al. 2005). North Australian geese carry low pathogenic strains of AIV, and the high pathogenic strains are fatal (AHS 2006; AQIS 2006). Faecal-oral transmission (Friend & Franson 1999) may be high where geese aggregate on large shallow-water wetlands and mix with migratory shorebirds and numerous other waterfowl (Tracey et al. 2004).

West Nile Virus (WNV) is a zoonotic virus that belongs to the Japanese encephalitis virus antigenic complex and is primarily transmitted by mosquitoes (Hess & Pare 2004). Susceptibility appears to vary among species with high mortality rates in young domestic geese: 692 of 2 731 goslings (25%) over 10 days in the USA (Austin et al. 2004), 160 of 400 goslings (40%) in Israel (Swayne et al. 2001), and 504 of 3 600 (14%) in Hungary (Glavits et al. 2005). The status of WNV and indeed, Japanese B encephalitis, in northern Australia is unknown, nor is the pathogenicity of flaviviridae in geese. It is possible that the species might act as a reservoir for WNV, or other Japanese encephalitis strains, were these to be introduced to northern Australia. Waterfowl are implicated in the cycle of many other arboviruses such as Murray valley encephalitis, Ockelbo virus, Sindbis virus and Usutu virus, and may act as susceptible dead-end hosts or reservoirs (Chvala et al. 2006; Chvala et al. 2007).

Outbreaks of haemorrhagic nephritis enteritis occurred in farmed goose flocks of 3 – 10 weeks in age, and mortality was between 4 – 67% (Palya et al. 2004). A distinct polyomavirus species comprising variable strains was attributed as the cause (Palya et al. 2004).

3.4.2 Bacterial diseases

Bacterial infections are a more common cause of mortality in waterfowl than are viral diseases (Friend & Franson 1999). Bacteria of the genus *Clostridium* in particular are responsible for more wild bird deaths than other disease agent, and avian cholera has become the most important infectious disease of waterbirds in North America (Friend & Franson 1999; Friend 2002). Although some data are available on bacterial disease outbreaks in temperate regions, few exist for the tropics.

Avian botulism has been responsible for the deaths of many thousands of individual waterfowl (Friend 2002). Anaerobic bacteria (*Clostridium botulinum*) Type C produce dormant spores that remain viable and widely distributed in wetland sediments for decades (Rocke & Samuel 1999). Neurotoxin is produced after the spores germinate, usually under anaerobic conditions and high temperatures (30–37°C), and ingestion leads to lethal paralysis and death (Rocke & Samuel 1999). Outbreaks are likely to occur where birds occupy shallow, stagnant waters where dissolved oxygen content is low, temperature exceeds 20°C, and decaying animal material is abundant (Rocke & Samuel 1999). Losses of waterfowl (due to botulism) have been high; on the Salton Sea, Friend (2002) documented large-scale mortality events where 2,000 to 6,000 waterfowl perished. In tropical Australia, mass mortality (up to thousands) of geese on the floodplains of the Mary River during the hot, late dry season of 1989 has been witnessed (P. Whitehead, pers. comm., Australian Government).

Avian cholera is a contagious disease that results from infection by the bacterium (*Pasteurella multocida*) (Friend & Franson 1999). Environmental contamination from diseased birds is a primary source for infection, and high concentrations of *P. multocida* have been found in waters several weeks following waterfowl mortality events (Friend & Franson 1999; Waldenstrom et al. 2003). Ingestion appears to be the most common form of infection, particularly for grubbing waterfowl species, followed by bird-to-bird contact and aerosols (Friend & Franson 1999). It is likely that most bird species may become infected with *P. multocida*, but pathogenesis appears to depend on the bacterium strain, host susceptibility and the infectious dose (Samuel et al. 2007). Chronic low-level mortality may continue throughout the year and so account for a substantial portion of annual population loss, yet it may be overlooked because it does not lead to mass kills (Samuel et al. 2007). Mortality events in lesser snow geese (*Chen caerulescens*) have been recorded for 20,000 – 30,000 individuals (Blanchong et al. 2006). These authors also found that wetland water conditions are not strongly associated with the risk of cholera outbreak, but that eutrophication and El Niño climate events can cause *P. multocida* to flourish.

Of 20 known strains of *Mycobacterium avium* causing avian tuberculosis, three lead to disease in waterfowl (Friend & Franson 1999). Transmission is through bird-to-bird contact or ingestion of contaminated water. Disease appears to be present within most wild bird populations

(Friend & Franson 1999). The status of avian tuberculosis in north Australian geese is unknown, but *M. avium* can survive for long periods outside of the host, and because transmission is typically faecal-oral (Friend & Franson 1999), infection is likely.

Other bacterial diseases caused by species such as *Clostridium perfringens* have caused mass mortality in waterfowl species; following an abrupt change in diet, the bacterium proliferates and produces toxins (Wobeser & Rainnie 1987). *Salmonella* bacteria also cause disease in avian species, notably salmonellosis (Friend & Franson 1999). Transmission is usually through ingestion and the longevity of the bacteria outside of hosts makes some tropical waterfowl species vulnerable.

3.4.3 Fungal diseases

It is likely that disease-causing fungi are common on tropical floodplains, and opportunistic infections may occur when birds are immuno-suppressed. Three basic types of avian disease are caused by fungi: mycosis (direct invasion of tissues by fungal cells), mycotoxicosis (from ingestion of toxic fungal metabolites) and allergic disease (Friend 2002). Respiratory tract infection may result from aspergilliosis (*Aspergillus fumigates*) caused by a saprophytic mould growing on damp soils, organic debris and decaying vegetation. Aspergilliosis is reported worldwide and outbreaks have occurred in waterfowl, usually acting concomitantly with immuno-supression precipitated by lead poisoning, injury or drought (Friend & Franson 1999).

3.4.4 Parasites

Many tropical waterfowl are infected with parasite fauna. Anecdotal evidence suggests that geese have a waterfowl-typical helminth parasite fauna: cyclocoelid flukes are prominent during the tropical dry-wet transition months, and high loads of *Echinostoma* flukes have been found in magpie goose goslings (W. Freeland, pers. comm., Australian Government). Further, avian malaria is a known threat to migratory waterfowl using tropical wetlands (Wikelski et al. 2004; Mendes et al. 2005). The symptoms of these are unknown, but it is possible that parasites reduce body condition and so contribute toward bird mortality during periods of nutritional stress or injury.

In summary, duck plague, strains of the AIV, avian botulism, cholera and aspergilliosis are most likely to cause catastrophic mass mortality events among tropical geese populations, and tropical waterfowl species in general. High temperatures, anaerobic wetland conditions and mass aggregations of waterfowl might precipitate epizootics. The frequency and severity of these is unknown, but we speculate that the predicted rise in mean atmospheric temperatures in tropical Australia by as much as 7.2°C by 2070, and more frequent hot days and nights (IPCC 2007) will facilitate increased disease outbreaks.

Our review highlights the array of diseases that do and potentially could affect mortality rates in tropical waterfowl, and demonstrates two important aspects relevant to population persistence. First, failure to incorporate the probability of mass mortality events (catastrophes *sensu* Reed et al. 2003a) arising from disease could seriously compromise estimates of population extinction, and tropical waterfowl are particularly susceptible given their general foraging mode, migratory behaviour and exposure to a wide range of pathogens (Tracey et al. 2004). Indeed, the inclusion of disease in population viability analyses of threatened avian species populations greatly increases extinction risk (Brook & Kikkawa 1998). Second, mortality arising from disease can go unnoticed because it does not necessarily occur in punctuated mass events; rather, disease reduces average survival rates below that expected naturally or from hunting and predation (Ives & Murray 1997).

To illustrate these aspects and their implications for population persistence, we next model the dynamics of a well-studied species of tropical waterfowl, incorporating natural, disease-related and predation (traditional and recreational harvest) mortality to examine their relative and interacting contributions to extinction probability under climate change. Further, our work addresses recent concerns about the lack of realistic population models in avian research (Beissinger *et al.* 2006).

3.5 Persistence of magpie geese in northern Australia

3.5.1 Ecology, life history and threats

Native to Australia and New Guinea, and sole members of the family *Anseranatidae*, magpie geese are estimated at ~ 3.5 million individuals in the NT of Australia alone (Bayliss & Yeomans 1990; Whitehead et al. 1992). Populations depend on extensive sub-coastal wetlands for forage and breeding (Bayliss & Yeomans 1990). During the dry months (June through October), geese aggregate in flocks of up to 250,000 on shallow-water wetlands, and grub for tubers of the sedge plant *E. dulcis* (Whitehead et al. 1992). Ephemeral floodplains with dense plant growth are used for nesting following monsoonal rains, and dispersal is seasonally nomadic, typically between favoured forage and nesting sites (Whitehead et al. 1992). Mean adult weight is 2.8 and 2.0 kg for males and females, respectively (Frith & Davies 1961).

Current threats to tropical Australian populations include habitat loss to invasive plants, saline water intrusion and eventual inundation through sea level rise (Lonsdale 1994; Hennessy et al. 2007), wetland alteration by non-native swamp buffalo (*Bubalus bubalis*) and pigs (*Sus scrofa*) (Bradshaw et al. 2007), poisoning by spent lead shot (Whitehead & Tschirner 1991), emerging infectious diseases (as discussed previously), and unsustainable hunting rates (Brook & Whitehead 2005b). Recreational harvest of geese in northern Australia is estimated at ~ 30 000 birds year^{-1} (Brook & Whitehead 2005b), and is regulated through a licence system (Whitehead et al. 1992). Unregulated aboriginal harvest is estimated to be ~ 50 000 to 150 000 birds year^{-1}, and recreational harvest is considered sustainable if the current environmental conditions prevail (Brook & Whitehead 2005b). We note that shooting by tropical fruit-growers and mortality through injury (by lead shot) has not been estimated, and is likely to raise these figures (see for example Noer et al. 2007).

3.5.2 Response to global warming

Physiologically, geese are adapted to cope with tropical extremes of heavy rainfall and high temperatures (Frith & Davies 1961; Whitehead et al. 1992). It is unlikely that temperature shifts will affect geese directly, other than the most extreme projections. There is some support from climatological models for a change in the return time or intensity of El Niño-Southern Oscillation, and instability of the tropical monsoon (IPCC 2007), but their implication for northern Australian ecosystems remains unclear. Ecologically, geese are generalist herbivores capable of dispersal in response to food availability (Frith & Davies 1961), and present populations are large enough to maintain genetic heterozygosity and evolutionary adaptability (Franklin & Frankham 1998). There is evidence, however, that changed hydrological regimes may affect geese nesting habits to the detriment of tropical populations (Whitehead 1998).

Habitat loss, infectious disease, and unchecked harvest (Brook & Whitehead 2005b) pose the most serious global warming-linked threats to tropical geese populations. Below we model likely population scenarios where disease outbreaks are included and where harvest is regulated or allowed to continue.

3.5.3 Minimum population size, disease and harvest

To test quantitatively the effect of disease on north Australian geese, we incorporated an additional mortality factor in a stage-structured metapopulation model of geese developed by Brook and Whitehead (2005a). In that study, the long-term impacts of recreational and aboriginal hunting on geese were considered, based on available survey data on population size and spatial distribution, dispersal, survival and site-specific harvest regimes. The details of the original model constructed using RAMAS Metapop Ver. 4 (Akçakaya & Root 2001) are described in Brook and Whitehead (2005b).

To consider the role of novel or climate change-enhanced infectious disease, we sampled from a broad „parameter space" of a likely epizootic frequency and severity in geese in the modified population models, with and without harvest. We first constructed a dataset for a population reduction multiplier – i.e., a factor that reduces the population abundance according to the estimated die-off from disease (severity). For example, to estimate additional mortality due to disease of 10%, a population reduction multiplier of 0.9 is used. We derived 100 reduction multipliers by sampling randomly from a uniform distribution with a range of 1 – 99%. We then followed the same process for the frequency of an outbreak. Here we considered the probability of occurrence to fall realistically between 0 to 25% per time step (year) – i.e., from no chance of an outbreak through to an average of one outbreak every four years, and derived a random dataset (100 points) of these values. RAMAS-based PVAs allow both of these parameters to be specified (see Akçakaya & Root 2001). The severity and frequency datasets where then randomly paired by sampling each parameter (without replacement) until 100 sensitivity scenarios were produced.

Each parameter combination was then iterated 100 times in the base RAMAS model, and the population was projected 100 years into the future. We ran simulations for two harvest scenarios where: (1) harvest was 130 000 birds yr^{-1} based on field data for northern Australia (Brook & Whitehead 2005b); and (2) no harvest was allowed. Outputs for these were final population size and Expected Minimum Abundance (EMA) of the total goose population over the 100-year projection interval. EMA is the average of the smallest population size attained in each iteration, and is a useful indicator of the propensity for species decline because it is not a bounded [0 – 1] measure like extinction probability, where large regions of the scenario space may produce predictions of either 0 or 1, and are therefore uninformative (McCarthy & Thompson 2001).

We used generalised linear mixed-effects models to examine the relationship between frequency and severity of disease and harvest on EMA, fitting these via maximum likelihood in the R Language (R Core Development Team 2007). An index of Kullback-Leibler (K-L) information loss was used to assign relative strengths of evidence to the different competing models, and Akaike‟s Information Criterion (AIC_c) was used as an objective means of model comparison (see Burnham & Anderson 2001). Hunting mortality had a stronger influence on EMA than the probability of disease (R^2=0.71 for EMA ~ hunting mortality and R^2=0.27 for EMA ~ probability of disease), but the interaction between these variables provided the best model fit (AIC_c weight [$wAIC_c$]=0.552, deviance explained = 97%). We controlled for harvest type by including it as a random effect.

PVA results for both harvest and no-harvest scenarios show that geese populations are more resilient to disease when harvest is disallowed. Fitted linear regression between mortality and EMA (Fig. 3.1 a, b) show a delayed (threshold) decline of the goose population when harvest is absent, but a more consistent linear response, and a reduced population viability across a broad range of disease scenarios, under current harvest pressure. These threshold *versus* linear response predictions are best illustrated where we fit smoothed three-dimensional plots of EMA both to disease severity and probability of an outbreak occurrence (Fig 3.2 a, b). Field studies have shown that harvest and disease can act in synergy to drive species to local extinction (Rizkalla et al. 2007; Vogel 2007). Total restriction on traditional harvest of geese is unrealistic, but these findings do nonetheless highlight the ecological importance of ensuring that harvest is constrained, particularly if populations are challenged simultaneously by habitat loss and epizootics.

A review of available literature suggests that catastrophic die-offs are likely to occur with probability of ~ 0.14 generation^{-1} in vertebrate populations (Reed et al. 2003a). Generation length in Reed et al. (2003a) was the average age of mothers across all offspring produced. We speculate that this may be ~ 5 years in wild geese based on field research (Frith & Davies 1961). As such, abrupt mortality events caused through disease outbreaks may occur with a probability of ~ 0.0169 year^{-1} in the absence of climate change. We modelled catastrophes (where severity was 50% decline in population abundance) in the geese population using the above frequency estimator, and found that EMA for magpie geese was ~ 368 000 individuals where harvest continues and ~ 1 657 000 where harvest is strictly controlled.

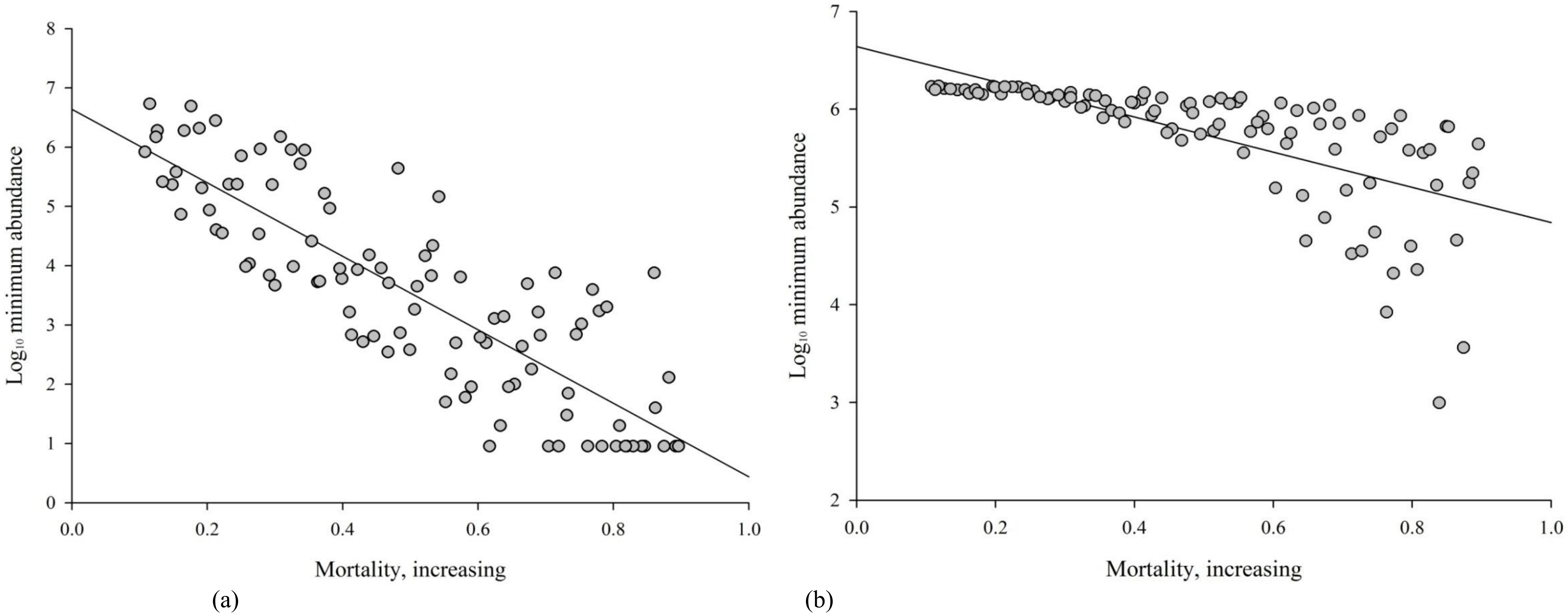
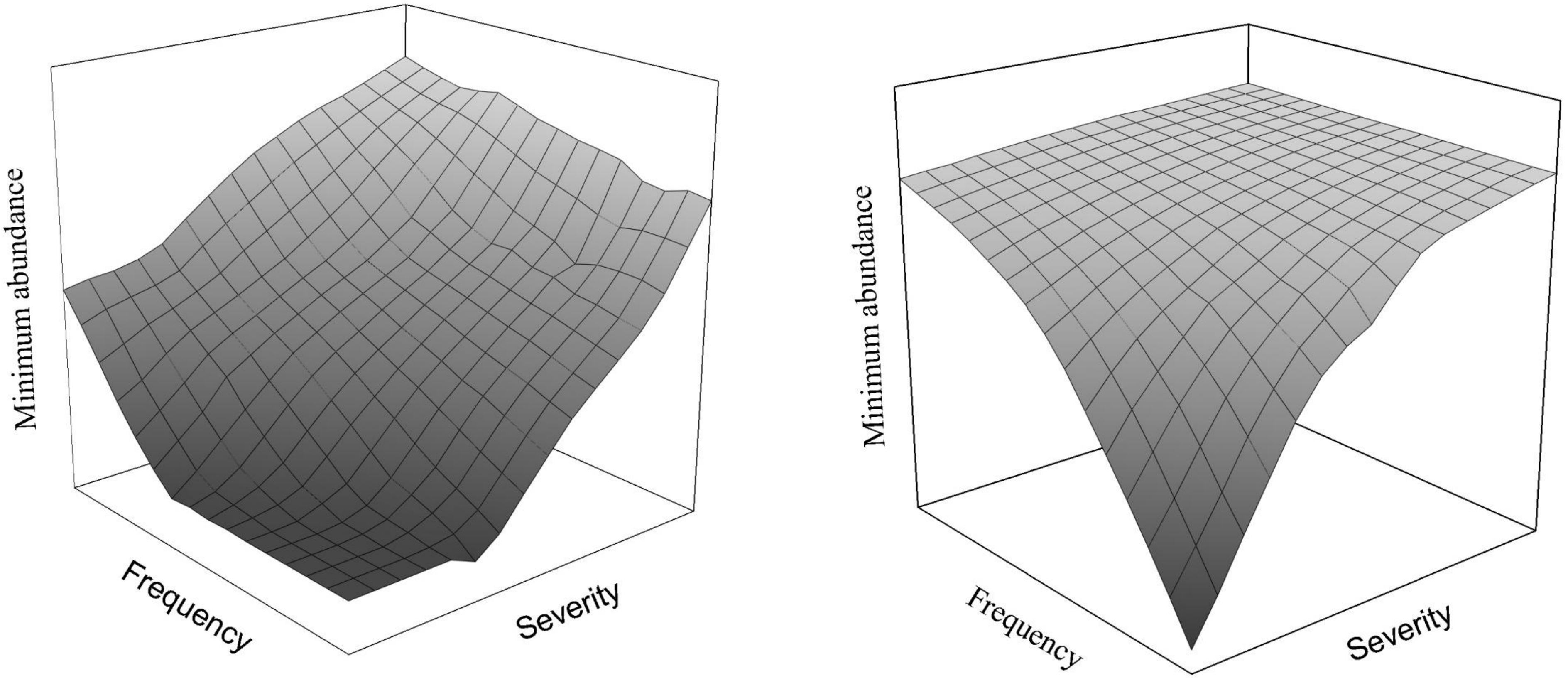


Figure 3.1 Interaction between the expected minimum abundance ($\log_{10}N$) and % disease-driven mortality (simulating scenarios of increasing disease severity) based on a stochastic stage-structured metapopulation model of magpie geese: (a) Harvest at 130 000 birds year^{-1} spread proportionally across floodplains ($R^2 = 0.710$); (b) No harvest ($R^2 = 0.456$). Lines show the least-squares fits.

Based on these results, climate change would need to enhance the frequency and severity of epizootics greatly to threaten geese (in the absence of harvest) due to the predicted lack of sensitivity to disease risk. However, under current harvest regimes, climate change-induced enhancement of epizootics would act additively with hunting to diminish long-term population viability progressively. Avian botulism, avian cholera, high pathogenic avian influenza and aspergilliosis are the diseases most likely to cause mass mortality in tropical geese populations that will lead to local extinctions if hunting continues at its current intensity and if climate change progresses unabated.



(a) (b)

Figure 3.2 Fitted surface plots of the interaction between expected minimum abundance ($\log_{10}N$), and disease mortality (disease severity) and increasingly probabilities (frequency) of disease outbreak based on a stochastic stage-structured metapopulation model of geese: (a) harvest at 130 000 birds year^{-1} spread proportionally across floodplains; (b) No harvest.

3.6 Discussion

Infectious disease can weaken the resilience of populations that might otherwise have been relatively robust to human sources of stress (Pedersen et al. 2007; Plowright et al. 2008b), and may even be the direct cause of the final extirpation of small, isolated, or otherwise vulnerable populations (Hale & Briskie 2007; Lips et al. 2008). Conservation biologists have long recognised the role of catastrophic disease in species extinction (Terborgh & Winter 1980; Roelke-Parker et al. 1996), and the chronic role of pathogens and parasites in reducing the reproductive fitness of individuals within populations (Packer et al. 1991). Indeed, infectious disease is considered to be one of the top five causes of global species extinctions and was listed as a contributing factor in ~ 4% of recorded species extinctions over the last 500 years (Smith et al. 2006).

Infectious diseases have precipitated avian extinctions, often acting in synergy with other deterministic factors such as habitat loss and harvest (Smith et al. 2006). Waterfowl appear to be particularly susceptible to catastrophic mortality events because of their tendency to form large seasonal breeding and feeding aggregations which facilitate pathogen transmission (Converse & Kidd 2001; Chen et al. 2005). Although avian disease has received less attention in the Australian tropics compared to temperate regions (see Tracey et al. 2004), inference is possible from measurements of infectious diseases common across geographic regions (Friend & Franson 1999; Hess & Pare 2004).

Recent and ongoing shifts in climate following global warming (IPCC 2007), and the direct and indirect impacts of climate change on tropical regions (Hennessy et al. 2007) are anticipated to increase a species‟ extinction probabilities, especially via synergistic interaction with other drivers of decline (Zell 2004; Pascual et al. 2008). Harvest might undermine population resilience further through loss of genetic variation and population fragmentation (Frankham et al. 2002; Rizkalla et al. 2007), making these more vulnerable to catastrophic events (Caughley 1994; Clegg et al. 2007). The case study of geese we described supports this expectation and suggests an increased resilience to disease outbreaks when harvest is tightly controlled. The review highlights the breadth of infectious disease that potentially threatens geese, and yet there is a lack of detailed ecological and epidemiological knowledge on frequency and severity of disease. Our disease review sets a precedent for similar and future studies that explore the viability of populations threatened by global change, particularly where other drivers of decline (such as hunting) already exist. We recognise the lack of available data on projected habitat loss through sea level rise for this region, and how this may further enhance the disease-harvest-climate synergy (see Finlayson et al. 2006). This recognition underscores the need to develop quantitative hydrological models of this system for a broader evaluation of the risks faced by geese under global change.

Our results apply equally well to other waterbird populations across the tropics that are vulnerable to infectious disease. Tracey et al. (2004) documented ~18 waterbird species that are vulnerable to viral disease in tropical Australia that use similar habitats to geese. Notable among these are the Australian pelican (*P. conspicillatus*), plumed (*Dendrocygna eytoni*) and wandering (*D. arcuata*) whistling ducks, Radjah shelduck (*Tadorna radjah*) and grey teal (*Anas gracilis*). Moreover, infectious diseases are not unique to birds, and many other vertebrate populations may be vulnerable (Young 1994; Reed et al. 2003b), especially under a shifting climate. For example, flying foxes native to tropical Australia and Asia are threatened by emerging viral diseases (Breed et al. 2006), and new infectious diseases pose an identified risk to tropical Australia‟s livestock industry (Mackenzie et al. 2001; Pulliam et al. 2007). Interestingly, extinction of the Australian thylacine (*Thylacinus cynocephalus*) was attributed, in part, to introduced pathogens acting in synergy with overhunting by people (Smith et al. 2006).

Future disease-oriented research on tropical waterfowl needs to focus on

1) possible types of climate change impacts on regional tropical weather systems (e.g., effects on El Niño and monsoonal stability);

2) the sensitivity of waterfowl (or any other species of concern), directly or indirectly, to climate change;

3) further evidence for disease enhancement, spread or novel emergence through climatic changes; and

4) evidence for synergies between disease and other drivers of global change.

Studies tackling these issues, based on multiple working hypotheses of the additive or interactive effects of multiple drivers (Brook et al. 2008), will allow robust evidence-based conservation decisions that will withstand scrutiny (Burnham & Anderson 2001; Kovats et al. 2001) and best aid applied decision-making to maximise conservation outcomes.

4. MIRNDE AND GABBAL: SEASONAL AGGREGATIVE RESPONSE OF A UNIQUE TROPICAL WATERFOWL AND IMPLICATIONS FOR ITS CONSERVATION

Submitted as a research paper to *Oecologia* by Lochran W. Traill and Barry W. Brook

Lead author Traill conducted all field-based research, analysed all data and prepared draft manuscripts (0.9). Brook (0.1) co-conceived the work, guided the field programme, gave advice on data analyses and commented on draft manuscripts.

The co-author agrees that this manuscript can be submitted as a chapter for a PhD thesis.

Abstract

We describe the aggregative response of a unique tropical waterbird, the magpie goose to the dynamics of the ephemeral sub-coastal floodplains of northern Australia. We find that birds migrate in large numbers to feeding sites and aggregate in response to the availability, abundance and size of the root tubers of a wetland sedge plant, *E. dulcis*. The presence of large numbers of foraging birds was most strongly influenced by water depth, which determined the availability of foodplants. Despite intense predation by geese on *E. dulcis* root tubers, there was no evidence of a negative-density feedback mechanism between plant and herbivore populations, suggesting that the system is driven by environmental parameters. A gain in bird body condition over the aggregative period does however suggest an important role of *E. dulcis* – dominated floodplains in the ecology of magpie geese, particularly as feeding occurs during the late dry season when food resources are relatively scarce. Sensitivity of *E. dulcis* to saline water will lead to the loss of the foodplant under rising ocean waters, thereby threatening the long-term viability of dependent magpie geese populations.

4.1 Introduction

The temporal and spatial configuration of consumers in relation to resource abundance and availability is a central theme within ecology (Heck & Valentine 2006), and underlies effective wildlife management based on systems ecology (Rowcliffe et al. 2001). Herbivores may respond to foodplant availability through migration (Nolet et al. 2001), aggregation (Bos et al. 2004) or through demographic fluctuation (Jefferies et al. 1994). Conversely, herbivores have the ability to alter plant community structure through over-consumption and altered competitive interactions (Jefferies & Rockwell 2002; Brathen et al. 2007). Theory on plant-herbivore interaction is based principally on the (predator-prey) work of Holling (Holling 1959a; Holling 1959b) and Rosenzweig and MacArthur (1963) and is conceptually well-developed. The theory has also been confronted with evidence from field research, with studies showing the functional, numerical and aggregative responses of herbivores to resources (Jefferies et al. 1994; Rowcliffe et al. 1999).

Abundant, large-bodied herbivorous waterfowl are known to influence foodplant community composition and distribution in some situations (Badzinski et al. 2006), and are, in turn, constrained by available resources (Jefferies et al. 1994). Studies of wetland-waterfowl interactions are important for informing best-practice systems-wide conservation (for example by preservation of key habitat) and also underlie wildlife management where waterbirds are hunted (Brook & Whitehead 2005b; Nichols et al. 2007). To date, waterfowl-habitat research has been based principally in temperate regions with little information on tropical waterfowl, despite their importance to both wetland ecology (Frith & Davies 1961; Finlayson et al. 2006) and the informal economies of local communities (Whitehead et al. 1988; Whitehead et al. 2000). Moreover, tropical waterbirds face growing threats from the increased pressures of expanding human populations in the developing world and environmental shifts via global change (Bradshaw et al. 2008). The sustainable management of waterfowl populations thus requires research that identifies the underlying drivers of key interactions between herbivorous waterbirds and their foodplants at a population level.

Magpie geese, also known as *Mirnde* to aboriginal Australians, are an iconic waterbird native to Australia and New Guinea, and are the only extant member of family Anseranatidae (Frith & Davies 1961). Once prevalent across south and south-eastern Australia, magpie geese are now restricted to the tropical north because of the synergistic historical impacts of drought, habitat loss (principally agricultural displacement and draining of wetlands), deliberate poisoning, over-exploitation and predation by introduced vertebrates (Nye et al. 2007). The relative abundance of tropical magpie geese populations (Bayliss & Yeomans 1990), their ecological importance as a keystone species (Whitehead 1998) and cultural value as „bush-tucker“ (Whitehead et al. 1988) has contributed toward ongoing research and the identification of key knowledge gaps.

Magpie geese gather on sub-coastal wetlands of northern Australia (known as *Gabbal*) and southern New Guinea during the dry season, principally to forage for the root tubers (or culms) of the sedge *E. dulcis*, or water chestnut (Frith & Davies 1961; Whitehead 1998). In these environments, the relatively large, long-legged birds do not dive for food but grub with their heavy bills in glutinous clay soils, and so are limited by the depth of water that they are able to stand in. Although broad-scale habitat associations have been shown between geese and floodplains dominated by *E. dulcis* (Bayliss & Yeomans 1990), wetland-scale associations have not been quantified. Moreover, the drivers of seasonal dispersal and body condition are not known. Such interactions are important to the building of more realistic population models that incorporate ecological drivers and test management scenarios under climate change (see Keith et al. 2008).

Here we quantify an aggregative response in geese to seasonal wetland dynamics. We identify the influence of foodplants and environmental parameters on bird aggregation, body condition and departure, and discuss these findings in the context of tropical waterfowl ecology and conservation.

4.2 Methods

4.2.1 Study area

Fieldwork was undertaken on the seasonal floodplain system of the (macro-tidal) South Alligator River, Kakadu National Park (Fig. 4.1). The South Alligator (SA) floodplains are representative of sub-coastal wetlands across northern Australia (Whitehead et al. 2000; Finlayson et al. 2006) and have been documented as important feeding sites for magpie geese during the tropical dry period (Frith & Davies 1961; Whitehead 1998).

North Australian wetland systems were formed in the recent Holocene following the stabilisation of sea levels at 6 000 to 4 000 years BP (Mulrennan & Woodroffe 1998). Systems are dynamic, alternating between annual wetting and drying and tracking intensely seasonal rainfall patterns (Bayliss 1989). The climate of the „Top End" of Australia"s NT is marked by two distinct seasons: the wet (November – April), associated with the north-western monsoon, and the dry season (May – October).

Figure 4.1 Location of study site on the Nourlangie Creek, South Alligator River confluence, Kakadu National Park, NT of Australia. Also shown are sub coastal floodplains in white / vegetation and the tarred roads through Kakadu.

Many NT floodplains are heavily grazed by managed livestock and feral ungulates (Whitehead et al. 1990; Corbett & Hertog 1996), and introduced pasture grasses are prevalent (Lonsdale 1994). Native floodplain vegetation is dominant in designated and protected conservation areas, such as the World Heritage listed Kakadu National Park (KNP), and these support numerous native and non-native vertebrates, including a diverse waterfowl guild

(Finlayson et al. 2006). Magpie geese rely on such sub-coastal wetlands for forage and breeding activity (Whitehead & Tschirner 1990). Migration is seasonally nomadic, usually between preferred feeding and nesting sites (Whitehead 1998).

4.2.2 Field sampling

Experimental design required that we estimated (1) bird abundance on floodplains, to test an aggregative response, *viz.* a relationship between predator density and prey abundance (Rowcliffe et al. 1999), (2) an index of bird body condition, and (3) the likely drivers of bird migration, or „giving-up thresholds" for the key resource (as per Vickery et al. 1995). Field work was restricted to the dry season only (June through November), because this is the period when geese aggregate as available water declines. Monitoring ran from 2005 through 2007.

Two study sites were chosen (within one extensive floodplain area) at the South Alligator River and Nourlangie Creek confluence (Fig. 4.1). The floodplains at this confluence have been documented in the past as important forage sites for geese (Bayliss & Yeomans 1990; Whitehead 1998). The distance between sites was ~ 10 km; we were restricted to this spacing due to logistical and financial constraints.

We constructed three plots at each of the two sites (six plots in total), all within reach of access roads. Plots were designed so that we could estimate both bird and foodplant abundance, as well as environmental parameters. All plots were 200 x 50 metres (1 ha equivalent) in size, starting ~ 5 m from the water"s edge and separated by no less than 1 000 m. Plots were demarcated using 2.5 m steel pickets, with white plastic pipes (50 mm gauge) secured at the top of each of these. The 2005 field season was dedicated to experimental design, plot demarcation, and for resolving a number of logistical issues such as floodplain-access.

We required access to study sites situated within flooded areas (so that we could count root tubers and measure wetland parameters). Large estuarine crocodiles (*Crocodylus porosus*) prevented wading, and dense floodplain vegetation restricted the use of an (outboard) motorised boat. A four-seat, 4.8 m airboat (or fanboat) was hired and we found this to be the safest and most efficient method of traversing floodplains. Wetlands flooded following the tropical monsoon rains in December each year. Water levels rose up to 5 m, and inundation made site-access impossible using a four-wheel-drive vehicle. Floodplain waters slowly receded during the dry season, and by June or July of each year, site access was possible by 4WD vehicle (needed to drag the airboat to the water"s edge). Note, birds cannot access foodplants before this time and thus field-data collection commenced by June.

Those habitat variables most likely to influence herbivore abundance were given careful *a priori* consideration (see Models section). We required estimates of bird abundance, *E. dulcis* tuber abundance, and environmental parameters such as water depth, soil depth and viscosity. Bird density was estimated from a single trailer-mounted boom-lift (maximum height, 10 m). The lift was towed to each plot, and placed ~ 30 m from the shoreline, so as not to disturb grubbing birds. From the raised lift, two observers counted the total number of geese in each plot at every hour, for an 8 hour period, thus accounting for daily variation in goose aggregation (note that birds typically moved to *Melaleuca* woodland roosting sites at nightfall). On each hour, three separate counts were taken to reduce sampling error. The mean value of each hourly count was calculated, and then the median value taken across all eight counts to derive a central estimate of bird abundance. Goose abundance was thus derived every month from June to November 2006 and July to October 2007.

We used bird weight (in grams) as a measure of an individual"s robustness (see Kight & Swaddle 2007) in 2006. From 2007 we used an index (bird weight in grams / bird body length) that better reflected relative body condition. Following subsequent review of literature (see Green 2001) we elected not to use these data to test response to environmental parameters. We sourced magpie geese in two ways: first from live-bird capture done in collaboration with Australian Quarantine as part of national disease surveillance, and second from dead geese shot on behalf of the traditional owners of KNP. Birds were secured each month during the field season, aged, sexed and weighed (also colour-neck-banded when live-caught). Individual geese were placed in a large cotton bag and weighed using a hanging scale (5 kilogram maximum, in 2 g increments). Total length was taken by laying each adult bird on its back, and using a tape to measure length (mm) from tip-of-beak to tip-of-tail (see Lowe 1989).

Tuber and floodplain-parameter data were measured on-site using the (Charles Darwin) University airboat. Immediately following bird counts (typically 3 days), we drove the airboat to plots for plant collection. The noise of the airboat disturbed the geese, and thus the necessity of plant tuber counts following bird counts. We randomly selected (using a numbered grid overlain on a satellite image of each plot and using values from a computer-based pseudo-random number generator) 3 points within each plot prior to travel, and used a handheld Global Positioning System (GPS) to locate these. We used a handheld core extractor (65 mm diameter x 350 mm depth core, 1.2 m arm) to sample soil and extract root tubers. We took 10 samples (at each of the 3 points within each plot) by walking around the airboat perimeter and leaning overboard. This allowed estimation of tuber abundance at each plot. Tubers were separated from the soil core using a wire-mesh pan (held overboard), washed, counted and stored in sealed and numbered paper bags. Following field excursions, *E. dulcis* tubers were taken to the University campus in Darwin, cleaned, dried (in a drying oven), measured and weighed.

At each plot, we also collected data on parameters likely to influence or drive the abundance of geese. *A priori* consideration of the system (*sensu* Burnham & Anderson 2001), based on a literature review, guided development of multiple competing hypotheses, expressed as generalised linear mixed effects models (GLMM) with different combinations of independent predictors. Parameters used to build the model set included water depth in mm (measured using a 1.5 m gradated rod, 3 samples at each subplot), soil depth in mm (from the top of the soil to the base where the muddy strata met a hard, rocky substrate, and measured using a rod), soil viscosity (2007 only and after cursory analysis of 2006 data) and an index of pig-rooting. Soil viscosity was estimated using a qualitative index of stickiness (after DPI 2004), and derived from samples at each point (30 from each plot). Viscosity was scored from 0 – 3 using hands to judge texture, with 0 being not „sticky‟ and 3 very „sticky‟. Water depth was categorised following field observation of bird grubbing behaviour, thus 0 for water below 10 mm, 1 for water between 10 and 450 mm and 2 for water deeper than 450 mm. Pig-rooting data were ultimately discarded as negligible.

Further, departure thresholds and giving-up densities, as shown in some temperate waterfowl populations (Vickery et al. 1995; Rowcliffe et al. 2001), have not been defined for geese. Here we used a binary indicator of bird absence from floodplains, and tested factors correlated with departure (as above). Owing to logistical constraints, we were not able to collect wetland parameter data following bird departure in 2007 and we therefore analysed 2006 data only.

4.2.3 *A priori* model set

As noted above, we determined, *a priori*, the possible drivers of geese aggregation and departure thresholds on tropical floodplains, and then measured these in the field. We were interested in the influence that tuber abundance and size had on bird abundance and body condition through the dry season. We further sought to determine a decline in tuber density below a threshold beyond which grubbing effort was no longer worthwhile (see Nolet et al. 2001), or whether bird departure was determined by environmental factors such as water level.

We took a multiple working hypotheses approach to data collection and analyses (after Burnham & Anderson 2001). That is, multiple working hypotheses were developed, with data being used as an arbitrator via confrontation with the model set based on likelihood and parameter-fitting bias (Hilborn & Mangel 1997) – see *Analyses* for details on statistical inference. Relative support for each model allowed the derivation of a best-approximating model, or best „explanation" of the biological system (Burnham & Anderson 2001). Following field work in 2006, we revised our hypotheses slightly to incorporate new parameters; after a better working-knowledge of the system. All models are listed in Tables 4.1 and 4.2 and Appendix 1.

4.2.4 Analyses

Three model sets for testing bird abundance were collated for data from 2006, 2007 and both years. Models were also prepared to test bird departure using bird absence as a response. To gauge the relative importance of each predictor variable, we fitted a series of GLMMs to bird abundance and bird absence (the two alternative dependent variables) using the `lmer` function in the R-language environment (R Core Development Team 2007). The random effects error structure within the GLMM was used to correct for spatial and temporal non-independence of data (Koenig 1999), given the likelihood of spatial correlation between plots and sites, and temporal correlation between month (sampling took place once each month) and year (two years), which were not measured directly and not captured within the fixed effects (predictor variables).

Asymptotic measures of relative information loss were used to assign strengths of evidence to the competing models (Burnham & Anderson 2001), with both Akaike"s information criterion corrected for small sample sizes (AIC_c) and the Bayesian information criterion (BIC) weights used as an objective means of model comparison (McCarthy 2007). We chose a Bayesian method of model selection in addition to Akaike"s information criteria, because the BIC tends to select simpler models which reflect main effects (dominant drivers), whereas AIC will include tapering effects, if sufficient data is available, and so often selects „saturated" models (see McCarthy 2007).

4.3 Results

4.3.1 Aggregative response

Geese moved to the South Alligator floodplains at the onset of the dry season for both 2006 (July-August) and (July) 2007. There was a marked increase in bird abundance over these periods (Fig. 4.2), followed by a decrease in abundance at the end of the dry season (October-November) when access to foodplants was restricted by floodplain drying. Mean number of geese ha^{-1} rose from 0 at the onset of dry 2006 to 85 ha^{-1} at peak. The 2007 foraging period was shorter, but peak abundance was higher, at 115 birds ha^{-1}. If we assume that the study area at the Nourlangie Creek – South Alligator floodplain interface is ~ 800 ha^{-1}, then maximum geese abundance (for this time period and on these floodplains only) was ~ 68 000 in 2006 and ~ 92 000 in 2007.

Trends in body condition through the dry periods of 2006 and 2007 show slight gains in bird weight as the season progressed. During 2007, body condition indices (adult birds only) show a peak early during the aggregation and with a gradual decline toward October (Appendix 2). Nonetheless, we note that birds gain net condition following sustained consumption of *E. dulcis* tubers, and body weights are indicative of healthy adult magpie geese (see Frith & Davies 1961).

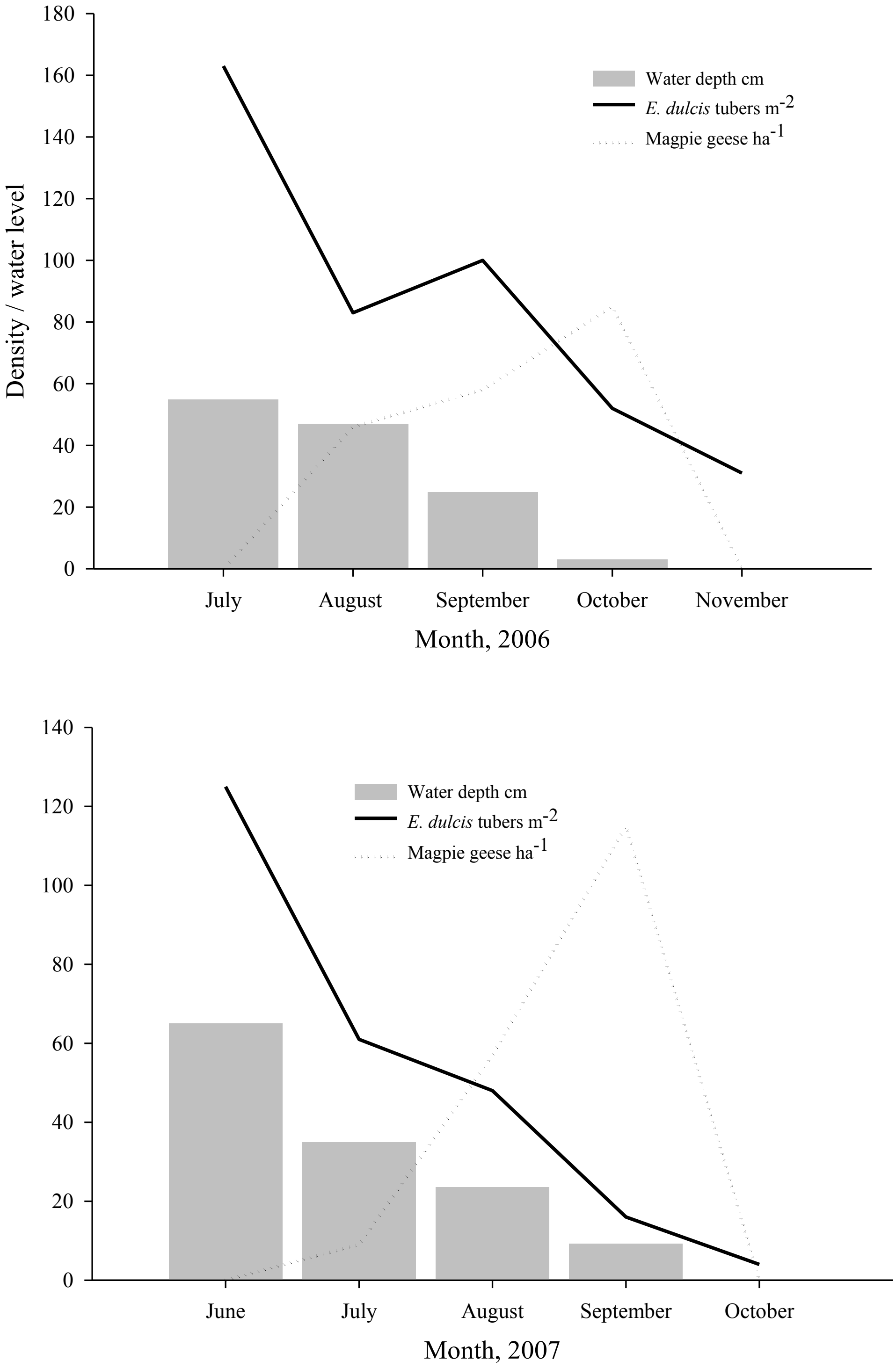


Figure 4.2 a, b Decline in root tuber abundance of *E. dulcis* as the dry season progresses, and for 2006 (a) and 2007 (b). Also shown are the aggregative response of magpie geese in response to tuber density and access. *E. dulcis* taken as mean tuber density m^{-2}, and geese abundance taken as mean individuals‟ ha^{-1} and per month.

Using AIC$_c$ and BIC to select the most parsimonious models, we found that water depth was the best predictor of bird abundance in 2006 and across both years (Table 4.1a, c). All fixed effects (global [saturated] model) were the best predictors of goose abundance during 2007 (Table 4.1b). These findings indicate the role that rainfall ultimately has on restricting access to foodplants, with seasonal rain driving the flooding and drying of wetlands. We took these analyses a step further and omitted water depth from models testing bird abundance during the aggregative period only. Results indicate that root-tuber density and size were key drivers of abundance (Appendix 1), but the relatively low deviance explained suggests the overwhelming influence that water depth has on this system.

Bayliss and Yeomans (1990) used a regression analysis to test the broad-scale (across the north Australia) response of geese to percent cover of *E. dulcis* and found a fairly strong relationship ($R^2 = 0.45$). Geese aggregate on floodplains dominated by *E. dulcis* in large part due to the nutrient provided by the root tubers. Of interest here though, is that our examination of the plant-herbivore relationship, at a finer resolution than that done by Bayliss and Yeomans (1990), shows that wetland environmental parameters (essentially the presence and extent of floodplain waters) determine feeding opportunity.

Candidate models where response is bird abundance	**k**	**AIC$_c$**	**ΔAIC$_c$**	***w*AIC$_c$**	**ΔBIC**	**% DE**
Tuber density + water depth	7	1256.57	0.000	0.63	0.0	44.7
Tuber density + tuber weight (size) + water depth	8	1258.16	1.584	0.28	3.9	44.7
Global (interaction between tuber density and weight + water depth)	9	1260.52	3.950	0.09	8.4	44.7
Water depth	6	1383.12	126.550	0.00	124.2	39.0
Water depth + tuber density	7	1385.03	128.461	0.00	128.5	39.0
Tuber weight	5	2229.00	972.427	0.00	967.7	1.2
Tuber density + tuber weight	6	2230.30	973.727	0.00	971.4	1.2
Null, random effects only (plots nested in site and month)	4	2253.03	996.455	0.00	989.4	0.0
Tuber density	5	2254.01	997.438	0.00	992.8	0.1

Table 4.1 a

Table 4.1. Results from generalised linear mixed-effect models (GLMM) of the aggregative response of magpie geese (abundance and presence/absence) to floodplain dynamics during the dry season. All GLMMs include site as a random effect. Shown are the number of model parameters, including random effect variance decomposition (k), Akaike‟s corrected information criterion (AIC$_c$), difference from best model (ΔAIC$_c$), Akaike weight (*w*AIC$_c$) scaled relative to a total sum of 1, Bayesian Information Criterion (BIC), and percent deviance explained (% DE) as a measure of goodness-of-fit. Included are data collected 2006 (a), 2007 (b) and (c) pooled across 2006 and 2007.

Candidate models where response is bird abundance	**k**	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**ΔBIC**	**% DE**
Global (interaction between tuber weight and density + water depth + soil viscosity)	11	149.75	0.000	0.44	2.8	73.4
Water depth	6	150.22	0.475	0.35	0.0	69.8
Interaction between tuber weight and density + water depth	9	151.26	1.507	0.21	3.5	71.5
Soil viscosity	6	406.24	256.490	0.00	256.0	12.9
Tuber density + tuber weight	7	437.87	288.117	0.00	288.6	6.5
Tuber density	5	441.87	292.118	0.00	290.5	4.3
Null, random effects only (plots nested in site and month)	4	458.85	309.100	0.00	306.2	0.0
Tuber weight	5	461.05	311.304	0.00	309.7	0.1

Table 4.1 b and c

Candidate models where response is bird abundance	**k**	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**ΔBIC**	**% DE**
Water depth	7	1804.17	0.000	0.53	0.0	53.2
Global (interaction between tuber density and weight + water depth)	10	1804.38	0.211	0.47	8.4	53.4
Interaction between tuber density and weight	8	3775.94	1971.777	0.00	1974.5	1.7
Tuber density + weight	7	3799.14	1994.970	0.00	1995.0	1.1
Tuber weight	6	3802.84	1998.672	0.00	1995.9	0.9
Tuber density	6	3824.80	2020.629	0.00	2017.8	0.3
Null, random effects only (plots nested in site and month)	5	3835.26	2031.095	0.00	2025.5	0.0

4.3.2 Departure threshold

We found that goose abundance decreased with a reduction in the availability of root tubers (Fig. 4.2). Birds appear to reach a point where reward (for foodplants) no longer matched grubbing effort, but water is the driving factor here (Table 4.2). The loss of floodplain water to evaporation leads to the rapid drying of the floodplain soils and so grubbing effort is difficult, if not impossible to the birds.

Of interest, *E. dulcis* root-tuber density immediately following bird departure was 3.7 m^{-2} (median = 3, *n* = 150), and mean density at the last measurement prior to departure (3 weeks earlier) was 7.1 m^{-2} (median = 7, *n* = 370).

Candidate models where response is bird absence	**k**	**AIC_c**	**ΔAIC_c**	**$wAIC_c$**	**ΔBIC**	**% DE**
Water depth	6	27.28	0.000	0.53	0.0	77.9
Global (interaction between tuber density and weight + water depth)	7	27.50	0.220	0.47	2.0	81.4
Tuber density	5	60.42	33.141	0.00	31.2	21.8
Tuber density + tuber weight	6	61.95	34.668	0.00	34.7	23.2
Null, random effects only (plots nested in site and month)	4	71.90	44.626	0.00	40.8	0.0
Tuber weight	5	72.19	44.911	0.00	43.0	3.2

Table 4.2. Generalised linear mixed-effect model results on the migration threshold (coded as a binary value: absence = 1, presence = 0) of magpie geese to seasonal floodplains during the dry season 2006.

4.4 Discussion

Geese aggregate on floodplains dominated by *E. dulcis* during the early tropical dry season where they forage for *Eleocharis* root-tubers. When foraging in these environments, they gain body condition and accrue reserves that help carry them through the late dry season when the floodplains dry and tubers become inaccessible and other foods are sparse (Frith & Davies 1961). While bulbs are accessible, geese respond to both root-tuber availability and size, and are restricted by water depth and soil viscosity. Essentially, aggregation is driven by seasonal rainfall. These findings build on past work that has linked geese to the presence of *Eleocharis* on seasonal floodplains (Bayliss & Yeomans 1990), but at a finer spatial scale.

Aggregative response by magpie geese is consistent with the hypothesis that herbivore (waterfowl) aggregation is largely driven by (wetland) resource availability and access (Sutherland & Allport 1994; Rowcliffe et al. 1998). A large proportion of the region‟s goose population uses *Eleocharis* – dominated floodplains during the late-dry season (Bayliss & Yeomans 1990), in preference to other extensive available habitats and foodplants, such as floodplains dominated by native *Hymenachne* or introduced *Urochloa* grass species. Up to 70% of the population uses the Kakadu wetlands at and around our study sites in the mid- to late-dry season (Whitehead 1998). Aggregative response by (non-related) geese has been shown in temperate regions, typically by migratory populations (Vickery et al. 1995; Rowcliffe et al. 1998; Bos et al. 2004).

Other factors that we have not considered explicitly may drive dry season site-selection by geese, such as predator avoidance or access to roosting sites (Frith & Davies 1961; Whitehead 1998) – although these were embedded implicitly within our random effects. While large sub-coastal floodplains, such as those in our study, do provide refuge from terrestrial predators, it is implausible that these factors alone drive an aggregative response because there are large areas that offer both deep water and adjoining roosting sites elsewhere in these large floodplain systems (Bayliss & Yeomans 1990; Whitehead 1998).

Further, while we were unable to measure directly the functional response of geese to foodplants (Holling 1959b; Rowcliffe et al. 1999), Whitehead (1998) has documented the daily feeding patterns of geese. In relation to this, we did not witness aggressive or interference behaviour between individuals while feeding, as has been shown in temperate waterfowl assemblages (Rowcliffe et al. 1999). Undoubtedly though, geese do compete for plant tubers, with mature and larger birds tending to forage more efficiently (Whitehead 1998). An increase in feeding intensity as the season progressed was not obvious (as per Vickery et al. 1995).

Aggregative association by geese is a response to an ecological „window-of-opportunity". The apparent increase in bird condition during this period highlights the ecological importance of *E. dulcis*. Indeed, Whitehead (1998) suggested that access to *E. dulcis* is an important source of reserves needed to carry birds through the resource-restricted period from the drying of floodplains until resumption of monsoonal rainfalls. The initial peak in goose condition is interesting, and we speculate that birds simply lose condition as contest-type competition increases. The increase in root-tuber size (measured as dry-weight) is also interesting, because biomass allocation may be a plant strategy that allows effective tuber re-growth following goose eviction after wetland-drying and during later wet season inundation. We note that gut-content of harvested geese comprised > 90% (by volume) *E. dulcis* root-tubers (Traill, unpublished data).

While we failed to show a convincing „giving up" density, where forage effort is no longer worthwhile (e.g., Nolet et al. 2001), it appears that geese abandoned preferred forage sites when tuber density fell below 4 m^{-2}, although this figure is likely to vary with other influences on foraging costs, such as the increasing glutinousness and ultimately hardness of dry clay soils. Of note, magpie geese have been observed returning to study sites to forage for tubers following sporadic dry season rains sufficient to provide wetland surface water and soften soils (D. Lindner, pers. comm., Kakadu Buffalo Farm).

Periods of herbivore exclusion may allow *E. dulcis* plants opportunity to regenerate, but there is no evidence that predation by geese drives a shift in plant community structure away from *Eleocharis* (e.g., Jefferies et al. 1994). We believe, however, that rainfall regime, floodplain water quality (especially level of salinity) and period of inundation all strongly influence the growth and abundance of *E. dulcis* plants, and this requires further investigation. Indeed, it is possible that the nutrient input and grubbing action of magpie geese may benefit seed germination (Zacheis et al. 2002).

Sensitivity of *E. dulcis* to saline water is a driving factor in the spatial and temporal distribution of the plants (Eliot et al. 1999; Paynter 2004). *E. dulcis* does not tolerate saline water > 33 ppt (Midmore 1998), and past saline water intrusion possibly associated with feral buffalo *Bubalus bubalis* damage affected habitats on parts of the South Alligator floodplains and larger areas of the nearby Mary River (Corbett & Hertog 1996). Projected saline water intrusion due to ongoing and accelerating sea level rise and associated higher storm surge extreme events could affect floodplains across north Australia within the coming decades (Eliot et al. 1999). Our work here implies that the loss of *E. dulcis* through a shift in the hydrological regime will cause a decline of geese across tropical Australia and impose severe limitations on aboriginal harvest (Whitehead et al. 2000). Moreover, it is not known how the synergistic interactions between invasive weeds and saline water intrusion will affect *E. dulcis*, but is likely that these interactions will be to the detriment of geese (Paynter 2004).

The onus is on relevant conservation authorities to protect tropical sub-coastal wetland systems and allow for adequate adaptation to global change (control of weeds and ferals, and carefully-planned construction of buffers against sea level rise), thus providing forage to magpie geese and persistence of this unique species into the foreseeable future.

CHAPTER FIVE

5. TROPICAL NOMADS: SATELLITE TRACKING OF MAGPIE GEESE IN NORTHERN AUSTRALIA

Submitted as a research paper to *Emu* by Lochran W. Traill, Corey J. A. Bradshaw and Barry W. Brook

Lead author Traill carried out all field-based research, accessed and analysed all telemetry data, conducted GIS-based analyses and prepared draft manuscripts (0.9). Bradshaw commented on draft manuscripts and assisted with generalised linear models (0.05). Brook gave feedback on research design and commented on draft manuscripts (0.05).

All co-authors agree that this manuscript can be submitted as a chapter for a PhD thesis.

Abstract

Documenting the movement patterns and habitat use of tropical waterfowl will assist in long-term bird and wetland conservation because such data provide essential information on population connectivity necessary to predict resilience to global environmental change. We monitored the seasonal movements of geese in tropical north Australia using satellite telemetry. Ten wild-living birds were captured in Kakadu National Park (KNP) in late 2006 and fitted with KiwiSat® satellite transmitters. Migration was multi-directional and the maximum linear distance moved by an individual was 114 km from the release site, over 38 weeks of tracking. Migration did appear to be related to seasonal environmental fluctuations. Most monitored birds remained resident within the National Park. Individuals selected floodplains, woodland billabongs and paperbark forest over other habitat types, and median elevation of land used was 8 m above sea level. Accurate data were not obtained for any longer than 12 months, with most birds apparently losing their backpacks within six months. Just 62% of point location data were accurate to within 1 000 metres. We recommend indirect genetic tests to assess more comprehensively the connectedness of geese and other waterfowl sub-populations across tropical Australia.

5.1 Introduction

Migration includes temporary and permanent emigration and immigration (Dingle 1996) and is principally an adaptive population-level response to seasonal peaks and troughs in resource abundance (Alerstam et al. 2003; van der Graaf et al. 2006). From a genetic perspective, migration describes the movement of alleles between semi-isolated populations (Slatkin 1985; Lande 1988), and the term „dispersal" describes the movement of an individual from its place of birth to the place where it reproduces (Levin 1992). These behaviours are driven in part by density-dependent habitat use, where gains in survival and reproduction are balanced by the costs (lost foraging opportunity, energy demands and mortality) of migration (Roshier et al. 2008). Predator avoidance and responses to disturbance might also encourage movement (Tankersley 2004). Understanding these processes aids in the development of effective conservation strategies, especially for threatened species (IUCN 2008) because population connectivity is one of the principal determinants of threat risk among different taxa (Hanski et al. 1997; Brook et al. 2008). Indeed, individual movement between fragmented sub-populations (Fahrig & Merriam 1994) is a major determinant of long-term metapopulation persistence (Dunning et al. 1992; Saccheri et al. 1998).

Study of animal movement is also relevant to the prevention of wildlife disease (Plowright et al. 2008). Migrating individuals may increase the range of a pathogen by acting as a vector (Lips et al. 2008), or infected individuals can transfer pathogens or parasites into naïve populations. The transfer of infectious diseases can be catastrophic for small and isolated populations (e.g., Clegg et al. 2007).

The study of avian migration has, to date, focused on temperate bird species, particularly across Europe and North America (e.g., Hestbeck et al. 1991; Drent et al. 2003). Relatively less is known about migration patterns of tropical birds, especially waterfowl (although see Roshier et al. 2008). This is a concerning knowledge gap because of the threats faced by biodiversity in the region through global change (Bradshaw et al. 2008; Colwell et al. 2008) and the rising incidence and prevalence of avian disease (Tracey et al. 2004). Here we help address this deficiency by providing data on seasonal movement and habitat use patterns of geese in tropical north Australia.

Endemic to Australia and New Guinea, magpie geese are the sole members of the family Anseranatidae. Populations are mainly distributed across tropical north Australia (and southern New Guinea) and are especially abundant in the Northern Territory of Australia (up to 3.5 million individuals – Bayliss & Yeomans 1990). Geese were common in southern and south-eastern Australia prior to European settlement, but have now been reduced to small, isolated and conservation-dependent populations through the additive and synergistic impacts of habitat loss, over-exploitation, predation and drought (Nye et al. 2007). Tropical magpie geese populations depend on extensive sub-coastal floodplains for both forage and breeding activity (Whitehead & Tschirner 1992; Whitehead 1999). During the tropical dry season (May through November), geese aggregate in flocks of up to 250 000 individuals on shallow-water wetlands to grub for the nutrient rich root-tubers of the sedge plant *E. dulcis* (Frith & Davies 1961) prior to migration for breeding (Whitehead 1998). Radio telemetry has in the past been used to track bird movement (Whitehead 1998), but these data lack the resolution and reliability provided by satellite telemetry.

Geese are known as a nomadic migratory species, moving from nesting and feeding sites during each season (Whitehead 1998). Birds breed following the tropical rains from March onward, and are known to forage on wetland sedge plants during the tropical dry season, from July-August through to November (Frith & Davies 1961).

Although geese are currently listed as *Least Concern* in the IUCN"s Red List (IUCN 2008), saline water intrusion via sea level rise is predicted to shift *E. dulcis*-dominated floodplains toward mangrove communities and saltflats (Mulrennan & Woodroffe 1998a) – to the detriment of geese and other tropical waterfowl. Other threats to geese include habitat loss to invasive plants (Lonsdale 1994), wetland degradation by non-native buffalo *Bubalus bubalis* and pigs *Sus scrofa* (Bradshaw et al. 2007), toxicosis from spent lead shot (Whitehead & Tschirner 1992), infectious diseases and potential over-harvest (Brook & Whitehead 2005b).

In this paper we use satellite telemetry to track individual bird movement over 12 months during 2007 – 2008, and discuss the implications of seasonal migration for disease transfer and tropical waterfowl conservation. Further, we test mass-biased movement rates of birds during the wet and dry seasons and quantify habitat selection. Data on habitat use by geese will guide the conservation of preferred wetlands. Finally we describe the challenges experienced with using transmitters fixed to harnesses and overall data quality. We use the terms „movement" and „migration" interchangeably to describe multi-directional movement of wild birds in response to environmental fluctuation. We do not use the term „dispersal" (movement from place of birth to place of breeding) because of the short observation period relative to generation length.

5.2 Methods

5.2.1 Study site and species

The capture and release of geese was done entirely within Kakadu National Park (KNP) in Australia"s Northern Territory. The World Heritage-listed National Park (Fig. 4.1) covers 19 804 km^2 and supports numerous native vegetation and vertebrate species, including a diverse waterfowl guild (Finlayson et al. 2006). Climate is marked by two distinct seasons (Whitehead 1998); the „wet‟ (Dec – Apr) associated with the north-western monsoon, and the „dry‟ (May – Nov).

Geese rely on the extensive sub-coastal floodplains of KNP for forage and nesting (Bayliss & Yeomans 1990) and are harvested regularly by resident aboriginal people (Whitehead et al. 2000). We were interested in fixing satellite transmitters to geese that used the sub-coastal floodplains within KNP to document the extent of ex-Park movements. KNP was chosen as a capture-and-release site (and geese as a study species) because: (1) magpie geese are a likely reservoir and dispersal agent for strains of the avian influenza and Newcastle disease viruses (Tracey et al. 2004; Traill et al. 2009a), with large aggregations during the dry season (Bayliss & Yeomans 1990) allowing potential mutation of avian viruses (Tracey et al. 2004), and goose movement outside of these areas having implications for animal and human health (AQIS 2006); (2) an important aspect of the ecology of geese, large-scale migration to (and from) the South Alligator River floodplains (Whitehead 1998), has not been documented using satellite telemetry; and (3) large dry season aggregations of geese allowed for greater opportunity to catch and tag individual birds.

5.2.2 Tag deployment

During October and November 2006, we secured free-ranging geese using a baited cage trap (Ashley & North 2004). Capture was done in collaboration with the Australian Quarantine and Inspection Service (AQIS) to monitor waterfowl for strains of the avian influenza and Newcastle disease virus (AQIS 2006). The trap was set at the verge of an ephemeral floodplain (132º 36′, 43″ E; 12º 50′ 60″ S) at the start of October 2006 while geese were foraging for the root tubers of *E. dulcis*. We built a hexagonal-shaped cage using 2.5-m steel pickets and steel wire mesh (5 × 1.0 mm). The side height was ~ 3 m and maximal diameter ~ 6 m. Cages were baited with crushed maize for ~ 21 days prior to capture of birds (for habituation).

Over 60 birds (magpie geese and plumed whistling duck *Dendrocygna eytoni*) were caught November 2006, and from these we selected 10 geese to be fitted with Kiwisat 202 (www.sirtrack.com) Platform Transmitter Terminals (PTT). We deliberately chose both adults and sub-adults and males and females. All selected geese were assessed as healthy by body weight (relative to mean across all birds captured, see Appendix 2). Birds were placed in a large cotton bag, and weighed using a hanging scale (max 5 kg in 2-g increments) accounting for both PTT and bag weight. The sex of each bird was determined using cloacal pliers (Whitehead 1998). Birds were aged on general body size, height of the cranial knob and development of tracheal loops (Whitehead 1998) and categorised into one of adult, sub-adult and juvenile age classes.

Selected geese were transported to a holding pen (15 m diameter and 3 m height) located ~ 100 m from the capture site. The holding pen allowed us to test the effectiveness of backpack design, and monitor bird response to harnesses such as discomfort behaviour (see Garrettson et al. 2000). We further required that data sourced through the Argos system (www.cls.fr) were adequate. The holding cage allowed free movement and short flight, and birds were fed and supervised by an Aboriginal Traditional Owner.

PTTs (70 × 30 × 25 mm; ~ 45 grams total weight including harness) had antennae ~ 150 mm in length. Units were set with a repetition rate of 75 seconds and a duty cycle of 8 hours on/160 hours off. Units were powered by one AA cell and one $^{2}/_{3}$ AA battery allowing a longevity of 900 – 1 000 days (www.sirtrack.com). Backpacks (or harnesses) comprised two double-stitched nylon ribbons (10 × ~ 300 mm) and were designed to fit under and over the bird"s wings. A stainless-steel trace (1.5 mm gauge) was fed through each PTT and crimped (2.0 mm aluminium crimps) at both ends to allow loops for ribbon attachment. Harnesses were adjusted individually to each bird and the ribbon stitched at loops. All ten PTTs were fitted January 2007 and birds monitored for another 2 weeks. Individual geese were caught every 7 – 10 days and checked for injuries or general discomfort. PTTs were turned on and data sourced through the Argos data web site to confirm accuracy. All birds were released February 2007 after we were satisfied with the harnesses and data. We used data from 01 March 2007 onward (transmitted at weekly intervals).

For all birds, PTTs and harnesses were ~ 2% of body weight. This was in accordance with recommendations by Cooke et al. (2004). We were aware at the onset of the study that harnessed devices can modify bird behaviour (Blouin et al. 1999; Garrettson et al. 2000), but felt that these were superior to neckbands given the grubbing behaviour of geese on floodplains (Whitehead & Tschirner 1992).

5.2.3 Data acquisition and analyses

We received data transmissions via Argos until 31 March 2008. Archived data were purchased through Argos and transferred to a spreadsheet in comma-delimited format. We deleted all location data with error > 1 000 m (see www.cls.fr). We then categorised data for each individual PTT by season; thus, data were grouped into the wet season (beginning Dec to end Apr) and the dry season (start May and end Nov). Location data were exported to ArcGIS version 9 (www.esri.com). These were converted to shapefiles and we used the *Analysis* tool in ArcGIS to determine minimum, maximum and average distance moved by each bird. We fitted linear models to ($\log_{10}$-transformed) bird mass and distance moved using the `lm` function in the R language (R Core Development Team 2009).

We determined the strength of evidence for hypothesised relationships based on information theory: Akaike‟s information criterion corrected for small samples (AIC_c) using evidence ratios (*ER* = AIC_c weight of slope model ÷ AIC_c weight of intercept-only model, see Burnham & Anderson 2002). The *ER* is useful even for a comparison of a null model to a single alternative, in concept being akin to Bayesian odds ratios (see McCarthy 2007). For example, an *ER* of 5 would indicate that the hypothesised model was 5 times more likely to be a better biased-corrected model than the null, given the available data. The *ER* is preferable to a classic null hypothesis significance test because the likelihood of the alternative model is explicitly evaluated (not just the null). We determined migration dates and used *Draw* tools in ArcGIS to outline movement (Fig. 5.1 a, b).

We converted presence data to raster files and used the *Extract* function in ArcGIS to determine habitat use (based on vegetation communities) and habitat-specific altitude. Vegetation shapefiles were sourced from Geoscience Australia (www.ga.gov.au). To compare habitat selected (presence data) to proportion habitat available, we first used the *Minimum Convex Polygon* function within ArcGIS to calculate proportional breakdown of vegetation communities (within the *MCP* only). We calculated frequency of bird occurrence within each habitat (number of location hits by each vegetation community) and habitat availability (as above). For each habitat type we calculated a χ^2-like statistic of observed deviance from expected use ([observed use – expected based on habitat availability]^2/expected) in R and estimated the probability that the habitat-specific metrics could be generated at random based on a multinomial randomisation of expected values (probabilities based on 100 000 iterations).

5.3 Results

5.3.1 Movement

Across both wet and dry seasons, the maximum (linear) distance moved was 114 km, indicating that geese are not likely to migrate far when adequate resources are available. There was no apparent difference in migration between the sexes (Table 5.1), although samples sizes were small. Sub-adults stayed closer to the release site (maximum distance moved = 23 km). There was considerable variation in individual movement patterns and distance (Fig. 5.1 a, b). Some birds migrated north along the South Alligator floodplain system while others moved to the Mary River region and another to the East Alligator system (Fig.5.1). Five birds migrated back to the South Alligator during the late dry period.

Dividing movement by season (wet/dry) showed that individuals followed consistent movement trends (Appendix 3). In other words, if an individual moved at a high rate during the wet season, this trend continued throughout the dry season (information-theoretic evidence ratio [*ER*] = 973.4, $R^2 = 0.81$). However, dry season movement rates were slightly lower than wet season movement rates (Appendix 3). Comparing maximum and weekly mean movements to the weight of birds at time of release suggested that heavier birds may be travelling farther than lighter birds; however, the evidence ratios for all relationships by season and metric indicated no (i.e., $ER < 1$) or only weak evidence of effect (Fig. 5.2).

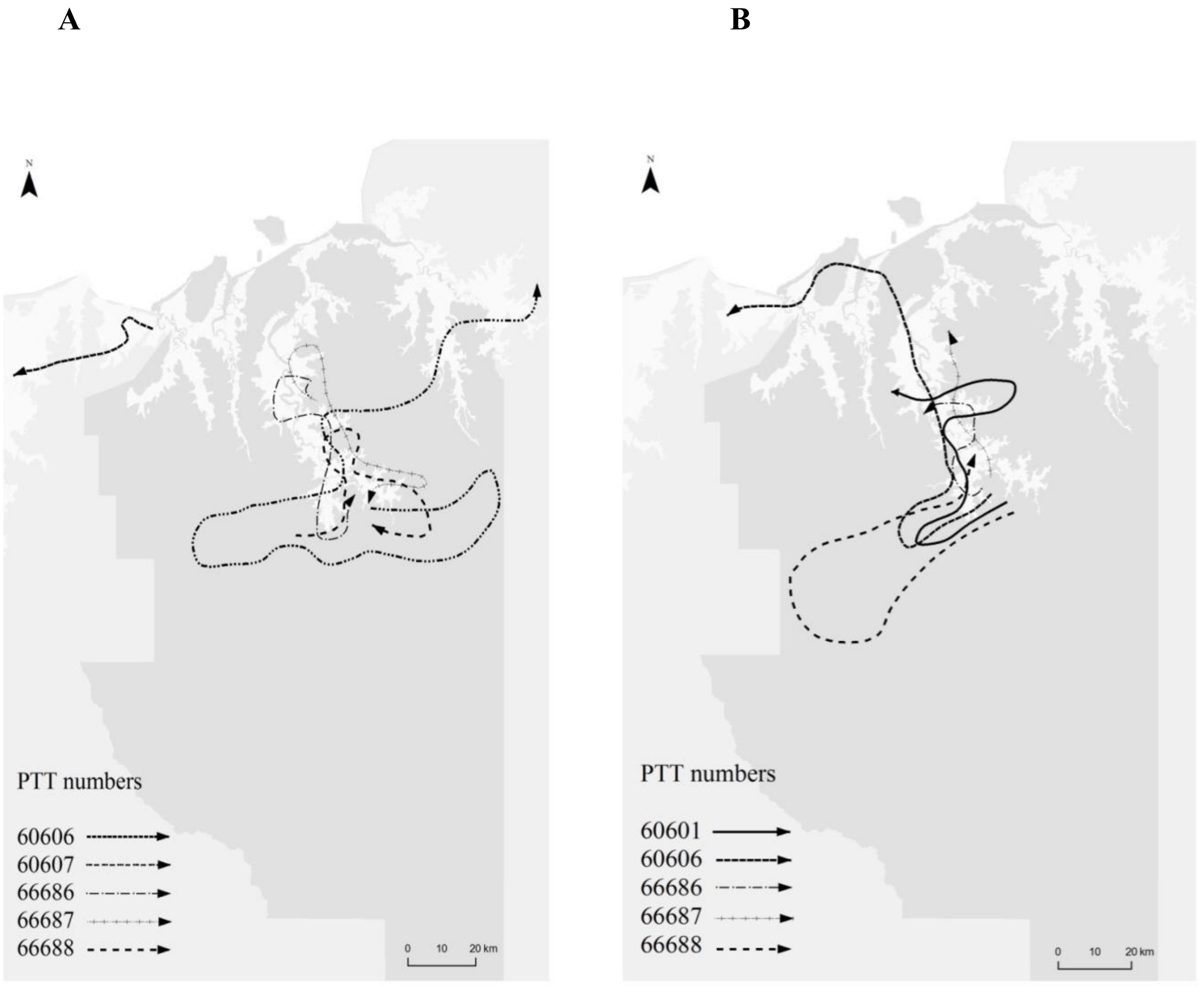


Figure 5.1 (A) Movement data for magpie geese during the wet season immediately post release (March – end April 2007). Platform Transmitter Terminal numbers are represented by dotted or straight lines. Sub-coastal floodplains are shown in white and the outline of Kakadu Park is shown in dark grey. (B) Movement data birds during the dry season (May through November 2007). Note: data only shown where birds moved > 25 km during the season. Release site at the origin of arrows (2A only).

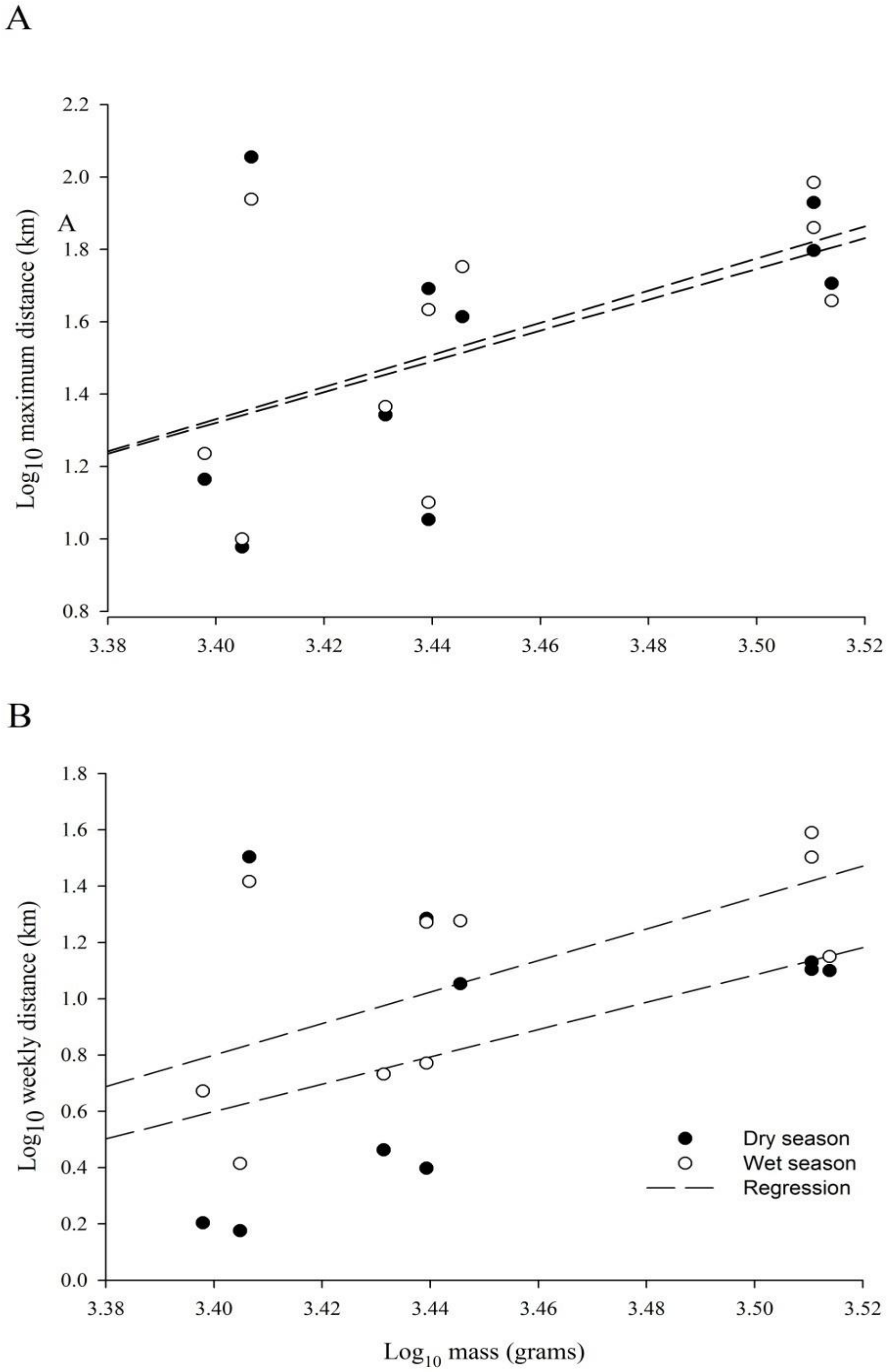


Figure 5.2 (A) Maximum and (B) weekly mean distance migrated by birds relative to body weight ($\log_{10}$) at time of departure during the dry and wet seasons. All data pooled by gender. Information-theoretic evidence ratios (ER, see text) were < 1 (i.e., the null model had most support) for all relationships except for weekly mean wet season movement rate relative to body mass (ER = 1.5, R2 = 0.33).

PTT number	Age	Gender	Body weight at release (g)	Activity (weeks)	Max distance (km), wet / dry	Mean weekly distance (km), wet / dry	Habitat use in protected area (%)
60600	Sub-adult	Female	2540	10	10.0 / 9.5	2.6 / 1.5	100
60601	Adult	Female	2790	36	56.5 / 41.1	18.9 / 11.3	100
60603	Sub-adult	Female	2500	26	17.2 / 14.6	4.7 / 1.6	100
60604	Sub-adult	Male	2750	14	12.6 / 11.3	5.9 / 2.5	100
60605	Sub-adult	Male	2700	36	23.2 / 22.0	5.4 / 2.9	100
60606	Adult	Male	3240	40	96.5 / 85.0	38.9 / 12.7	34
60607	Adult	Female	2550	38	86.8 / 113.5	26.1 / 31.9	99
66686	Adult	Female	2750	32	43.0 / 49.1	18.7 / 19.3	100
66687	Adult	Male	3265	64	45.5 / 50.8	14.1 / 12.6	100
66688	Adult	Male	3240	64	72.5 / 62.7	31.8 / 13.5	100

Table 5.1 Length of data transmission in weeks, maximum distance moved by season and proportion of habitat used within protected areas for captured magpie geese fitted with satellite transmitters.

Vegetation Communities	**Observed χ^2**	**Pr(random)**	**Conclusion**
Coast Rainforest / Myrtle - Pandanus Savanna	24.965	0.368	random
Coast Rainforest / Deciduous Rainforest	242.703	0.049	random or weak evidence of selection
Floodplain Sedgeland	486.597	< 0.001	selection
Mangroves	48.937	0.366	random
Myrtle - Pandanus Savanna	52.237	< 0.001	selection
Open Forest	254.925	< 0.001	avoidance
Paperbark Forest	14.317	0.001	selection
Woodland	86.021	< 0.001	avoidance
Hill-Woodland	13.252	0.005	avoidance

Table 5.2 Habitat selection by 10 satellite-tracked magpie geese from March to December 2007. Multinomial randomisation (100 000 iterations) to test the probability that a habitat type was selected, used in proportion to availability (random) or avoided are shown based on observed χ^2 and Type I error probabilities (chance observed deviance from expected use based on availability was random – Pr(random)).

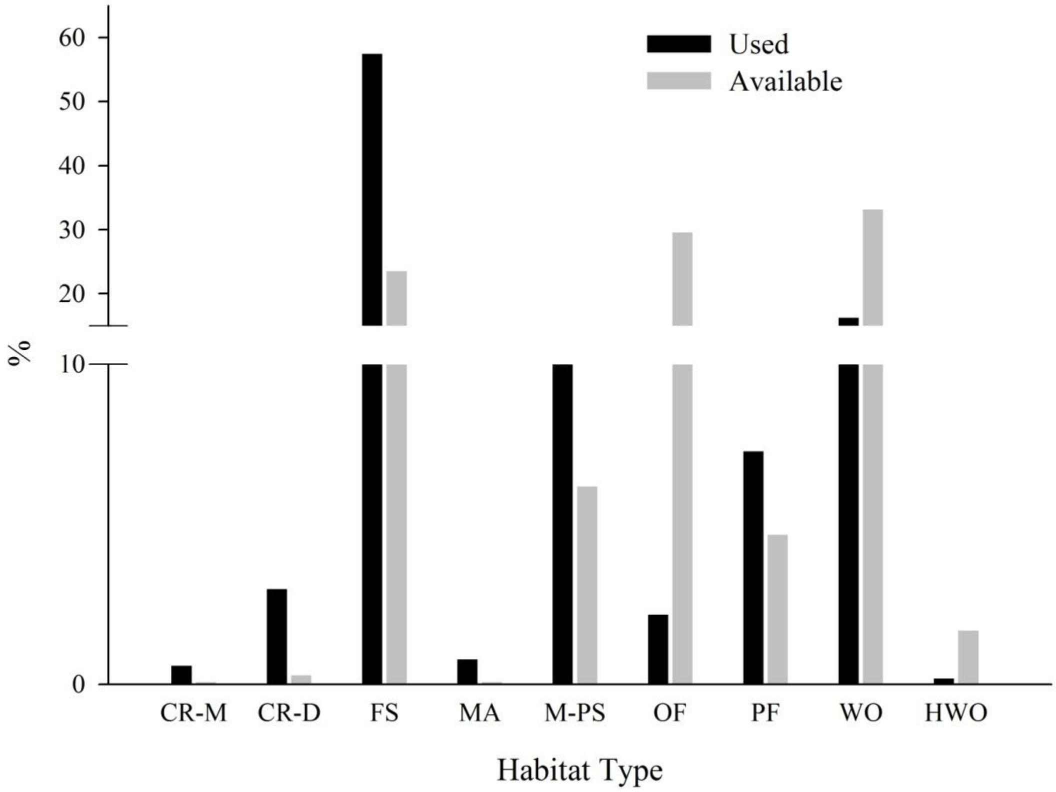


Figure 5.3 Bar chart comparing broad vegetation communities used by geese during both wet and dry seasons (per cent value) versus availability within Kakadu National Park. Selection, random use and avoidance tests shown in Table 5.2. Vegetation communities are CR-M (Coast Rainforest / Myrtle - Pandanus Savanna), CR-D (Coast Rainforest / Deciduous Rainforest), FS (Floodplain Sedgeland), MA (Mangroves) , M-PS (Myrtle - Pandanus Savanna) , OF (Open Forest), PF (Paperbark Forest), WO (Woodland), H-WO (Hill woodland) .

Most birds showed an association with KNP (Table 5.1). Notably, one individual (60606, adult male) moved onto pastoral-lease land on the Wildman River. We found that birds selected sedge-dominated floodplains, woodland and Myrtle-Pandanus savanna over other habitat types (Fig. 5.3 and Table 5.2). We note that use of woodland and savanna is likely to represent either roosting areas, or is a product of targeting transient billabongs within broad woodland communities (see Whitehead 1998). Birds did not use habitat > 10 m above sea level (median for all data, 8 m above sea level).

5.3.2 PTT reliability

By December 2007 we cancelled transmission for all but three PTTs because these were either no longer relaying data, or the animals had not moved for > 3 months (Table 5.1). After 12 months, only two PTTs were still transmitting location data. The two PTTs transmitting for longer than 12 months were stationary after 13 months and the harnesses had likely come loose. In sum, despite the time taken to construct adequate harnesses and thorough design and checks on PTT quality, accurate data were not obtained beyond 12 months of bird release. Location data were adequate, but not of the highest quality. Of all transmission (n = 1847), only 62% of location data were accurate to within 1 000 m (Table 5.3). Although magpie geese tend to forage and nest in open areas, data transmission might have been degraded by contact with floodplain substratum. The two transmitters retrieved from wild birds were in good condition, and the antennae had not been damaged.

Data quality	***n***	**%**
3	231	13
2	378	20
1	527	29
0	207	11
A, B and Z	504	27

Table 5.3 Accuracy of location data sourced through the Argos satellite system, where $3 \leq 150$ m, 2 = 150 – 300 m accuracy, 1 = 350 – 1 000 m, $0 \geq 1\,000$ m, A and B = no estimate of accuracy and Z = invalid location.

5.4 Discussion

Our satellite telemetry data has added to our understanding of goose movement by providing more detailed information at finer spatial scales. We observed extensive variation in distance moved and direction of movement. Only one adult bird moved farther than 100 km and most birds were resident to Kakadu during the study period. Past research on geese movement based on tag (leg-band) returns and radio telemetry has documented the nomadic movement patterns of North Australian populations in response to temporal and spatial variability in resource availability (Frith & Davies 1961; Whitehead 1998). Seasonal habitat associations by geese have also been documented (Bayliss & Yeomans 1990), and geese tend to associate with low-lying black clay floodplains during the period following the monsoonal rains and transient or permanent lagoons during the dry season. Rainfall is the principal driver of migratory behaviour in geese (Bayliss 1989; Whitehead 1998), although precipitation amount *per se* is not likely to instigate migration directly; it does affect resource availability. The seasonal drying of floodplains dominated by *E. dulcis* locks away the foodplant tubers under hard clay, forcing the departure of hundreds of thousands of geese in search of alternative forage (Frith & Davies 1961; Whitehead & Tschirner 1992). The very flooding and drying of transient floodplains allows the continued persistence of *E. dulcis* communities despite repeated predation (L. W. Traill, unpublished data). These plant communities in turn support numerically abundant geese populations typical of Northern Australia (Whitehead 1998).

Despite finding relatively limited movement, anecdotal evidence suggests that birds are capable of moving up to 500 km in one event during catastrophic periods of resource scarcity (Frith & Davies 1961), and geese have been observed flying over the Torres Strait between Australia and Papua New Guinea (Draffan et al. 1983). Whitehead (1998) also found that some birds moved farther than 114 km using VHF-telemetry over a longer period than our study (~ 5 years).

It appears that geese pursue a ranging-type behaviour (see Roshier et al. 2008), moving between sites in response to resource availability, and possible behavioural responses not examined here. From our (small) sample, we found that adults moved farther than sub-adult birds. Whitehead (1998) suggests that birds do not typically breed until their fifth year (although they attain sexual maturity by 24 – 36 months), and the first 3 – 5 years of life is used to gather knowledge of seasonal variation in resource availability. Further, the potentially greater distances moved by larger birds may be attributed to their increased foraging efficiency and thus body condition (Whitehead & Tschirner 1992). Acknowledging the limited inference provided by small sample sizes, we found no apparent differences between male and female adult birds, possibly due to shared breeding responsibility (Whitehead 1999).

Although geese do not pursue the migratory behaviour typical of ecologically similar temperate Anatidae (Blouin et al. 1999; Jefferies & Drent 2006), seasonal movement of more than 100 km (linear distance between sites) has implications for disease transfer. Geese might transfer parasites or pathogens to naïve populations thereby causing disease. Further, geese are a potential reservoir to highly pathogenic diseases, including H5N1 avian influenza (Tracey et al. 2004) and are of key interest to Australian health officials (AQIS 2006). Although these avian viral strains are fatal to individual geese, fine-scale movement between subpopulations will facilitate disease spread and mass mortality events. Spatial models that attempt to emulate zoonotic disease spread (e.g., Hess 1996; Plowright et al. 2008) will need to account for connectedness among the magpie goose metapopulation, and potential for the rate of spread to be higher than fadeout (Hess 1994). If the birds sampled from KNP are typical of sub-populations across northern Australia, we can assume that individual movement is seasonal, uni-directional and birds are capable of moving 100 - 500 km in one week.

Regarding the suitability of our method, it appears that bird mortality or the loss of harness was the likely outcome for half of our sample. Such technology is possibly best used for large birds and where movement between subpopulations is unknown.

From a conservation perspective, geese are mainly reliant on low-lying sub-coastal floodplains. Recent projections of future sea level rise by the year 2100 are up to 1.4 m (Rahmstorf 2007) and an eventual rise of > 14 m following ice sheet melt (USGS 2000). Of more immediate concern, habitat loss is likely even where sea level rise is less than 0.5 m, through saline water intrusion and the loss of (saline sensitive) *E. dulcis* communities (see Finlayson et al. 2006). Habitat loss will lead to fragmentation of the tropical metapopulation and the potential loss of genetic heterozygosity (Frankham & Ralls 1998; Spielman et al. 2004). Further, isolated populations will be vulnerable to demographic and environmental fluctuations and especially catastrophic events such as drought or epizootics (Caughley 1994; Traill et al. 2007). Habitat protection (including levees to protect wetlands against salt water intrusion), and maintenance of continued genetic transfer between viable subpopulations will be important for the long-term persistence of magpie geese in tropical Australia.

We recommend more research on tropical geese populations using molecular genetic analyses to define more systematically metapopulation structure, migration patterns, and demographic histories of subpopulations across their range (Frankham et al. 2002). These data will focus conservation effort and provide the information required if future translocations are required to maintain viable population.

CHAPTER SIX

6. WETLAND CONSERVATION AND SUSTAINABLE USE UNDER GLOBAL CHANGE: A TROPICAL AUSTRALIAN CASE STUDY USING MAGPIE GEESE

Published as a research paper at *Ecography* by Lochran W. Traill, Corey J. A. Bradshaw, Steven Delean and Barry W. Brook

Lead author Traill sourced GIS data, analysed these, ran population models and prepared all draft manuscripts (0.9). Brook conceived the work, checked models and read draft manuscripts (0.05). Bradshaw (0.025) and Delean (0.025) assisted with analyses and read draft manuscripts.

All co-authors agree that this manuscript can be submitted as a chapter for a PhD thesis.

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Abstract

Imminent shifts in environmental parameters due to climatic change might have profound ramifications for wetlands listed under the Ramsar convention. Although the exact mechanisms by which global change will affect these systems are not known, models that simulate component drivers, particularly at a broad spatial scale, can nevertheless allow for more informed conservation decision-making. Such general inference is particularly needed for wetlands across the tropics, where less knowledge and fewer resources are available to mitigate the impacts on important conservation sites. Here we develop a case study of wetland loss to sea level rise across tropical north Australia (including Ramsar listed sites), and link these to a metapopulation model for a keystone endemic waterbird, the magpie goose. We projected published models on sea level rise through to the year 2400, and found a non-linear trajectory of inundation up to 20 m above present levels. Digital elevation models were used to simulate sea level rise and the spatially differentiated loss of wetland habitat used by geese. Range retraction was linked to decline in ecological carrying capacity, and we coupled wetland-specific habitat loss projections to a spatially explicit demographic metapopulation model. Additionally, we included alternate harvest strategies based on present-day estimates of indigenous and nonindigenous offtake of geese, and examined the synergy between wetland loss and hunting on extinction risk. Our results suggest that Australia‟s once-abundant and widespread magpie goose will be reduced to a fragmented population of just a few thousand individuals within the next 200 – 300 years. Harvest could continue for some time, up to a „tipping point‟ at around 5% loss of current wetland habitat, after which the decline of geese is rapid. Given the inexorable nature of sea level rise, short- to medium-term conservation of waterbirds across Ramsar wetlands must prepare for adaptive wetland management, such as through buffer-placement, and ongoing monitoring of harvest.

6.1 Introduction

Global climate change poses a serious threat to tropical biodiversity (Deutsch et al. 2008). Populations already undermined by habitat loss, over-exploitation and competitive invasive species (Sodhi et al. 2004) are now challenged by environmental perturbation through global warming (Thomas et al. 2004). The potential for synergistic interactions among deterministic threats will make matters worse (Brook et al. 2008), and small, restricted populations are not likely to persist (Caughley 1994; Traill et al. 2009b).

The geographic and socio-political impacts of climate change will be asymmetrical; tropical regions are likely to experience a relatively greater loss of biodiversity than other regions (Bradshaw et al. 2008) and many of the world"s developing economies are situated within the equatorial belt. Climate change will include rising oceans, increased concentration of CO_2, rising temperatures and altered rainfall regimes (IPCC 2007; Church et al. 2008). The impacts of these will vary, but sea level rise will undoubtedly have a direct and marked effect on coastal biodiversity (for example Mulrennan & Woodroffe 1998a). Saline water intrusion inland will precipitate a shift in wetland plant community structure away from fresh-, or brackish-water adapted plants toward salt-adapted species, and with consequences for dependent fauna (Eliot et al. 1999). Resultant ecological shifts across coastal biomes will be expedited by sinking deltas (through sediment trapping and removal; see Syvitski et al. 2009), more intense cyclonic activity and storm surges (IPCC 2007).

Projections of sea level rise differ, ranging from ~ 20 cm (Raper & Braithwaite 2005) through to several metres (Hansen 2007), and up to 25 m (± 5 m) within the coming century (Rohling et al. 2008). There is concern that many Ramsar listed wetlands (which include rivers, swamps and marshes, wet grasslands and peatlands, estuaries, deltas and tidal flats, near-shore marine areas and mangroves) will be affected by such changes (http://ramsar.org).

As per listing criteria, Ramsar sites are wetlands that are home to threatened ecological communities, regions of high biodiversity and species endemism, aggregations of more than 20 000 waterbirds, and wetlands that provide food or other resources to human societies. Many Ramsar sites in the tropics are coastal, and thus the conservation and cultural implications of global change on these cannot be ignored. Indeed, change will occur, and any attempt to simulate such changes in the context of adaptive wildlife management will allow prevention of species extirpation events.

In tropical North Australia, up to eight separate wetlands are listed under the Ramsar convention, including the extensive floodplain systems of World Heritage-listed Kakadu National Park (Eliot et al. 1999). Indeed Kakadu and the nearby floodplains of Cobourg Peninsula are exemplar Ramsar sites because they support (1) high biodiversity (Finlayson et al. 2006), including endemic flora and fauna, (2) seasonal waterbird aggregations in excess of 2.5 million individuals from over 60 species and, (3) traditional and sustainable resource use by resident Aboriginal communities (Delaney et al. 2008).

To date, some research has addressed the possible outcomes for tropical north Australia under climate change (Eliot et al. 1999; Hennessy et al. 2004) but no quantitative assessment of the nature and extent of change to coastal wetlands through sea level rise has been done. Such research has important ecological and socio-political outcomes for wetlands across the tropics, including waterbird conservation and indigenous harvest. Here we address this deficiency by developing a comprehensive case study based in tropical Australia. We project sea level rise based on published scenarios and link the consequent wetland habitat loss to a predictive metapopulation model for a keystone endemic waterbird, the magpie goose. We include the recreational and traditional harvest of geese as an important form of human use. We discuss the realities of sea level rise for Ramsar sites such as those within North Australia, and the outcomes for dependent waterbirds and human communities.

6.2 Materials and Methods

6.2.1 Case study system and species

As a case study, we focused on geese populations across Australia‟s Northern Territory and the seasonal subcoastal floodplains (Fig. 6.1) that support these. Magpie geese are relatively well-studied and are economically and culturally important to indigenous and nonindigenous Australians (Delaney et al. 2008), thus the suitability of these for case study. Further, we use the term floodplains here to separate these from the mangrove systems, tidal flats and estuaries that additionally form part of the Ramsar listed wetlands in tropical Australia. Magpie geese rely on the subcoastal floodplains of tropical Australia and New Guinea for food and nest material (Whitehead 1998).

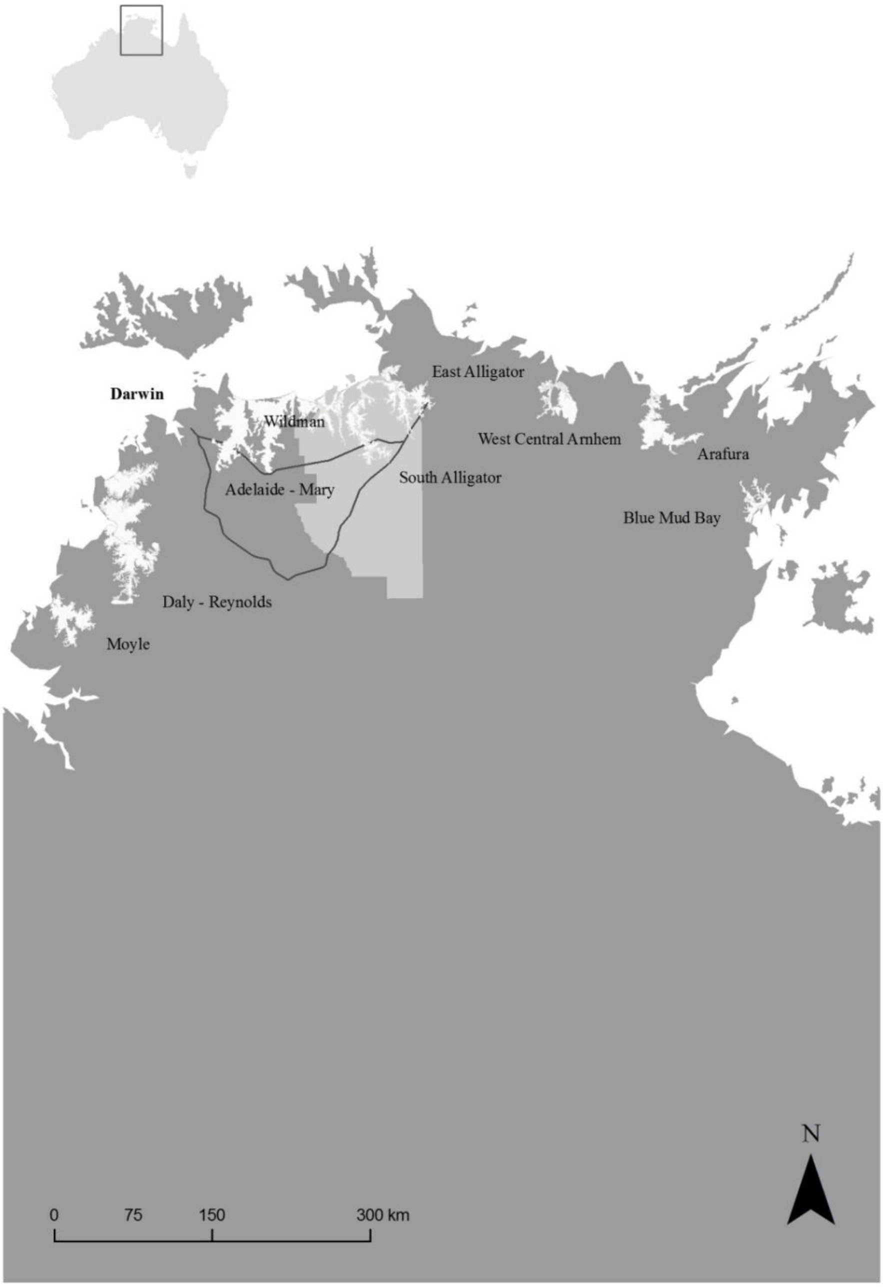


Figure 6.1. Subcoastal floodplains across the Northern Territory of Australia. Floodplains shown in white are used by magpie geese throughout the year. Kakadu National Park is highlighted in light grey and main access roads to the city of Darwin are represented as dark lines.

The numerous and extensive low-lying floodplains or tropical Australia flank macro-tidal seasonal rivers (Bayliss & Yeomans 1990). Formation of these was initiated in the recent Holocene: a transgressive phase began ~ 7 000 years BP following a rise in sea levels, followed by a large (mangrove) swamp phase as ocean levels stabilised ~ 6 000 years BP (Mulrennan & Woodroffe 1998b). Progadation of the coast and large river channels occurred primarily ~ 6 000 – 4 000 years BP and gross coastal morphology has changed little in ~ 1 500 years (Mulrennan & Woodroffe 1998b). Importantly, floodplain nutrient deposition over this period allowed for abundant floodplain plant growth – thus the numerous vertebrate populations in evidence today (Finlayson et al. 2006). Native plants are generally dominant on floodplains within protected areas, and these in turn support native and non-native vertebrates including a diverse waterfowl guild (Finlayson et al. 2006).

Magpie geese, endemic to Australia and New Guinea, are the sole member of family Anseranatidae and are estimated at 2 - 3 million individuals in the Northern Territory alone (Delaney et al. 2008). During the dry season, birds aggregate in numbers of up to 250 000 on shallow water floodplains, where they grub for tubers of the sedge plant *E. dulcis* (Frith & Davies 1961). The size of the aggregations and impact of herbivory alter wetland plant community structure. Population models for geese suggest that present day hunting estimates (median of 100 000 geese year^{-1}) are sustainable, assuming that current environmental conditions prevail (Brook & Whitehead 2005b).

6.2.2 Sea level rise

Saline water intrusion of tropical Australian wetlands has received scientific attention for almost two decades (Whitehead et al. 1990; Mulrennan & Woodroffe 1998a; Eliot et al.

1999). Heightened sea levels will alter coastal, estuarine and floodplain plant communities and will likely precipitate a decline in the carrying capacities of dependent waterbirds (for example, Jefferies et al. 1994). However, no past studies have explicitly modelled sea level rise or its impacts on tropical waterbirds.

As an example of likely outcomes for waterbirds under sea level rise, we tested the quantitative response of the Northern Territory magpie goose metapopulation to altered wetland habitat availability. To do this, we (1) predicted future rising ocean levels and used these projections to calculate wetland-specific habitat loss through inundation, (2) linked habitat loss to a decline in the ecological carrying capacity (K) of geese, and (3) incorporated the revised K into a spatially explicit metapopulation viability analysis that included harvest at present day rates.

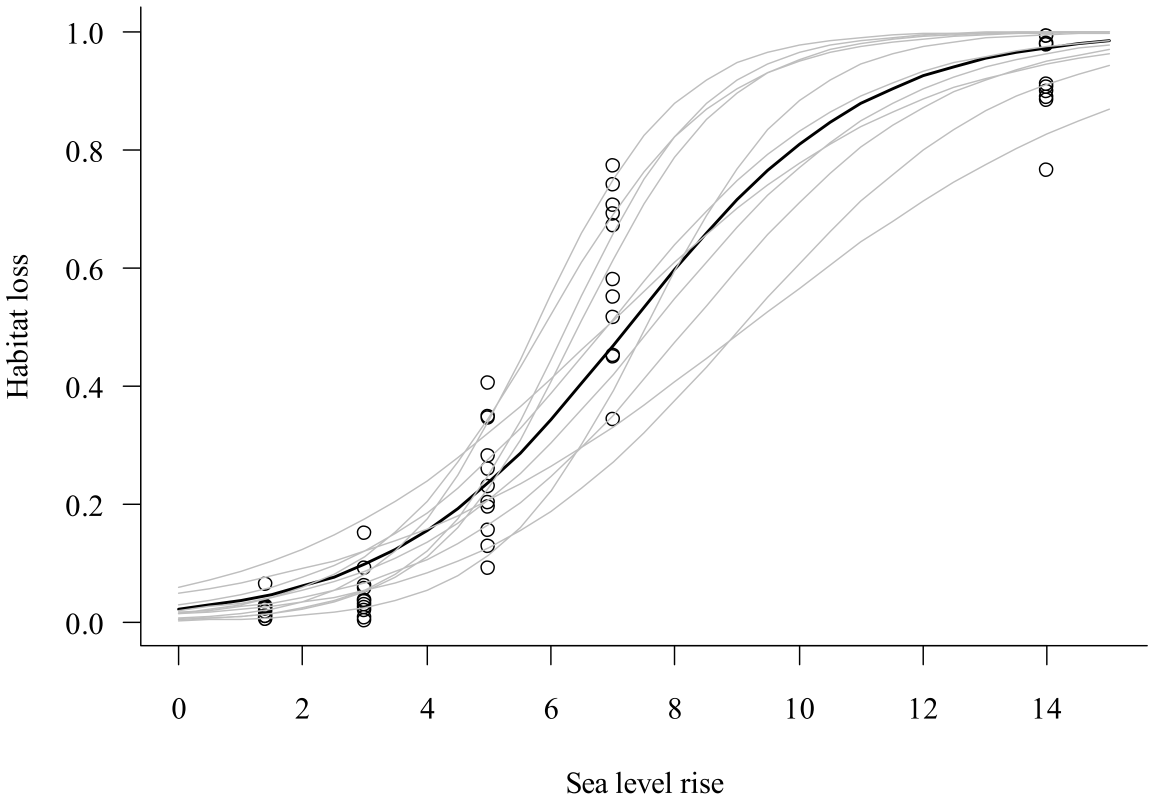


Figure 6.2. Relationship between sea level rise and wetland habitat loss. Individual data represent each of the eleven major coastal wetland systems across the Northern Territory of Australia, under sea level rise (1.4 m, 3 m, 5 m, 7 m and 14 m). Lines represent generalised linear model fits for each wetland (grey) and all (black).

Specifically, we simulated coastal inundation using digital elevation models in the Geographic Information System software ARCINFO version 9.2 (ESRI 2008). Digital elevation models were based on 90 m Shuttle Radar Topography Mission data, processed by the Consortium for Spatial Information (Jarvis et al. 2006). These were sourced in ASCII format and processed in ARCINFO. High-quality digital terrain models derived through commercial Light Detection and Ranging (LiDAR) exceeded our budget. Digital elevation models were converted to raster images, and five sea level rise scenarios (1.4, 3, 5, 7 and 14 m above 1990 levels) were created using the *extract* function in ARCINFO, assuming inundation of land surface lower than the specified elevations. For reference, the 1.4 m figure is the upper bound for 2100 calculated by Rahmstorf (2007).

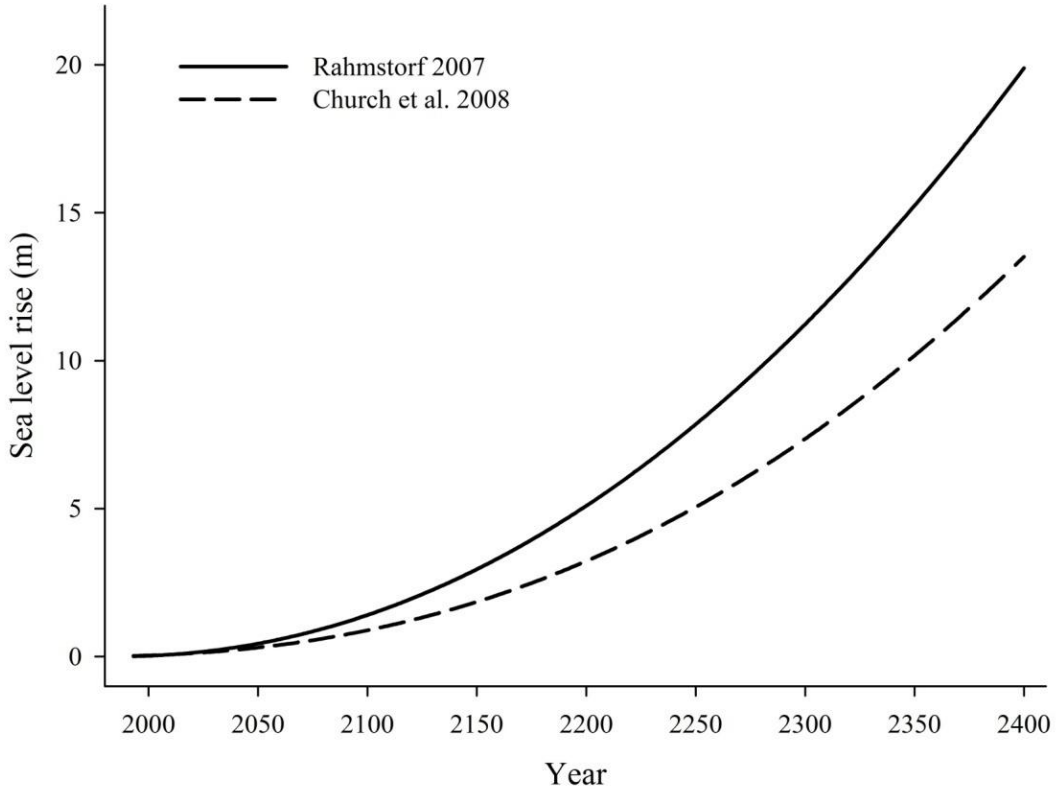


Figure 6.3. Sea level rise projections from 1994 to 2400, based on an extrapolation of the model projections of Rahmstorf (2007) and Church et al. (2008). Predictions were based on linear models fitted to power-transformed (0.48 and 0.43, respectively) sea level rise values and were back-transformed for display (see Methods).

To calculate floodplain loss in the NT, we sourced these as shapefiles from Geoscience Australia (Geoscience Australia 2008). Wetlands are determined by Geoscience Australia using vegetation communities, elevation and tidal projections. More detail can be found at http://ga.gov.au. Shapefiles were first projected to converge with the co-ordinate system used by digital elevation models, and then edited in ARCINFO to derive one wetland shapefile using the *merge* function. Floodplain area (and thus potential habitat available to magpie geese) was calculated in ARCINFO. We assumed that floodplains provided both foodplant and nesting material to geese, thus accounting for seasonal variation in use (Whitehead 1998). Raster digital elevation models were converted to vector shapefiles, and we used the *clip* function in ARCINFO to calculate habitat loss (of the floodplain shapefile).

Percent habitat loss under each sea level rise scenario was calculated for each of the 12 floodplains (except for the inland Barkley Tablelands, thus 11). We assumed that inundation (by ocean water) would result in the loss of both forage and nest material (see Whitehead 1998). *E. dulcis* in particular does not tolerate saline water greater than 33 ppt (Midmore 1998). We estimated habitat loss for each individual wetland over the range of sea level rise scenarios using a generalised linear model with a logit link and binomial variance function in R (R Development Core Team 2008). The logistic models fitted here were the basis for future sea level projections (Fig. 6.2).

We chose to project ocean rise beyond 2100. The nonlinear trajectory of rising ocean levels are typically not shown in medium- to long-term projections, such as used by the IPCC. Projections up to the year 2400 were used because we were confident that upper limits of sea level rise of at least 14 m (resulting from ongoing thermal expansion, complete mountain ice cap loss, and large-scale melting of the icesheets of Greenland and West Antarctica; USGS 2000) would be attained within that timeframe (Hansen 2007). To project sea level rise beyond 2100, we chose two scenarios based on mean ocean level increase over the past few decades, namely the 106-year projections published by Rahmstorf (2007) and Church et al. (2008). We digitised electronic images of graphs given by these authors (upper-bound projection Fig. 4, Rahmstorf 2007) and (upper-bound Fig. 6, Church et al. 2008) to derive the data.

The nonlinear increase in sea level over time was linearised using a power transformation of sea level values. Power transformation was determined using a Box-Cox profile likelihood function based on a linear model of rise against time. The estimated transformations were a better fit than the square root (0.5); a power of 0.48 for data derived from Rahmstorf (2007) and 0.43 for data from Church et al. (2008). We then fitted a linear model to the relationship between transformed sea level rise and time. Visual inspection of plots of model fitted values *versus* residuals indicated no systematic pattern that would indicate undue heteroscedasticity. The fitted linear model was used to predict future ocean rise outward to 2400, and these predictions were then back-transformed to the original scale (Fig. 6.3). The proportion of floodplain habitat loss at each modelled time step (i.e., each year) was predicted from the sea level rise projection based on the fitted models described above for each major floodplain.

Assuming a 1:1 relationship between predicted habitat loss and K, the decline in (ceiling) K over 400 years was estimated as the initial population size (N) multiplied by the proportional decline in wetland habitat for each year. We used the initial N values across all floodplains given by Brook and Whitehead (2005a, b). However, we adjusted these estimates downward from ~ 3.5 to ~ 2.65 million birds based on a recent census (Delaney et al. 2008). The projected annual K over 400 years was estimated using habitat loss predictions based on the sea level scenarios of both Rahmstorf (2007) and Church et al. (2008).

6.2.3 Population models, magpie geese

We used a spatially explicit stochastic population model of magpie geese developed by Brook and Whitehead (2005a, b) to test the effect of habitat loss on long-term population viability. Implemented in RAMAS Metapop v4 (Akçakaya 2001), the original model tested sustainable limits to recreational and aboriginal hunting across the NT. Here we used v5 of the RAMAS software.

In brief, the model was based on a discrete-time vital-rate transition matrix and included four age classes, sex-structure, demographic and environmental stochasticity, and a polygynous mating system (Brook & Whitehead 2005a, b). Reproductive rates were determined from published life-history data and surrogate data from ecologically similar geese where these were not available. Age at reproductive maturity for female magpie geese was ~ 2 – 3 years, and annual egg production averages 4.7 per female (Whitehead 1998). Hatchling survival was 0.45, and sub-adult and adult survival thereafter determined as 0.9. Adult survival was estimated using surrogate snow geese *Anser caerulescens* data. Density feedback was included as affecting survival and fecundity rates (Brook & Whitehead 2005a, b). A partially age-structured Leslie-Lefkovitch transition matrix was used to determine finite rate of population increase (λ), stable age distribution and expected generation time. Maximum intrinsic rate of increase (r_m) was taken as λ. The demographic transition matrix was configured within RAMAS with outlined survival and recruitment rates (Brook & Whitehead 2005a).

The spatial component of the model was based on a caricature of the major river-wetland systems across the NT (Brook & Whitehead 2005b). Subpopulation structure was inferred from aerial census data (Bayliss & Yeomans 1990), and updated here after Delaney et al. (2008). Dispersal between subpopulations was modelled as a function of connectivity, with nearby populations more likely to mix than farther subpopulations. The rates of dispersal varied from year to year, in keeping with annual rainfall fluctuation. As described above, we revised the initial N estimates to 2.65 million birds and linked the temporal decline in K estimated above individually to each coastal subpopulation.

We included indigenous and recreational harvest as an important component of mortality in magpie geese across the NT. Harvest can be specified within RAMAS Metapop at each time step (see Akçakaya 2001). Magpie geese are an important food source to the aboriginal people of Northern Australia (Whitehead et al. 2000), and are popular with recreational shooters (Whitehead et al. 1988). Recreational harvest is estimated at ~ 30 000 birds year^{-1} (Whitehead et al. 1988) and aboriginal harvest at 50 000 – 150 000 year^{-1}. We took the lower estimate of indigenous harvest (50 000 birds year^{-1}) and added 5 000 birds each year culled by tropical fruit growers and 15 000 birds that are estimated to die each year following injury sustained from shot (see Noer et al. 2007). Thus, total conservative harvest at each time step (year) was 100 000 birds.

Two harvest strategies were adopted: (*i*) Estimates of proportional harvest of each subpopulation (quota system) were derived from past records and by reviewing the proximity to recreational and aboriginal hunters (see Brook & Whitehead 2005b). Thus, total birds harvested declined in proportion to total abundance (at each time step), as expected if a quota management system were put into place. If implemented in practice, this requires annual monitoring of population size at each wetland; (*ii*) Estimates of fixed off-take at 100 000 birds each year derived for each wetland using the above multipliers to estimate subpopulation off-take and then standardising to equate to a total metapopulation harvest of 100 000 at each time step (year). Hunting therefore continued at present rates even when bird numbers declined. In practice, such a strategy would likely be terminated if population decline became severe. It is offered here as an illustrative scenario only.

All above scenarios were projected forward for 400 years and repeatedly simulated 10 000 times each to capture the variance in individual model runs adequately and to allow for a robust estimate of probability of decline. We ran an initial 50 time steps (excluding decline in K) to allow for stabilisation following density feedback (thus stabilisation at ~ 1.5 million birds, Fig. 6.4). Model outputs selected were median final metapopulation size after 400 years (median N) and the expected minimum abundance (EMA) of the metapopulation. EMA is the average of the lowest population size reached in each iteration. EMA is a useful indicator of propensity for species decline because unlike extinction risk, it is not bounded between 0 – 100%, and estimates the area under a quasi-extinction risk curve (McCarthy & Thompson 2001).

We identified approximate „tipping points‟ (curve inflexions) beyond which decline in geese abundance is more rapid than previously experienced, using mean N from proportional harvest simulations because these showed a nonlinear trajectory over time (Fig.6. 4 a, b). We calculated the change in abundance by estimating $(N_{t+1} - N_{t-1})/2$ at each time step (t), which gave us a gradient of decline through time. Visual inspection of the plotted gradients allowed inference on tipping points.

6.3 Results

Projections from the 90 m digital elevation models do not show a substantial loss of habitat under 1 – 3 m of inundation (Fig. 6.2). However, near-total loss of present day subcoastal floodplains occurs with sea level rise of 10 – 14 m. It is worth noting here that habitat loss will be disproportionate, with key wetlands such as those on the South Alligator system entirely eradicated, and other, non-Ramsar sites such as the Adelaide and Barkley remaining relatively intact.

According to our simulation of coastal inundation, the pace of wetland habitat loss due to rising oceans will be slow this century, but will increase in pace 150 – 300 years from now (Fig. 6.3). However, the coarseness of available digital elevation models does not allow simulation of saline water intrusion through channels, nor does it capture the effect of temporary storm surges, and so damage caused by saline water intrusion (and habitat degradation) will likely occur at a faster pace than our landscape-scale models predict.

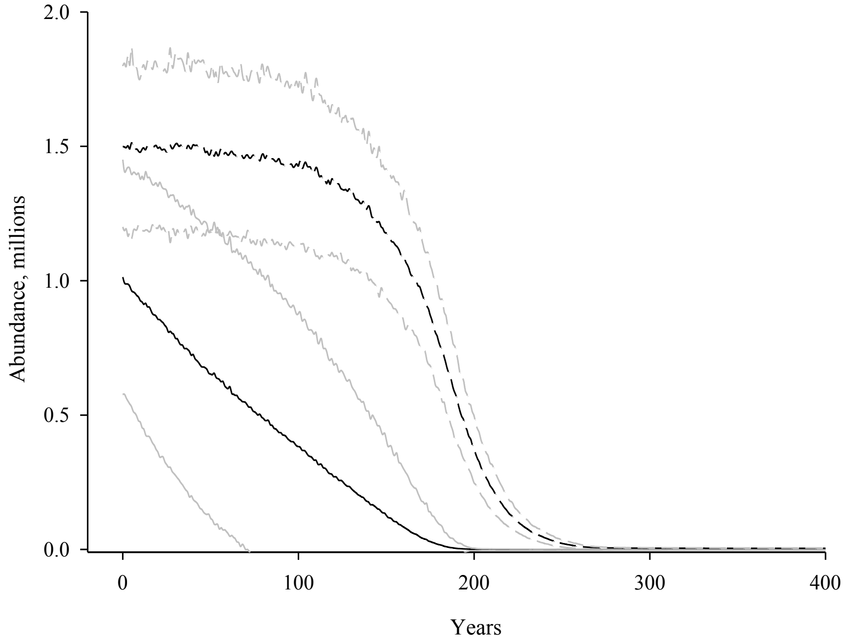
The implications of this century-scale change for the long-term persistence of magpie geese are serious. Indeed, despite the fact that relatively large expanses of floodplains used by geese will remain in the next 100 years, the goose metapopulation will be reduced to just a few thousand individuals by 2200 (see EMA values, Table 6.1). If future aboriginal harvest is not regulated by quota, magpie geese will be extinct in the „Top End" of Australia in a few hundred years (Table 6.1). Our population models suggest that harvest at present-rates can continue for some time. However, even regulated harvest (according to a quota system) is sustainable up to a threshold (~ 5% less habitat than that available today for both scenarios), after which decline is rapid (Fig. 6.4 a, b).

Harvest strategy	Sea level rise projection	Population size variable	2100 (year)	2200	2300	2400
Wetland-specific* proportional harvest quota	Rahmstorf 2007	*N*	1 444 209	368 647	4 790	4 358
		EMA	998 526	313 786	3 343	2 414
	Church et al. 2008	*N*	1 458 697	1 191 077	51 069	5 039
		EMA	998 727	896 513	43 353	3 012
Fixed upper limit† of 100 000 birds year^{-1}	Rahmstorf 2007	*N*	361 330	995	31	2
		EMA	260 659	841	20	2
	Church et al. 2008	*N*	427 556	63 577	40 220	18
		EMA	290 482	48 977	11 120	14

Table 6.1. Population size estimates from spatially explicit population viability analysis for magpie geese under two scenarios of sea level rise and two harvest strategies. Results are presented for the years 2100, 2200, 2300, and 2400. All stochastic simulations were run 10 000 times and for 400 steps (years). *N* = median final population size; EMA = expected minimum abundance (minimum population size for each simulation run, averaged across all 10 000 iterations).

*Wetland-specific denotes harvest unique to each major wetland and proportional to metapopulation size across the Northern Territory.

†Denotes harvest across the Northern Territory fixed at a total of 100 000 birds year^{-1}.



A (above) and B (below)

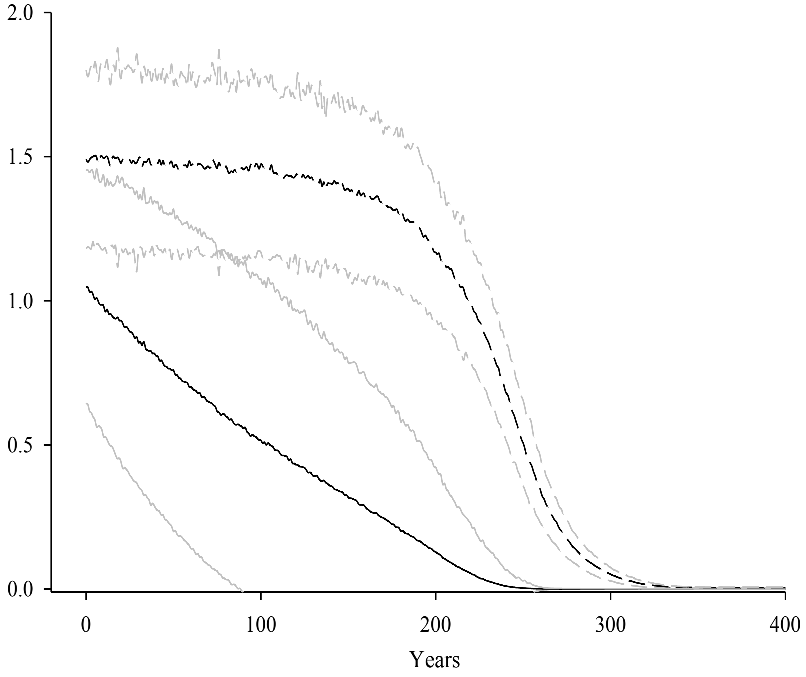


Figure 6.4. Results of a spatially explicit population viability analysis for magpie geese in the Northern Territory of Australia, based on sea level projections by (A) Rahmstorf (2007) and (B) Church et al. (2008). Stochastic simulations were run for 400 years with 10 000 iterations. Harvest scenarios were either wetland-specific, set at a proportional value (quota system as dotted black line, SD in grey), or a fixed harvest of a total 100 000 birds year^{-1} across all floodplains (solid black line, SD in grey). An initial fifty years of „burn in‟ simulation allowed „smoothing‟ of density-dependent

oscillation and thus the drop to under 2 million individuals at initial *N* (zero time point is the year 2000).

Note: One *standard deviation* (SD) provided either side of mean *N* for each scenario, in grey lines.

6.4 Discussion

Sea level rise across Northern Australia will follow a nonlinear trajectory, with near-total inundation of present-day coastal regions within 300 – 400 years; a scenario likely to be played-out across the Asian-Pacific. This estimate is conservative because the underpinning semi-empirical models project an ongoing acceleration of polar ice sheet dynamics that is no more rapid than reflected in historical trends – an assumption with considerable scientific uncertainty (Hansen 2007). Apart from the social impacts, radical shifts in tropical wetland ecology will be of serious consequence to dependent waterbirds such as magpie geese. Loss of just 5% of wetland habitat available to magpie geese today will be to the detriment of North Australian populations and possibly signal an ecological point-of-no-return. The short- to medium-term (100 – 200 year) resilience of North Australian geese is thus attributable solely to their numerical abundance (see Soulé 1987).

We note that vertical accretion and the possible re-establishment of freshwater floodplains further inland are unlikely to be sufficient to support large waterbird aggregations. Present day north Australian floodplains are the product of ~ 4 000 years of deposition (Mulrennan & Woodroffe 1998b) and nutrient input, which has determined the ability of these to support current vegetation and associated resource densities (Finlayson et al. 2006). We are unaware of the formation process for analogous Asian wetlands, but suggest that the outcomes will be similar: the rate of change will exceed the adaptive capacity of dependent flora and fauna.

Our modelled „tipping point" in time, (after which decline under harvest is sudden), at 100 – 150 years from now and following ~ 5% loss of present day wetlands, is alarming. In reality, this could occur sooner than our inundation projections would indicate because of fine-scale habitat degradation and localised inundation that is not captured by our coarse-digital elevation model-based mapping. Moreover, we do not account for the 1:100 multiplicative factor (*Bruun* Rule) of shoreline retreat in response to rising ocean levels (see Bruun 1983). Advanced hydrological models are required to deal with these features, perhaps based on LiDAR imagery. Our work has also identified an important issue regarding indigenous harvest in northern Australia: it needs to be monitored. We do not suggest punitive action against traditional harvest, but promote the implementation of annual monitoring of geese populations (as per Delaney et al. 2008) and off-takes. When required, upper limits on hunting will need to be implemented. Conservation managers need to consider that sub-coastal wetlands across the tropics are the result of thousands of years of nutrient deposition and these will not simply move inland and continue to support present day levels of biodiversity. The change will occur faster than species like magpie geese have capacity to adapt to and thus their decline.

Failure to look beyond the next 100 years (a common time frame used for conservation and climate change policy making) misses a critical point: sea level rise is an inexorable process that will have increasingly serious and cumulative consequences for coastal ecological systems, even if early impacts are apparently adaptable and not immediately threatening to species" viability. Plausible models outlined here show that upper estimates of sea level rise (at 14 m after USGS 2000, not considering any substantive melting of East Antarctica) will likely occur within the next 300 – 400 years. Unless global warming is substantially mitigated (IPCC 2007), tropical waterfowl that are dependent on coastal wetlands will, within a few centuries, exist only as relictual subpopulations within a fragmented landscape, and no longer able to function in their former ecological role. Aboriginal and recreational harvest of such waterbirds will have to be monitored and potentially regulated.

Our case study should be indicative of the sort of changes that will occur to subcoastal wetlands across the Asia-Pacific region. Shifts in wetland plant community structure will occur at a pace faster than resident waterbirds can adapt. This does not necessarily imply extinction, but rather declines in habitat available to waterbirds and subsequent loss of hunting opportunity to many communities. Whilst we acknowledge that we cannot contemplate the future adaptive and mitigation responses of human society as major changes progress, we point out that many of the coastal ecological systems (and dependent species) that we witness, use and appreciate today, are not likely to persist.

CHAPTER SEVEN

7. PRAGMATIC POPULATION VIABILITY TARGETS IN A RAPIDLY CHANGING WORLD

Published as a review paper at *Biological Conservation* by Lochran W. Traill, Barry W. Brook, Richard Frankham and Corey J. A. Bradshaw

Lead author Traill conducted the review and wrote all manuscripts (0.8). Bradshaw (0.1) and Traill co-conceived the work and Frankham (0.05) and Brook (0.05) contributed toward the intellectual development of the work and commented on all draft manuscripts.

All co-authors agree that this manuscript can be submitted as a chapter for a PhD thesis.

Abstract

To ensure both long-term persistence and evolutionary potential, the required number of individuals in a population often greatly exceeds the targets proposed by conservation management. We critically review minimum population size requirements for species based on empirical and theoretical estimates made over the past few decades. This literature collectively shows that thousands (not hundreds) of individuals are required for a population to have an acceptable probability of riding-out environmental fluctuation and catastrophic events, and ensuring the continuation of evolutionary processes. The evidence is clear, yet conservation policy does not appear to reflect these findings, with pragmatic concerns on feasibility over-riding biological risk assessment. As such, we argue that conservation biology faces a dilemma akin to those working on the physical basis of climate change, where scientific recommendations on carbon emission reductions are compromised by policy makers. There is no obvious resolution other than a more explicit acceptance of the trade-offs implied when population viability requirements are ignored. We recommend that conservation planners include demographic and genetic thresholds in their assessments, and recognise implicit triage where these are not met.

7.1 Introduction

Extinction is the natural endpoint in the evolutionary process, with most species typically persisting five to ten million years (Frankham et al. 2002). Evolutionary theory and numerical simulation of population persistence (or demise) has allowed the estimation of thresholds, or key „turning points‟, after which extinction is more likely. The turning point in the trajectory of a population is complex, such that simplifications of the process are often used to make conservation decisions in an imperfectly measured world. This is why the concept (and applied use) of population viability and minimum viable population size (MVP) gained momentum in the early years of conservation biology (Beissinger & McCullough 2002), and why population thresholds remain in use today (Traill et al. 2007), albeit concomitant with extinction correlates such as habitat loss (Mace et al. 2008). Importantly, these thresholds imply the moment at which a *declining* population becomes a *small* population, with increased vulnerability to extinction (Caughley 1994). Small populations are uniquely vulnerable to demographic stochasticity at this crucial stage (Melbourne & Hastings 2008). Moreover, the number of individuals required to maintain the *small* population is generally underestimated.

But are people really listening to the key, inconvenient truths that emerge here? The present day increase in the rate of extinction is rapid and can be principally attributed to an explosion of modern human activity (IUCN 2008). In response to the perceived biotic crisis that looms as a result, multi-lateral conservation organisations such as the World Conservation Union (IUCN) and the scientific community have worked hard to understand and quantify extinction risk, and communicate this knowledge to policy-makers, governments and the general public (Beissinger & McCullough 2002). Here we review the evolutionary and demographic requirements of populations and argue that evidence-based scientific estimates of what is required to achieve viability are (often considerably) larger than targets outlined by conservation organisations. While we cannot provide an exhaustive review of the practical challenges of conservation biology, we suggest that most vulnerable species are not really being managed for viability (continued existence under trying environmental circumstances); rather, conservation targets in most cases merely aim to maximise short-term persistence and fit with complex political and financial realities. The problem is similar to the dilemma faced by climate scientists, where national and international policy seems incapable of meeting the emissions reduction implied by the available geophysical and biological evidence to avert severe anthropogenic interference with the climate system, let alone to reverse the damage already done (Hare 2009). Numerous socio-political impediments (IPCC 2007; Working Group III) do not invalidate the science behind climate change and its impacts (Working Group I and II); rather, they capitulate to the reality of what is considered politically possible. Here we argue that preventing species extinctions by applying knowledge derived from the discipline of conservation biology has an analogous problem, admittedly with no immediate resolution.

7.2 The scientific basis for minimum viable population sizes

Despite a good deal of empirical development of the concept of minimum viable population size (Frankham 1995; Frankham & Franklin 1998; Reed et al. 2003b; Brook et al. 2006; Traill et al. 2007), there is a disconnect between associated theory and conservation practice. It is irrefutable that population size matters for extinction risk, with small and isolated populations being particularly vulnerable to: (1) demographic fluctuation due to random variation in birth and death rates and sex ratio, (2) environmental fluctuation in resource or habitat availability, predation, competitive interactions and catastrophes, (3) reduction in co-operative interactions and subsequent decline in fertility and survival (Allee effects), (4) inbreeding depression reducing reproductive fitness, and (5) loss of genetic diversity reducing the ability to evolve and cope with environmental change (see Caughley 1994; Frankham 1995).

The idea of a MVP has its foundation in efforts to capture, in population viability analyses (PVA), the many and interacting determinants of extinction risk. In this original context, MVP is defined as the smallest number of individuals required for a population to persist in its natural environment (Shaffer 1981). The likelihood of success is measured on a probability scale (0 – 1), and projections into the future can be scaled to years or generations (Reed et al. 2003b).

Alternatively, evolutionarily determined MVPs are based solely on the maintenance of evolutionary potential, that is, the population size required at equilibrium to balance the loss of quantitative genetic variation with the gain from mutation (Franklin 1980; Franklin & Frankham 1998). Although the arguments are theoretically different, both recommend similar turning points toward extinction, as we demonstrate below.

7.2.1 Empirical MVP

Estimates of MVP size can be derived by empirical simulation, experiments, or long-term monitoring. An example of long-term census study is that by Berger (1990) who evaluated the persistence of isolated populations of bighorn sheep (*Ovis canadensis*) over 50 years. Populations < 50 individuals went locally extinct, while those containing ≥ 100 individuals generally persisted.

Most empirical MVPs are probabilistic estimates of population persistence over a stipulated period: by arbitrary convention at least 90% certainty of persistence for at least 100 years (Shaffer 1981). Typically, PVAs are stochastic systems models which project changes in population abundance over time and account for demographic and environmental variation, catastrophic events, density dependence (including density feedback) and inbreeding depression (Gilpin & Soulé 1986). PVAs are used to predict population persistence in the short (a few years) to medium term (10s to 100s of years) and allow quantitative comparison and qualitative ranking of alternate management strategies. Persistence over generations (from as low as 3 to 40 or more generation spans) is used as an alternate to time steps in years, and is seen as biologically more appropriate when working across taxonomic groups (O'Grady et al. 2008). Simulation models can be individual- or matrix/cohort-based and implemented using generic computer software packages (see Lindenmayer et al. 1995) or tailored models. Most estimates of empirical MVP have been obtained using PVAs; indeed, a recent review of MVP-related literature found that 95% of 141 published articles used PVA as their basis for estimating extinction risk (Traill et al. 2007).

Median estimates of the empirical MVP derived from PVAs range from ~ 1 300 (Brook et al. 2006) to ~ 5 800 individuals (Reed et al. 2003b), depending on the method and underlying assumptions. The lower estimate derives from scalar population growth models that do not include demographic stochasticity, fluctuation in age structure or genetic deterioration. The upper estimates of MVP (Reed et al. 2003b) accounted for all major deterministic and stochastic threats and some positive feedbacks, including inbreeding depression. Of note, Melbourne and Hastings (2008) find that most population analyses have under-estimated viability by not accounting for all major factors contributing toward stochasticity.

A recent review and meta-analysis reported that 60% of published PVAs included genetic effects (Traill et al. 2007). Yet, even PVAs that take genetic factors into account usually underestimate their impacts on extinction risk. First, these only encompass the deleterious genetic impacts of inbreeding on reproduction and survival (inbreeding depression), but do not consider the loss of genetic diversity which effectively reduces a population‟s ability to evolve and cope with environmental change (Visser 2008). Second, all studies that include inbreeding depression underestimate its effect on population viability. Many use small impacts of inbreeding depression based on juvenile mortality in captive populations, rather than those for all components of reproduction and survival in wild populations (O'Grady et al. 2006). Further, all assume Poisson-type variation in family size, but variation is typically much greater leading to lower effective population sizes (Box 1), more rapid inbreeding and greater reduction in reproductive fitness (Frankham et al. 2002).

Critics argue that PVAs are only practically useful for predicting extinction risk where data are extensive and reliable and projection time frames are short (Fieberg & Ellner 2000). Further, the IUCN Red List does not base the categorisation of any threatened species on PVAs alone (IUCN 2008). However, Boyce (1992) and Burgman (2006) suggest that PVAs are indispensable when done properly because they cause assumptions regarding the processes leading to decline to be made explicit, and bring together scientists and policy-makers to assess the costs and benefits of alternative approaches to population management.

7.2.2 Evolutionary MVP

Few conservation programs (for wild-living populations) explicitly incorporate genetic goals or attempt to maintain wild populations large enough to retain a substantial fraction of genetic diversity (Frankham et al. 2002). Genetically viable populations are those large enough to avoid inbreeding depression, prevent the accumulation of deleterious mutations, and maintain evolutionary potential. Small populations can persist in the wild for some time, but the reproductive fitness of these, and especially the ability to adapt to change (evolutionary potential) is compromised and extirpation is likely (Spielman et al. 2004). So what population sizes are required to ensure genetic viability, and how do these compare to empirical MVPs?

The MVP to retain evolutionary potential in perpetuity is the equilibrium population size where loss of quantitative genetic variation due to small population size (genetic drift) is matched by gains through mutation. Franklin (1980) estimated this to be a genetically effective population size (N_e) of ~ 500 individuals (50 to avoid inbreeding). Critically though, the mean ratio of the N_e to the census population size (N) is ~ 0.1 (Frankham 1995) and therefore a census population of ~ 5 000 adults. The concept of N_e is described in Box 1, but we note here that the estimation of the census N allowed biologists to move on from the 50/500 rule (after Franklin 1980). Other estimates of the evolutionary MVP have attained a N_e of ~ 5 000, corresponding to an adult population size of 50 000 (Lande 1988; Franklin & Frankham 1998).

Unfortunately, the population sizes of many threatened species are likely to fall below this range (perhaps > 2 000 species, given the total number of *Critically Endangered* populations in the Red List; IUCN 2008). The loss of genetic variation within these populations can be regenerated through mutation, but this will typically take hundreds to thousands of generations (Frankham et al. 2002). Small populations have therefore reached a point-of-departure: away from the ability to adapt to changing environmental circumstances and toward inflexible vulnerability to these same changes (Frankham & Ralls 1998).

7.3 Generalities

The bottom line is that both the evolutionary and demographic constraints on populations require sizes to be at least 5 000 adult individuals. These seem to be large requirements, but a number of studies across taxonomic groups have made similar findings: the median MVP derived from PVA of 102 vertebrate species was 5 816 individuals (Reed et al. 2003b), and 4 169 individuals from a meta-analysis of 212 species (Traill et al. 2007). The census-based MVP of 5 500 reported by Thomas (1990) is also remarkably congruent; all similar to the recommended census *N* of 5 000 individuals (Frankham 1995). We note though that similarities are not strictly equivalent, and are a result of evaluation of some non-overlapping factors, meaning MVP in many circumstances will be larger still.

Box 1 – Genetically effective population sizes

The genetically effective population size (N_e) is a measure of a population"s genetic behaviour relative to that of an „ideal" population (Frankham et al. 2002). Technically, it is the size of an idealised population that would result in the same inbreeding or loss of genetic diversity as that in the population under study. An idealised population is a conceptual closed, random-mating population of hermaphrodites that have Poisson variation in family size, constant numbers of breeding individuals in successive, non-overlapping generations, and no mutation or selection (Wright 1931). Real populations deviate from the idealised population due to fluctuations in population size, unequal sex ratios, family size variation greater than Poisson and overlapping generations. The first three factors reduce N_e to below the census size, while the effects of overlapping generations are not consistent in direction (Frankham 1995). Genetic impacts depend on N_e, rather than *N*, with genetic diversity being lost at a rate of

$1/(2N_e)$ per generation within closed populations, and inbreeding increasing at this same rate in random-mating populations. The N_e is the „currency" used to describe the evolutionary MVP.

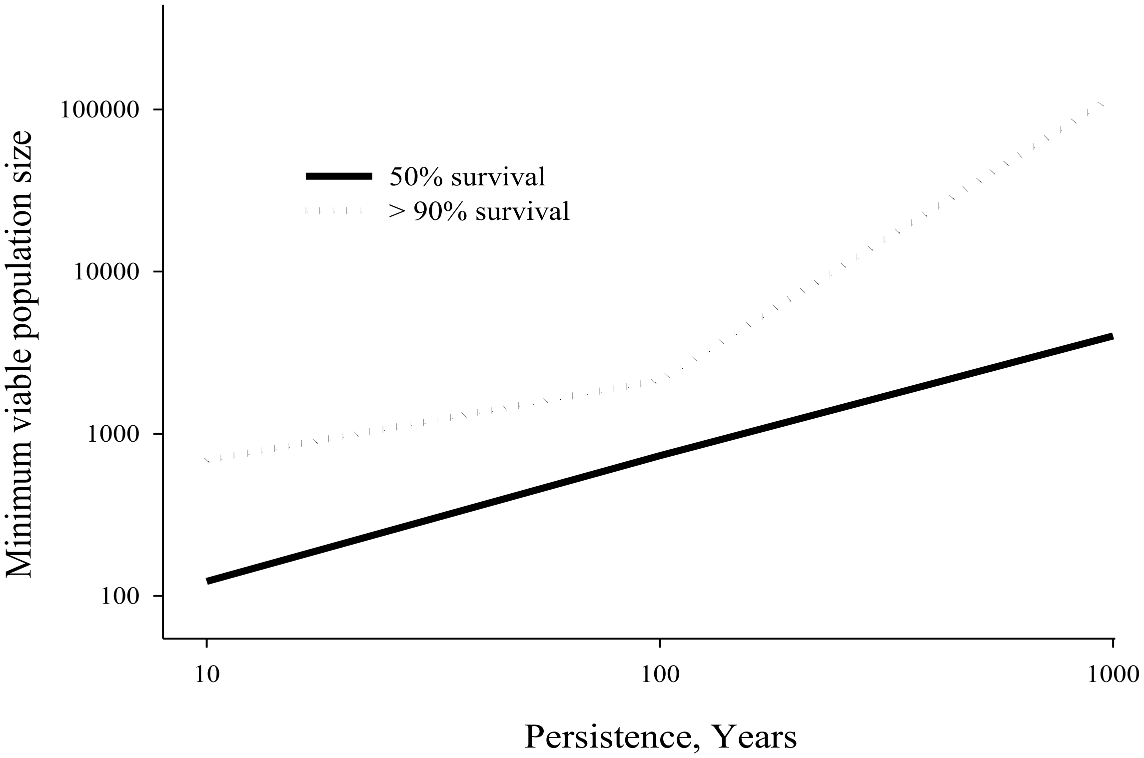


Figure 7.1 Line plot of median minimum viable population estimates (scaled to $\log_{10}$) for 1 198 species derived from time series analyses (see Brook et al. 2006) along a logged timescale (10 – 1 000 years). The full line represents median MVP size at 50% probability of persistence. The dotted line is the median MVP at greater than 90% probability of persistence

7.4 Conservation in the long term

The science of more than 30 years of empirical and genetic research on the viability of wild-living populations thus implies that the number of individuals (required to avoid a turning point toward extinction) is greater than generally appreciated or implemented within conservation management. Although our contention that conservationists often manage below a biologically reasonable extinction threshold is not new (see Reed et al. 2003b), debate persists. Disagreement hinges on two main issues: (*i*) the accuracy of predictions and (*ii*) their real-world applicability to conservation action (Beissinger & Westphal 1998; Coulson et al. 2001).

Regarding accuracy, criticism centres on the general low quality of available population data and the high sensitivity of predictions to assumptions made. A response to this is that the rapidity with which the extinction crisis is unfolding means that biologists and managers cannot afford to wait for the collection of the necessary high-quality data before making decisions (Lee & Jetz 2008) – and that given their relative simplicity, most biases are likely to underestimate rather than overestimate risk. Many conservationists also question the real-world relevance of MVP estimates given their high associated uncertainty bounds and the wide cross-species range. For example, some published PVAs have specified MVP sizes as low as 20 individuals (Sæther et al. 1998) and others as high as 100 000 (Reed 2005). However, variation arises in part from the complexity, biological reality and type of PVA used, and median confidence intervals from meta-analysis of standardised MVPs still provide reasonable guidance on the most likely targets that will be required (e.g., 3 577 – 5 129, 95% CI; Traill et al. 2007). Further, conservationists working within developing nations will rarely have the resources available to collect the demographic and other data necessary to model viability for specific species or taxa; there is thus a compelling argument to develop rules of thumb for population size extinction-risk thresholds. Moreover, related species tend to have similar characteristics and response.

Differences between published MVP estimates, even for the same species, can also be explained by the different survival probabilities and timescales used. For example, median MVP values estimated from time series models fitted to of 1 198 species (Brook et al. 2006) differed substantially (by up to 10 000 individuals) depending on whether the risk criteria specified a > 50 or > 90% probability of survival (Fig. 7.1). The first is a „coin toss" level of risk acceptance, the latter is equivalent to being listed as *Threatened* by the IUCN (Criterion E). Further, median MVP values increase by many thousands of individuals as the projection interval increases from 10 to 1 000 years (Fig. 7.2). The implication here (of selecting a particular frame of reference) is that conservation decision-makers must explicitly choose a period over which they are managing for persistence, and with a specified certainty of success. Beyond that chosen frame of reference, nothing useful can be said about the longterm persistence of a given species.

The science of integrated population biology is now clear enough that we can state that if conservation practitioners purportedly manage for population viability with a few hundred individuals or less, then they effectively manage at a 50:50 odds of success on a century time scale (see Fig. 7.1). Clearly, any conservation project that is serious about the long-term survival (and continued ability to evolve) of a species must aim for a metapopulation of thousands of individuals (Fig. 7.1 and 7.2), or else re-evaluate their stated position. Practitioners can validly take issue with high population targets, because of the impracticality of preserving adequate contiguous habitat, especially for large-bodied species (e.g., Armbruster & Lande 1993). In reality, most populations presently exist as fragmented subpopulations within a larger metapopulation (Akçakaya & Brook 2008), with their successful conservation depending on genetic exchange among units to maintain high genetic heterozyosity (Frankham et al. 2002).

Box 2 – Ecological triage

Ecological (or conservation) triage is a concept enveloped in an evolving, but unfortunately acrimonious, debate at the centre of conservation biology. Polarity centres on two fundamentally different approaches toward conservation, *viz*. „no species extinction, at any cost‟ and „extinction is inevitable for some species, let‟s manage the process rationally‟ (e.g., Jachowski & Kesler 2009).

The debate has a long history. Walker (1992) advocated the prioritisation of species (conservation status) according to the necessary functions that species or populations provided to ecosystem function; and the abandonment of functionally redundant, or highly diminished species. While few conservationists explicitly advocate extinction of no-hopers, triage is implicit through recognition that current threats to biodiversity outweigh the resources available to mitigate these. Thus, a number of approaches can be taken to optimise conservation effort, albeit acknowledging that preventing extinction altogether is at the very least daunting. For example, Hobbs & Kristjanson (2003) advocate adaptive management strategies ranging from *no immediate management action* (say, for non-threatened species) to *urgent protection or restoration,* without stating that populations should be abandoned. Carefully thought-out resource allocation thus allows more efficient conservation effort, and hopefully, better outcomes.

Recent advances include „prioritisation protocols‟ that optimise (conservation) resource allocation through cost-benefit analyses (Murdoch et al. 2007) and the likelihood of management success. The authors build on the *Noah‟s Ark* framework (Weitzman 1998) through consideration of conservation costs and benefits, species utility and value; but take these a step further by accounting for the probability of management success. Wilson et al. (2007) developed a conservation prioritisation framework that addressed geographic priorities, fund allocation and area-specific threats. By applying this framework across Mediterranean ecoregions, they found that more species could be conserved through targeted conservation actions than through sole reliance on acquisition of appropriate habitat.

Conservation planning uses many criteria to guide decisions on conservation action, principally based on (biodiversity) representation and persistence. Among the principles relevant to biodiversity persistence are population viability and evolutionary potential. Nonetheless, the point we make is that even (conservation) planners practice an implicit form of triage through recognition that entire conservation networks are not feasible. Conservation is one form of land use among many, and planners optimise conservation outcomes given the constraints.

Criticism of triage basically comes down to „defeatism‟. Pimm (2000) argues that triage is inappropriately seductive because “it combines the semblance of tough decision-making style with the substance of doing nothing.” The argument to let species X go will be repeated years later for species Y. Further, triage inhibits science; saving the very rarest pushes the technical frontiers of conservation biology. To quote Pimm (2000) again, “nothing concentrates the mind like impending extinction, nor so openly tests whether our knowledge of ecology, genetics and behavior is up to task.”

More recent critics point out that a shift in philosophical stance by conservation biologists will have ramifications far beyond the current debate. If conservation biologists, the very people dedicated to prevent extinction via scientific investigation and restorative problem solving, sanction this, then what is there to stop others with no sympathy for conservation from justifying extinction (Jachowski & Kesler 2009)? Others highlight conservation success stories such as the whooping crane (*Grus americana*), or indicate new funding possibilities for conservation through carbon financing (Pimm 2000; Parr et al. 2009).

The debate is not likely to go away. In the interim, and on a positive note, the explicit nature of triage-based analyses will likely prompt funding from Government and donor sources that may not otherwise have been freed.

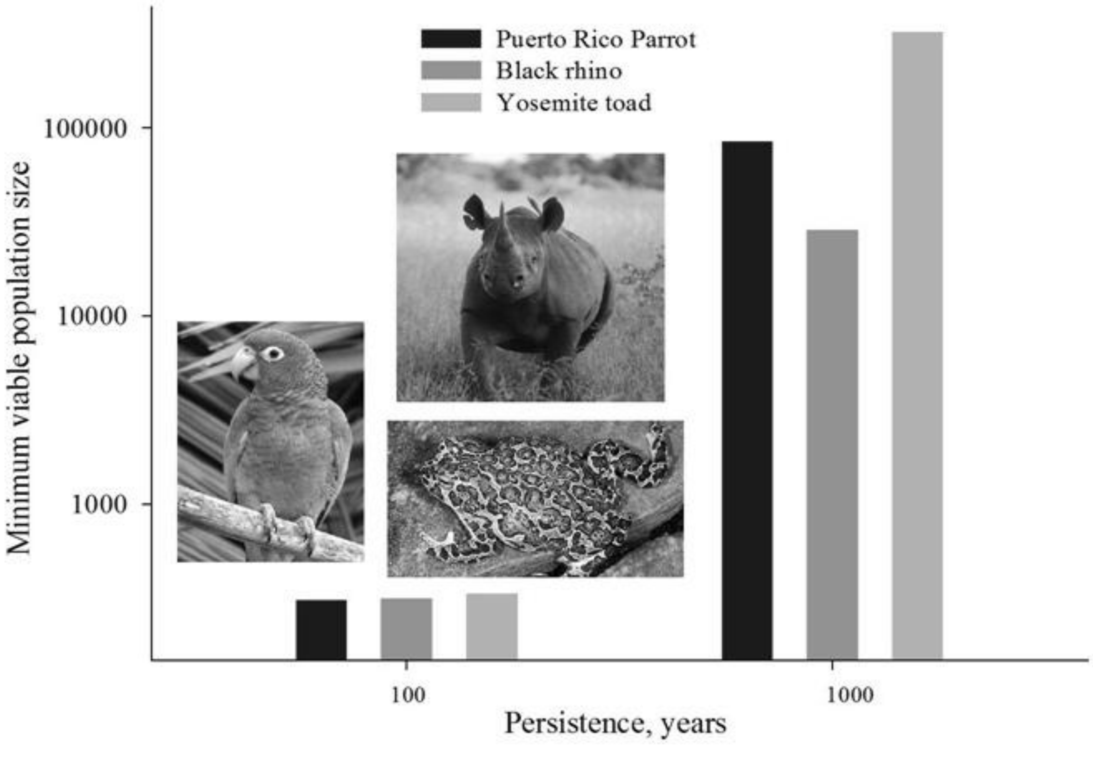


Figure 7.2 Bar chart of ($\log_{10}$) MVP estimates for three threatened vertebrate species from time series population viability analyses (Brook et al. 2006). Selected species are the Yosemite toad (*Bufo*

canorus), black rhinoceros (*Diceros bicornis*) and the Puerto Rico parrot (*Amazona vittata*). Data are model-averaged MVP values for 100 years (90% probability of survival, as used by the IUCN 2008) and 1 000 years (99% probability of survival). Images, PR parrot (http://kevinschafer.com), black rhino (http://wildcast.net) and Yosemite toad (http://calacademy.org)

7.5 Conclusions

We maintain that given demographic, genetic and phenomenological consensus, the concept of the minimum viable population is a useful benchmark, and highly relevant in today‟s biodiversity crisis. The poor implementation of empirically derived MVP targets is not the fault of the available data or theory arising; rather, we argue it is more constrained by political and logistic challenges. In other words, MVP estimates bring scientific frankness to the socio-political arena. Geophysical scientists use climate models to advise decision makers on the risks posed by global warming associated with different scenarios of carbon emission reductions (IPCC 2007). Similarly, conservation biologists have a critical role to play in providing a scientific reality check on whether, and to what degree, decisions made in the interests of threatened species management or under the motivation of avoiding extinctions, will be effective. This can be done openly, thereby avoiding the tag of stealth policy (see Wilhere 2008). By explicit presentation of threshold data at alternate probabilities of success (Fig. 7.1), biologists leave the ultimate decision to the political process.

Current evidence from integrated work on population dynamics shows that setting conservation thresholds at a few hundred individuals only is a subjective and non-scientific decision, not an evidence-based biological one which properly accounts for the synergistic impacts of deterministic threats (Brook et al. 2008; Visser 2008). Many existing conservation programs might therefore be managing inadvertently or implicitly for extinction – a clearly illogical and counter-intuitive aspiration. If practitioners cannot justify using conservation triage to alleviate problems associated with unrealistic targets (see Box 2), where small, inbred populations are neglected in preference to more viable options, then they must manage for biologically relevant MVPs at least 5 000 adult individuals (or 500 simply to prevent inbreeding) whilst addressing the concomitant mechanisms of decline (Balmford et al. 2009).

One partial remedy is for prioritisation of conservation funds to be based on indices of the distance of species population sizes from MVP. So for example, a small population of 50 individuals will score 0.01 (percent of 5 000), and the inverse of this can be used as a modifier for fund allocation. A simple scoring system such as this can be the basis of a decision-framework for threatened species within a particular management region, and conservationists can factor in other considerations such as likelihood of success and economic value. Indeed, both demographic and evolutionary MVPs have been, and continue to be influential to real-world conservation planning. As with the use of biodiversity surrogates in conservation planning , rules of thumb on species" demographic and genetic requirements are often the only option when dealing with the current crisis under conditions of great uncertainly and severe resource constraints.

Further, MVPs are legitimate and concrete targets that policy-makers can digest and implement. While scientists debate MVP variance, the extinction crisis deepens. Thresholds at 500/5 000 are communicated more effectively to policy-makers who do not have the time to read the extensive literature surrounding viability. Indeed, the lack of communication between science and conservation policy can be improved through dissemination of generalities (such as thresholds) that can be formulated as policy.

If, on the other hand, scientists regard MVP thresholds to be too high to implement practically, then what are the alternatives? Is managing for hundreds of individuals over short time-frames sensible? If biologists believe that metapopulations numbering less than a few thousand individuals are capable of survival in a globally changing world, then this needs to be argued with relevant empirical and genetic data as support. Other than that, a more explicit and honest acceptance of the biological trade-offs implied in ignoring MVPs on logistical grounds is needed, for credibility‟s sake.

CHAPTER EIGHT

8. Synthesis of research

In summary, the major findings of my research are:

1) Global change in the tropics will alter present-day wetland plant community structure and distribution, with subsequent ramifications for magpie geese (Chapter 2). This will likely take place through saline water intrusion and disruption to competitive (plant) interactions through increased temperatures, rainfall regimes and atmospheric CO_2.

2) In the absence of climate change, catastrophic epizootics will reduce the present day NT geese metapopulation from ~ 3.5 million to ~ 368 000 birds in 100 years and under current harvest regimes (Chapter 3). Increased severity and frequency of epizootics are likely under climate change and highlight the need to monitor harvest carefully. Offtake of geese will need to be managed respectfully but efficiently should mass mortality events occur in the future.

3) Magpie geese aggregate in large numbers during the dry season to eat *E. dulcis* root tubers, and subsequently gain body condition (Chapter 4). Access to foodplants is restricted by floodplain water depth and soil viscosity and departure is forced by drying of the floodplains. The potential reduction in availability of *E. dulcis* will adversely affect magpie geese given that present day wetland habitat is likely to be degraded and reduced under global change (Chapter 2).

4) Migration of geese outward from feeding sites (following the drying of the floodplains) is multi-directional and generally no further than 115 km (Chapter 5). Geese are capable of moving up to 500 km should resource scarcity force this. Magpie geese also select subcoastal floodplains relative to availability.

5) Digital elevation models coupled to population viability analyses predict resilience of magpie geese across the NT to sea level rise up to 1.4 m (Chapter 6). Present day harvest rates will likely force extirpation of subpopulations if habitat loss occurs through saline water intrusion. Fragmentation of geese populations will occur and the persistence of these will depend on dispersal ability of adult birds. Further, the coarseness of the available models prevents fine-scale mapping of saline water intrusion through paleochannels, as is likely to occur.

6) It will be difficult to maintain viable subpopulations of any species if they fall below 5 000 individuals. This minimum is required to avoid the deleterious effects of inbreeding, loss of genetic diversity and susceptibility to environmental fluctuations (Chapter 7). Again, the transfer of genetic material between populations is vital to the continued persistence of geese, and artificial transfer may be required in the future.

I elaborate further on these findings in this closing chapter, and outline management options and future research.

The reduction and possible loss of tropical populations of the unique magpie goose will be a tragedy given the species" wide-scale extirpation across Southern Australia (Garnett 1992). If the global imperative of dangerous climate change is avoided or effectively mitigated, then there is no reason for widespread extirpations to occur, given that Australia has the expertise and resources available to focus effective conservation effort. Attempts here to model the likely outcomes of habitat loss through sea level rise and increased incidence of disease are preliminary attempts – *first generation* models – in an ongoing process of model development and adaptive management. Thus the conservation management of magpie geese must be a progressive process, where conservation biologists and wildlife managers learn and adapt to a changing world. These efforts of learning-by-doing and effective demonstration of evidence-based tropical systems management (outlined below) will further benefit native waterbirds and wetland plants, and the sustained harvest of geese can continue under a better-informed environment.

8.1 Management options

A starting point for the management of magpie geese across North Australia will be to learn from the mistakes made in Southern Australia. Habitat loss, hunting and catastrophic droughts interacting with diversion of natural water flows caused an extinction event that conservationists in southern states are still trying to redress (with limited success). Frith and Davies (1961) made a highly pertinent statement in their closing comments on the study of geese as a „pest“ species:

> “Geese will not be a continuing problem to the (rice) industry as settlement develops; rather the advance of settlement could virtually eliminate the magpie goose from the Northern Territory.”

Climate change aside, the increased human population and agricultural land use will continue to undermine the viability of geese populations across the NT. A multi-pronged approach is required, based on rigorous science and informed management. These can be grouped into four classes: habitat loss, population structure, disease and harvest.

1) Habitat loss. The loss of wetland habitat to saline water intrusion, invasive weeds and feral ungulates, will continue to be pressing environmental issues in the NT. Current threats are principally loss of wetland habitat to introduced grasses and weeds that prevent nesting and

feeding by geese. Management strategies are in place for these (see http://weeds.gov.au), but it is not adequately understood how these weeds and ferals will respond to global warming. Further targeted research is required which can feed into management plans. For example, questions such as “Which weeds are likely to benefit from tropical climate change and what are the most likely sources of spread?” need to be answered.

Although the GIS-based models presented herein showed the impact of sea level rise under 1.4 m to be marginal, the relatively coarse resolution of the available digital elevation data meant that it was not possible to account for fine scale saline water intrusion through channels or the natural erosion of levees. Past management techniques developed to control and turn back saline water intrusion on the Mary River may be useful (Whitehead et al. 1992). Strategically-placed barrages will allow a buffer against saline water intrusion, or at least retard the process. Wetland maintenance and restoration of floodplains will go a long way toward conserving magpie geese and other tropical waterbirds under moderate climate change impacts.

Further, a systematic compilation of photographic and satellite imagery of wetland habitat can be used to plot changes in vegetation cover through time (for an example, see Banfai et al. 2007). A triage approach to the decision-making process (see Chapter 7) will allow for efficient allocation of funds toward more crucial (and less degraded) habitat via a ranking system. In addition, an up-to-date database of viable wetland habitat and especially coverage of *E. dulcis*, will inform choices about agricultural development. The triage approach can again be adopted to allocate land that has already been degraded or lost to invasives, and where the cost of restoration is too high to justify conservation. Furthermore, spatial refuges (Wolff 1980) can be identified and funds allocated toward the protection of those in preference to under-used sites.

2) Population structure. It is critical that relevant authorities continue to monitor magpie geese across the NT (see Delaney et al. 2008). A well-developed strategy that allows consistent methods (with the inevitable turnover of staff) and based on rigorous quantitative approaches that allow for the estimation of observation error, observability, and bias correction (e.g. for aerial surveys), will make detection of trends in population decline (or increase) most readily apparent. These can be coupled to rainfall records and other climatic variables, disease records and the above-mentioned records on wetland habitat in order to make more robust predictions of short-term changes in abundance and distribution. Further, these can be linked to the monitoring of harvest which I discuss below. From a management perspective, the maintenance of a rigorous, long-term database of population dynamics allows for powerful inference on the population ecology of geese, including development of density-dependent time series projections that can be used to test future scenarios (Brook et al. 2006).

Continued monitoring of geese populations across North Australia will also permit development of more spatially realistic metapopulation models (see Brook & Whitehead 2000a,b). With sufficient information on habitat and climatic preferences, metapopulation structure can be mapped reliably to landscape suitability (Anderson et al. 2008). Finally, ongoing, well-calibrated monitoring of geese populations will allow the detection of population crashes in response to drought or other catastrophic events such as disease outbreaks (Chapter 3). Catastrophic declines will require urgent action to avoid the extirpation of subpopulations (as using minimum population guidelines as discussed in Chapter 7). Harvest will need to be tightly regulated under these circumstances until populations recover to viable levels. Largely unquantified Aboriginal harvest will need to be more effectively monitored.

Conservation managers in stronghold areas such as Kakadu National Park will be required to work to prevent population fragmentation and isolation of subpopulations below 5 000 individuals. Even though the species is mobile, small populations remain vulnerable to catastrophic events and there is a risk of disaggregation of the north Australian super-metapopulation over time.

3) Disease. Although probably not as serious a threat habitat loss, mass mortality events need to be monitored closely (Chapter 3). Records on local disease outbreaks will detect trends in spatial and temporal occurrence and correlates of epizootics, such as periods of very high temperature regimes or resource scarcity (Plowright et al. 2008b).

4) Harvest. The coupling of current harvest rates to models of habitat loss and increased mortality through epizootics show that historic intensity of harvest might not be sustainable in the future due to local and global change. While regulation of harvest appears to be a quick and effective conservation measure, this should only be implemented widely if other strategies fail. The hunting of geese by Aboriginal persons has cultural significance (Vardon et al. 1996; Whitehead et al. 2000) and recreational shooters provide employment through spin-off industries.

Maintenance of a sustainable harvest will be a great challenge to future conservationists, but this can be done by focusing effort on a whole system-based approach habitat and population management, as outlined above. Responsible management may necessitate periods of harvest restriction, but collaboration with landholders and Aboriginal land management authorities will provide opportunity to monitor offtake and build these data into models that project geese population decline and test management strategies (Fordham et al. 2008). Lead shot will need to be phased out as soon as possible. Mortality of geese and other waterfowl through lead toxicoses has been shown explicitly (Whitehead & Tschirner 1991) and its continued use is unnecessary given the availability of alternatives (e.g. steel and bismuth shot).

8.2 Further research

Finally, the research reported in this thesis has indentified some key aspects of magpie goose ecology and the ramifications of sea level rise and increased habitat loss, but there is scope for ongoing development of these approaches. This thesis has built on past research and applied a suite of new ecological research methods to study the population and habitat dynamics of magpie geese, but obviously only go part of the way toward sufficient knowledge.

The quantification of an aggregative response by magpie geese, and the part played by the environment in restricting access has been shown. However, the biological and ecological mechanisms that allow the return of *E. dulcis* following sustained predation are not known. Frith and Davies (1961) inferred that water salinity and the timing of floodplain inundation determined the success of *E. dulcis*, but did not test this explicitly. In this study, I chose to focus on the metapopulation ecology of geese under global change but did not have the opportunity to test germination of *E. dulcis* plants directly. Future experimental work should address this gap through laboratory-based work that tests the success of both seed germination and propagule success under varying environmental scenarios, such as period of inundation, water salinity and predation. Drivers of *E. dulcis* abundance (under current climatic conditions) can be derived in this way, and based on multi-model inference (Burnham & Anderson 2001). Further, experiments can replicate projected changes under global change (Chapter 2). These can include altered temperature, frequency of extreme heat events and flooding regimes (reflecting changes in rainfall and cyclonic activity), changes in water salinity due to periodic inundation of wetlands from storm surges, and increased CO_2, CH_4, N_2O and O_3 levels in the atmosphere.

Such research will go a long way towards predicting wild plant response to climate change and can be built into predictive models that link the success or failure of *E. dulcis* to magpie geese habitat suitability, and building upon the models developed here. Such models have recently been tested on different systems (Keith et al. 2008) but there is opportunity to develop the new art within a tropical context.

As outlined previously, research will also need to address the response of the geese to climate change and susceptibility to disease outbreak (Chapter 3). With sufficient field data, correlative modelling can be used to further test synergies between current and projected threats (Brook et al. 2008) and identify life history parameters sensitive to change, such as juvenile recruitment or adult survival (Beissinger & McCullough 2002). GIS-based models of habitat loss (Chapter 6) will need to incorporate higher resolution digital elevation and coastal bathymetric models as these become available (see http://ga.gov.au) and possibly employ the use of LIDAR imagery for fine-scale (centimetre-scale resolution) mapping of sea level rise. Collaboration with experts from the field of surface hydrology will test more realistic models of changes in river channel structure and resilience and thus floodplain resilience under sea level rise. These models will also permit identification of levees likely to be breached by rising ocean levels and thus direct the construction of costly river buffers.

Increasingly complex metapopulation viability or cell-based landscape models can incorporate feral animal and weed dynamics under global change (Akçakaya & Brook 2008). Models such as these can additionally be tested in the field with well-thought out tests on ungulate and avian population dynamics. Finally, ongoing monitoring of magpie geese for avian disease (AQIS 2006) provides ideal opportunities to determine the genetic structuring of magpie geese subpopulations and levels of interbreeding between these (also allowing indirect inference of dispersal rates). Genetic data will allow informed decisions by conservation biologists regarding reintroduction programmes (Frankham et al. 2002), should these ever be necessary.

In closing, conservation biologists have unique but time-constrained opportunity to preserve an ancient and unique waterbird for the continued enjoyment of future Australians and ecological health of North Australian wetland systems. Almost five decades of thorough research has been done on geese. There is little excuse for failure.

Appendices

Appendix 1. Aggregative response of magpie geese to *E. dulcis* and floodplain parameters (excluding water) during the aggregative period only (data pre- and post-feeding are omitted).

Candidate models where response is bird abundance	**k**	**AIC$_c$**	**ΔAIC$_c$**	***w*AIC$_c$**	**ΔBIC**	**% DE**
Global (interactive term between tuber weight and density)	7	2141.16	0.000	1.00	0.0	3.2
Tuber weight	5	2155.72	14.560	0.00	11.4	2.3
Tuber density + tuber weight	6	2156.21	15.054	0.00	13.5	2.4
Null, random effects only (plots nested in site and month)	4	2203.77	62.609	0.00	57.8	0.0
Tuber density	5	2203.82	62.663	0.00	59.5	0.1

Appendix 1a

Candidate models where response is bird abundance	**k**	**AIC$_c$**	**ΔAIC$_c$**	***w*AIC$_c$**	**ΔBIC**	**% DE**
Global (soil viscosity and interaction between tuber size and density)	9	295.91	0.000	0.72	0.0	9.5
Interaction between tuber size and density	7	297.79	1.888	0.28	0.9	6.8
Tuber density	5	306.87	10.970	0.00	8.2	1.8
Soil viscosity	6	309.69	13.782	0.00	12.0	1.8
Tuber weight	5	309.70	13.792	0.00	11.0	0.9
Null, random effects only (plots nested in site and month)	4	309.81	13.905	0.00	10.0	0.0

Appendix 1b

Appendix 2. Mean body weight (in grams) of adult male and female magpie geese (a) 2006 and (b) 2007. Included are body condition (BC) indices for geese (2007 only) following the collation of bird length data.

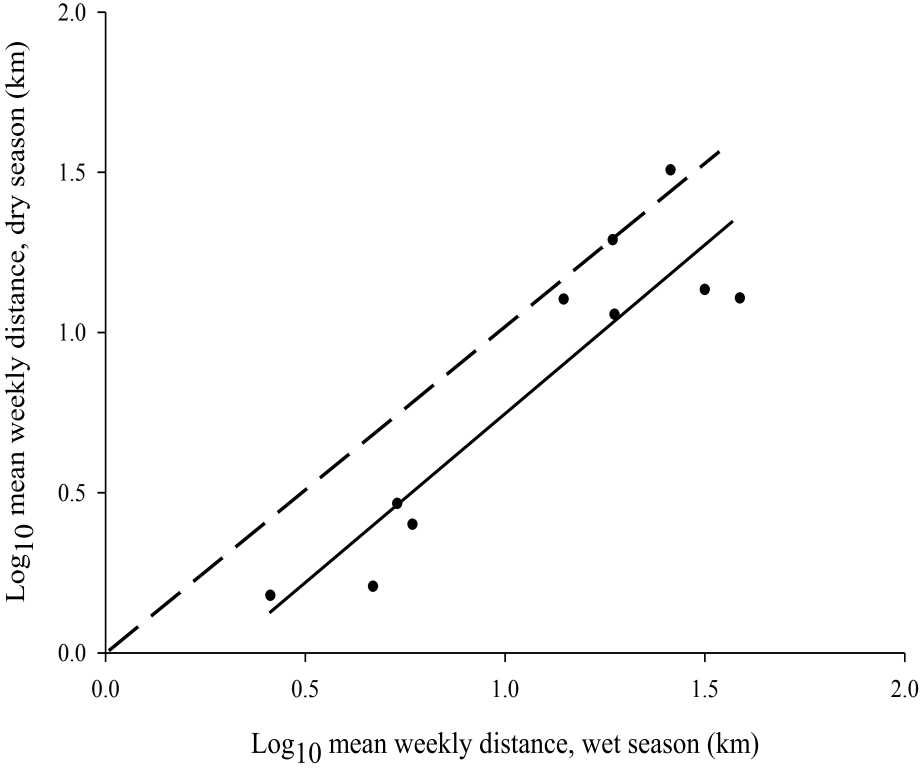
Month, 2006	**Sex (adult geese)**	**Mean weight in grams (with standard error)**	***n***
September	Male	2900 (223)	12
	Female	2733 (497)	6
October	Male	2986 (289)	66
	Female	2649 (295)	53

Appendix 2a

Month, 2007	**Sex (adult geese)**	**Mean weight in grams (with standard error)**	**Mean BC index (weight/length)**	***n***
July	Male	2868 (223)	3.39	6
	Female	2383 (254)	3.03	14
August	Male	3131 (246)	3.58	89
	Female	2956 (324)	3.48	71
September	Male	3030 (232)	3.46	88
	Female	2913 (317)	3.37	55
October	Male	3062 (162)	3.43	17
	Female	3040 (190)	3.43	10

Appendix 2b

Appendix 3 Weekly mean distance (km) travelled during the wet versus dry seasons for all birds tracked (sexes pooled). Dashed line indicates the 1:1 relationship; clearly, dry-season (DS) movements were less than those occurring during the wet season (WS).



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Addendum.

Response to thesis examiners

<u>Examiner One</u>

Chapter 1

The opening paragraph sets the context of this thesis as global change and the use of population models to guide the conservation and management of threatened species. The remainder of the chapter reviews the ecology and biology of the magpie goose, before returning onto page 12 to the assertion that global warming is "*the biggest medium to long-term threat facing tropical magpie geese populations* ..." This assertion is supported by several references that discuss climate change impacts on tropical floodplains and the capacity of agencies to manage those changes. If these references refer directly to magpie geese this needs to be made explicit. In addition, there is a need here to elaborate on the mechanisms by which magpie geese are likely to be affected by global change given the previously reviewed ecology. The candidate refers to his own work in chapters 3, 6 and 7 to support the assertion. This is inappropriate and this section needs a clear statement of the questions to be answered in the thesis and the approach to be taken. Currently this does not appear anywhere in the thesis.

<u>Response</u>. Reference to global change through Hennessy et al. (2004) and Finlayson et al. (2006) is appropriate, given that these refer to the changes that will take place across the sedge-dominated floodplains that magpie geese depend on for forage and nest material. Finlayson et al (2006) do refer to magpie geese (page 391 and 394 of original thesis).

The mechanisms by which magpie geese are likely to be affected by climate change are provided on pages 27-28.

If the context of this thesis is global change and the use of population models to guide the conservation and management of threatened species then these topics should be reviewed. In particular, the mechanisms by which global change differentially impacts tropical and temperate systems or migratory and sedentary species; global change impacts on other waterfowl species; and successes and failures in the application of population models to the conservation of threatened species.

Postscript. The Introduction should now include the following text:

"*Global change will act across biogeographic regions, affecting these in somewhat different ways. The tropics, in particular tropical south-east Asia and Australia, support high levels of species diversity and endemism, but lack the capacity to mitigate changes effectively (Lee and Jetz 2008). Temperate regions may have less diversity (partly thanks to past anthropogenic impact – Fritz et al. 2009), but generally have the resources available to deal with change.*

Critical to the success of conservation effort in the tropics is the identification of thresholds to population resilience to change, especially where species are used by local communities as a food items or other uses (Du Toit et al. 2004). There is a paucity of data available for such thresholds across the tropics, particularly for waterbirds. This is cause for concern where tropical waterbirds are threatened by habitat loss through climate change (principally sea level rise, Garnett and Brook 2007). Sodhi and Smith (2007) found that the greatest threat to tropical bird species were habitat loss and degradation, invasive species and shifts in climatic variables. Of course, a greater threat is when these factors act additively or synergistically (Brook et al. 2008). South East Asia has experienced more loss of habitat than other regions in recent times (Fritz et al. 2009) and projections of likely changes in climatic parameters will worsen the situation (IPCC 2007).

Little research has been done, to date, on the impacts of climate change on waterbirds. The only notable findings in recent-times for temperate waterbirds are apparent shifts in winter distribution (Brook et al. 2009), shifts in the timing of spring events (Walther et al. 2002) and projected decline in waterbirds abundance across the Arctic through global *change (Wrona et al. 2006). Not surprisingly, populations that have dispersive capacity will fare better than those that lack capacity to migrate (Thomas et al. 2004). Even less data is available for tropical waterbirds. Garnett and Brook (2007) find that habitat loss and degradation is the biggest threat to tropical Australian waterbirds*

One method for addressing conservation concerns and directing future research is the development of population models for species-of-concern or even multiple species. Simulation models for species populations have been used for over three decades (Traill et al. 2007), and while some concern lingers over the accuracy of these, the real value is heuristic (Ball et al. 2003). Viability analyses underscore many conservation planning programs and increasingly robust models are used to project range shifts for species and the outcomes at a management level."

Page 1, para 2. Assertions about habitat loss, overexploitation and global warming need references. It would help the reader if the aspects of the ecology of magpie geese that have been „*relatively well studied*" were listed and referenced.

Postscript. The thesis should now include the following text:

"*Magpie geese have been of interest to science over the last for decades for a number of reasons. First, the species were seen as a threat to agriculture (Frith and Davies, 1961), second the mere abundance of the birds makes these ecologically important with the ability to alter their environment, and third the birds are an important food item to aboriginal Australians (Whitehead 1999).*

Frith and Davies (1961) produced a record of the life history of the birds that is useful to this day. Indeed, by addressing the concerns of the-then fledgling rice industry (that since failed), the authors covered species distribution, habitat use, movements (using VHF telemetry), food preferences, breeding behaviour, sexual cycle, clutch size, hatching success and population response to control measures. Since that time, numerous articles have *addressed aspects of the ecology of the species, mostly building on the work done by Frith and Davies. These have included further work on the distribution of the species (Bayliss and Yeomans 1990; Morton et al. 1990; Halse et al. 1996; Wilson 1997; Nye et al. 2007), nesting phenology (Whitehead and Saalfeld 2000), sexual dimorphism (Whitehead 1999), variation in foraging strategies (Whitehead and Tschirner 1992), fatality from lead shot ingestion (Harper 1990; Whitehead and Tschirner 1991) and population ecology including harvest (Bayliss and Yeomans 1990; Brook and Whitehead 2005 a,b)."*

Page 2, para 3. Reword the sentence beginning „The species has …" to improve clarity. The next sentence doesn"t make sense.

Postscript. Should now read: "*The species has maintained evolutionarily constancy over the past 4 million years, with recent (South Australian) fossil identification from the Pliocene Tirari formation …*"

Figure 1. A point of interest is that in 2007 magpie geese bred in the Riverina for the first time since the 1930s at Fivebough swamp near Leeton in the Rutherglen region.

Postscript. Noted as a footnote.

Figure 2. The figure does not work on greyscale graphic. Perhaps more illustrative if colours were changed and less of southern NT shown.

Response. This and subsequent Figures throughout the thesis have been published in peer-reviewed manuscripts and provide adequate illustration.

Page 9 and 10. The assertion that „*population regulation of geese populations are likely driven by per capita forage availability*" needs to be referenced. There is a large body of literature on the regulation of goose populations in Europe and North America by authors such as J Madsen ….. This section is critical to the development of later arguments about climate change and hunting effects and should be reviewed thoroughly.

Postscript. Should now read: "*... population regulation of geese populations are likely driven by per capita forage availability (Bayliss 1989; Bayliss and Yeomans 1990; Whitehead 1999).*"

Page 11 para 1. Add references to last sentence.

Postscript. "*Other drivers include predation by introduced predators such as foxes (*Vulpes vulpes*), poisoning and the diversion of water flows for crop irrigation (Nye et al. 2007).*"

Page 11 para 2. The literature on the effects of lead shot on waterfowl is large. This paragraph needs rewording to improve clarity as to what assertions are general and the evidence as related to magpie geese.

Response. Both Harper (1990) and Whitehead & Tschirner (1991) explicitly refer to magpie geese.

Page 11 para 3. The first sentence takes two large ideas, additive and synergistic effects in populations (Brook 2008) and the dynamics of declining and small populations (Caughley 1994) to make a statement about the extirpation of southern geese populations. These ideas should be pulled apart and elaborated on. Moreover, the citations are inappropriately used here as neither cited author makes any assertion about southern magpie geese populations.

Postscript. The page should now include*:* "*The work done by Caughley (see 1994 as key reference) was ahead of its time - in that Caughley found that the deterministic drivers of population decline may not cause extirpation once a population reaches a threshold (thereafter the small population). Once small, populations are vulnerable to demographic and environmental stochasticity (Caughley 1994), as well as inbreeding (Spielman et al. 2004). Additive and synergistic effects are where drivers of decline (such as habitat loss, predation and competition from invasive species) act additively (self-explanatory) or synergistically (where the* whole *of the impact is greater than the* sum *of the parts) to drive an extirpation or extinction event (Brook 2008). The concept of synergy has gained recent traction since global change will likely act in synergy with known drivers of decline (habitat loss and exploitation) to drive future species extinction (Brook et al. 2008).*"

Note further, the appropriate reference to magpie geese here is Nye et al. (2007).

Page 12 para 1. The reference to Wikelski et al. 2004 is inappropriate as written. That paper discusses disease dynamics in bird populations on the Galapagos Islands.

Response. The use of Wikelski et al. (2004) here is contextual; no references are available for extirpation events among magpie geese and thus the use of surrogate species to illustrate an ecological process.

Page 13 para 2. The authors claim to have conducted an „*exhaustive review of the literature*" doesn"t stand up to scrutiny and should be deleted.

Postscript. Sentence should read "*I conduct literature reviews …*"

Chapter 2

This Chapter once again starts with the threat posed by global warming before setting off on a wide-ranging discussion on plant-herbivore interactions, predator prey dynamics, threatening process, functional and numerical response in population models, migration triggers in birds, differential grazing, compensatory growth and others. Most of these topics are well studied and are supported by a large body of literature. The chapter lacks a narrative that helps the reader understand the relevance of the many topics to the primary subject of the thesis. For instance, on page 17 paragraph 2 identifies plant-herbivore dynamics as a „*key ecological interaction*" which it is, and cites 3 references, one on savanna systems, another on goose grazing and another on sea grass meadows. What precisely is the author endeavouring to convey to the reader and what is the relevance of the literature cited? Be explicit.

Response. The relevance of these references is contextual, and further, ecological interactions are similar across biogeographic regions and taxa. Key interaction between magpie geese and their preferred foodplant *E. dulcis* has been shown at a broad-scale (Bayliss and Yeomans 1990) but not at a fine-scale and thus the importance of Chapter four.

The narrative then jumps from a broad statement on ecological interactions to the specific example of the possible threats posed by climate change to the coastal floodplains tropical Australia and geese. Why was this example selected as a case study? What is the relationship of plant-geese interactions in northern Australia to other types of plant-herbivore interactions that make it a good exemplar of a key ecological interaction? Be explicit.

Response. The references cited in this paragraph discuss the importance of seasonal sub-coastal tropical floodplains to present-day populations of magpie geese. The system is exemplar because it features an interaction principally between one plant (*E. dulcis*) and one herbivore (geese) with no apparent feedback mechanism (discussed further in Chapter 4). The reliance of the birds on *E. dulcis* is discussed by Whitehead (1999).

As written the chapter does not demonstrate a coherent understanding of the relationship of the thesis to the literature and the chapter should be reorganised and perhaps some of the topics reviewed used to support arguments in Chapter 1.

Response. The Chapter has been published in Emu (DOI: 10.1071/MU09003) and I think adequately addresses the contextual (that is, under global change) relationship between tropical waterbird populations and seasonal wetlands, and likely outcomes under climate change.

Page 20 para 1. Tracey et al. (2004) make no assertions about emerging infectious diseases as a general threat to magpie geese or any other Australian waterfowl. That paper discusses specifically the ecology of avian influenza and pathways for infection into Australia.

Postscript. The paragraph should now read: *"Known threats to magpie geese in northern Australia are habitat loss to invasive species and saline water intrusion (Lonsdale 1994; Hennessy et al. 2004), wetland alteration by non-native ungulates (Bradshaw et al. 2007), and unsustainable harvest (Brook and Whitehead 2005b).*"

Page 22 para 1. See comment above re page 9.

Response. See change above re page 9.

Page 23 para 2. It should not be assumed that density-dependent effects exist, or that observed effects in related species in other biomes are relevant to highly mobile fauna in Australia where responses to variable patterns of resource abundance are highly individualistic (see

Roshier et al. 2008). This section barely touches the subject matter and doesn‟t support the application of density-dependent herbivore models even though their application may be entirely appropriate.

Postscript. Sentence should read: *Numerical response is difficult to parametise in highly mobile populations typical of many waterfowl. Functional type responses have been demonstrated in waterfowl (see Rowcliffe et al. 1999), although more typically, work has shown an aggregative response (Bayliss & Yeomans 1990; Bos et al. 2004).*

Page 25 para 2. Neither review nor insight and should be expanded or deleted. The data or justification for the application of giving-up densities should be moved to the methods in chapter 4.

Postscript. Paragraph should be considered removed.

Page 26 para 2. Hughes (2003) makes no assertions about the effects of climate change on magpie goose populations on northern coastal floodplains and the citation should be deleted. The only reference to magpie geese by Hughes is the unusual occurrence in South Australia by Baxter et al. (2001).

Response. The reference does not explicitly refer to magpie geese, but that makes this no less relevant when the point being made is that climatic shifts will have potentially have outcomes for species such as magpie geese (and other waterbirds). Had past research shown the response of magpie geese to climatic shifts, then there would have been no need for my work.

Page 28, para 2. The first sentence is premature speculation and should be deleted.

Postscript. Consider deleted.

Page 28, last para. Last sentence uses the first person and then cites a reference that the candidate did not author. Reword.

Postscript. Text now reads: "E. dulcis *is resilient in this respect, being adapted to switch between C3 and C4 photosynthesis and so will likely remain competitive under changes in CO2 levels (Cowie et al. 2000).*"

Page 29, para 2. Again Chambers et al. (2005) only discuss magpie geese in relation to unusual sightings in South Australia. Hence the citation is misleading. Beaumont et al. (2006) do not mention migratory waterfowl. Moreover, Australia does not have any long-distance migratory waterfowl with observable consistency in arrival and departure dates. Hence, the sentence is wrong and the citation inappropriate. Similarly, the last sentence is a selective citation to support a particular argument.

Postscript. Consider the offending paragraph omitted.

Page 30, para 3. Italicise species name.

Postscript. Italicised.

Page 32, para 1. Capitalise north.

Postscript. Capitalised.

Page 32, para 2. Reword sentence „*This process acts aids in* …"

Postscript. Consider re-worded as "*this process aids in*…"

Chapter 3.

No comment made by reviewer (Chapter published in *Biotropica* at time of thesis submission).

Chapter 4.

This chapter reports on changing patterns of goose abundance and condition on a coastal floodplain. While the methods and conclusions appear sound the chapter is let down by inadequate citation of the relevant literature and an inappropriate structure that intertwines results with discussion. The work of Marcel Klaassen and Bart Nolet and their students on the feeding behaviour Bewicks swans in the Netherlands is particularly relevant to this study. Both species feed predominately on flooded tubers when they are available but apparently contrast in the nature of the plant-herbivore interaction with density-dependent effects in one system and not the other. This is noteworthy as a point of discussion as it tells us much about the nature of these interactions in systems with contrasting patterns of resource distribution.

Response. The Chapter has been changed for journal review since original submission and the suggested authors included in the manuscript (currently in Review).

Page 66 para 4. It is not clear whether counts are an estimate or an absolute count. If the three plots are the population used in the analysis then the counts are an absolute count with an estimation of error. If the three plots are a randomly selected sample of the floodplain population then it is not clear how or whether the counts were used to estimate the total population of the floodplain. This needs clarification.

Response. The counts are an estimate. The total population size inferred from these was a crude estimation (page 70 original thesis), and the total is not used as a response variable for any model. The offending total abundance data should be considered omitted from the thesis.

page 67, para 1. The use of weight as an index of body condition needs justification. The reference cited is for small passerine, while routinely used measures in geese such as abdominal profile are not mentioned. See Klaasen et al 2006. Journal of Avian Biology. Moreover, a sample of birds should be used to verify the applicability of the body condition index used.

Response. Body weight measures should no longer be considered as valid here. Note, no generalised linear models use body weight as a response or predictor variable.

Page 68, para 1. If the data collected and the analysis undertaken are relevant to the thesis, then the methods used need to be explained in full.

Postscript. Text should now read: "*Parameters used to build the model set included water depth in mm (measured using a 1.5 m gradated rod, 3 samples at each subplot), soil depth in mm (from the top of the soil to the base where the muddy strata met a hard, rocky substrate and measured using a rod), soil viscosity (2007 only and after cursory analysis of 2006 data) and an index of pig-rooting (after Bowman and McDonough 1991). Soil viscosity was estimated using a qualitative index of stickiness (after DPI 2004), and derived from samples at each point (30 from each plot). Viscosity was scored from 0 – 3 using hands to judge* *texture, with 0 being not „sticky" and3 very „sticky". Water depth was categorised following field observation of bird grubbing behaviour, thus 0 for water below 10 mm, 1 for water between 10 and 450 mm and 2 for water deeper than 450 mm. Pig-rooting data were ultimately discarded as negligible*."

Page 70. It is scientific convention that the Results section should not contain Discussion and the citation of the work of others here is inappropriate.

Postscript. Offending paragraph should be considered omitted.

Page 74. See comment page 70. Appendix 1 should appear as a table in text.

Response. The Table was transferred to Appendices to avoid unnecessary clutter in text (as is practice in many Journals where authors can transfer additional material to the Supplementary Online section).

Page 70 para2. The last two sentences need rewording to improve clarity. The pulsed nature in many Australian aquatic systems means that food resources are either very abundant or very scarce. Thus competition for food resources is often transient. „*Undoubtedly though, magpie geese do compete for tubers* ..." needs justification.

Response. These sentences (that refer to total population size at study site) are for interest only and should thus be considered omitted from the thesis.

Page 80, para 2. The references cited in the last sentence refer to North American systems. This needs to be made explicit as neither author cited refers to magpie geese.

Postscript. Sentence to now read: "*Indeed, it is possible that the nutrient input and grubbing action of magpie geese may benefit seed germination (see for a Temperate-system example Cargill & Jefferies 1984; Zacheis et al. 2002).*"

Page 81. Delete last sentence.

Postscript. Readers to consider this omitted.

Chapter 5

This chapter is the first tracking study of magpie geese using satellite tags. These data are used to describe movements and habitat use. The introduction includes text on migration, metapopulations, disease ecology, waterbird ecology and conservation. All are dealt with in a cursory manner and the context or significance of the study is not clear to the reader.

Response. The context intended by the Introduction is: Migration in important to the maintenance of genetic material between populations (subpopulations within a metapopulation, see Frankham et al. 2002), migration may introduce pathogens and or parasites into a naïve population and thus precipitate an epizootic (Epstein 2002), and the conservation of waterbirds is dependent on an understanding of migration for the above-mentioned reasons. Thus the need for the broad review of these topics.

Location data from CLS Argos relies on Doppler shift to determine distance from the sensor on the satellite to the deployed tag and potentially has large errors. The data have a nominal accuracy based on the 68th percentile for each location class but some data may be many kilometres from the true location, even for the higher location classes used in this study. It is usual to filter the data based on set criteria defined by the ecology of the study organism and study objectives. In particular, location error may significantly affect analyses of habitat use and should be commented upon.

Response. Location accuracy of the data are provided below, where 3 = < 150 m, 2 = 150 – 300 m accuracy, 1 = 350 – 1000 m, 0 = > 1000 m, A and B = no estimate of accuracy and Z = invalid location.

Data quality	***n***	**%**
3	231	13
2	378	20
1	527	29
0	207	11
A, B and Z	504	27

Making statistical inference from the relocation data raises issues of independence among animals and of independence of relocations of the same animal (see Erikson et al 2001). The methods described to determine habitat use are simplistic and it is not clear precisely how the data were handled. Were all data points of a certain class or classes induced in the analysis? The author does not review or refer to the large body of literature on this topic.

Response. Since submission, habitat use data were re-analysed. The results are thus:

Vegetation Communities	**Observed** χ^2	**Pr(random)**	**Conclusion**
Coast Rainforest / Myrtle - Pandanus Savanna	24.965	0.368	random
Coast Rainforest / Deciduous Rainforest	242.703	0.049	random or weak evidence of selection
Floodplain Sedgeland	486.597	< 0.001	selection
Mangroves	48.937	0.366	random
Myrtle - Pandanus Savanna	52.237	< 0.001	selection
Open Forest	254.925	< 0.001	avoidance
Paperbark Forest	14.317	0.001	selection
Woodland	86.021	< 0.001	avoidance
Hill-Woodland	13.252	0.005	avoidance

The methods used to derive these are: "*For each habitat type we calculated a -like statistic of observed deviance from expected use ([observed use – expected based on habitat availability]2/expected) in R (Table) and estimated the probability that the habitat-specific metrics could be generated at random based on a multinomial randomisation of expected values (probabilities based on 100 000 iterations).*"

Moreover, this analysis is not referred to in the discussion and does not contribute to the narrative and could be deleted. If habitat use or occupancy is considered important then there are more statistically robust techniques available. For example, bird locations and fixed-kernel statistical techniques can be used to develop probabilistic measures of resource use – „utilisation distribution‟ (Marzluff et al 2004).

Response. As above.

Para 85, para 1. This is hyperbole. Tracey et al 2004 discuss possible vectors of highly pathogenic avian influenza, don"t mention other pathogens or disease and make no comment on the „*incidence of avian disease*" in the region.

Postscript. Consider omitted.

Page 86, para 2. Why not simply refer to movement and not complicate matters by reference to migration or dispersal?

Postscript. Consider reference to migration and dispersal omitted.

Page 88, para 1 and 2. If attachment methods were tested then this needs to be described and results reported. What was deemed adequate in terms of data density and accuracy from Argos?

Response: The practical methods developed were not recorded and we quickly chose the back-pack design outlined (at length) in paragraph 2. This is adequate for replication. For data accuracy, we considered any data A, B or Z as unworthy (see Table above).

Page 89, para 3. Reword to improve clarity. Altitude of what?

Postscript. Paragraph should read: "*Further, we converted presence data to raster files and used the Extract function in ArcGIS to determine altitude (that is, the habitat height above sea* *level that the birds used). Finally, we used these presence data to determine habitat use. These were based on vegetation communities derived from Geoscience Australia*."

Page 90, para 2. Did the PTTs have an activity sensor to show whether the bird was dead or alive at time of transmission?

Response. No.

Page 90, para 3. The data are high quality as few telemetry studies have more than 60% of location fixes LC > 1.

Postscript. Text should now read: "*Location data were of relative high-quality*."

Page 90, para 4. Need to be consistent in the use of migration and movement.

Postscript. Consider text to read movement throughout.

Page 96, para 3. Dingle‟s book on Migration (1996) is the primary source of the term ranging behaviour. Also see Bennetts and Kitchens (2000).

Postscript. Reader to consider reference to Dingle (1996) to be made here, as suggested. Dingle H. 1996. Migration: The biology of life on the move. Oxford University Press, UK.

Also, Bennetts RE, Kitchens WM. 2000. Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? Oikos 91, 459-467.

Page 99, para 1. Need to be consistent in the use of movement terminology. Change dispersing to moving.

Postscript. Text to use „movement" throughout.

Page 99, para 3. Delete last sentence. Reintroductions by whom and in response to what?

Postscript. Offending text to be considered omitted.

Chapter 6

This chapter is the first of two modelling chapters and these are the strength of the thesis and provide the most original component. However, irritations about the use of citations persist and lead the reader to question the veracity of the support for the assertions made. Once again, the structure of the chapter does not follow scientific convention and Results appear in the Methods, other authors work is cited in the Results, and placement of tables and figures does not support the text as they are often several pages removed from where they are referenced. Hence the chapter needs to be significantly restructured.

Postscript. The Chapter has been substantially revised since submission and is now In Press at *Ecography*. Appropriate changes have been made.

To improve the narrative through the thesis this chapter should be linked to the previous chapter on movements. This would strengthen the case for examining local effects of saltwater intrusion.

Postscript. As above.

Page 105, para 3. Remove reference to Tracey et al 2004 as this paper does not support the assertion of a threat to goose populations.

Postscript. Consider deleted from the text.

Page 111. It is the responsibility of the candidate to demonstrate familiarity with the literature and methods used. Referring the reader to a review article helps no one. Moreover, the details of the model structure and parameter estimation should be reproduced here.

Postscript. The review referred to here (Shaffer 1981) is an outline of the first published PVA and is a benchmark to all further work in the field. Readers are advised to source Brook and Whitehead (2005) for all details on model parametisation.

Page 115, para 2. Citation in first sentence is inappropriate. Reword or elaborate.

Postscript. Offending sentence to be considered deleted.

Page 117, para 2. Citations in first sentence is inappropriate. Reword or elaborate. Pulliam (1998) makes no comment as to whether "*The South Alligator River floodplains provide* *critical source habitat …*‟ Remove citation. Discussion of barriers is speculative and irrelevant.

Postscript. Offending sentence and reference to be considered deleted. Reference to the South Alligator as critical habitat now to be Bayliss and Yeomans (1990).

Chapter 7

This chapter reviews minimum viable population models. The chapter makes no reference to magpie geese and therefore needs contextual statement in the first or last chapter to integrate it with the narrative of the thesis (see below). The writing is markedly better developed than earlier chapters and the narrative flows from one idea to the next. The only irritant here is that the structure of the chapter follows that of the journal to which it was submitted and does not complement that of the thesis.

Postscript. Formatting now corrected to follow that of the entire thesis.

Chapter 8

This chapter makes claims that are overstated. For instance, „*Global change in the tropics will .., with subsequent ramifications for magpie geese*.‟ While climate change may have ramifications for geese, there is no certainty in this assertion. The modelling was based on a set of assumptions, not all of which are articulated and these need to be stated.

Postscript. All reference to models to now read "*Global change will potentially have ramifications for magpie geese, principally though habitat loss to coastal inundation*."

Note: Each Chapter based on population simulation does state assumptions and these have undergone peer-review. Assumptions regarding sea level rise are stated and SD used for projections. The results of models that project outcomes under disease are illustrative of additive impacts.

Much of the discussion of management is on topics unrelated to the outcomes of the research and doesn‟t provide the contextual statement that draws together the various threads of research undertaken. This leaves the reader uncertain about how the outcomes of one chapter inform other chapters or the relationship of the thesis to the literature. This is symptomatic of inadequate reference to the existing literature in a number of chapters and is unconvincing that the thesis relates the topic of research to the broader framework of the disciplines within which it falls.

Examiner Two

Chapter 1

As written, this chapter provides as acceptable introduction to the goose and the rest of the dissertation.

Chapter 2

According to the abstract, this chapter‟s goal is to use magpie goose-wetland interaction as model for examining the effects of climate change on waterfowl in general. Through page 26, we get a review of waterfowl-plant interactions. Certainly this material should be read and understood by the author and the review appears to be up-to-date. At the same time it‟s hard to believe there isn‟t a more comprehensive review already available. Next, on page 27 we get a list of potential impacts of climate change on the Australian tropical coast. Following the list, we get what becomes a case study and it‟s at this point that I became less satisfied. Although the objective is a case study, all we get is superficial expansion of the points on the list with reference to the natural history of magpie geese. For example, on page 28 we learn that the important food plant *E. dulcis* can switch between C3 and C4 photosynthesis, so it should remain competitive. Are we to assume that‟s the whole story? What about water stress and heat stress as a function of photosynthetic pathway, or about photosynthetic pathways as competitors? Then we go on to the next point, plant growth in the face of temperature change, then disease, and so on. I‟ll hardly call this a case study.

Postscript. The sentence (page 28 of original submission) *"E. dulcis is resilient .., being adapted to switch between C3 and C4 ... and so we predict that it will remain competitive under changes in CO2 levels"* should be considered deleted as this is speculative.

Next we read how the idea of multiple competing hypotheses can be used to determine what will happen to magpie geese in the face of climate change. I have two major problems with this. First, the physical setting will inevitably take precedence over the biotic interactions - the system is inevitably hierarchical. The story in this chapter increasingly revolves around *Eleocharis*. I suggest that before we care at all about the biotic interactions we need to look at the physical setting. As we‟ve seen here in Louisiana US, herbivores don‟t mean a thing if the plants die from saltwater intrusion. These physical factors are mentioned but not in a way that can get to a quantitative prediction. Second, to apply the information-theoretic approach, you must have a single dataset that can be used with all models. I can‟t see what such a dataset would look like based in what we get in the chapter.

Response. Regarding the physical setting, the biotic interactions indeed do become irrelevant under sea level rise and thus my analysis in Chapter six.

Overall this chapter wasn‟t a good lead-in to the rest of the dissertation and should it be published, I doubt that it will be useful to anyone who manages waterfowl that aren‟t magpie geese.

Chapter 3

This chapter includes two parts, a literature review of potential disease threats to magpie geese and addition of disease parameters into an existing PVA. The catch is meant to be the exacerbating effect that climate change will have on disease risk. I don‟t see any major problems with the chapter but I also don‟t see it as being particularly informative for either disease risk or population modelling.

I can sympathise with the author‟s difficulty in finding much relevant data on disease risk and climate change for magpie geese. In the end, all one can do is make a list of known risks based on other waterfowl. At this point the precise systematic position of Anseranas becomes important, as it may differ from all other waterfowl for phylogenetically constrained disease. This point deserves more attention. Similarly, despite a flurry of papers on climate change and disease, there‟s really not enough information available to make more than a guess about what might change for magpie geese in a warmer climate. Overall, I saw this part of the paper as a useful summary of the literature (with the caveat that I don‟t know this literature, so I can‟t really say how complete the summary may be).

The models are somewhat difficult to understand in the absence of the original model from Brook and Whitehead. It seems like the new parameters on population reduction and outbreak frequency don‟t have much basis in reality. Why choose 10-90% mortality? I suppose that range will safely include the realm of possibility, but it also makes the model hard or even impossible to interpret.

Response. The range of mortality is coupled with severity. We do this to project all possible outcomes under realistic scenarios. The results are illustrative of outcomes if both severity and frequency of epizootics increase, or indeed, if only severity increases or frequency. Thus, the full parameter space of these scenarios.

Can you model past population fluctuations better by including known disease outbreaks than with the existing model?

Response. Data on disease outbreaks are sketchy and past population data lacks consistency.

The thrust of this analysis is the difference in response depending on whether hunting pressure is included. Perhaps I‟m missing something, but I don‟t think it is reasonable to model hunting pressure as a constant 130k/birds per year. For much of the abundance values in Figure 3.1a, there appear to be fewer than 100k birds. Surely the hunting pressure either through Government regulation or simply the difficulty in finding birds wouldn‟t be constant? With density-dependent hunting mortality, I bet the two curves would have a similar shape with the hunting + disease curve falling below the disease-only curve?

Response. Again, the scenario is illustrative of what will eventuate if Aboriginal harvest is not regulated under global change. This has direct outcomes for wildlife management since indigenous harvest is completely unregulated and not even monitored.

Without offering comment on the original model, which might be excellent, this addition to it seems fairly simplistic and without a tangible connection to climate change. It is probably a useful exercise for a dissertation, but I‟m a bit surprised that it was accepted by *Biotropica*. I was downright disturbed to see this chapter later cited as evidence that magpie geese are under threat by disease (p85-86). Nothing in this chapter shows any level of threat that isn‟t so vaguely defining as to be true for any population on the planet.

Postscript. Consider any reference to this Chapter in the context of threat through disease as omitted.

Chapter 4

I‟m convinced that geese show a response to water depth and tuber biomass, but much of this chapter isn‟t very satisfying. There‟s probably too much analysis for this basic point, and the figures and tables could do a better job of showing the relevant pattern. Here are some specific comments, in sequential order:

1. Abstract. Not much of the statements of fact end up being supported by the data or even addressed directly by the data. For example, the 90 000 bird estimate is a sketchy extrapolation (see below), the effects of drying vs. tuber abundance is not disentangled and there‟s nothing in the data relevant to the question of saltwater intrusion or population processes of the plant.

Postscript. The Chapter has been revised following submission to peer-reviewed journals. The abstract should now read:

"We describe the aggregative response of a unique tropical waterbird, the magpie goose (Anseranas semipalmata) *to the dynamics of the ephemeral sub-coastal floodplains of northern Australia. We find that birds migrate in large numbers to feeding sites and aggregate in response to the availability, abundance and size of the root tubers of a wetland sedge plant,* E. dulcis. *The presence of large numbers of foraging birds was most strongly influenced by water depth, which determined the availability of foodplants. Despite intense predation by geese on* E. dulcis *root tubers, there was no evidence of a negative-feedback mechanism between plant and herbivore populations, suggesting that the system is driven by environmental parameters. A gain in bird body condition over the aggregative period does however suggest an important role of* E. dulcis *– dominated floodplains in the ecology of magpie geese, particularly as feeding occurs during the late dry season when food resources are relatively scarce. Sensitivity of* E. dulcis *to saline water will lead to the loss of the foodplant under rising ocean waters, thereby threatening the long-term viability of dependent magpie geese populations."*

2. Introduction, last paragraph. Give a clear and explicit statement of objectives so the reader can determine the dependent and independent variables that will be addressed.

Postscript. Introduction should now include: "*Here we quantify an aggregative response in magpie geese to seasonal wetland dynamics. We identify the influence of foodplants (tuber abundance and mass) and environmental parameters (water depth, soil depth, soil viscosity and an index of pig rooting) on bird aggregation, body condition and departure, and discuss these findings in the context of tropical waterfowl ecology and conservation*."

3. Methods. Make it clear how many samples go into the information-theoretic analysis. It is six samples in each of three plots at each of two sites in 2006 and four/plot/site in 2007? It seems to me that the time in the season should also be considered. If you are looking at how birds choose where to forage, it"s more important to compare their choices in the same month than to confound months.

Postscript. Methods have changed following submission of this Chapter to peer-reviewed journals. Month is included as a random effect (temporal correlation) and plots were nested within sites to account for spatial auto-correlation. Methods should now read: "*Three model sets for testing bird abundance were collated for data from 2006, 2007 and both years. Models were also prepared to test bird departure using bird absence as a response. To gauge the relative importance of each predictor variable, we fitted a series of generalised linear mixed models (GLMM) to bird abundance and bird absence (the two alternative dependent variables) using the lmer function in the R-language environment (R Core Development Team 2007). The random effects error structure within the GLMM was used to correct for spatial and temporal non-independence of data (Koenig 1999), given the likelihood of spatial correlation between plots and sites, and temporal correlation between month (sampling took place once each month) and year (two years), which were not measured directly and not captured within the fixed effects (predictor variables).*

Asymptotic measures of relative information loss were used to assign strengths of evidence to the competing models (Burnham and Anderson 2001), with both Akaike"s information criterion corrected for small sample sizes (AIC$_c$) and the Bayesian information criterion (BIC) weights used as an objective means of model comparison (McCarthy 2007). We chose a Bayesian method of model selection in addition to Akaike"s information criteria, because the BIC tends to select simpler models which reflect main effects (dominant drivers), whereas AIC will include tapering effects, if sufficient data is available, and so often selects „saturated"models (see McCarthy 2007)."

4. Body condition. First, just using mass without correcting for size is unacceptable, so 2006 should be dropped. Second, these data are presented without any analysis or even a sd. I don"t see any pattern from the means. Third it isn"t clear how these samples relate to the abundance or food availability data. Do you know that the birds used in the body condition sample were even eating *Eleocharis*? In the end, I see no reason to include these data at all.

Postscript. Has changed following submission of this Chapter to peer-reviewed journals. These data should not be considered by the reader

5. Results, aggregation. Figure 2 shows considerable variation among plots within months, which makes Figure 3 an oversimplification. To me this variation among plots within months is the most interesting part of the data. We need to see data for geese and tubers for individual plots or plot/month combinations. Also I"m extremely leery of taking the mean from your plots and scaling up to the 90k estimate without accounting for goose patchiness. Notice also a mistake in the exponent in 800 ha in the next to last line of the next to last paragraph on page 70.

Postscript. Data for individual plots are:

Geese only 2006 (July [0], August [43,114,2,3,0,55], September [66,62,146,78,16,0], October [259,46,59,149,0], November [0]) and 2007 (July [13,5,2,2,7,19], August [71,74,48,23,67], September [35,206,43,174], October [0]).

The 90k estimate should be considered removed.

6. Discussion. I don‟t see how the results really get to most of the points mentioned in the first paragraph. Birds apparently respond to water depth and tuber biomass (although this could be presented better), yes. Soil viscosity, I don‟t think so. Preference to *Eleocharis*? There‟s no way to say from these data; how do you know what they were doing when they weren‟t on your plots?

Response: soil viscosity is a measure of the difficulty of grubbing behaviour, so the more viscous the soils become (as the floodplains dry up), so the more difficult it is for the birds to feed for the plant root-tubers. Preference for *Eleocharis* is assumed, and we found that > 90% of bird gut content consisted of the root-tubers of *E. dulcis* during this feeding period (*n* = 120 Traill, unpublished data). Remaining gut content consisted grass leaf parts.

Chapter 5

This chapter suffers from the inevitable small sample size of many telemetry studies. It does provide reasonable data on bird movements, albeit for a single year and a few birds. I have a few suggestions and comments.

1. Title. Catchy, but I‟d hardly call movements of this scale nomadism.

Postscript. Title should now be considered as: "*Movement patterns and habitat use by north Australian magpie geese* (Anseranas semipalmata)."

2. Abstract. Once again, the abstract promises more than the paper delivers. How would you know if you did see departure thresholds? I think that you can say more about the data, such as association with sedge wetlands, and less about the transmitter and data problems.

Postscript. The abstract has changed following submission (and subsequent revision) to peer-reviewed journals. This now reads: "*Documenting the movement patterns and habitat use of tropical waterfowl will assist in long-term bird and wetland conservation because such data provide essential information on population connectivity necessary to predict resilience to global environmental change. We monitored the seasonal movements of magpie geese* (Anseranas semipalmata) *in tropical north Australia using satellite telemetry. Ten wild-living birds were captured in Kakadu National Park (KNP) in late 2006 and fitted with KiwiSat® satellite transmitters. Migration was multi-directional and the maximum linear distance moved by an individual was 114 km from the release site, over 38 weeks of tracking. Migration did appear to be related to seasonal environmental fluctuations. Most monitored birds remained resident within the National Park. Individuals selected floodplains, woodland billabongs and paperbark forest over other habitat types, and median elevation of land used was 8 m above sea level. Accurate data were not obtained for any longer than 12 months, with most birds apparently losing their backpacks within six months. Just 62% of point location data were accurate to within 1000 metres. We recommend indirect genetic tests to assess more comprehensively the connectedness of geese and other waterfowl sub-populations across tropical Australia*."

3. Introduction. This while business about migration *vs.* movement is fuzzy. I suggest you drop „*migration*‟ as a term and as a conceptual basis for this paper. These birds aren‟t migrating, they‟re just moving around a relatively local area, probably in response to food availability.

Postscript. The text should now read „movement" throughout.

4. Methods, IT analysis. The description on page 89 is painful to read and impossible to understand. What are the dependent and independent variables? For the distance measurements, what are the time intervals?

Postscript. The methods and results of this Chapter have changed following peer-review at International journals. The Chapter is currently in Review at *Emu Austral Ornithology*. The Results now read: "*Across both wet and dry seasons, the maximum (linear) distance moved was 114 km, indicating that magpie geese are not likely to migrate far when adequate resources are available. There was no apparent difference in migration between the sexes (Table 5.1), although samples sizes were small. Sub-adults stayed closer to the release site (maximum distance moved = 23 km). There was considerable variation in individual movement patterns and distance (Fig. 5.1 a, b). Some birds migrated north along the South Alligator floodplain system while others moved to the Mary River region and another to the East Alligator system (Fig.5.1). Five birds migrated back to the South Alligator during the late dry period.*

Dividing movement by season (wet/dry) showed that individuals followed consistent movement trends. In other words, if an individual moved at a high rate during the wet season, this trend continued throughout the dry season (information-theoretic evidence ratio [ER] = 973.4, R2 = 0.81). However, dry season movement rates were slightly lower than wet season movement rates (Figure 5.2). Comparing maximum and weekly mean movements to the weight of birds at time of release suggested that heavier birds may be travelling farther than lighter birds; however, the evidence ratios for all relationships by season and metric indicated no (i.e., ER < 1) or only weak evidence of effect (Fig. 5.2)."

Note, the time intervals were weekly.

5. Table 5.3. Can you look at seasonal variation in availability of the wetlands? You can also actually test the use *vs.* availability of particular habitats.

Postscript. Methods have changed following submission of this Chapter to peer-reviewed journals. Methods should now read: "*We calculated frequency of bird occurrence within each habitat (number of location hits by each vegetation community) and habitat availability (as above). For each habitat type we calculated a -like statistic of observed deviance from expected use ([observed use – expected based on habitat availability]2/expected) in R and estimated the probability that the habitat-specific metrics could be generated at random based on a multinomial randomisation of expected values (probabilities based on 100 000 iterations).*"

6. Isn‟t there anything more you can get from these data? Identification of roost sites? Short-term patterns of day-time foraging patches and roosts? Identification of colonies?

Response. No, data at weekly intervals are adequate for habitat use and movement only.

Chapter 6

Here we get a useful look at the possible changes to the physical setting. This work seems to be a straightforward extension of map data to the existing metapopulation model. I have a couple of comments. First, how can you be so sure that the modelled loss of wetlands absolutely will not be partially offset by additional wetlands that develop? We get only the most superficial discounting of this possibility, but not even a map to help support it. The caveats on pages 116-117 help, but what about effects of changes in rainfall or temperature? I agree that a complex hydrological model is beyond the scope of this model, but maybe there‟s something out there already, perhaps in the IPCC report that incorporates these factors.

Response. This point was raised by reviewers following submission of this Chapter to *Ecography*. Following revision, our rebuttal to the possibility to new wetland development is incorporated in the text and is as follows: "*We note that vertical accretion and the possible re-establishment of freshwater floodplains further inland are unlikely to be sufficient to support large waterbird aggregations. Present-day north Australian floodplains are the product of ~ 4 000 years of deposition (Mulrennan and Woodroffe 1998b) and nutrient input, which has determined the ability of these to support current vegetation and associated resource densities (Finlayson et al. 2006).*"

and;

"*The numerous and extensive low-lying floodplains or tropical Australia flank macro-tidal seasonal rivers (Bayliss and Yeomans 1990). Formation of these was initiated in the recent Holocene: a transgressive phase began ~ 7 000 years BP following a rise in sea levels, followed by a large (mangrove) swamp phase as ocean levels stabilised ~ 6 000 years BP (Mulrennan and Woodroffe 1998b). Progadation of the coast and large river channels occurred primarily ~ 6 000 – 4 000 years BP and gross coastal morphology has changed little in ~ 1 500 years (Mulrennan and Woodroffe 1998b). Importantly, floodplain nutrient deposition over this period allowed for abundant floodplain plant growth – thus the numerous vertebrate populations in evidence today (Finlayson et al. 2006). Native plants are generally dominant on floodplains within protected areas, and these in turn support native and non-native vertebrates including a diverse waterfowl guild (Finlayson et al. 2006).*"

Second, why does this set of models include variable hunting pressure when the disease models in the earlier chapter does not?

Response. The models simulating disease were of heuristic value and illustrative of scenarios. We do not make any explicit management recommendations based on the work done in Chapter three (published in *Biotropica*) and state explicitly within that manuscript that our models test alternate scenarios. The population model in Chapter three ably demonstrates the resilience of the bird population (under increased pressure from pathogens and parasites) when human predation is tightly controlled, versus the lack of resilience under *status quo*. Our models do not make projections on final population size and base management recommendations on these.

Third, even the minimum estimate of sea level rise seems high to me. Can this be justified? I"m not saying it can"t, but based on the numbers we use here; it seems on the high end for 2100. I think you need to state explicitly what the ranges of predictions are that apply to your area. I"ll add that this applies to the other climate predictions that appear in the dissertation. Especially if the source is the IPCC, please give enough information that the reader can find the exact number for themselves.

Postscript. Methods have changed following submission of this Chapter to peer-reviewed journals. Methods should now read: "*We chose to project ocean rise beyond 2100. The nonlinear trajectory of rising ocean levels are typically not shown in medium- to long-term projections, such as used by the IPCC. Projections up to the year 2400 were used because we were confident that upper limits of sea level rise of at least 14 m (resulting from ongoing thermal expansion, complete mountain ice cap loss, and large-scale melting of the ice sheets of Greenland and West Antarctica; USGS 2000) would be attained within that timeframe (Hansen 2007). To project sea level rise beyond 2100, we chose two scenarios based on mean ocean level increase over the past few decades, namely the 106-year projections published by Rahmstorf (2007) and Church et al. (2008). We digitised electronic images of graphs given by these authors (upper-bound projection Fig. 4, Rahmstorf 2007) and (upper-bound Fig. 6, Church et al. 2008) to derive the data.*

The nonlinear increase in sea level over time was linearised using a power transformation of sea level values. Power transformation was determined using a Box-Cox profile likelihood function based on a linear model of rise against time. The estimated transformations were a better fit than the square root (0.5); a power of 0.48 for data derived from Rahmstorf (2007) and 0.43 for data from Church et al. (2008). We then fitted a linear model to the relationship between transformed sea level rise and time. Visual inspection of plots of model fitted values versus residuals indicated no systematic pattern that would *indicate undue heteroscedasticity. The fitted linear model was used to predict future ocean rise outward to 2400, and these predictions were then back-transformed to the original scale (Fig. 6.3). The proportion of floodplain habitat loss at each modelled time step (i.e., each year) was predicted from the sea level rise projection based on the fitted models described above for each major floodplain*."

The Chapter has been revised and accepted for Publication at *Ecography* (see http://wiley.com/bw/journal.asp?ref=0906-7590).

Chapter 7

This chapter lists MVP estimates for a variety of species and uses existing reviews of the importance of N and Ne to conclude that most MVP estimates are too low. I suppose they are, but I doubt that anyone in the business of working with these populations will need this review to tell them so. At the same time, conservation biologists don"t need another review of the importance of population size for evolutionary potential or Allee effects.

After reading the beginning of this chapter, I thought that it might be useful as a lecture to graduate students, until I got to your vision of how management should work (page 130-131). We get the advice that once MVP targets are set, we should be able to begin „captive breeding and translocation" when population drop below the target. Maybe in a perfect world, but how can there be possible resources to do so (aside from the practical problems of accurate counting)? My initial impression that this was utter delusion was tempered by reading the comments on triage that conclude the chapter, so I"m now left with the conclusion that the management ideas were just poorly reasoned.

Overall, I don"t see any new empirical revelation or theoretical insight that would convince me that this chapter should be published.

Response. Chapter has subsequently been revised and published in Biological Conservation (DOI: 10.1016/j.biocon.2009.09.001).

Chapter 8

Looking at the set of points that begin this chapter: the first one can‟t be called conclusion of this research; the second makes it sound like the wildly speculative parametisation of the disease models represent a realistic model of threats; the third emphasises questionable condition data; the fourth seems mostly ok, but doesn‟t really address the potential for geese to find appropriate habitat. In the end, we don‟t get a very compelling synthesis, although I agree with the recommendations for further research.

Postscript. See changes to synthesis as per response to Reviewer One.

Concluding remarks

After reading these comments, you can say I‟ve been quite harsh. Here‟s why - understanding how climate change will affect biological systems will be a major challenge from here into eternity. You appear to be taking a path toward least publishable units rather than really getting down to problem solving. The literature on biological effects of climate change is already bloating with fluff. Your chapters 2, 3 and 7 are more of it. Too bad you didn‟t do some mesocosm or exclosure experiments with Eleocharis instead: they might have been revealing and useful to future managers of magpie geese. You‟re just beginning your career so there‟s time to channel your obvious energies more productively.

Examiner Three

Overall

This is an excellent PhD thesis and I am certain many papers will come out of it. Each Chapter is of publication quality. I liked seeing the proportional effort score for each chapter. This is an approach I had recommended in a previous paper.

Chapter 1

Good overview of the issue.

Page 10. Some numbers and references on these important demographic parameters should be provided.

Postscript. Should now read: "*There is risk of under-estimate of total mortality as these figures do not account for culling by tropical fruit-growers (Lindner, D. pers. comm., Kakadu Buffalo Farm), or mortality through injury by shot, as high as 0.7 wounded bird per bagged one (see Noer et al. 2007).*"

Pg 12. Can you provide data on area taken over by these invasive species?

Response. The extent of land lost to invasive weeds across the Top End is difficult to quantify because this varies according to efficacy of control. There are Australian State and Commonwealth bodies that specifically deal with weed control. The most notable species are *Mimosa pigra*, *Salvinia molesta*, *Urochloa mutica*, *Echinochloa polystachya* and *Hymanachne amplexicaulis*. From personal experience in the Top End, I‟d say 25-45% of floodplain flora consist of these species.

Of note, Paynter and Flanagaan (2004) state that there is over 800 km^{-2} of *Mimosa pigra* in the Top End. Paynter Q, Flanagan GJ. 2004. Integrating herbicide and mechanical control treatments with fire and biological control to manage an invasive wetland shrub, Mimosa pigra. Journal of Applied Ecology 41, 615-629.

Pg 17. See Figure 2a of Sekercioglu et al 2008 for an example of the non-linearity of climate change impacts.

Postscript. The reference mentioned here, for the benefit of readers is: Sekercioglu, CH; Schneider, SH; Fay, JP, et al. 2008. Climate change, elevational range shifts, and bird extinctions. Conservation Biology 22, 140-150. DOI: 10.1111/j.1523-1739.2007.00852.x

Chapter 3

Good review and interesting model provide an excellent example for similar studies elsewhere. I"d be curious to know if climate-related droughts could increase the concentration of magpie geese in shrinking wetlands and thus increase infection rate.

Postscript. The text in the Discussion should now include a caveat as "*Should populations be forced to use shrinking wetlands during times of drought - then outbreaks are more likely, particularly when the condition of birds may be weakened. Again, avian cholera and botulism are the most likely sources of mass mortality events here*."

Pg 40. A more relevant example would be the shift in Hawaiian mosquitoes and avian malaria.

Postscript. The reference to this is: Atkinson et al. 2009. Introduced avian diseases, climate change, and the future of Hawaiian honeycreepers. Journal of Avian Medicine and Surgery 23, 53 DOI: 10.1647/2008-059.1

Pg 48. Increased drought can lead to reduced fruit harvest and fewer food resources for magpie geese, both of which would increase conflict with farmers and the number of birds killed.

Postscript. Text should now include a caveat that includes reference to increased conflict between geese and agriculturalists, particularly under stressful conditions such as periods of drought.

Pg 52. This also shows the importance of collecting more accurate data on total human-caused mortality.

Response. None necessary.

Chapter 4

Pg 70. Then this peak abundance of ~11500 per km^{-2} is higher than the previous record?

Response. Text reads 115 birds km^{-2} – and this is not as high as the densities recorded by Bayliss and Yeomans (1990) of 3460 birds km^{-2}.

Chapter 5

This is very interesting and hard field work. The findings are valuable. However, I would have like to see a one page review of previous work on magpie geese satellite tracking and how your results compare with these.

Postscript. To date, no previous work has used satellite tags to track magpie goose migration. Whitehead (1999) used VHF telemetry and found results similar to ours that is birds are seasonally nomadic and move between preferred forage and breeding areas (notably the Mary and South Alligator Rivers systems). Our rational to use satellite telemetry was to test anecdotal evidence of long distance dispersal (~ 500 km) – VHF telemetry does not allow the testing of this, unless the researcher travels those distances. So, data received from VHF transmitters depend on „sighting“ of the birds, that is to say the researcher is required to be close enough for the signal to be read. Satellite telemetry does not require this and therefore tracks movement no matter the location of the researcher relative to the study species.

Chapter 6

Why was not a combined model with harvest, disease and habitat loss used?

Postscript. The models that outlined the interaction between disease and harvest were illustrative of the likely outcomes of increased frequency and severity of disease occurrence under climate change and under one of two management scenarios, *viz*. tightly regulated aboriginal harvest and unregulated harvest (as it occurs today). The models linking habitat loss through sea level rise to magpie goose carrying capacity did include diseases as a catastrophic mass-mortality event (where severity was 50% decline in population abundance) using the frequency estimator of 0.0169/year (after Reed et al. 2003).

Chapter 7

Excellent review and of critical conservation relevance. However, a paragraph or two linking this synthesis to the magpie goose work would be valuable, as this is an example of a relatively abundant species which nevertheless may experience large population declines due to combined effects of climate change, habitat loss, hunting and disease. It is an excellent real work example of why MVPs should be in the thousands.

Pg 131. 5000/1000=5 – this was confusing

Postscript. Consider this to be omitted; moreover the Chapter has since changed following revision for *Biological Conservation*.

Chapter 8

This was a well-written synthesis and I especially enjoyed the section on future directions.

No further corrections.

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End of thesis