Predicting and measuring the impacts of climate change and habitat loss on Southeast Asian and Australian birds

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To my parents.

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Abstract

The evil quartet of habitat loss, overharvesting, introduced species, and extinction cascades threatens approximately 13% of the world's birds with extinction. Under a mid-range greenhouse gas emissions scenario, climate change and its synergistic interaction with the quartet may threaten an additional 20% of the global avifauna by 2100. Yet, studies of climate impacts on birds, particularly from the tropics, are so uncommon that it is difficult to assess extinction risk. Indeed, the International Union for the Conservation of Nature (IUCN) has no formal framework for evaluating extinction risk from climate change, largely because of the scarcity of measurements of climate-change impacts and uncertainty in model predictions.

In this thesis I measure and predict the effects of climate change on tropical birds, forecast climate-change impacts on a threatened Australian cockatoo, and analyse the U.S. national threatened species list's coverage of globally imperilled animals. The first chapter reviews studies on the effects of climate change on tropical birds and highlights urgent research avenues. Chapter two is the first field measurement of climate-change-induced range shifts in Southeast Asian birds. The third chapter combines abundance patterns along elevational gradients with climate and land-use change scenarios to forecast the additive effects of deforestation and climate change on endemic birds in Sulawesi. In chapter four I analyse autumn arrival dates in Singapore for the first study of climate change impacts on avian migration phenology in the tropics. The fifth chapter is a detailed case study where I link demographic and bioclimatic models to forecast extinction probability of an Australian cockatoo (*Calyptorhynchus lathami halmaturinus*) under climate-change, conservation-management, disease, and wildfire scenarios. Chapter six evaluates the coverage of IUCN-listed species by one of the world's leading national threatened species lists, the United States Endangered Species Act (ESA).

Main Findings: Chapter two showed that ranges of Southeast Asian birds appear to moving upslope, with unknown consequences for bird communities. Model-based estimates in chapter three indicated that deforestation is likely to leave endemic species little scope for responding to climate change. Chapter four showed that arrival of long-distance waders and raptors is becoming delayed over time, which may impact other events in species' annual cycles. In chapter five I found that high emissions climate change or reduced brush-tail possum management is likely to threaten the cockatoo, and showed how coupling population and bioclimatic models serve to make predictions more realistic. Chapter six found that 40-95% of IUCN-listed animals found within the U.S. are not ESA-listed.

In conclusion, my results support previous predictions that many upland tropical species, which are currently considered secure, are likely at risk from climate change and its synergy with habitat loss. More measurements of climate-change-induced phenology and range changes are needed, especially from the tropics. Lastly, uncertainty in climate-biodiversity models can be minimised by using coupled demographic-bioclimatic approaches.

Originality Statement

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution to J. Berton C. Harris and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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J. Berton C. Harris, 1 May 2012

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Introduction

The world is facing a sixth mass extinction, this time caused by anthropogenic actions (Butchart et al. 2010). The principal drivers of observed extinctions are the "evil quartet" of habitat loss, introduced species, extinction cascades, and overexploitation (Diamond 1989). The status of the world's species is monitored by the International Union for the Conservation of Nature (IUCN) which maintains the Red List of threatened species, the leading classification of its kind (Mace et al. 2008). The Red List is often used to prioritise management actions to direct efforts to species that are most threatened (de Grammont and Cuarón 2006). Management actions are usually implemented at the regional or local level, which highlights the potential importance of national governments following IUCN listings when conserving species (see Chapter 6).

Birds are excellent study organisms for investigating extinction risk because they are diverse, widely distributed, and well-studied. Approximately 13% of the world's 10,000 bird species are currently considered by the IUCN to be threatened (Fig. 1.1). In accordance with Diamond (1989), habitat loss in its various forms threatens the majority of birds, followed by invasive species, hunting, and several other minor threats, including climate change, which is currently implicated with threating only 200 species. Predictive models indicate that climate change could threaten up to 35% of the world's bird species with extinction by 2100 (Williams et al. 2003; Sekercioglu et al. 2008), but uncertainty surrounding model projections have made the IUCN weary of integrating climate change impacts into their assessments (Akçakaya et al. 2006).

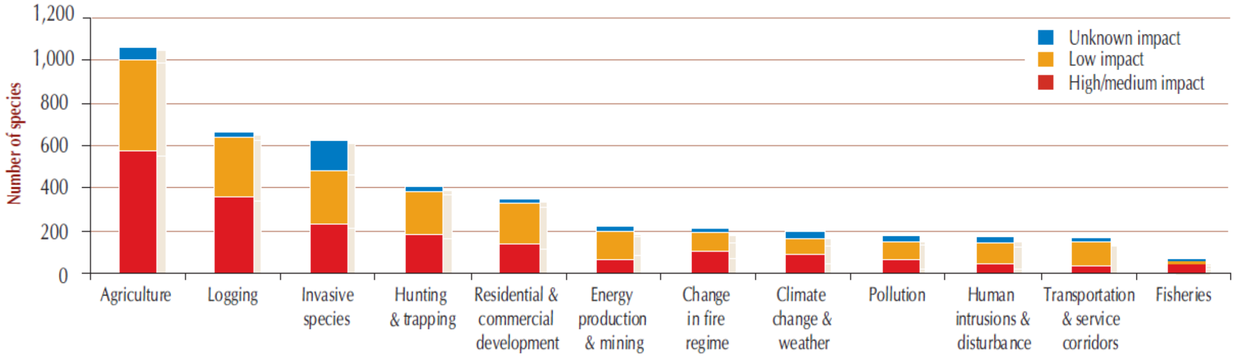

Figure 1.1 Breakdown of factors threatening the world's birds with extinction. Figure from BirdLife International (2008a) used by permission.

Habitat loss and fragmentation

Habitat loss and fragmentation have caused extinctions in temperate and tropical birds (Sodhi et al. 2004a; Elphick et al. 2010) and continue to be the primary threat to global bird diversity (Fig. 1.1). Habitat loss *per se*, combined with high rates of nest predation and parasitism from fragmentation, are thought to be the cause of many bird population declines (Garnett et al. 1999; Wilcove 2008; see Chapter 5). Fragmentation tends to reduce populations of top predators that require large areas of intact habitat, leading to mesopredator release (Wilcove 1985). In addition, generalist competitors and predators, as well as brood parasites, often benefit from habitat fragmentation (Grey et al. 1997; Robinson and Robinson 2001).

Many tropical species are more sensitive to habitat loss and fragmentation than temperate species because most tropical birds evolved in more homogeneous habitats (Stratford and Robinson 2005; Sodhi et al. 2008). Understory and ground-dwelling tropical species often have poor dispersal abilities (Stratford and Robinson 2005; Moore et al. 2008) and are probably most vulnerable to nest predation (Robinson 1999). There is much variation in extirpation vulnerability from fragmentation by dietary guild, but species that eat insects, fruit or both tend to be most vulnerable (Kattan 1992; Sekercioglu et al. 2002; Sodhi et al. 2004a). Species with large body sizes tend to be most vulnerable, probably because of hunting pressure and low reproductive rates (Sodhi et al. 2006a).

Habitat loss and fragmentation have been the primary foci of conservation biology thus far (Sutherland et al. 2009). Climate change is likely to become the world's second most important extinction driver, especially because of the way it interacts with other threats (Brook et al. 2008), but studies of climate-change impacts on biodiversity are still in early development compared to their equivalents for habitat loss (Parmesan 2007). Measurements of the effects of climate change on tropical birds (Chapters 1, 2, 4), and detailed predictions of climate impacts (Chapters 3, 5) are particularly lacking.

The first four chapters of the thesis focus on the effects of climate change on tropical birds. Tropical latitudes are home to most hotspots of species richness, endemism, and threatened species (Orme et al. 2005), which makes tropical research a clear priority for the future. Yet, the tropics are not receiving their share of studies (Giam et al. 2012), and Southeast Asia in particular should receive more research effort based on the number of endemic and threatened species and rapid habitat loss in the region (Sodhi et al. 2004b, 2006b).

Climate change

Climate scientists have a good understanding of the emissions-climate relationship and the various pathways to keep temperature change below 2 °C (Meinshausen et al. 2009; Rogelj et al. 2011). If we are to avoid >2 °C of warming, near zero emissions will be required by 2100 (zero emissions by 2150), necessitating abrupt reductions because of the already high levels of greenhouse gasses in the atmosphere (Rogelj et al. 2011). The world is currently exceeding the high-emissions reference scenarios, and political inaction is the norm, indicating there is a moderate likelihood that global warming will exceed 3 °C by 2100 (IPCC 2007). It is therefore imperative that conservation biologists increase efforts to monitor ecosystem responses to climate change and refine predictions of climate-biodiversity impacts (Brook 2008).

Prehistoric climate change caused much movement of species ranges and contributed to extinctions. Pollen core studies from the tropics show that ancient plant communities moved up and down mountains along with the glacial/inter-glacial cycles following their preferred climates (e.g. Bush et al. 2004). Phylogenetic studies show how species’ ranges contracted to climatic refugia during changes (e.g. Carstens and Knowles 2007). In addition, climate change, along with direct human impacts such as hunting, apparently contributed to most megafaunal extinctions (Brook and Barnosky 2011). These historical patterns suggest that we can expect species to shift their ranges to higher latitudes and altitudes as the climate warms and that there will be ‘winners’ and ‘losers’ from climate change. One substantial difference during the current phase of warming is that the landscape has been heavily fragmented and degraded by people exacerbating stresses to species. In addition, the pace of contemporary warming may be faster than past changes (Brook 2008; but see Hof et al. 2011).

Although there are few examples of recent climate-related extinctions (e.g. amphibians in Costa Rica, Pounds et al. 2006), numerous species are shifting their ranges in response to climate change. Many range changes have been documented in the temperate zone, where species are shifting to northern latitudes (La Sorte and Thompson 2007) and higher altitudes (Moritz et al. 2008). In the tropics, gradual temperature changes across latitude make latitudinal shifts much less likely, especially for species with poor dispersal (Colwell et al. 2008). Instead, species are expected to either shift to higher elevations or cooler microclimates. If species occur far away from potential refugia they will likely have to adapt or face lowland biotic attrition (Wright et al. 2009; Feeley and Silman 2010a). The few published examples of climate-related altitudinal range shifts in the tropics suggest that species are moving upslope slower than predicted by the adiabatic lapse rate (temperature loss as a function of elevation gain; Raxworthy et al. 2008; Chen et al. 2009; Forero-Medina et al. 2011a; but see Chapter 2, Peh 2007). So far it is unclear if this results from local adaptation, a lag in shifts of plants, insects, or avian competitors, or just the birds’ inability to move (with the lower part of the population suffering from attrition whilst the upper part can’t keep pace). Clearly, more measurements of range changes are urgently needed, especially from poorly-studied tropical regions such as Southeast Asia.

Shifts in phenology (timing of events in the annual cycle) have also been attributed to climate change. For example, in Holland, spring oak budburst, caterpillar emergence, and hatch dates of the insectivorous pied flycatcher *Ficedula hypoleuca*, and predatory sparrowhawk *Accipiter nisus* are all advancing over time (some not statistically significant), but at different rates (Both et al. 2009). If the changes continue at different rates, trophic interactions may be disrupted (Brook 2009). Bird migration timing is also being affected, with many North American and European studies showing that spring arrival on the breeding grounds has advanced (Knudsen et al. 2011). On the other hand, autumn departure from the northern hemisphere breeding grounds is much more variable, with many studies showing no change, and others showing advances or delays (Cotton 2003; Mills 2005; Thorup et al. 2007; Van Buskirk et al. 2009). These changes may have significant impacts on species because fitness may be tied to spring arrival timing, which can be linked to habitat quality on the wintering grounds (Marra et al. 1998; Norris et al. 2004). Two studies have evaluated changes in migration timing in the southern hemisphere, finding advances for several species (Beaumont et al. 2006; Altwegg et al. 2011). But no study to date has quantified changes in migration in the tropics, where hundreds of migratory birds pass through and spend the non-breeding period. This important problem is addressed in chapter 4 of my thesis.

In addition to monitoring range and phenology changes, it will be essential to build realistic forecasts of climate change impacts on species if we are to mitigate extinctions. One popular method is using bioclimatic envelope or species distribution models that correlate species occurrence data to environmental variables and then project into the future (Pearson and Dawson 2003). If a study species' range is projected to contract under future climates, then it could be threatened. The utility of bioclimatic models is limited, however, because: (i) they are correlative and do not model a mechanism between climate and population size (Kearney and Porter 2009), (ii) they usually do not consider species interactions or population demographics (Araújo and Luoto 2007; Brook et al. 2009), (iii) they suffer from uncertainty surrounding bioclimatic model (Araújo and Rahbek 2006), global climate model (Fordham et al. 2012a,b), and emissions scenario (Beaumont et al. 2008) choices. Furthermore, extinction risk characterisations based on projected changes in range size alone are problematic because population size changes are often non-linearly-related to range size (Shoo et al. 2005a; Fordham et al. in press-a). Coupled demographic-bioclimatic models are more mechanistic than bioclimatic models alone, and circumvent some of the above problems.Chapter 5 describes a detailed conservation-management case study using this approach.

In mountainous tropical areas, weather station coverage is often poor, and climate changes rapidly, depending on elevation and aspect (Hijmans et al. 2005). There are so few weather stations in countries such as Madagascar that it is impossible to create high quality downscaled climate surfaces (grids) (Raxworthy et al. 2008). In these cases, the adiabatic lapse rate can be used to project elevational range changes. The lapse rate is usually a loss of 5-7 °C per 1,000 m of elevation gained (Smith and Young 1987; Whitten et al. 2002; Colwell et al. 2008). If abundance data are available, projections can be made by shifting the elevational abundance distribution upslope based on different climate scenarios to forecast future population sizes (Shoo et al. 2005a,b; Gasner et al. 2010). Lapse-rate models are simplistic, but are a useful way to model potential changes in population size from climate change. This sort of predictive modelling can begin to identify which species are most vulnerable to the immediate impacts of climate change based on species traits such as abundance and altitudinal range size (Shoo et al. 2005b; Williams et al. 2008; Isaac et al. 2009). The reality is, however that forest is being lost so rapidly in most tropical regions that many species may have no forested refuges to which to retreat during climate change (Sodhi et al. 2004b; Shearman et al. 2012). To date, no studies have combined climate models and land cover projections at a fine scale to evaluate if enough forest will remain to enable species to respond to climate change. Chapter 3 addresses this deficiency for Sulawesi in Southeast Asia.

In this thesis I measure and predict the effects of climate change and habitat loss on tropical (mainly Asian) and temperate Australian birds. I present new data from the field to measure range changes and build predictive models of future impacts. I also explore coupled bioclimatic-demographic modelling and a leading national threatened species list’s coverage of IUCN-listed animals. The questions I evaluated in this work included:

(1) Does the IUCN Red List underestimate the number of threatened birds in the upland tropics?
(2) Is there evidence for climate-related range changes in Southeast Asian birds?
(3) Will deforestation or climate change be more potent extinction drivers in Southeast Asia?
(4) Is climate change altering the timing of bird migration in Asia?
(5) How effective are coupled bioclimatic-demographic models for predicting population viability under climate change?
(6) Does the United States Endangered Species Act protect IUCN-listed species?

Chapter 1

The tropical frontier in avian climate impact research

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STATEMENT OF AUTHORSHIP-CHAPTER 1

The tropical frontier in avian climate impact research.

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J. Berton C. Harris: Conceived the idea, wrote the paper.

I hereby certify that the statement of contribution is accurate.

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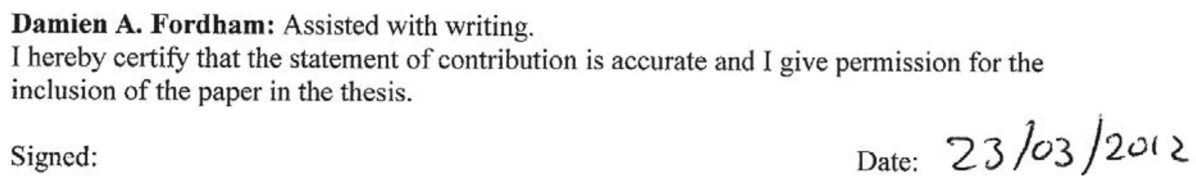

Damien A. Fordham: Assisted with writing.

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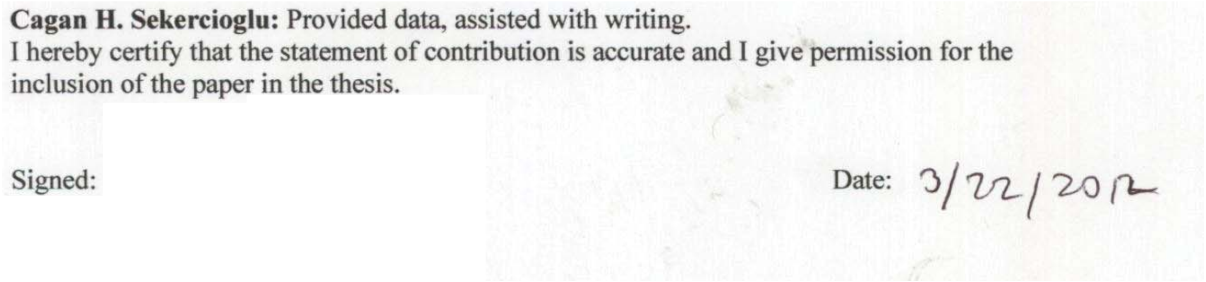

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Chapter 1 - The tropical frontier in avian climate impact research.

The impacts of climate change on tropical biodiversity are a subject of active debate. Global reviews show that climate change is having far-reaching effects on biodiversity (Sala *et al.* 2000, Walther *et al.* 2002, Root *et al.* 2003, Parmesan & Yohe 2003, Parmesan 2006, Rosenzweig *et al.* 2007, 2008; Miller-Rushing *et al.* 2010), but these studies tend to focus on temperate environments, with rare mention of changes in the tropics (Laurance *et al.* 2011). Of the c. 30 000 studies reviewed for the IPCC 2007 report, <1% were from the tropics (Rosensweig *et al.* 2008). The lack of research on climate impacts on tropical biodiversity, combined with the perception of a small absolute magnitude of projected temperature and rainfall changes (Sala *et al.* 2000, but see Stainforth *et al.* 2005, Chen *et al.* 2009), has helped fuel disagreement about the vulnerability of tropical species to ongoing and projected changes. Some studies argue that the effects of climate change will be small relative to the overwhelming impacts of habitat loss (Sala *et al.* 2000, Sodhi *et al.* 2004b). By contrast, several modelling analyses predict that climate change will be an important extinction driver in the tropics (Williams *et al.* 2003, Thomas *et al.* 2004, Shoo *et al.* 2005a, Colwell *et al.* 2008, Sekercioglu *et al.* 2008, Hole *et al.* 2009).

Tropical birds have received less study than temperate birds despite the fact that tropical latitudes harbour the vast majority of bird species (e.g. Sodhi *et al.* 2006b). The lack of studies makes it difficult to measure and predict the impacts of climate change relative to other extinction drivers such as habitat loss, invasive species, disease, and over-exploitation (Sodhi *et al.* 2011). We reviewed the literature and here highlight examples of innovative studies that were able to uncover important information on the effects of climate change on upland tropical birds. We then discuss further research avenues, including new avian monitoring and experiments, with a focus on efficient methods that can provide useful results with minimal investment of time and money. In addition, we point out the need for increased climate monitoring, highlight the potential for literature-based traits analyses, and briefly discuss conservation of upland tropical birds under climate change.

Rising temperatures from climate change have been shown to cause upslope range shifts in multiple studies of temperate animals (e.g. Tryjanowski *et al.* 2005) and plants (e.g. Lenoir *et* *al.* 2008), but few studies have documented altitudinal range shifts in the tropics. Climate-induced upslope range shifts have been shown in very few field-based studies of tropical animals (e.g. Pounds *et al.* 1999, 2005; Seimon *et al.* 2007; Raxworthy *et al.* 2008; Chen *et al.* 2009, 2011). For birds, Peh (2007) compared altitudinal ranges of generalist bird species (that are likely little affected by habitat loss) in Southeast Asian field guides from 1975 to 2000. Of 306 species studied, Peh (2007) found that 84 species shifted their upper range margin upslope with a stable lower margin, 7 species shifted their lower margin with a stable upper margin, and just 3 species shifted both margins. The under-representation of tropical range shifts is likely explained by low research effort in the tropics, mostly short-term studies focused on presence-absence, and the difficulty of disentangling multiple drivers of range changes, such as habitat loss, invasive species, and climate change (Brook *et al.* 2008).

Distributional shifts from climate change are poorly documented in the tropics, but these changes demand attention because extinctions might be avoided if suitable refuges exist, species are able to disperse, and species interactions are not seriously altered (Parmesan 2006). Mid-range emissions scenarios predict that, by 2100, large areas of the lowland tropics will either experience climates hotter than currently exist anywhere on Earth, or be >1 500 km from the equivalent of the current climate (New *et al.* 2009). In a process called lowland biotic attrition, lowland species that are found far from cool, upland refuges will be unable to shift and extinctions may result unless species can adapt (Colwell *et al.* 2008, Wright *et al.* 2009). Upland species that have narrow altitudinal ranges may suffer from range-shift gaps where they are unable to keep up with advancing climates up mountainsides (Colwell *et al.* 2008; Fig. 1.1). In forested areas, birds may be less affected by range-shift gaps than some plants, insects, and reptiles and amphibians that are poor dispersers or are strongly philopatric. But habitat loss may substantially constrain distributional shifts that tropical animals will need to make under climate change (Forero-Medina *et al.* 2011b). Mountaintop extinctions of high elevation species may result when preferred climates shift off the tops of mountains (Williams *et al.* 2003) and low elevation competitors expand their distributions upslope (Jankowski *et al.* 2010). Lastly, tropical species may be particularly vulnerable to climate change because they experience minimal fluctuations in annual temperature and are already near their maximum thermal tolerance (Tewksbury *et al.* 2008).

Approximately 10 percent (CHS unpubl. data) of the world's bird species are confined to small geographic and elevational ranges in tropical upland (≥500 m elevation) habitats. Correlative distribution and abundance and models suggest many of these species are likely to be threatened by climate change (Jetz *et al.* 2007, Sekercioglu *et al.* 2008, Gasner *et al.* 2010, La Sorte & Jetz 2010a), yet most are classified as least concern by the IUCN (Sekercioglu *et al.* 2008, BirdLife International 2009) because of the uncertainties surrounding model predictions (Akçakaya *et al.* 2006). The causes of uncertainty in forecasts of climate change impacts on biodiversity are varied, but broadly speaking, uncertainty results from a lack of long-term empirical data on climate-biodiversity impacts combined with model-based uncertainty derived from biodiversity and climate modelling techniques, including a failure to incorporate biological processes (Araújo & Rahbek 2006, Heikkinen *et al.* 2007, Beaumont *et al.* 2008).

Below we discuss avian monitoring and experiments (first and second sections), and species traits analyses and climate monitoring (third section), that will yield valuable data on climate change impacts on upland tropical birds. We focus on efficient approaches that could be readily applied by many scientists, but we also discuss the importance of targeted intensive research.

Monitoring climate change impacts

Studies from Costa Rica show that climate change can cause compositional changes in tropical upland bird communities, but the shifting ecology of these novel communities remains to be investigated. Pounds *et al.* (1999) studied birds from 1979 to 1998 in a forested plot at Monteverde reserve (1 540 m). The authors documented the colonisation of 15 low elevation species (usually found below 1 470 m), and showed that these avian community changes were correlated to decreased mist frequency from climate change. Furthermore, Pounds *et al.* (2005) observed that high elevation species are declining (e.g. Resplendent Quetzal *Pharomachrus mocinno*) or moving upslope (e.g. Fiery-throated Hummingbird *Panterpe insignis*), probably in response to climate change and consequent changes in species interactions. This sort of documentation of bird community shifts from climate change is urgently needed from other tropical regions. Similar processes are likely occurring outside of Costa Rica, but very few studies have been done, so it is difficult to generalise from these results except to say that most studied species showed changes.

There are many ways forward from the pioneering work of Pounds *et al.* (1999, 2005). One efficient approach would be to rapidly survey bird communities along elevation gradients.

Such work generates broad estimates of abundance for many species, and all that is required is identification ability, binoculars, and a global positioning system. In a recent project JBCH (unpubl. data) recorded bird abundances with point counts and transect surveys on trails from the base to the summit of four mountains in Borneo. Abundances of 234 species were recorded from 275–4 095 m in just two months. Abundance data are essential in climate impacts research for quantitative historical-current comparisons (Tingley & Beissinger 2009), and spatial modelling to predict potential changes in population size (Shoo *et al.* 2005a).

Most temperate studies that have been able to detect climate impacts on birds were long-term projects (reviewed in Crick 2004, Møller *et al.* 2010); thus, while most long-term projects are expensive and difficult to maintain, it will be important to repeat surveys at regular intervals, at least every five years (Magurran *et al.* 2010). If similar repeated, rapid surveys are done in different tropical regions, generalisations could perhaps be made on which lowland species are likely to invade highland areas, and which range-restricted highland endemic species are prone to decline. Studies need to incorporate well-protected areas to control for the effects of habitat loss and land use.

Reproductive information is urgently needed to document changes in the breeding avifauna of a site and to allow quantification of reproductive fitness. Fundamental information can be efficiently collected with nest searching to rapidly improve our understanding of reproduction in upland tropical birds. For example, eight trained nest searchers located 700 nests in a Venezuelan upland tropical forest in a four month field season (T. E. Martin pers. comm.). Such large sample sizes allow monitoring of changes in reproductive output for many species that can be linked to changes in climate or, perhaps, competition. Video monitoring of nests can efficiently quantify baseline nest predation and brood parasitism (from, for example, cuckoos *Cuculus* sp. and cowbirds *Molothrus* sp.), and detect changes from invading nest predators and parasites over time, providing a clearer picture of any climate-driven change. Since so few data are available, results from individual studies will be of great use, but again, efficacy will be markedly improved if studies are repeated over time (e.g. Martin 2007).

Intensive research methods such as mark-recapture studies are also sorely needed in tropical uplands, but these methods are expensive, often logistically challenging, and difficult to maintain, so studies should be carefully allocated to taxa and regions that are most likely to produce results that can be generalised. Long-term mark-recapture datasets are potentially critically important for bettering our understanding of the effects of climate change on birds because they provide a statistically rigorous method for quantifying climate impacts on avian survival, enable us to measure breeding status and age distribution, allow population modelling, and enable robust inference on density and population trends (Grosbois *et al.* 2008). In a temperate example, mark-recapture analysis was able to link climate to changes in White Stork *Ciconia ciconia* survival using ringing and resighting data from 1947–1985 in France (Grosbois *et al.* 2008). Mark-recapture studies have been done on upland tropical birds (e.g. Parker *et al.* 2006) but long-term datasets are rare (e.g. Newmark 2006). Some of the difficulties of maintaining a long-term mark-recapture program could be mitigated if programs are linked to permanent research stations. As a starting point, we propose long-term (a goal of >30 years) mark-recapture programs be established at at least one research station in each tropical region (Asian tropics, Afrotropics, and Neotropics). Suitable locations for establishing these programs include the Smithsonian's Center for Tropical Forest Studies plots (www.ctfs.si.edu) which are foci of long-term ecological research. Candidate sites where baseline ecological research is already underway are La Planada, Colombia (1 796–1 891 m; Restrepo *et al.* 1999) and Doi Inthanon, Thailand (1 660–1 740 m; Khamyong *et al.* 2004). In Africa, where relevant studies on birds are the rarest (Laurance *et al.* 2011), the Usambara Mountains, part of the Eastern Arc Mountains biodiversity hotspot, are an ideal candidate, with a long-term bird mark-recapture study that was established over two decades ago (Newmark 2006).

While site-specific studies will be informative, continental- and global-scale monitoring programs will be best able to identify climate-induced shifts in avian distribution and abundance, which tend to occur at broad spatial scales. These programs draw on the large pool of skilled volunteer birdwatchers that can repeatedly and accurately collect occurrence data over large spatial and temporal scales. Data from continental-scale monitoring programs have been used to identify responses of many temperate species to climate change. For example, the North American Christmas bird count (La Sorte & Thompson 2007) and breeding bird atlas (Zuckerberg *et al.* 2009), and the British bird atlas (Thomas & Lennon 1999), have all been used to detect climate-related latitudinal shifts in bird distributions. Global monitoring schemes such as the Tropical Ecology Assessment and Monitoring Network (TEAM; www.teamnetwork.org) and Global Observation Research Initiative in Alpine Environments (GLORIA; www.gloria.ac.at) will also be important for comparing avian responses to climate change globally.

Avenues for experimental work

We know little about baseline competitive, parasitic, and symbiotic interactions in tropical upland bird communities, and virtually nothing about the changes to these dynamics caused by climate change. For example, due to upslope expansion, the cavity-nesting nest predator Keel-billed Toucan *Ramphastos sulfuratus* now nests alongside cavity-nesting Resplendent Quetzals at Monteverde, Costa Rica (Pounds *et al.* 1999), likely competing with them for cavities and preying on their eggs and young. Further, the importance of abiotic (e.g. Ghalambor *et al.* 2006) and biotic (e.g. Price & Kirkpatrick 2009) factors in determining tropical range boundaries are still poorly understood. The only study that has tested the importance of biotic interactions in this context used audio playback experiments and found that interspecific interactions are likely to be important for determining range boundaries in Monteverde (Jankowski *et al.* 2010). These authors also found that the mountaintop *Catharus fuscater* (Slaty-backed Nightingale-thrush) is tolerant of the middle elevation *C. mexicanus* (Black-headed Nightingale-thrush), while *C. mexicanus* is aggressive towards *C. fuscater*. This finding suggests that high elevation species may be under asymmetric pressure from low elevation species, and mountaintop endemics may be outcompeted. This pattern seems to fit into taxon cycle theory, where endemics have historically been squeezed by generalists into higher elevations (Ricklefs & Bermingham 2002). Asymmetric competition from low elevation generalists is likely to interact with other extinction pressures on high elevation species under climate change. Nonetheless, Jankowski *et al.* (2010) observed asymmetric competition in just one of two genera studied, and these results come from a single field site, so generalisations are so far difficult to make.

While Jankowski *et al.* (2010) made progress on baseline interspecific interactions in upland tropical birds, avian interactions under climate change and their effects on ecosystem function apparently remain to be investigated (Mooney *et al.* 2009). One clear way forward is to use field-based experiments to examine interspecific interactions. Our survey of the literature found no examples of experiments that were used to measure potential effects of climate change invaders on resident tropical birds (e.g. Lepetz *et al.* 2009), yet experimental analyses could be efficient and effective methods to test for interactions among invaders and residents. In this section, we highlight the potential for efficient artificial nest experiments and more intensive audio playback and introduction/removal experiments for examining species interactions under climate change.

Combining artificial nest experiments with video monitoring of natural nests would be an efficient way to evaluate the effects of colonising nest predators and brood parasites on resident upland birds. Artificial nests allow researchers to systematically quantify nest predation along elevational gradients, and monitoring is more efficient than filming natural nests because the lack of adult attendance allows motion-sensing camera traps to be used. Nonetheless, artificial nests are subject to a number of biases (Moore & Robinson 2004) which necessitate supplementing experiments with studies of some natural nests (see above). Modest investment in motion sensing cameras and video cameras combined with minimal nest searching would allow researchers to rapidly check for nest predation or brood parasitism from lowland invaders. If funding allows, it would be ideal to repeat studies over time to look for changes in predation and parasitism.

Audio playback experiments are useful for studying avian behaviour and stimulating territorial responses (Kroodsma 1989), and playback techniques are well established, promoting comparability across species and study sites (Martin & Martin 2001). In climate research, controlled playbacks of upland resident songs to potentially competitive invaders could efficiently test for aggressive responses and identify potential ‘problem’ invaders. Experiments where songs of invaders are played to residents could evaluate if residents are naive to novel invading competitors or predators (Reudink *et al.* 2007). Territory mapping combined with playbacks could characterise interactions between sympatric and neighbouring species (Jankowski *et al.* 2010) and predict potential changes in interactions as species’ distributions shift, but these methods require substantial effort.

Removal and introduction experiments would be an informative way to test for interspecific effects and associated ecosystem functions under climate change, but these experiments are potentially risky and difficult to implement. Grey *et al.* (1997) removed aggressive Noisy Miners *Manorina melanocephala* from temperate Australian woodlands and documented rapid colonisation of the habitat by several subordinate bird species. Similar judicious removal experiments of exotic or ‘pest’ species on tropical mountains could test for the competitive effects of invading climate change colonists. Introduction experiments with range-restricted upland species could test hypotheses on factors that limit populations such as dispersal barriers, habitat quality and physiological tolerances (Cooper & Walters 2002), and be used as pilot studies for assisted colonisation (Hoegh-Guldberg *et al.* 2008). Such experiments would be particularly interesting where anthropogenic disturbance is degrading native habitats and limiting dispersal to higher elevations. In all cases, the advantages and disadvantages of removal and introduction experiments will need to be carefully evaluated (e.g. Ricciardi & Simberloff 2009).

Other topical research directions

Above, we focused on empirical research methods for rapidly improving our knowledge of climate impacts on upland tropical birds. An alternative, little-explored, strategy would be to combine elevational range data with species trait information from the literature to evaluate if traits can predict colonisation success of low elevation species, or extirpation vulnerability in highland residents. Results from this kind of analysis could help direct monitoring to species that may be most threatened by climate change or most likely to become ‘problem’ species. Previous work has shown that range size, specialisation, mobility, and local abundance are related to resistance to extinction (Kattan 1992, Sekercioglu 2007), and elevational range, dispersal ability, reproductive output, migratory behaviour, and climatic niche breadth are likely to influence a species’ ability to respond to climate change (Isaac *et al.* 2009, Laurance *et al.* 2011). Species traits analyses could be readily implemented with existing data and would yield interesting results from each tropical region.

Accurately determining the relationship between key climate variables and species abundance will also depend on substantially increasing the collection of site-specific, long-term climate data. In tropical uplands, interpolated spatial climate layers are often impacted by poor spatial and temporal coverage of weather stations (Raxworthy *et al.* 2008), and steep topography where climates change rapidly over small horizontal distances. Automated portable weather stations that are established and carefully maintained at long-term study sites will improve the precision and accuracy of present day climate data and provide scope for downscaling future climate projections to ecologically relevant spatial scales (≤ 5km). Furthermore, improved weather station coverage will strengthen biodiversity-climate impact studies that rely on correlative approaches such as range shift analyses, species distribution modelling, and mark-recapture derived survival analyses. In addition, spatial models that incorporate fine scale climate data from portable weather stations can delineate key cool refuges and prioritise protection and reforestation in light of future range shifts (Shoo *et al.* 2011).

Conservation planning

The information gathered from the methods proposed above should be used to inform conservation status evaluations and active adaptive management programs. Although uncertainties surrounding models of climate-biodiversity impacts have so far precluded most conservation status assessments from including climate change (Akçakaya *et al.* 2006), combining advanced modelling techniques with new empirical data should dramatically improve the precision of predictions, and eventually allow conservation status evaluations in light of climate change. For example, coupled population and distribution models (Brook *et al.* 2009, Fordham *et al.* in press-a) and mechanistic process-based models (La Sorte & Jetz 2010b) show promise for substantially reducing uncertainty, but neither approach has been applied to tropical birds. As climate change impacts worsen, conservation biologists will have to judge between using uncertain projections of climate-induced shifts in range and abundance or ignoring the effects of climate change on obviously threatened species (e.g. Emperor Penguin *Aptenodytes forsteri*, Jenouvrier *et al.* 2008).

New data should be rapidly integrated into active adaptive management plans to increase our chances of mitigating extinctions and test management hypotheses (Wilhere 2002). For example, results could be used to design species-specific conservation programs for critically threatened species, or ‘hotspot’ habitats. Species traits analyses and removal experiments can be used to identify potential problem colonists and cautiously make predictions for other regions. Once altitudinal movements from climate change are better understood, models can be used to identify potential refuges (usually nearby higher elevation sites), and management action can be adjusted accordingly (Shoo *et al.* 2011). At a broader scale, systematic reserve planning can be used to combine new empirical data with spatial models (Hole *et al.* 2009) to design optimally connected networks of protected areas that maintain suitable climate space and encourage dispersal. Overall, management under climate change will have to be dynamic and adaptive, with ever-changing strategies and biodiversity goals, as novel communities emerge and species are lost (Manning *et al.* 2009).

Conclusion

Several modelling studies predict that tropical birds will be threatened by climate change but so few empirical data are available that it is difficult to judge the importance of climate change among other interacting extinction drivers. Combining efficient, local-scale research, targeted, intensive mark-recapture studies, and continental- and global-scale monitoring programs will maximise the outcome per unit effort for gathering information on the effects of climate change and other extinction drivers on upland tropical birds. Effective planning and adaptation will only be possible if we have adequate measurements of the effects of climate change on tropical upland species.

Chapter 2

Using diverse data sources to detect elevational range changes of birds on Mount Kinabalu, Malaysian Borneo

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Using diverse data sources to detect elevational range changes of birds on Mount Kinabalu, Malaysian Borneo

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J. Berton C. Harris: Conceived the idea, applied for funding and permits, performed the analysis, wrote the paper.

I hereby certify that the statement of contribution is accurate.

Signed:

Date: 2 Apr 2012

Ding Li Yong: Conceived the idea, identified bird recordings, assisted with writing.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

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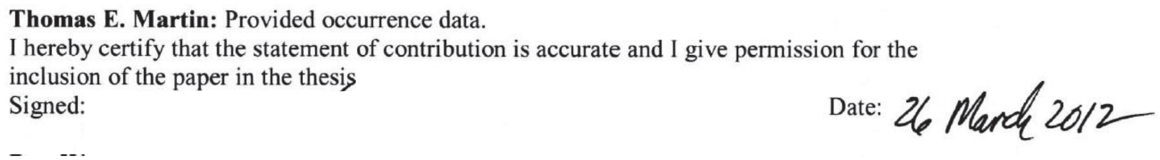

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Signed: Date: 1 May 2012

Chapter 2 - Using diverse data sources to detect elevational range changes of birds on Mount Kinabalu, Malaysian Borneo

Abstract

Few empirical studies have measured the effects of climate change on tropical biodiversity, and this paucity has contributed to uncertainty in predicting the severity of climate change on tropical organisms. With regards to elevational changes, most studies have either re-sampled historical systematic survey sites or analyzed time series of occurrence data at long-term study sites. Such data sources are unavailable for most tropical mountains, so other methods of detecting elevational changes must be sought. Here we combine data from published checklists, recent field work, peer-reviewed literature, unpublished reports, birdwatchers' trip reports, databases of birdwatchers' observations, audio recordings, and photographs to compare historical (pre-1998) and current (post-2006) bird distributions on Mt. Kinabalu in Sabah, Malaysian Borneo. Records were carefully checked by experts on Bornean birds. More species are now known from Mt. Kinabalu, but historical data provided elevational range estimates for more species than current data because of extensive mountain-wide collections and surveys. Most elevational comparisons for this study had to be limited to the 1450–1900 m elevational band, where most of the recent work has been done. Information was compiled into an annotated list of 342 species from 200–4095 m. We present this list to encourage refinement of the dataset and future work on elevational distributions on the mountain. Of 58 species with sufficient data from 1450 m to the summit, 38 appear to have shifted their ranges (24 species upslope and 14 downslope). A total of 22 resident species have recently been observed above their published maximum elevation for Borneo. Some species that have shifted upwards, such as *Chalcophaps indica* and *Pellorneum pyrrogenys*, are now common or breeding at elevations above their published maximum. Fifteen species appear to have declined on the mountain, probably as a result of habitat loss outside the protected area. Several of the upslope shifts are probably attributable to climate change, but many downslope shifts may be artifacts of incomplete recent sampling. The upward shifts agree with the few other tropical range comparisons that have been published. Our approach demonstrates the viability of combining diverse data sources (of varying accuracy and bias) to detect distributional shifts from climate change.

Introduction

Approximately 1,000 bird species are restricted to tropical mountains (Harris et al., 2011). Most of these species are considered of 'least concern' because their upland ranges are typically forested (BirdLife International, 2011), yet they may be particularly vulnerable to climate change because their montane and often narrow ranges put them at risk of mountaintop extinctions and range shift gaps (Colwell et al., 2008; Sekercioglu et al., 2008). New modeling approaches have made progress in predicting which tropical species may be most vulnerable to climate change (e.g. La Sorte & Jetz, 2010a), but so few studies have measured the effects of climate change on tropical birds that our understanding is still rudimentary (Harris et al., 2011). In addition, weather station coverage is extremely sparse in many tropical uplands in both space and time, which makes climate monitoring and associated biodiversity studies difficult (Raxworthy et al., 2008).

The few published distributional comparisons from tropical mountains—studies of moths on Gunung [=Mount] Kinabalu in Malaysian Borneo (Chen et al., 2009, 2011), birds in Peru (Forero-Medina et al., 2011a), reptiles and amphibians in Madagascar (Raxworthy et al., 2008), and multiple taxa in Costa Rica (Pounds et al., 1999, 2005)—have found upward shifts in species distributions, which will likely cause changes in the ecology of montane communities. Chen et al. (2009) analyzed climate data and compared moth (Lepidoptera) distributions from 1965 to 2008 on Mt. Kinabalu. They found that temperatures have increased by c. 0.7 ºC on the mountain since 1965, and distributions of 102 moths have shifted upwards by 67 m on average (which is less than the adiabatic lapse rate prediction of 127 m of elevation change with temperature change). Peh (2007) took a broader approach and compared elevational ranges of 300 generalist bird species (to control for the effects of habitat loss) from Southeast Asian field guides between 1975 and 2000. He found that 84 species shifted their upper range margin upslope while maintaining a stable lower margin, seven shifted their lower margin upslope with a stable upper margin, and three shifted both margins. Peh's (2007) results suggest that birds are shifting their ranges upslope in the region (especially the upper margins), but his analysis was restricted to generalist species at a regional scale.

To develop a database and compare elevational distributions of birds from prior to 1998 to after 2006 on Mt. Kinabalu, we surveyed birds on the mountain and compiled information from checklists, citizen science observations, the literature, and unpublished reports. We also checked for changes in species abundance when comparing historical and current patterns, as has been done with other checklist comparisons and re-surveys of historically-sampled sites in the tropics (Sodhi et al., 2006a; Pearson et al., 2010).

At 4095 m, Mt. Kinabalu is the tallest mountain between New Guinea and the Himalayas. It is the “most important biogeographic feature of Borneo” (Sheldon et al., 2001: 49) and potentially an essential refuge of endemism from climate change-induced range shifts (Chen et al., 2011). Kinabalu Park, which covers c. 753 km^2, was declared protected in 1963. Most of the park is above 1200 m, but elevations descend to 200 m at Serinsim (Fig. 2.1). In 1978, 289 bird species were known from Mt. Kinabalu (Jenkins & de Silva, 1978). In 1996, this number had increased to 306 species (Jenkins et al., 1996). Weather station coverage is poor in the Mt. Kinabalu region, but gridded data in the 5 x 5º cell that encompasses Mt. Kinabalu shows an increase in mean annual temperature of +0.48 ºC from 1998–2007 (Chen et al., 2009). The lapse rate on Mt. Kinabalu was estimated as c. 0.55 ºC per 100 m of elevation gain (Kitayama, 1992), so the observed temperature change could have theoretically driven an 87 m upward shift during our study period, assuming a linear relationship between climate and species distributions (Ghalambor et al., 2006).

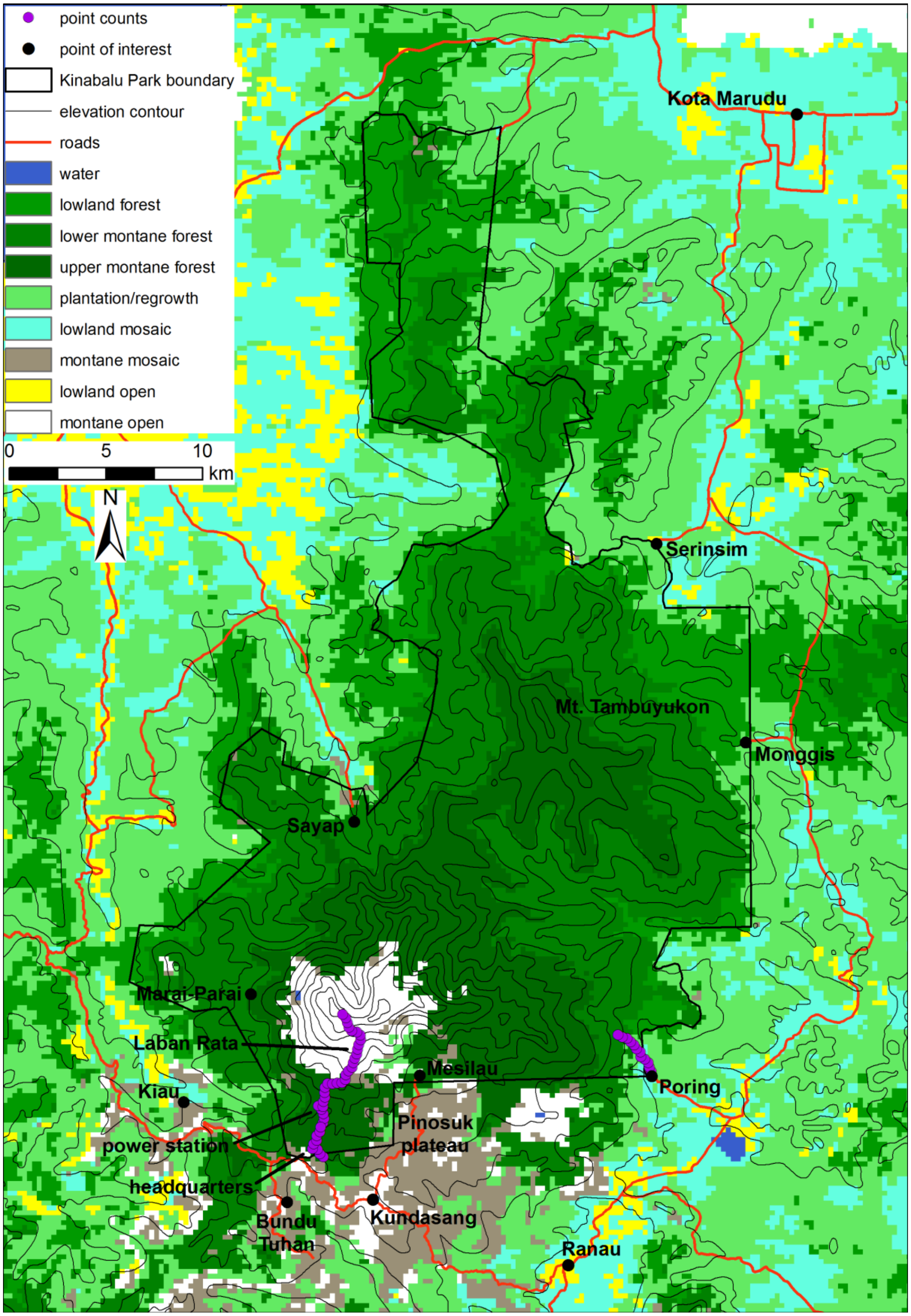

Figure 2.1. Map of Kinabalu Park, Sabah (solid black line). Land cover from 2010 (Miettinen et al., 2011), JBCH's point count locations, elevation contours (303 m intervals), roads, and points

of interest including towns and collecting localites are shown. Timpohon gate is c. 50 m from the power station; the summit trail extends from the power station to the summit (shown by JBCH's points).

Most of Kinabalu Park has remained largely undisturbed since 1963, which makes it ideal for studying range shifts from climate change independent of the effects of habitat loss. But areas outside the park have become increasingly disturbed (Beaman & Beaman, 1990; McMorrow & Talip, 2001), and the extensive submontane forest on the Pinosuk plateau near Kundasang was degazetted from the park and deforested in the early 1980s to develop a copper mine and other land uses (Fig. 2.1; Sheldon, 1986). Therefore, some submontane species that were once recorded on the plateau (e.g., by Gore, 1968, and Smythies, 1964) are no longer found there, and populations of submontane forest birds below park headquarters are much reduced (Sheldon et al., 2001). This situation makes it difficult to compare past and current lower range margins for some species, and the limited submontane forest bird community below the headquarters may affect climate-related community changes at higher elevations. Nonetheless, much of the historical data we analyzed comes from after 1980, and upward range shifts above the headquarters should be little affected by these habitat changes.

The citizen science data we collected from Mt. Kinabalu varied in spatial coverage, methods, effort, and observer bias (Harris & Haskell, 2007; Boakes et al., 2010; Dickinson et al., 2010) that made it difficult to conduct standardized historical to current comparisons. We attempted to address these problems by: (1) restricting range estimates to areas that have received more research and birdwatching compared to the rest of the park; (2) consulting experts on Bornean birds to remove suspect records; and (3) contacting birdwatchers, scientists, and bird tour companies to verify time, place, and identification details for many records.

Given the usually strong relationships between climate and species distributions (e.g. Bush et al., 2004), and the results of similar studies (for examples, see Pearson et al., 2010; Chen et al., 2011), we hypothesized: (1) warming temperatures have caused elevational increases in some resident birds on Mt. Kinabalu, and (2) declines in forest bird species would be apparent, likely as a result of habitat loss outside the park. We examined these possibilities with diverse data sources and report the results here.

Methods

Data sources

We compared “historical” distribution data collected prior to 1998 (a few records came from as far back as the late 1800s) to “current” data from 2007–2011. We also reviewed intermediate information from 1998–2006, and present these data in the online appendix to promote further study, but we did not use these years in the elevational comparisons to allow a 10 year gap. Elevational range shifts from climate change were found after 10 years in a previous study on reptiles and amphibians (Raxworthy et al., 2008), and the marked temperature increase shown during this interval (0.48 ºC; Chen et al., 2009) indicated that shifts would likely be observed. Tropical birds have also been shown to shift their ranges in response to small temperature changes (Pounds et al., 2005; Forero-Medina et al., 2011a). Data came from published checklists, recent field work, peer-reviewed literature, unpublished reports, birdwatchers’ trip reports, audio recording databases (Xeno Canto, www.xeno-canto.org; and AVoCet, http://avocet.zoology.msu.edu), Oriental Bird Images (OBI; a photographic database; http://orientalbirdimages.org), Global Biodiversity Information Facility specimen records (GBIF; http://data.gbif.org), and two online databases of georeferenced occurrence data, mostly from birdwatchers’ observations: eBird/Avian Knowledge Network (AKN; http://www.avianknowledge.net) and Bird I Witness (BIW; www.worldbirds.org/malaysia). Mt. Kinabalu is one of Asia’s most frequently visited birdwatching sites, and there are many trip reports available from the region. We collected trip reports from independent birdwatchers (on Surfbirds (http://www.surfbirds.com), Birdtours (http://www.birdtours.co.uk), and World Twitch (http://www.worldtwitch.com)), and professionally-led bird tours (from Victor Emanuel Nature Tours, Birdtour Asia, Tropical Birding, Bird Quest, and Rockjumper Birding Tours). We contacted the aforementioned tour companies as well as WINGS, Field Guides, and King Bird tours to ask for historical trip reports but none were available. In all, we obtained 52 reports covering the historical and current time frames from these bird-watching sources.

Historical (pre-1998) data.–The main historical data sources are two published checklists of the birds of the Kinabalu region (Jenkins & de Silva, 1978; Jenkins et al., 1996). The checklists combined data from specimens, the literature, unpublished scientific reports, and sight records to produce species accounts and elevational ranges (see Sheldon et al., 2001 for details on areas covered by historical expeditions including a figure showing collecting localities). Jenkins and de

Silva (1978) and Jenkins et al. (1996) focused on bird records from (1) Kinabalu Park headquarters (c. 1575 m) up to the summit (4095 m) along the power station road and the summit trail, and (2) Poring Hot Springs (c. 500 m, but many historical Poring records did not have elevations specified) (Fig. 2.1). The checklists also include records from other areas on the mountain, particularly from older specimens. Overall, Jenkins et al. (1996) made minor edits to the 1978 checklist, making it difficult to find range changes between the two lists. We therefore included Jenkins et al.'s (1996) additions and treated the checklists as a single data source.

Data from Biun's (1999) study of elevational distributions of birds on Mt. Kinabalu provided a substantial supplement to the checklists. Biun (1999) surveyed birds in 1996 and 1997 at five sites (primary forest at Poring, 700 m; park headquarters, 1600 m; Kemburongoh, 2100 m; Layang-Layang, 2600 m; and Paka cave, 3100 m) during six sampling periods (June, September, and December 1996, and April, June, and October 1997). He spent four days at each site during each sampling period, amounting to 120 days of sampling effort. He sampled birds with 30 12-m mist nets that were open day and night, and one hour of aural and visual observations along a 500 m transect at each site. This research would have served as an adequate benchmark for future comparisons, but Biun's (1999) abundance data are no longer available.

Additional historical data came from the literature (Gore, 1968; Smythies, 1981, 1999; Sheldon & Francis, 1985; Sheldon et al., 2001; Mann, 2008), unpublished scientific reports (Sheldon, 1977; Phillips, 1986; Batchelor, 1991; Rahman et al., 1998), Xeno Canto (n = 1), AVoCet (n = 25), Oriental Bird Images (n = 3), Global Biodiversity Information Facility specimens (n = 88), Avian Knowledge Network observations (298 records total; P. Bono, 1997, Kinabalu Park; W. Nezadal, 1991, Poring c. 975 m; D. Roberson, 1988, Kinabalu Park and summit trail), Bird I Witness observations from park headquarters (n = 16), and birdwatchers' trip reports (Wall & Yong, 1985; Johnstone, 1989; Vermuelen, 1996). In the Methods we use "n" to refer to the number of records coming from each data source; this differs from the sample sizes (number of range margins) used in the range comparisons.

Intermediate data (1998–2006) .–Intermediate data came from the literature (Moyle, 2003), unpublished reports (Moyle & Sheldon, 2000; Sheldon et al., 2004), Xeno Canto (n = 52), AVoCet (n = 10), Oriental Bird Images (n = 189), Global Biodiversity Information Facility specimens (n = 208), Bird I Witness (53 total records from Mt. Kinabalu trails (Liwagu and Silau Silau), power station road, Kinabalu headquarters area, Poring (Langanan trail), and Mesilau headquarters and trail), Avian Knowledge Network observations (690 records total; C. Artuso, 2000, Poring c. 560 m; E. Barnes, 2005, Silau Silau trail c. 1570 m and Poring c. 560 m; R.

Carratello, 2003, Kinabalu Park; A. Lazere, 2005, Kinabalu Park; D. Roberson, 2003, Kinabalu Park) and trip reports (Benstead & Benstead, 2001; Addison, 2002; Clayton & Thomas, 2002; Rheindt, 2003; White & Clarke, 2003; Benstead, 2004; Gandy, 2004; Hall & Kroll, 2004; Ericsson, 2005; Hornbuckle, 2005; Babic & Babic, 2006).

Current (post-2006) data.–Substantial current data came from recent field work by JBCH, AJB, and JAE. From March to April 2010 JBCH conducted systematic point count and transect surveys on Mt. Kinabalu along the Liwagu and summit trails from 1450–4095 m, and at Poring along the waterfall trail from the headquarters car park up to Langanan waterfall (500–1000 m). The point counts were conducted for 10 minutes and covered a 50 m radius. They were separated by 250 horizontal meters along continuous elevational gradients on mountain trails (Ralph et al., 1995; Fig. 2.1; see Table S2.1 for coordinates of points, to enable re-sampling). Occurrence data were also collected along ‘transects’ in between the points to 50 m on either side of the trail. Systematic surveys were done in the morning from 600 until 1030, and sites were opportunistically re-surveyed in the afternoon. JBCH also revisited the points and transects at night to sample nocturnal birds, however, only every other point was surveyed because low bird abundance made point count detections uncommon. Transects were found to be more effective for sampling nocturnal birds on the mountain. As suggested by Ralph et al. (1995), estimates of the distance of singing birds from the point were made more accurate by conducting trials with audio playback and a measuring tape. A Nikon Forestry 550 laser range finder was used to verify visual distance estimates.

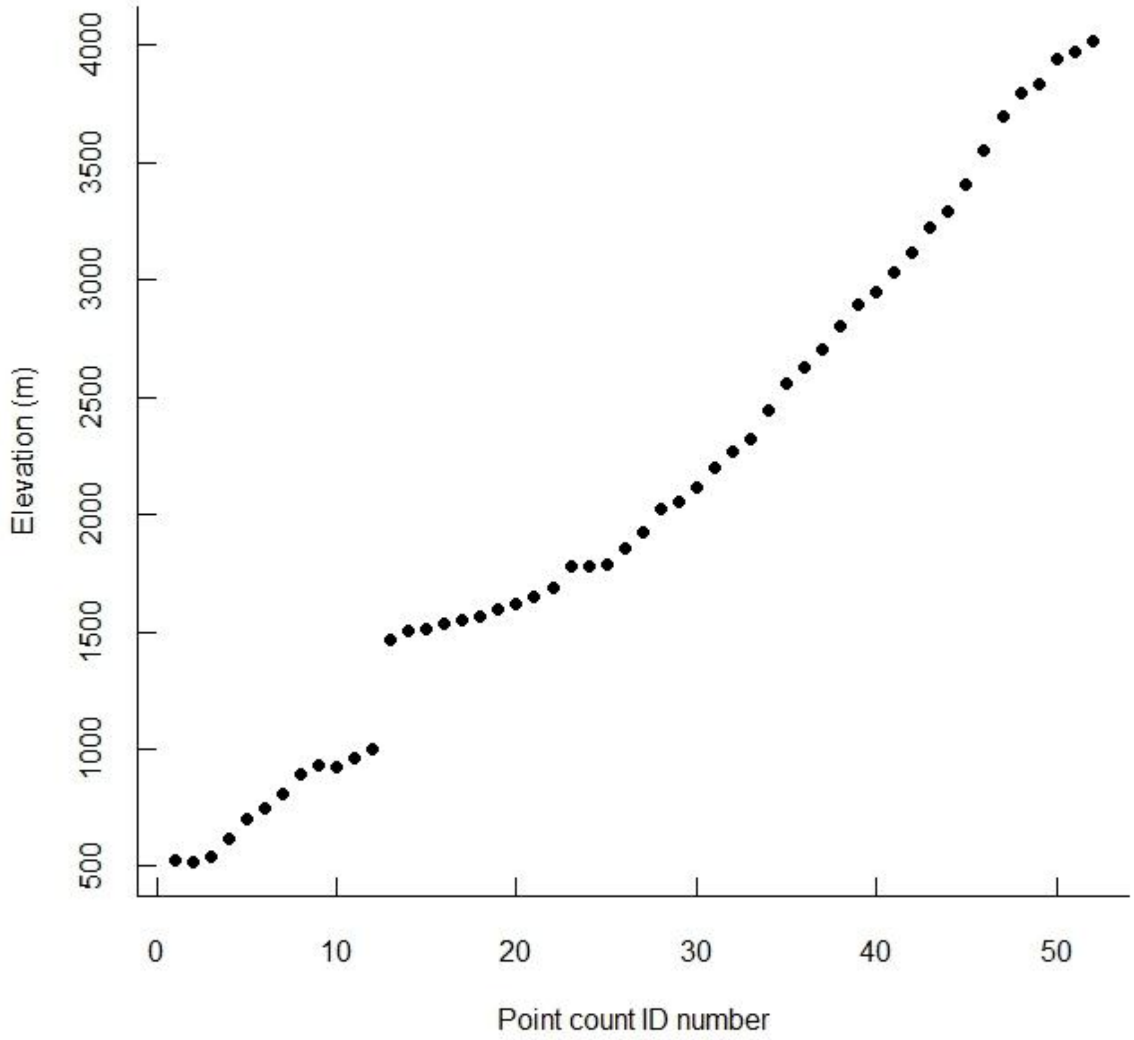

Figure 2.2. Plot of elevational coverage of point counts done by JBCH in 2010 at Poring (lower 12 points) and from near park headquarters to the summit (upper points). The break in points shows the divide between Poring and Mt. Kinabalu sampling sites.

AJB documented elevational distributions of birds on Mt. Kinabalu as part of TEM's long-term nest-searching and mist-netting project at the site. The data presented here are a combination of AJB's observations, GPS points taken at nests located by TEM and his field crew, and mist-net captures by his team. Mist-netting was conducted every day from 700 until 1300 with 12 9-m mist-nets set up in consistent locations within banding plots, which were distributed evenly across the study area. Nests were found using both parental behavior and systematic search techniques (Martin & Geupel, 1993). AJB spent a total of 12 months (from February to June) over three years (2009–2011) at the site. The majority of AJB's records come from forest between the junction of the Liwagu and Silau-Silau rivers up to Timpohon gate, on both sides of the power station road (1450–1900 m). Additional AJB observations come from Poring (10 field days), the Mt. Tambuyukon summit trail above Kampung Monggis (3 field days), and Kundasang (Fig. 2.1).

JAE has visited Mt. Kinabalu on 18 occasions, totaling c. 90 days from 2002–2010, specifically for birdwatching, both privately and leading birdwatchers for Birdtour Asia, covering all months except December to March and September. On each visit JAE spent at least one day at Poring (each time walking on the Langanan trail to at least km 3.1 (c. 975 m), and all the way to Langanan Waterfall on five occasions), one morning or afternoon at Mesilau (c. 1940 m), and two days walking from Timpohon gate to the summit and back. The majority of the time spent within Kinabalu Park was between the headquarters and Timpohon Gate, birdwatching along trails, particularly Bukit Ular and Mempening, with occasional visits to Silau-Silau and along the road.

Additional current data came from the literature (Mann, 2008; Sheldon et al., 2009), unpublished reports (Sheldon & Moyle, 2008), Xeno Canto (n = 152), AVoCet (n = 120), Oriental Bird Images (n = 307), Global Biodiversity Information Facility specimens (n = 32), Avian Knowledge Network (860 total records; J. Sevenair, 2010, Kinabalu Park; J. Watson, 2010, Poring c. 500 m and Kinabalu Park; S. Brown, 2011, Kinabalu Park, Poring c. 560 m, and Mesilau c. 2000 m; L. Harding, 2011, Poring c. 560 m, summit trail, and Mesilau c. 1930 m; J. Harrison, 2011, Kinabalu Park; R. Merrill, 2011, Kinabalu Park), Bird I Witness (1081 total records from Mt. Kinabalu trails (Bukit Ular, Liwagu, Mempening, Silau Silau, Kiau View), power station road, Kinabalu headquarters area, Poring (Langanan trail, canopy walkway), and Mesilau headquarters), and trip reports (Banwell, 2007; Low, 2007; Newnham, 2007; Shackelford, 2007; Woods, 2007, 2008; Dobbs, 2008; Harrap, 2008, 2010, 2011; Matheve, 2008; Valentine, 2008; Valentine & Thurmilangan, 2008a, b; Barnes, 2009; Chafer, 2009; Eaton, 2009, 2010a,b; Gear, 2009; Hutchinson, 2009, 2011; Roadhouse, 2009; Gurney, 2010; Lambert & Yong, 2010; Myers, 2011). Lastly, AB has worked at Kinabalu Park for the last 34 years and has collected supplemental data on the park's avifauna.

Data accuracy and comparing ranges

Records from the different data sources varied in certainty in identifications and spatial accuracy. They were carefully reviewed by two experts on Bornean birds (FHS and JAE) and questionable identifications were removed or considered hypothetical. To maximize spatial accuracy, we took the conservative approach of assigning approximate elevations only if a location could be sufficiently narrowed to a small elevational range. For example, we did not assign elevations to records from "Poring" because most observers cover elevations from 500–1000 m in a single visit. We considered Avian Knowledge Network records from "Kinabalu Park, 1845 m" to be located somewhere between park headquarters and Timpohon gate, and we did not assign an elevation. We conservatively considered Avian Knowledge Network records from "greater than 2000 m on the summit trail" to be from 2050 m (in many cases we contacted the observer to verify the locality). In total, we contacted 25 observers to clarify identifications and details on the place and time where sightings were made. We consider mist net records to be the most reliable, followed by published observations, and finally birdwatchers' trip reports.

We attempted to standardize datasets by compiling elevational range information only from records in the two focal regions of the checklists (Jenkins & de Silva, 1978; Jenkins et al., 1996) and JBCH's sample sites (see above). We decided a priori that it would not be appropriate to compare means of the lower and upper margins because of differences in sampling effort over time. Several lines of evidence indicate that historical sampling was more complete than recent sampling: (1) the historical dataset incorporated a much longer time period with a legacy of much ornithological research (Sheldon et al., 2001); (2) the historical data produced range margin information for more species than the current data, even though more species are now known from the mountain; and (3) the distance between the mean range margins across all comparable species is larger in the historical data (see Results). Historical sampling was most comprehensive from near park headquarters (c. 1450 m) to the summit, and recent sampling was most complete from park headquarters to Timpohon gate (1900 m). Given the overlap in sampling effort, we looked for upward and downward shifts from park headquarters to Timpohon gate. We also checked for range expansions above Timpohon gate (upward shifts) because these elevations were well surveyed historically and any expansions would likely reflect a genuine shift. Possible downslope shifts above Timpohon gate were marked in the online appendix, but we found these changes much less reliable because apparent range contractions above Timpohon gate could easily result from incomplete recent sampling at high elevations. Range changes of ≥100 m were considered to be outside the range of measurement error and marked as upward or downward shifts in online appendix. We also compared historical and current elevational ranges for each species to Borneo-wide ranges from Mann (2008) to weigh the evidence for a substantial shift. In some cases, Mann's (2008) maximum elevations disagreed with those of Sheldon et al. (2001), and we checked the original specimen data to find the Bornean maximum.

We also considered making range comparisons based on individual components of the dataset (e.g. JBCH data vs. Biun, 1999), but found such secondary comparisons to be poorly justified, given that our dataset is collated from multiple contributing sources with varying spatial and temporal coverage, and any one data source produces incomplete ranges for species. Instead, we plotted contributions of records from each data source to check for disproportionate effects from single data sources.

To organize species, we followed the classification of the International Ornithologists' Union (Gill & Donsker, 2011), except when published phylogenies indicated otherwise, e.g., for Bornean Forktail *Enicurus borneensis* (Moyle et al., 2005) and Bornean Spiderhunter *Arachnothera everetti* (Moyle et al., 2011).

Results

The historical data produced a list of 317 species for Mt. Kinabalu from the period prior to 1998. The current list comprises 342 species (51% of Borneo's total; Phillips & Phillips, 2011), including 42 endemics (82% of the total for Borneo; Phillips & Phillips, 2011), 39 non-breeding species, and seven hypothetical species (online appendix). Despite the increase in species, the current data provided less comprehensive overall coverage of species' ranges than the historical data: we were able to compile 229 lower and 239 upper margins from the historical data, compared to 218 lower and 200 upper margins from the current data. 170 species had historical and current data for the lower range margin, while 161 had historical and current data for the upper margin. The mean elevational ranges of comparable species (those with both historical and current data) were 601.2 m ± 19.9 SE to 1565.7 m ± 66.5 (historical lower and upper margins) versus 742.2 m ± 29.2 to 1314.9 m ± 56.4 (current lower and upper margins). The broader elevational band in the range means indicates historical sampling was more extensive than current sampling.

The checklists and Biun (1999) were the most important historical data sources, collectively contributing information on 75% of the species in the historical list, whereas birdwatchers' trip reports, JBCH's data, and unpublished reports were the most important intermediate and current data sources, contributing information on 63% of the species in the current list. Species that shifted their ranges (Table 2.1) generally were recorded in proportion to all species, except that AJB's data were especially important for detecting upward shifts, and JAE's data detected many downward shifts (Fig. 2.3). The trip reports contributed information on nearly 25% of the species but were less important for identifying shifts in elevations in our study because many records had inadequate spatial resolution.

Table 2.1. Birds that appear to have shifted their ranges on Mt. Kinabalu (from park headquarters, c. 1575 m, to the summit, 4095 m) by at least 100 m. Gray fill indicates a shift upward, gray fill with horizontal lines indicates a shift downward. Bold numbers indicate margins at least 100 m higher than the maximum previously recorded in Borneo (Mann, 2008). Underlined numbers are marginally higher than in Mann (2008). Ambiguities in the upper margin reported in Mann (2008) were checked against the literature and specimens to estimate the maximum. See the online appendix for data sources for each margin.

English name	Scientific name	Past lower margin (m)	Past upper margin (m)	Current lower margin (m)	Current upper margin (m)	Year range of records from shifting margin	Upper margin from Mann (2008)	Notes
Crested Honey Buzzard*	*Pernis ptilorhynchus*	818	848	500	**1500**	unspecified	to over 1000 m	Three recent records from Kinabalu Park (at least 1500 m).
Crested Goshawk	*Accipiter trivirgatus*	303	909	560	1500	1913 to 2009	to 2015 m "throughout Borneo"	Recently bred at 1500 m.
Common Emerald Dove	*Chalcophaps indica*	600	1600	1450	**1900**	before 1978 to 2009	up to at least 1590 m	Multiple recent mist-net captures from 1450–1850 m; recent sighting at 1900 m.
Chestnut-breasted Malkoha	*Phaenicophaeus curvirostris*	303	1061	539	**1600**	1962 to 2010	to 1220 m	Two recent sightings from c. 1500 m, one sighting at 1600 m.
Dark Hawk Cuckoo	*Hierococcyx bocki*	909	1835	1509	2023	1957 to 2010	to 1985 m	Recently heard up to 2023 m.
Collared Owlet	*Glaucidium brodiei*	1515	1600	1450	1900	1996/1997 to 2009/2010	to 1530 m on Mt. Kinabalu, to 2100 m on Mt. Trus	Recent sightings up to 1900 m.

							Madi	
Bornean Frogmouth	*Batrachostomus mixtus*	700	2540	1575	1850	before 1998 to 2011	to 2540 m	Inconspicuous. No recent sightings above c. 1850 m.
Rufous-collared Kingfisher	*Actenoides concretus*	500	1667	530	750	before 1968 to 2011	to 1680 m	No recent sightings above 750 m.
Rhinoceros Hornbill	*Buceros rhinoceros*	1061	1758	645	950	before 1978 to 2008	to 1750 m in Sabah (Sheldon et al., 2001)	No recent sightings above 950 m.
Bornean Barbet	*Megalaima eximia*	560	2121	600	1800	before 1978 to 2011	to 2140 m	No recent sightings above 1800 m.
Checker-throated Woodpecker	*Chrysophlegma mentale*	545	1667	600	1900	before 1940 to 2009/2010	to at least 1835 m, perhaps to 2160 m on Mt. Trus Madi	Recent sightings up to 1900 m.
Orange-backed Woodpecker	*Reinwardtipicus validus*		1561	818	1900	1986 to 2009/2010	to 1985 m on Mt. Murud, Sarawak	Recent sightings up to 1900 m.
Rufous Woodpecker	*Micropternus brachyurus*	700	1600	500	600	1996/1997 to 2010	to 1818 m (Gore, 1968)	No recent sightings above 600 m.
Whitehead's Broadbill	*Calyptomena whiteheadi*	700	1667	700	1900	before 1978 to 2009/2010	to 1850 m on Mt. Trus Madi, to 1700 m on Mt. Kinabalu	Recent sightings up to 1900 m.
Black-and-Yellow Broadbill	*Eurylaimus ochromalus*	303	700	530	1547	1996/1997 to 2010	to at least 1800 m	Recently heard at 1547 m.
White-bellied Erpornis	*Erpornis zantholeuca*	700	1515	516	1800	before 1978 to 2009/2010	to over 1750 m	Recent sightings up to at least 1800 m.

Black-and-crimson Oriole	*Oriolus cruentus*	700	1600	900	1900	1996/1997 to 2009/2010	to 2300 m on Mt. Trus Madi	Recent sightings up to at least 1900 m.
White-throated Fantail	*Rhipidura albicollis*	800	**3100**	975	**3290**	1996/1997 to 2010	to 2750 m	Recent sightings up to 3290 m.
Grey-headed Canary-flycatcher	*Culicicapa ceylonensis*	909	1667	700	1533	before 1978 to 2010	to 1700	No recent sightings above 1533 m.
Flavescent Bulbul	*Pycnonotus flavescens*	1575	3485	1900	3294	before 1978 to 2009/2010	to 3970 m	No recent records below 1900 m.
Yellow-vented Bulbul	*Pycnonotus goiavier*	500	1575	500	560	1970 to 2010	to 1590 m	Open country species. No recent sightings above 560 m.
Ochraceous Bulbul	*Alophoixus ochraceus*	700	2636	1452	1780	1970 to 2010	to 2650 m	No recent records above 1780 m below Timpohon gate, but recent records at Mesilau (c. 1940-2000 m).
Grey-cheeked Bulbul	*Alophoixus bres*	500	1485	500	927	before 1927 to 2010	to 1500 m	No recent records above 927 m.
Yellow-bellied Warbler	*Abroscopus superciliaris*	909	**1818**	530	1575	before 1996 to 2008	to 1530 m	No recent records above c. 1575 m.
Mountain Leaf Warbler	*Phylloscopus trivirgatus*	1515	3100	1450	**3221**	1929 to 2010	to 3100 m (Smythies, 1960; Sheldon et al., 2001)	Recent sightings up to 3221 m.
Yellow-bellied Prinia	*Prinia flaviventris*		1091		1500	before 1968 to 2010	to 1530 m	Open country species. Recent sightings up

								to1500 m.
Ashy Tailorbird	*Orthotomus ruficeps*	303	975	500	1500	1991 to 2007	to over 1500 m	Recent sightings up to 1500 m.
Chestnut-backed Scimitar Babbler	*Pomatorhinus montanus*	455	1667	530	1850	before 1960 to 2011	to 1700 m (Kinabalu), to 2200 m (Trus Madi)	Recent record at 1850 m.
Brown Fulvetta	*Alcippe brunneicauda*	500	1500	500	950	1985 to 2009	to 1432 m	No recent records above 950 m.
Temminck's Babbler	*Pellorneum pyrrogenys*	500	1575	975	**1900**	before 1996 to 2009/2010	to 1550 m	Several recent sightings up to 1650 m, one breeding pair at 1860–1900 m.
Velvet-fronted Nuthatch	*Sitta frontalis*	909	1970	1500	1762	before 1996 to 2010	to about 2100 m	No recent records above 1762 m in headquarters area, but seen at Mesilau (c. 1900 m) in 2008.
Orange-headed Thrush	*Geokichla citrina*	909	1800	1500	**1900**	1998 to 2009/2010	to 1800 m	Recent breeding records up to 1900 m.
Oriental Magpie-Robin	*Copsychus saularis*	500	939	523	1575	before 1940 to 2005	1530 m	Open country species. Recent sightings up to 1575 m.
White-tailed Flycatcher	*Cyornis concretus*	700	1667	630	975	before 1978 to 2009	to 1680 m, usually to 1200 m	No recent records above 975 m, except for a record with no details from "Kinabalu" (Hornbuckle

								2005).
Bornean Leafbird	*Chloropsis kinabaluensis*	600	2121	850	1800	before 1968 to 2009/2010	to 2200 m on Mt. Trus Madi, to 2140 m on Mt. Kinabalu	No recent records above 1800 m.
Little Spiderhunter	*Arachnothera longirostra*	500	975	530	1500	1991 to 2010	to at least 1500 m	Mist-netted in forest at 1500 m in 2010 and 2011.
Bornean Spiderhunter	*Arachnothera everetti*	700	1515	530	**2100**	unspecified	to 1530 m	Recently mist-netted at 2100 m.
Whitehead's Spiderhunter	*Arachnothera juliae*	1212	1667	1450	2000	unspecified	to 2100 m on Mt. Trus Madi	Recent sightings up to 2000 m.

**Pernis ptilorhynchus* has resident and migratory populations.

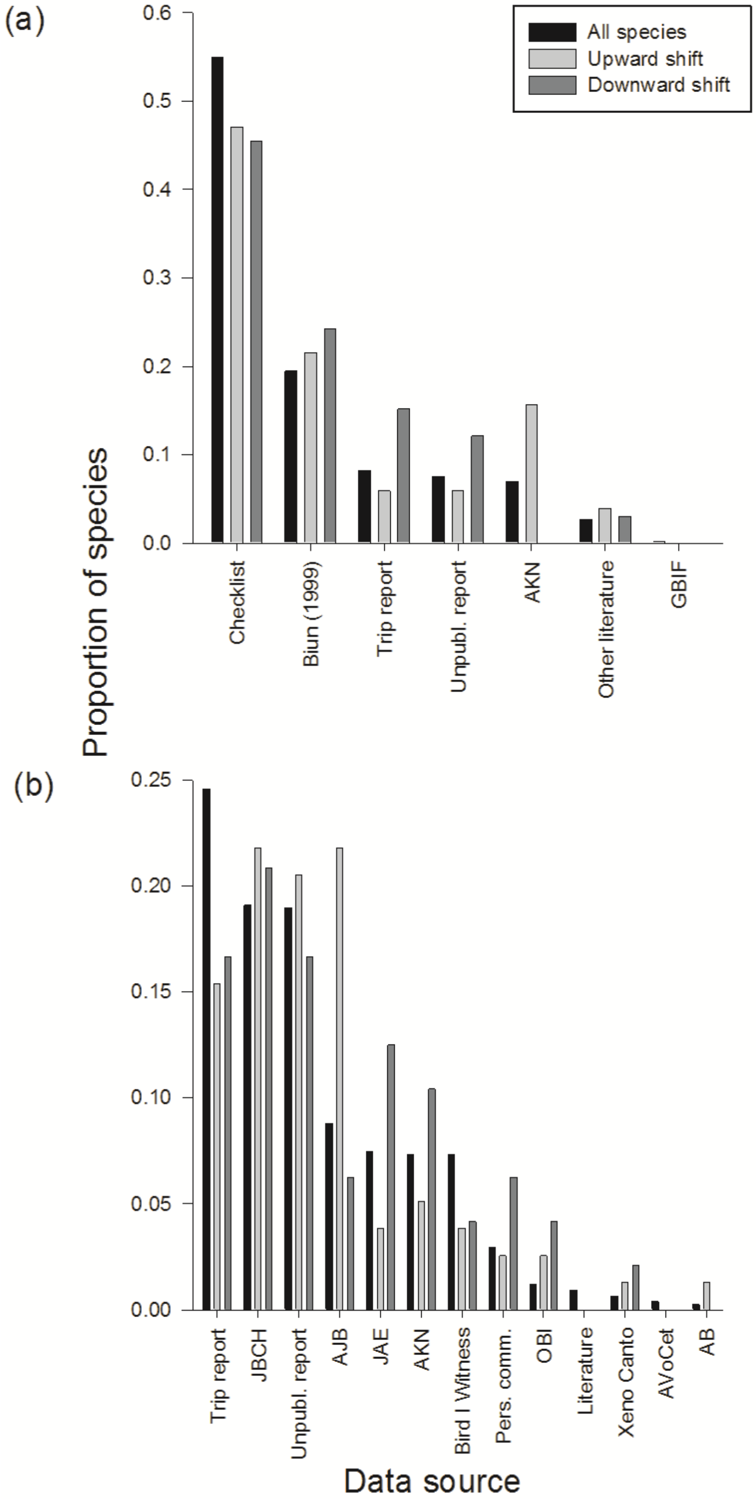

Figure 2.3. Contribution of various data sources to (a) historic and (b) current + intermediate species accounts (online appendix) for bird species in the Mt. Kinabalu region. Data source contributions are shown for all species and species exhibiting possible upward or downward range shifts. For example, in the historical data, checklists contributed information to ranges of 55% percent of the species known from Mt. Kinabalu, while checklists contributed data to ranges

for 47 and 45% of the species that showed upward or downward shifts, respectively. See Table 2.1 for a list of species that apparently shifted their ranges. Trip report refers to birdwatchers' trip reports; AKN to Avian Knowledge Network; GBIF to the Global Biodiversity Information Facility; JBCH, AJB, JAE, and AB to data from the authors; OBI to Oriental Bird Images.

Fifty-eight species had sufficient data from park headquarters to the summit (or from headquarters to Timpohon gate, for prospective downward shifting species; see Methods) to enable current-historical comparisons. Of these, 38 appear to have shifted their ranges; 23 may have shifted their upper margin upslope, 14 their upper margin downslope, and one its lower margin upslope (Table 2.1). An additional 35 species appeared to have moved downwards (online appendix), but these changes occurred above Timpohon gate, where many apparent downshifts likely resulted from incomplete current sampling. Birds showing possible upward shifts included six species that appeared to expand their ranges above Timpohon gate, three of which moved ≥100 m above their published Bornean maximum elevation (Mann, 2008). The period between sightings was at least 12 years for all species that shifted their ranges (Table 2.1). There were no clear taxonomic patterns in species that appeared to shift elevations, although two woodpeckers (Checker-throated Woodpecker *Chrysophlegma mentale* and Orange-backed Woodpecker *Reinwardtipicus validus*), two cisticolids (Yellow-bellied Prinia *Prinia flaviventris* and Ashy Tailorbird *Orthotomus ruficeps*) and three spiderhunters (*Arachnothera*) shifted upwards, and two bulbuls (Ochraceous Bulbul *Alophoixus ochraceus*, and Yellow-vented Bulbul *Pycnonotus goiavier*) shifted downwards.

Eight species in Table 2.1 and 25 other species, including seven migratory birds, have been observed above their published Bornean ranges since 1995 (Table 2.2). No species showed downward shifts ≥ 100 m below their published minimum, but Mountain Barbet *Megalaima monticola* was recorded at 700 m in 1996, which is marginally lower than its 750 m minimum (Mann, 2008). Fifteen species showed apparent decreases in abundance (Table 2.3).

Table 2.2. Birds recorded in the Mt. Kinabalu region above their Bornean elevational range (Mann, 2008). English names of migratory species are underlined. Number is bold if the margin is at least 100 m higher than the maximum in Borneo (Mann, 2008) or underlined if marginally higher. See online appendix for data source for each margin.

English name	Scientific name	Past upper margin	Current upper margin	Upper margin from Mann (2008)	Notes
Red-breasted Partridge	*Arborophila hyperythra*	**3100**	**3068**	to 1890 m on Mt. Kinabalu, to 2200 m on Mt. Trus Madi	Seen at 3100 m in 1996 (Biun, 1999) and recent records up to 3068 m.
Grey-faced Buzzard*	*Butastur indicus*	**1600**	**1650**	to 1500 m	Sighting from 1600 m in 1996 (Biun, 1999) and at c. 1650 m below Mesilau in 2010.
Crested Hawk-Eagle	*Nisaetus cirrhatus*		**1575**	to 1400 m	Recent records up to 1575 m.
White-breasted Waterhen	*Amaurornis phoenicurus*	1515		to 1530 m	Two recent records near Mesilau, at least 1900 m.
Little Bronze Cuckoo	*Chrysococcyx minutillus*		**1575**	*C. minutillus* is scarce, possibly into montane areas; *C. m. russatus* is scarce, up to 945 m	Recent sighting at c. 1575m.
Mountain Scops Owl	*Otus spilocephalus*	**3100**	**3036**	to 2705 m	Recent records up to at least 3036 m. This species may have been overlooked. It was considered "rare" and "rarely seen" (Jenkins & de Silva, 1978; Jenkins et al., 1996, respectively) but commonly heard on night surveys from 1800–2800 m in 2010 (JBCH).
Brown Wood Owl	*Strix leptogrammica*		**1900**	to 1500 m	Recent sightings from 1550–1650 m near park headquarters and at c. 1900 m at Mesilau (Phillips & Phillips, 2011).
Giant Swiftlet	*Hydrochous gigas*		**1900**	to about 1800 m	Recent sightings from 500–1900 m.
Maroon Woodpecker	*Blythipicus rubiginosus*	**2100**	**1921**	to 1800 m	Sight records at 2100 m in 1996/1997 (Biun, 1999); recently seen up to 1921 m.

Grey-chinned Minivet	*Pericrocotus solaris*	**2600**	2456	to 2440 m	Many observed at 2600 m in 1996/1997 (Biun, 1999).
Ashy Drongo	*Dicrurus leucophaeus*	**2600**	2052	to 2200 m or possibly 2400 m	Sight records up to 2600 m in 1996/1997 (Biun, 1999).
Crow-billed Drongo	*Dicrurus annectans*	**1600**	**1575**	up to c. 600 m	Seen at 700 m, netted at 1600 m 1996/1997 (Biun, 1999). Seen at park headquarters in 2008.
Hair-crested Drongo	*Dicrurus hottentottus*	**2050**	**2050**	to 1700 m	Historical and recent sightings up to 2050 m.
Greater Racket-tailed Drongo	*Dicrurus paradiseus*	**975**	**800**	to 650 m	Historical sightings up to 975 m, recent sightings to at least 800 m.
Yellow-browed Warbler	*Phylloscopus inornatus*		**1900**	The only previous record was from sea level in Sarawak.	Vocal individual photographed at 1900 m, 24 October 2008.
Sooty-capped Babbler	*Malacopteron affine*	**700**	**750**	to 550 m	Sight records from 700 m in 1996/1997 (Biun, 1999) and to 750 m in 2011.
Siberian Blue Robin	*Luscinia cyane*	700	**1850**	to 1680 m	Recent sightings up to 1850 m.
Ferruginous Flycatcher	*Muscicapa ferruginea*	1500	**1850**	to 1530 m	Recent sightngs up to 1850 m.
Narcissus Flycatcher	*Ficedula narcissina*		**1900**	to 1530 m	Recent sightings up to 1900 m.
Mugimaki Flycatcher	*Ficedula mugimaki*	**3100**	**3270**	to 2325 m	Recorded at 3100 m in 1996, netted at 3270 m in 2005, seen at 3255 m in 2010.
Thick-billed Flowerpecker	*Dicaeum agile*		**560**	below 200 m	Recent records from 500 and 560 m.
Plain Sunbird	*Anthreptes simplex*		560	to 1220 m	Netted at c. 1500 m in 1999 (Moyle, 2003).
Temminck's Sunbird	*Aethopyga temminckii*	**2100**	2050	to 1985 m	Sight record from 2100 m in 1996/1997 (Biun, 1999). Recent sight record from summit trail, at least 2050 m.
Eurasian Tree Sparrow	*Passer montanus*		**1940**	to at least 1400 m	Recent records up to 1550 m near park headquarters and c. 1940 m at Mesilau.
Grey Wagtail	*Motacilla cinerea*	**3100**	**1900**	to about 1800 m	Sight records at 3100 m in

1996/1997 (Biun, 1999).

*Resident and migratory populations

Table 2.3. Birds showing apparent changes in abundance from prior to 1998 to after 2006 in the Mt. Kinabalu region. See online appendix for more information on each species.

English name	Scientific name	Observations
Little Green Pigeon	*Treron olax*	Recorded at Poring, 500 m in 1985 (Phillips, 1986). No recent records.
Thick-billed Green Pigeon	*Treron curvirostra*	This species was considered the "commonest green pigeon at Poring hot springs" (Jenkins & de Silva, 1978). There was also a dead bird collected at park headquarters in 1988 (Jenkins et al., 1996). No recent records.
Barred Eagle-Owl	*Bubo sumatranus*	Historical records include an old specimen with no locality data; heard at Poring, c. 600 m (Wall & Yong, 1985); and recorded at 909 m. No recent records.
Black Hornbill	*Anthracoceros malayanus*	Seen at lower elevations of Poring (Wall & Yong, 1985). No recent records.
Black-and-Red Broadbill	*Cymbirhynchus macrorhynchos*	Was considered common at Poring (Jenkins et al., 1996). Wall and Yong (1985) and Batchelor (1991) also recorded the species at Poring. The only recent record is from Dobbs (2008) at the Poring hot pools. Seems to no longer be common.
Long-tailed Broadbill	*Psarisomus dalhousiae*	May have declined. Before 1978, 14 specimens were obtained from 3000–4500 ft (909–1364 m), and the species was recorded up to 1667 m. The only recent record from the headquarters area is of an active nest at 1500 m.
Rufous-winged Philentoma	*Philentoma pyrhoptera*	Netted at Poring in 1971. No recent records.
Bar-bellied Cuckoo-shrike	*Coracina striata*	Sight record from Poring and recorded up to 1212 m on Kinabalu (Jenkins & de Silva, 1978). Seen at canopy walkway, Poring (Vermeulen, 1996). No recent records.
Straw-headed Bulbul	*Pycnonotus zeylanicus*	Several historical records from Poring, including nine birds seen by Vermuelen (1996). No records after 1996, except a recent sighting from park

		headquarters that may have been an escapee (AB).
Bornean Bulbul	*Pycnonotus montis*	Was "fairly common around 3000 ft (909 m)" (Jenkins & de Silva, 1978) and recorded at Bundu Tuhan (Batchelor, 1991) and Poring, 700 m (Biun, 1999). Also Sayap, c. 1000 m (Moyle & Sheldon, 2000). No recent records.
Cinereous Bulbul	*Hemixos cinereus*	Was "common from 3000–6000 ft (909–1818 m) on Kinabalu" (Jenkins et al., 1996) and recorded up to 2727 m (Batchelor, 1991); now considered rare from 1450–1950 m (AJB).
Black-throated Babbler	*Stachyris nigricollis*	Seen at Poring, c. 500 m in 1989 (Batchelor, 1991). No records since.
Black-throated Wren Babbler	*Napothera atrigularis*	Netted at Poring, 700 m in 1996/1997 (Biun, 1999). No records since.
Malaysian Blue Flycatcher	*Cyornis turcosus*	Netted at Poring, c. 545 m (Sheldon, 1977); also recorded from Ranau (Jenkins & de Silva, 1978). No records since.
Van Hasselt's Sunbird	*Leptocoma brasiliana*	Collected at Poring in 1977 (Jenkins & de Silva, 1978). No recent records.

Discussion

In comparing species occurrence before 1998 and after 2006 on Mt. Kinabalu, we found evidence for upward shifts in 24 species and downward shifts in 14 species. Eight of the upward-shifting species were observed at least 100 m above their published maximum Bornean elevation (Mann, 2008), which suggests the observed shifts correspond to genuine range changes. Some species appear to be colonizing higher elevations. Common Emerald Dove *Chalcophaps indica* was known previously to reach only 1590 m in Borneo, but AJB observed this species near the power station (1900 m) on numerous occasions from 2009–2011, and it was commonly recorded in 2011 from 1450–1850 m. Temminck's Babbler *Pellorneum pyrrogenys* was formerly known only to range from 500–1575 m in Borneo, but now, on Mt. Kinabalu, it ranges from 975–1900 m, is fairly common from 1450–1650 m, rare to c. 1900 m and has nested at 1860–1900 m (AJB; online appendix). Other species have evidently increased in elevation above their previous maxima, including Chestnut-breasted Malkoha *Phaenicophaeus curvirostris* (seen three times at 1500–1600 m), White-throated Fantail *Rhipidura albicollis* (recent sightings up to 3300 m), Mountain Leaf Warbler *Phylloscopus trivirgatus* (recent sightings up to 3221 m), and Bornean Spiderhunter *Arachnothera everetti* (one mist-netted at 2100 m). Of the 25 additional species that were recorded above their Bornean maximum (Table 2.2), clear candidates for upward shifts include Crested Hawk-Eagle *Nisaetus cirrhatus* and Little Bronze Cuckoo *Chrysococcyx minutillus*.

Previous studies from tropical mountains have documented smaller shifts than predicted by the adiabatic lapse rate for most species (Raxworthy et al., 2008; Chen et al., 2009; Forero-Medina et al., 2011a). All apparent shifts we documented occurred over at least a 12 year span. Thus it is unsurprising that changes may have exceeded the 1997–2007 lapse rate prediction of 87 m upwards from +0.48 ºC. Given the spatial and temporal uncertainties from our various data sources, it is difficult to compare observed changes to predicted shifts based on the lapse rate. The widespread upward shifts, showing no clear signal of taxonomic or dietary bias, agree with results of other climate change studies from Southeast Asia (Peh, 2007; Chen et al., 2009, 2011), and other regions (Pounds et al., 1999, 2005; Seimon et al., 2007; Raxworthy et al., 2008; Forero-Medina et al., 2011a).

While some species may have moved upward as a consequence of climate change, other range changes can probably be explained by other factors. Three species, Oriental Magpie Robin *Copsychus saularis*, Yellow-bellied Prinia *Prinia flaviventris*, and Eurasian Tree Sparrow *Passer montanus*, are open country birds that likely expanded their ranges along roads as a result of habitat clearance in the region. Six species were migrants which may be less sensitive to warming, and Yellow-browed Warbler *Phylloscopus inornatus* is a vagrant with only two records for Borneo. Others, including Brown Wood Owl *Strix leptogrammica*, Bornean Frogmouth *Batrachostomus poliolophus*, Giant Swiftlet *Hydrochous gigas*, and Orange-headed Thrush *Geokichla citrina* are inconspicuous, rare, or difficult to identify, all of which make an accurate assessment of their ranges difficult or unreliable.

Our results also indicate that some species may have moved downslope since the 1990s. Perhaps the most convincing downslope shifts were shown in the upper range margins of two species, Bornean Leafbird *Chloropsis kinabaluensis* (formerly seen up to 2650 m, but no recent records above 1800 m) and Yellow-bellied Warbler *Abroscopus superciliaris* (formerly up to

1818 m, no recent records above 1575 m). We find these apparent changes convincing because these species are conspicuous and they have not been recorded recently in well sampled areas between park headquarters and Timpohon gate or at Mesilau. The influence of biotic and abiotic factors on lower and upper range margins are a subject of active debate (Lenoir et al., 2010; Gifford & Kozak, 2011), and detailed studies of downward shifting species are urgently needed. It would be interesting to investigate the incidence of downward range shifts as a function of species traits such as elevational range, presence of competitors, and tolerance to habitat disturbance. For example, range changes in *Chloropsis kinabaluensis* could be compared in Kalimantan where a lowland competitor (*C. cochinchinensis*) is present, and in Sabah where the competitor is absent, but *C. kinabaluensis* appears to be shifting its upper range margin downwards. It is unclear if changes in competitive interactions were related to downward shifts shown in the present study, but upward shifts in generalist species such as Little Spiderhunter *Arachnothera longirostra* (Table 2.1) could drive changes.

We suspect that many of the other possible downward shifts are due to past records of post-breeding dispersing birds (e.g. Brown Fulvetta *Alcippe brunneicauda*) or localized changes in abundance below Timpohon gate and incomplete sampling above the gate (e.g. Ochraceous Bulbul *Alophoixus ochraceus* and Velvet-fronted Nuthatch *Sitta frontalis,* both of which have been recently observed above 1900 m at Mesilau). In addition, it is possible that human disturbance (from increased numbers of hikers on the summit trail) could have contributed to reduced bird detection. Nevertheless, we think it is unlikely that disturbance from hikers could explain the lack of records for conspicuous species such as Bornean Leafbird, and many months of current observations (from AJB and TEM) come from lightly used trails in between park headquarters and Timpohon gate.

Our historical-current data comparison also uncovered an apparent reduction in abundance of 15 species. This reduction may be explained by habitat loss, hunting, the pet trade, climate change, or incomplete sampling. Most of the observed declines are probably related to habitat loss at lower elevations in Kinabalu Park near Poring, and deforestation on the Pinosuk Plateau. All lowland species in Table 2.3 except Straw-headed Bulbul *Pycnonotus zeylanicus* and Van Hasselt's Sunbird *Leptocoma brasiliana* are either known to be or thought to be negatively-affected by forest fragmentation or logging (Lambert & Collar, 2002; Edwards et al., 2011). The apparent declines of these species could have been caused by relatively recent disturbances, or delayed extinction debt from earlier habitat loss (Kuussaari et al., 2009). Hunting, especially of large bodied species such as Black Hornbill *Anthracoceros malayanus* and *Treron* pigeons could have also contributed to declines. The cage bird trade is likely to blame for the dramatic decline in Straw-headed Bulbul *Pycnonotus zeylanicus* at Poring and elsewhere in Borneo (Sheldon et al., 2009). Incomplete sampling at Poring may also be a factor, but all species in Table 2.3 are reasonably conspicuous, with the possible exceptions of Barred Eagle-Owl *Bubo sumatranus* and Black-throated Wren Babbler *Napothera atrigularis*. At higher elevations, observations of Long-tailed Broadbill *Psarisomus dalhousiae* and Cinereous Bulbul *Hemixos cinereus* from park headquarters upwards may have become less frequent because of population reductions caused by deforestation on the Pinosuk plateau in the early 1980s (Sheldon, 1986).

Our results indicate that citizen science data (including birdwatchers' trip reports and databases of audio, photographic, and birdwatchers' records) are invaluable resources for comparing bird distributions, but these data tend to lack adequate spatial or temporal details. We reiterate Boakes et al.'s (2010) call for birdwatchers "who intend their observations to be of practical use to others to carry a GPS".

The apparent range shifts documented here could help guide future research investigating changes in distribution and abundance of lowland colonists and highland endemics driven by climate change (reviewed in Harris et al., 2011). For example, it would be interesting to use playback experiments to study interactions among the three *Arachnothera* spiderhunters that now all occur at middle elevations on Mt. Kinabalu, and evaluate how interactions change with increasing elevation. In a similar situation, Jankowski et al. (2010) used playback experiments to discover that the higher elevation thrush *Catharus fuscater* was subordinate to the lower elevation *C. mexicanus*, which could have implications for the persistence of *C. fuscater* under climate change. Dark Hawk Cuckoo *Hierococcyx bocki* is a nest parasite of Chestnut-capped Laughingthrush *Garrulax mitratus* in Peninsular Malaysia and a probable nest parasite of Mountain Leaf Warblers on Mt. Kinabalu (Smythies, 1999). The apparent upward expansion of Dark Hawk Cuckoo and its possible effects on Mt. Kinabalu's high elevation avifauna (assuming flexible host preferences) would make for an interesting research topic. Lastly, our results, when used in future studies, should help validate and improve models that forecast avian distributional changes and extinction risk from climate change (Shoo et al., 2005a; Gasner et al., 2010).

In conclusion, we demonstrate a novel method for compiling avian occurrence data from diverse sources and attempting to account for varying temporal and spatial coverage and accuracy. Twenty-four species, eight of which were recorded above their published Bornean ranges, appear to have shifted their distributions upward. In addition, 14 species may have moved their ranges downslope and15 species may have declined in abundance. The ecological consequences of these shifts are still largely unknown and we hope our findings will be continually refined and stimulate further research on the mountain’s avifauna.

Chapter 3

Will rapid deforestation prevent endemic birds from responding to climate change in Southeast Asia?

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To be submitted to *Conservation Biology*.

STATEMENT OF AUTHORSHIP-CHAPTER 3

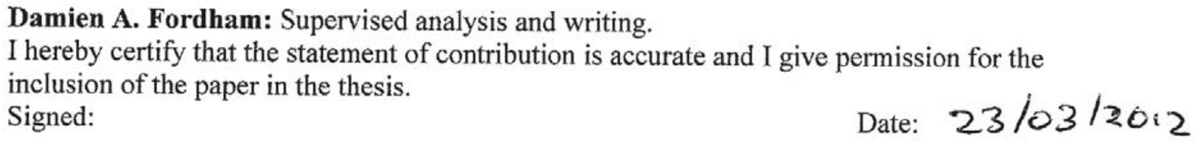
Will rapid deforestation prevent endemic birds from responding to climate change in Southeast Asia?

To be submitted to *Conservation Biology*.

J. Berton C. Harris: Applied for funding and permits, collected data, performed the analysis, wrote the paper.

I hereby certify that the statement of contribution is accurate.

Signed: Date: 2 Apr 2012



Damien A. Fordham: Supervised analysis and writing.
I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.
Signed: Date: 23/03/2012

Stephen D. Gregory: Performed the land cover analysis.

I hereby certify that the statement of contribution is accurate and I give permission for the
inclusion of the paper in the thesis.

Signed: Date: 4 April 2012

Dadang Dwi Putra: Collected data.

I hereby certify that the statement of contribution is accurate and I give permission for the
inclusion of the paper in the thesis.

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Dewi M. Prawiradilaga: Indonesian scientific counterpart, assisted with permits and data collection.

I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis.

Signed: Date: 28 March 2012

Dan Wei: Assisted with analyses.

I hereby certify that the statement of contribution is accurate and I give permission for the

inclusion of the paper in the thesis.

Signed: Date: 1 May 2012

Barry W. Brook: Supervised analysis and writing.

I hereby certify that the statement of contribution is accurate and I give permission for the

inclusion of the paper in the thesis.

Signed: Date:21 Mar 2012

Navjot S. Sodhi (deceased):Assisted with study design.

Chapter 3 – Will rapid deforestation prevent endemic birds from responding to climate change in Southeast Asia?

Abstract

It is unclear whether deforestation or climate change will cause more tropical bird extinctions. Here we report on the first effort to combine fine-scale climatic and dynamic land cover models to forecast vulnerability of tropical species. We sampled bird communities on four mountains across three seasons in Lore Lindu National Park, Sulawesi, Indonesia (a globally-important hotspot of avian endemism), to characterize relationships between elevation and abundance. We compared the relative impacts of climate change (projected using an ensemble of global climate models) and deforestation (based on historical rates) on abundance for two middle- and two high-elevation endemic species. Future forest area was projected under two land-use change scenarios − one assuming current deforestation rates, another assuming a 50% reduction in deforestation. Potential climate-change-induced range shifts were simulated by shifting species' abundance distributions upslope using a locally measured adiabatic lapse rate of –6.8 °C per 1,000 m of elevation gained. Lore Lindu National Park lost 11.8% of its forest area from 2000 to 2010 and Sulawesi as a whole lost 10.8%. Global climate models forecast that Central Sulawesi may warm by 0.7–0.9 °C by 2050 (for low- and high-emissions scenarios), which could translate into a lapse-rate-linked range shift of approximately 100 m upward. Our predictions suggest that high-elevation species will be buffered from deforestation by their isolated ranges, but potentially face steep population declines from climate change (by as much as 51%). Middle-elevation species are predicted to undergo moderate declines from half-rate deforestation or climate change (11–13% reductions), while deforestation at the current rate, or climate change combined with deforestation, is predicted to cause larger declines of 16–25%. If species are to track preferred climates, they will need large areas of remnant forest, which are unlikely to remain if current deforestation patterns continue. The biological richness and rapid deforestation now occurring inside Lore Lindu National Park emphasizes the need for increased enforcement of illegal clearing in the park. Further, our results indicate that climate change is a potentially serious threat to high-elevation endemics in Central Sulawesi. These findings are likely to be applicable to many other upland tropical sites where deforestation is encroaching from below and climate change is stressing high-elevation species.

Introduction

The successful maintenance of global biological diversity requires conservation of endemic hotspots (Orme et al. 2005). Endemic species, those that are restricted to certain areas such as islands or countries, are classic examples for the study of evolution and biogeography (e.g. Jetz et al. 2004), but their small ranges make them vulnerable to anthropogenic actions (Fordham & Brook 2009; Harris & Pimm 2008; but see Williams et al. 2009). Tropical mountain ranges are critical centers of avian endemism; approximately 1,000 of the world's bird species are restricted to tropical uplands (> 500 m elevation; Harris et al. 2011). Steep slopes and high elevations reduce the pressure of anthropogenic habitat degradation and other threats like hunting on many of these species, resulting in most upland tropical birds being considered of 'least concern' (BirdLife International 2011; Sekercioglu et al. 2008). Rapid habitat loss means that the bulk of threatened species in most tropical regions are found in the lowlands (e.g. Brooks et al. 1997). While upland species have been buffered from habitat loss in the past, human population growth is increasing pressure on higher elevation habitats (Shearman et al. 2012; Soh et al. 2006), and climate change threatens to reduce the available habitat for montane species (La Sorte & Jetz 2010).

It is unclear whether habitat loss or climate change will cause more extinctions in the tropics (Pimm 2008). Many upland tropical birds are faced with climate-change-induced range shifts (Forero-Medina et al. 2011; Harris et al. in press; Peh 2007; Pounds et al. 2005; Sekercioglu et al. 2012), that are likely to be particularly serious for mountaintop endemics and species with narrow elevational ranges (Colwell et al. 2008). Worryingly, the impacts of habitat loss, climate change, and other extinction drivers such as invasive species are likely to interact synergistically with one another (having impacts greater than the sum of their parts due to reinforcing feedbacks; Brook et al. 2008).

Studies that forecast vulnerability of species to extirpation due to habitat loss, climate change, and their interaction are urgently needed from the tropics. Two previous analyses used coarse land-cover scenarios and the adiabatic lapse rate (estimate of temperature loss with increasing elevation) to forecast vulnerability of the world's birds to climate change and habitat loss, and found that approximately 500 species (5% of the global total) may go extinct from mid-range warming by 2100 depending on emissions and habitat scenarios (Jetz et al. 2007; Sekercioglu et al. 2008). Yet, few analyses have focused on projecting tropical deforestation (Cannon et al. 2007; Soares-Filho et al. 2006), and no fine scale study has combined land cover and climate models to produce regional projections of extirpation vulnerability.

Southeast Asia's biological richness and severe on-going anthropogenic impacts make it a clear candidate for doing interactive habitat-climate modeling. Southeast Asia has one of the highest concentrations of endemic species in the world as a result of the region's numerous islands, tectonic history, and fluctuating sea levels (Sodhi & Brook 2006). Unfortunately, deforestation is so rapid in the region that many species may lose the majority of their range in the next 20 years (Bradshaw et al. 2009; Sodhi et al. 2004). Within Southeast Asia, Sulawesi is of special interest because it is among the world's richest hotspots of avian endemism, with 42 species found nowhere else (Coates & Bishop 1997). Despite this diversity, Sulawesi is ornithologically one of the least studied areas in the world, with higher elevations particularly poorly sampled, and new bird species still regularly described (Indrawan et al. 2008; Madika et al. 2011).

In this study we combine new data from the field with global climate and dynamic landscape models to forecast vulnerability of endemic birds in Lore Lindu National Park, Sulawesi (Indonesia). Lore Lindu is one of the island's most biodiverse national parks, but it is under threat from human encroachment (Cannon et al. 2007; Lee et al. 2009). We used four middle- and high-elevation endemic birds as case studies on the potential effects of habitat loss and climate change on Lore Lindu's birds. We identified predictors of deforestation from 2000 to 2010 and then projected the amount of forest remaining by 2050 based on scenarios assuming constant and halved rates of forest loss. Potential range changes from climate change were investigated by using the adiabatic lapse rate to simulate movement in species abundance-elevation relationships up mountains. Given that habitat loss is pervasive at lower elevations in Sulawesi (Cannon et al. 2007), and the findings of previous climate change studies (e.g. Colwell et al. 2008) we hypothesized: (1) habitat loss would threaten middle-elevation more than high-elevation species, and (2) climate change would particularly threaten narrow-ranged high-elevation species.

Methods

Study site

Lore Lindu National Park covers 2,290 km^2 of Central Sulawesi and is one of the island's most important protected areas for endemic flora and fauna (Fig. 3.1). Lore Lindu is one of the last refuges for large endemic mammals such as mountain anoa (*Bubalus depressicornis*) and babirusa (*Babyrousa babyrousa*) (Whitten et al. 2002), and approximately 78% of Sulawesi's endemic birds are found in the park (Coates & Bishop 1997; Lee et al. 2007). Worryingly, the national park is under considerable pressure from an increasing human population due to transmigration from more populous parts of Indonesia, expansion of cacao agriculture, and illegal logging (Clough et al. 2009; Lee et al. 2009; Weber et al. 2007). Most of the park is above 1,000 m elevation (Fig. S3.1) and 96% of the park was covered with primary forest in 2000.

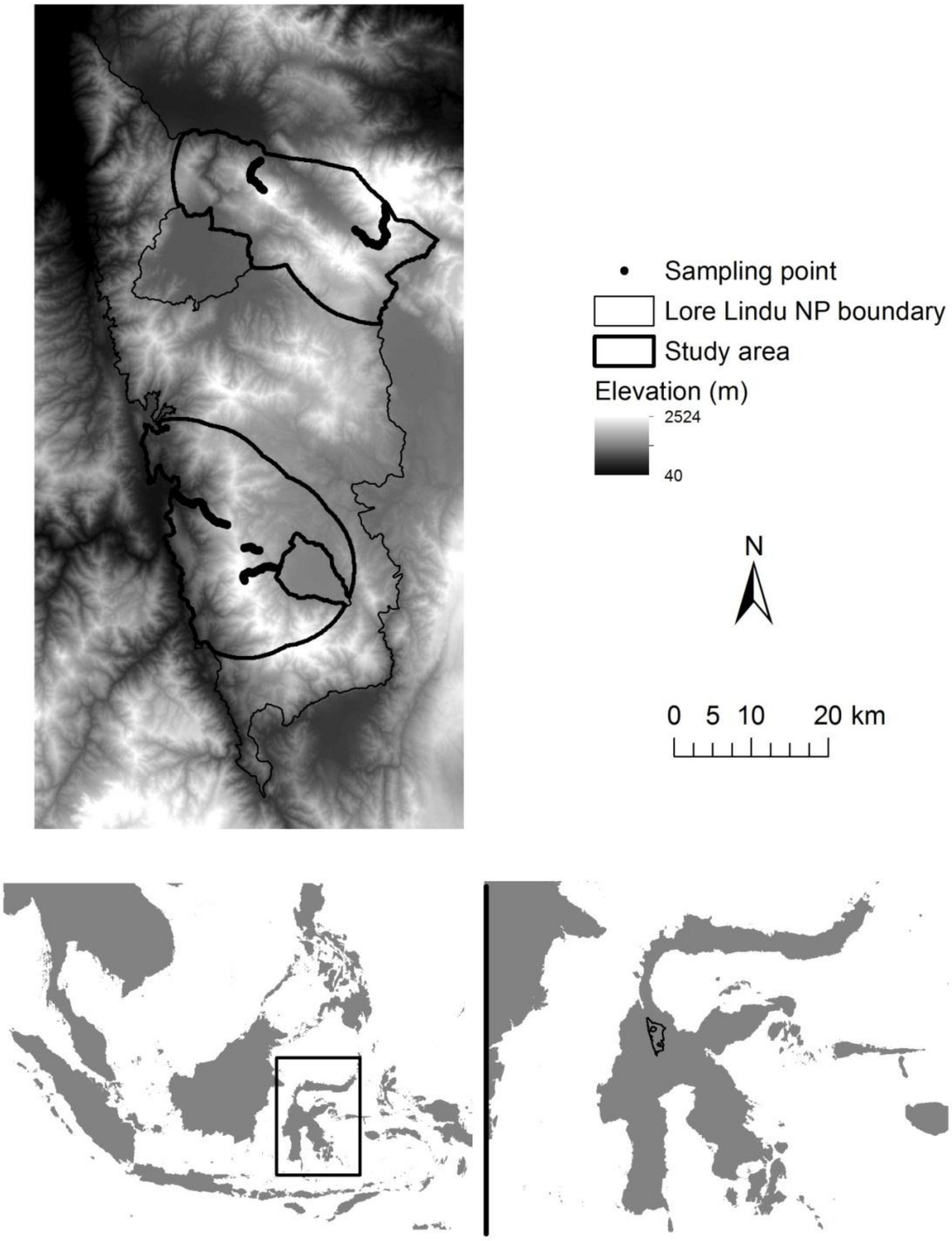

Figure 3.1. Location of Lore Lindu National Park and our study area and sampling sites. The two holes in the national park are annexed village areas.

Field sampling

We collected avian occurrence data on Mt. Nokilalaki (825–2365 m; S 1º 15.3’, E 120º 10’), Mt. Rorekatimbu (1265–2525 m; S 1º 17’, E 120 º 19’), Mt. Dali (1295–2280 m; S 1º 43’, E 120º 9’), and Mt. Rano Rano (480–1920 m; S 1º 39’, E 120º 7’) (Fig. 3.1; see Appendix 3.1 for point count coordinates). These four peaks are among the tallest mountains in Central Sulawesi and are located at opposite ends of Lore Lindu, providing broad coverage of elevations and regions of the park. Our sampling effort was broadly representative of the distribution of elevations in the park with middle elevations and forested areas most thoroughly sampled (Fig. S3.1).

We sampled bird communities with systematic point count and transect surveys in the morning and opportunistic re-surveys of the same areas, usually in the afternoon. We did 10-minute-duration, 50-m-radius point counts, separated by 250 m, along elevational gradients on mountain trails and roads (Ralph et al. 1995). When sampling along roads (only done at Mt. Rorekatimbu), we entered the forest ~ 50 m from the road to do the point counts. We also collected occurrence data along transects in between the points out to 50 m on either side of the trail. Variability in detection may affect abundance estimates (Thomas et al. 2010), however, surveys were standardized by only censusing birds in the morning on clear days with little wind (from dawn to 10:30). Furthermore, we minimized the effects of temporal variation in abundance by conducting surveys three times across the seasons (September–November 2009, May–June 2010, and January–February 2011). D.D.P who has >10 years' experience identifying Central Sulawesi birds by sight and sound was the primary observer in all surveys. We practiced distance estimation with audio playback and a measuring tape to make the aural 50 m estimate more accurate. A Nikon Forestry 550 laser range finder was used to check visual distance estimates. Visual detections declined, but aural detections increased with distance from the sampling points. These differences in visual/aural detection make it most parsimonious to assume uniform detection (Shoo et al. 2005b), which may overestimate overall abundance because aural detections formed 60–82% of observations for all species. In total, we sampled 149 points and approximately 58 km with systematic transects and opportunistic surveys.

Case study species

For case study species, we selected four endemic birds that differed in their altitudinal centres of abundance, and were common enough to reduce uncertainty in altitudinal abundance estimates: middle-elevation *Rhipidura teysmanni* (rusty-bellied fantail), and *Pachycephala sulfuriventer* (sulphur-bellied whistler), and high-elevation *Phylloscopus sarasinorum* (Sulawesi leaf-warbler), and *Myza sarasinorum* (white-eared myza). Our study was designed to characterise bird abundance in undisturbed forest. The four species are rarely or never seen in non-forest habitats in Lore Lindu (our data; Abrahamczyk et al. 2008; Maas et al. 2009; Sodhi et al. 2005; Waltert et al. 2004, 2005).

Population size characterisations

We compared the effects of climate change and deforestation on indices of population size calculated by multiplying abundance in elevation bands by forest area. This approach modeled the additive (not synergistic) impacts of habitat loss and climate change. Given the strong forest dependence of the study species (see above) we assumed cells without forest were unsuitable. We began by comparing the effects of elevation and aspect (derived from a 30 arc second digital elevation model; srtm.csi.cgiar.org) on bird abundance. Depending on study species, 47–75% of counts were zero, so we compared hurdle, zero-inflated, and Poisson regression approaches to model abundance (Zeileis et al. 2008; see supplementary material for more details). Hurdle models, which often outperform other approaches in data sets with high numbers of zeros relative to other values (Potts & Elith 2006), were top-ranked by AIC in three of four species (zero-inflated regression was best for *P. sulfuriventer*). Therefore, we used hurdle models to make the final comparisons. We found that elevation was a much better predictor of abundance than aspect for all species (Table S3.1). This finding, combined with the near 100% correlation between elevation and temperature on tropical mountains (Bush et al. 2004; Gaffen et al. 2000; Kitayama 1992; Sarmiento 1986; Smith & Young 1987), supported the use of a manual lapse-rate-driven habitat shift to simulate the effects of climate change on population size (see below).

Following Shoo et al. (2005a; 2005b), we calculated population size indices for our study species by multiplying mean abundance from the three sampling sessions in 100 m elevation bands (Fig. 3.2) by the number of forested cells in each band. Multiplying bird density by forest area gives a measure of the regional abundance of a species, but is not expected to yield true population size (Gasner et al. 2010; Shoo et al. 2005a; Shoo et al. 2005b). The resulting population size projections are more informative than range area metrics assuming cells of equal carrying capacity because **abundance ~ range area** relationships are often non-linear (Fordham et al. in press; Shoo et al. 2005b). Our sampling did not cover all areas of the national park so we restricted the analysis to areas within 10 km of our sampling sites (93,908 ha, approximately 42% of the park; Fig. 3.1). Analyses were done at the 30 arc second scale (~ 90 m) because the fine scale Shuttle Radar Topography Mission (SRTM) digital elevation model is of this resolution. Estimates were adjusted for differences in area between sampling sites (50 m point count circle = 0.79 ha) and the 30 arc second cells (0.85 ha in our region). Area of the 30 arc second cells varied so little in our study area that correction from latitudinal changes was unnecessary (Jenness 2004).

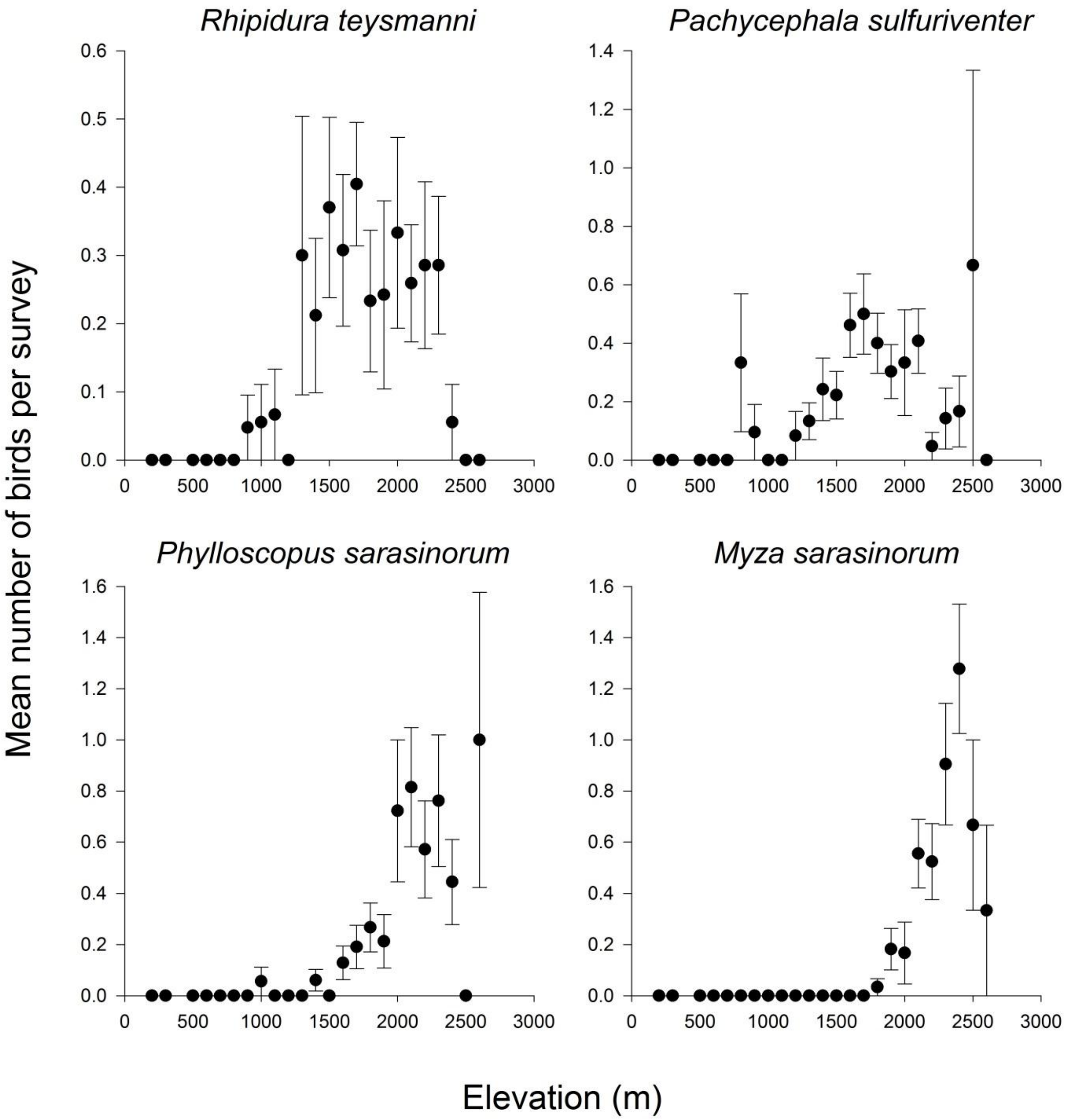

Figure 3.2. Abundance distributions of study species along elevational gradients on four mountains in Central Sulawesi. Average abundance per point count from three sampling sessions ± SE are shown.

Climate change

Climate-change impacts were simulated by linking a locally measured adiabatic lapse rate to predicted warming from an ensemble of global climate models. Ideally, spatial climate-change-biodiversity projections should incorporate fine scale climate layers, generated by downscaling coarse climate model projections to fine scale interpolated present day data (Fordham et al. 2012). Weather station coverage is incomplete in Central Sulawesi, limiting efforts to downscale climate model projections. The precipitation station coverage is very poor on Sulawesi (Hijmans et al. 2005) so we were unable to consider changes in precipitation due to high uncertainty. We feel confident that temperature change alone could exert a change in tropical bird distributions (Forero-Medina et al. 2011; Shoo et al. 2005b). Because climate changes rapidly over small horizontal distances, as is often the case on tropical mountains (Gasner et al. 2010; Raxworthy et al. 2008), we chose to use a fine-scale digital elevation model and a lapse rate to simulate upslope shifts from climate change. Our approach assumes full dispersal and the **abundance ~ elevation** relationship remains the same as the present day (Gasner et al. 2010; Shoo et al. 2005b). Globally, the lapse rate ranges from 5–7 °C of temperature loss per 1000 m of elevation gain (Bush et al. 2004; Gaffen et al. 2000; Kitayama 1992; Sarmiento 1986; Smith & Young 1987; Whitten et al. 2002). In Sulawesi, the lapse rate has been estimated as 7 °C on Mt. Rantemario from approximately five days of measurements (Whitten et al. 2002, pers. comm.) and ~ 6.8 °C in the Mt. Nokilalaki region (our calculations using Musser's (1982) data; see supplementary material). We chose to use Musser's (1982) measurements because he sampled for a comprehensive two months and Nokilalaki was one of our sampling sites.

For climate modelling we used the MAGICC/SCENGEN global climate emulation software to estimate possible changes in the climate of Central Sulawesi at the 0.5° scale (Fordham et al. 2012). Following Fordham et al. (2012), we evaluated model performance to choose seven regionally skilful climate models (BCCRBCM2, CCCMA–31, CSIR0–30, GFDLCM20, MIROCMED, CCSM–30 and UKHADGEM). Two scenarios, a no-climate-policy reference scenario (no greenhouse gas emission stabilization; MiniCAM Ref.) and a corresponding policy (stabilization) scenario (MiniCAM, Level 1) designed to stabilize at an equivalent CO_2 concentration of 450 ppm (Clarke et al. 2007; Wigley et al. 2009). These scenarios predicted warming of 0.70 °C and 0.88 °C in annual mean temperature in the Lore Lindu region for the mitigation and reference scenarios, respectively. These increases would yield 100–130 m upward shifts according to the 6.8 °C per 1,000 m lapse rate, assuming species track temperature change exactly and linearly (which is possible, given that there are often strong relationships between climate and species distributions; Bush et al. 2004; Ghalambor et al. 2006). Given uncertainties in climate model predictions, and the small differences between policy and reference scenarios, we chose to use the conservative 100 m upward shift in our subsequent decline estimates (see below).

Land cover

We used a raster land-cover dataset that was derived from MODIS imagery and created to monitor deforestation in Southeast Asia (Miettinen et al. 2011). Land cover was classified in 2000 and 2010 at a 250 m resolution (Miettinen et al. 2012). The relevant land cover categories for Lore Lindu are lowland (sea level to 750 m), lower montane (750–1500 m), and upper montane (1500 m +) forest (we collapsed these as “forest”), plantation/regrowth (young secondary vegetation), and mosaic and open (collapsed as “agriculture”). We evaluated the accuracy of the data by comparing the land-cover type we observed at each bird sampling point to the layer classification. We found the layer had 87% accuracy along our 149 points which is similar to the overall accuracy across the region (85%; Miettenen et al. 2012; Table S3.2).

We used the `LandUseChangeModelleR` program, written in R (S.D.G. unpubl. data), to relate observed land use change in the national park from 2000 to 2010 to four spatial variables: elevation, slope, distance from the park boundary, and distance from villages. We then used the program to project the amount of forest cover remaining in the park by 2050 based on two scenarios. The observed deforestation scenario maintained deforestation at the current rate, and the reduced scenario assumed increased enforcement and (arbitrarily) cut the deforestation rate by half. To simulate the loss of easily logged sites in this mountainous national park, both scenarios modelled a 50% decline in the rate of deforestation once 20% of the park’s forest had been converted. We chose not to project beyond the year 2050 because of high uncertainty about far-future forest management.

In the land-cover projections, deforestation represented the permanent conversion of forest to degraded (plantation/regrowth) or cleared (open/mosaic) land. We did not model forest regeneration because conversion is usually permanent in Central Sulawesi (Weber et al. 2007). The models were fit using patterns from across the national park but we also examined observed and predicted forest change in our study area. Deforestation was modelled as an annual transition matrix projected as a discrete transition Markov Chain (Takada et al. 2010). To identify which raster cells would be changed at each time step, and to which class they would change, we used 2010 land cover prediction probabilities from random forest models relating land cover change to the spatial variables mentioned above (Liaw & Wiener 2002). The models assigned each cell a probability of class membership in each land cover class calculated as the proportion of iterations in which they were assigned to that class. A cell's predicted 2010 land cover class is that which has the highest probability of class membership. We calculated each cell's vulnerability to change as the maximum probability of membership to any other land cover class (Eastman et al. 1995). For each time step, the land-cover change model calculated how many and which raster cells to change, based on the deforestation projections and cell vulnerabilities, and then altered their land-cover class to that with the second highest probability of class membership.

Results

Avian abundance patterns

We recorded 132 species (98 in systematic surveys, 34 in opportunistic surveys), 62 of which are endemic to the Sulawesi subregion (Coates & Bishop 1997; Harris et al. 2012). *Phylloscopus sarasinorum* and *Myza sarasinorum* had higher elevation and narrower ranges in our study area compared to *Pachycephala sulfuriventer* and *Rhipidura teysmanni* (Fig. 3.2). The high-elevation species also tended to be more abundant than middle-elevation species (Fig. 3.2). In Appendix 3.1 we list detailed coordinates of sampling sites and notes on their land cover in 2010 to promote re-surveys (full dataset available upon request from the corresponding author).

Land cover

Our analysis of Miettinen et al.'s (2011) data indicates that Lore Lindu National Park was deforested more rapidly than Sulawesi as a whole during the period 2000 to 2010 (11.8% compared to 10.8%) (Miettinen et al. 2011; Table 1). The Lore Lindu deforestation rate is similar to that of Borneo (12%) and higher than net deforestation across Southeast Asia (9.9%). The land-use-change models predict that massive deforestation of the national park may occur in the coming decades (34–40% of the park deforested by 2050), even if the deforestation rate is cut by half (Table 3.1; Fig. 3.3). Similarities in predicted forest loss between the two scenarios were the result of both scenarios quickly reaching 20% deforestation, and the deforestation rate consequently being halved. The forest loss and land conversion is predicted to be concentrated at the margins of the park boundaries. Changes in the study area and national park were comparable, but forest losses were greater in the study area, probably because the heavily impacted Dongi Dongi area near Mts. Nokilalaki and Rorekatimbu is inside the study area.

Table 3.1. Land cover percentages from 2000 and 2010, and projected changes to 2050 based on halved and observed (current) deforestation rates.

Land cover	2000	2010	2050 halved deforestation rate	2050 observed deforestation rate
Lore Lindu National Park				
forest	95.6	83.8	65.9	59.0
plantation/regrowth	3.1	10.9	27.4	33.7
agriculture (mosaic/open)	1.2	5.4	6.7	7.3
Study area				
forest	95.8	78.8	64.7	58.8
plantation/regrowth	3.1	12.6	26.0	31.3
agriculture (mosaic/open)	1.0	8.6	9.3	9.8

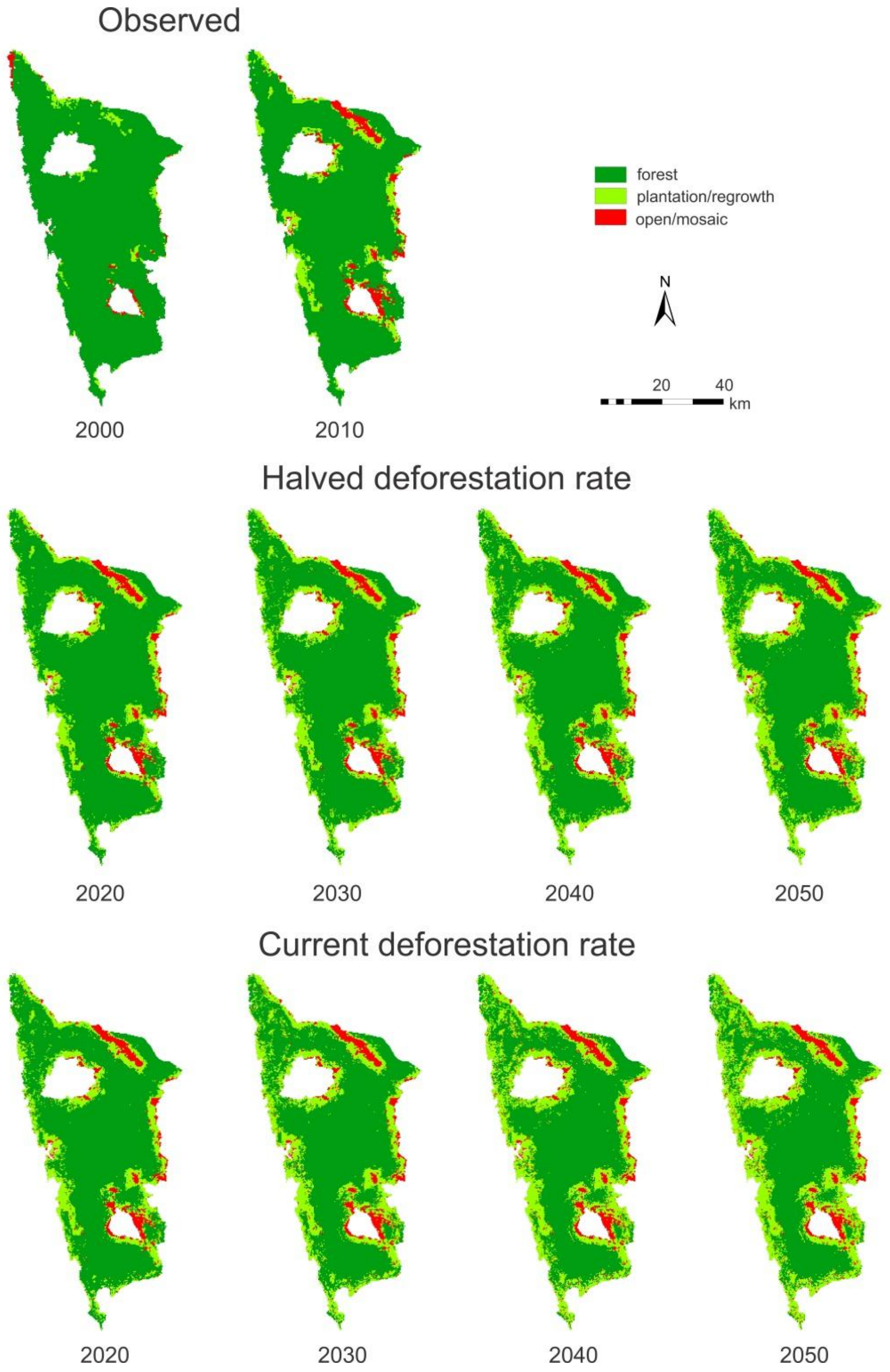

Figure 3.3. Observed (2000–2010) and projected (2020–2050) land cover change in Lore Lindu National Park. Observed data come from Miettenen et al. (2011). Land-cover-change models

were built by relating forest change from 2000–2010 to landscape variables and projecting to 2050 based on the current deforestation rate and half that rate. The two white sections in the park are annexed village areas.

Population size projections

The high-elevation species (*Myza sarasinorum* and *Phylloscopus sarasinorum*) are predicted to be relatively unaffected by simulated deforestation up to 2050 (Fig. 3.4). In contrast, the middle-elevation species (*Pachycephala sulfuriventer* and *Rhipidura teysmanni*) are predicted to decline by 11–18% due to deforestation alone (Table S3.3). Climate change (in the form of a 100 m shift based on the adiabatic lapse rate) is projected to cause substantial declines for all species, with especially severe impacts for high-elevation species (30–45% declines). When climate change and deforestation are combined, nearly additive 20–51% declines are predicted for all species (Fig. 3.4; Table S3.3). Halving the deforestation rate did not appreciably improve outcomes; all differences in population declines between the two scenarios were < 6%.

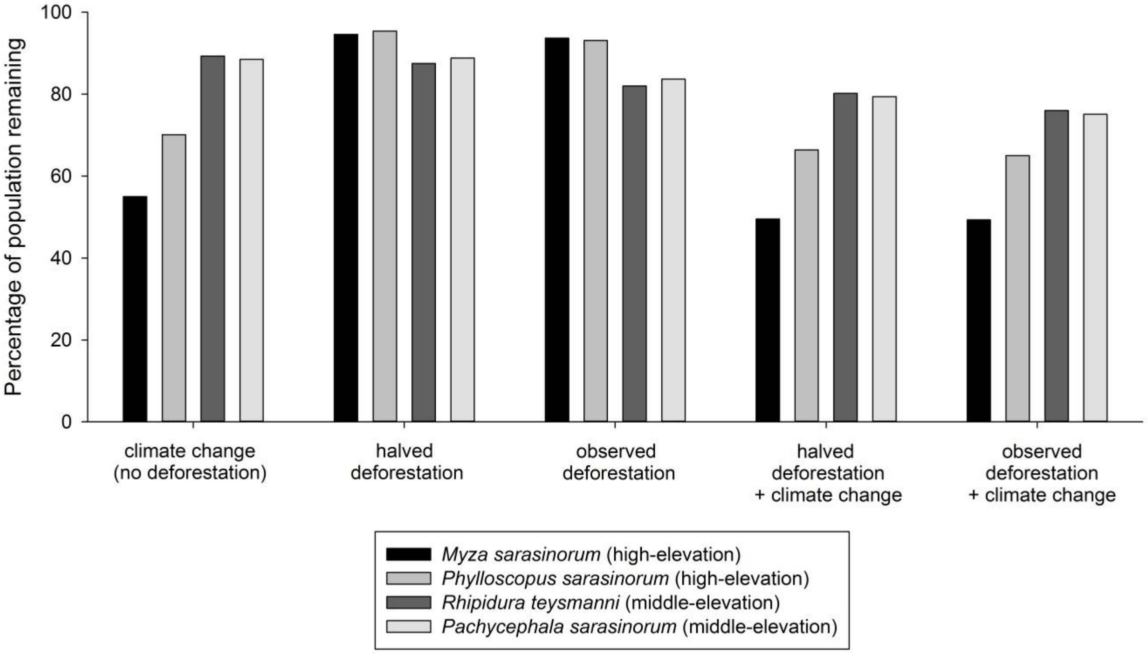

Figure 3.4. Projected percentage population declines from climate change and habitat loss for middle-elevation (*Rhipidura teysmanni*, *Pachycephala sulfuriventer*) and high-elevation (*Phylloscopus sarasinorum*, *Myza sarasinorum*) study species.

Discussion

Our results suggest that climate change will have a greater impact on high-elevation species, whereas deforestation will be more important for middle-elevation species. When climate change and deforestation are combined, all species will decline by at least 20%. The results indicate that management strategies in the region will likely need to be tailored to species based on their elevational distributions, with greater emphasis on mitigation of climate-change impacts for high-elevation species and deforestation on middle-elevation species. Our results agree with a growing body of studies that suggest upland tropical endemics (most of which are considered of least concern) are threatened with extinction in the medium term (Gasner et al. 2010; La Sorte & Jetz 2010; Sekercioglu et al. 2008; Shoo et al. 2005b; Williams et al. 2003). These findings contrast with the IUCN Red List's current emphasis on lowland species in Southeast Asia (BirdLife International 2011), and a previous analysis that postulated the Red List may overestimate the number of montane threatened species because their ranges were naturally small and not necessarily threatened (Brooks et al. 1999).

From 2000–2010 Sulawesi lost approximately 11% of its forest, and 12% of Lore Lindu National Park (which hosts 78% of the island's endemic bird species) was cleared. Our projections indicate approximately 40% the park will be deforested by 2050 if deforestation continues apace or the rate is cut by half, with serious implications for endemic biodiversity. Most deforestation in the region leads to permanent conversion, so substantial regeneration should not be expected (Clough et al. 2009). This rapid forest loss inside and outside the national park is threatening to substantially diminish the avian diversity of the endemic hotspot of Sulawesi, even before all the birds are described (King et al. 1999). It should be a priority of the Indonesian government and the conservation community to work towards halting deforestation inside the national park. Of broader concern for the region's biota, the deforestation patterns we found are not isolated to Sulawesi. Most of the biogeographic realms of insular Southeast Asia are undergoing rapid habitat loss outside and, perhaps to a lesser extent, inside protected areas (Miettinen et al. 2011).

Our lapse rate modeling approach could under- or over-estimate the impacts of climate change on tropical birds. The climate models predicted 0.7–0.9 °C of warming in the region by

2050, depending on the emissions scenario, which would correspond to a 100–130 m upward shift based on the local lapse rate. We conservatively assumed the 100 m shift based on mitigated emissions, but an additional 30 m shift would cause further projected population declines. The climate models predicted 2.3 °C of warming in the region by 2100 based on the high emissions scenario, which would correspond to a 340 m shift and major declines, assuming the lapse rate. By contrast, our results could over-estimate population declines if species shift slower than predicted by the lapse rate due to adaptation. Studies have documented moths, reptiles/amphibians, and birds shifting upwards more slowly than the lapse rate (Chen et al. 2009; Forero-Medina et al. 2011; Raxworthy et al. 2008), but other (lower resolution) studies had mixed results, with some birds shifting faster than predicted (Harris et al. in press; Peh 2007). Lastly, uncertainty in the lapse rate measurement (see supplementary material) could affect the results. The 6.8 °C per 1,000 m figure we used, while corroborated by other measurements in Sulawesi (Whitten et al. 2002), is at the upper end of lapse rates observed from the tropics (5–7 °C), and could overestimate range shifts.

Our approach made several other assumptions that should be considered when interpreting our results. When modeling population changes from climate change, we assumed full dispersal and that the current **abundance ~ elevation** relationship was maintained over time (Gasner et al. 2010; Shoo et al. 2005b). The approach also assumes homogeneous abundance within elevation bands, and disregards uncertainty around mean abundance per band, although the least certain points were at 2500 and 2600 m which had very few grid cells and therefore little impact on the population size index calculation (Fig. 3.2). We were also unable to consider species interactions (Gifford & Kozak 2011; Jankowski et al. 2010), vegetation shifts (or lack thereof) from climate change (Feeley & Silman 2010b), and other potential synergistic feedbacks, all of which can be important drivers of species distributions. In addition, all land-cover change inference was based on comparison between two time periods (2000 and 2010) because no other years were available.

Conclusion

If rapid deforestation continues inside Lore Lindu National Park, endemic species will have much less scope to respond to the stresses of climate change. Management efforts should account for the differential pressures of deforestation and climate change on middle- and high-elevation species. Furthermore, our results agree with other studies that suggest many more upland tropical birds are threatened with substantial population declines and possible extinction than are currently recognized. Our study demonstrates how models can be linked to predict the relative impacts of fine-scale habitat loss and climate change on population status in poorly-known tropical regions.

Chapter 4

Delay in autumn arrival date of migratory waders and raptors, but not passerines, in the Southeast Asian tropics

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In review, *Climatic Change*

STATEMENT OF AUTHORSHIP-CHAPTER 4

Delay in autumn arrival date of migratory waders and raptors, but not passerines, in the Southeast Asian tropics.

In review, *Climatic Change*.

J. Berton C. Harris: Collated data, performed the analysis, wrote the paper.
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Signed: Date: 2 Apr 2012

Ding Li Yong: Gathered and reviewed data, assisted with writing.
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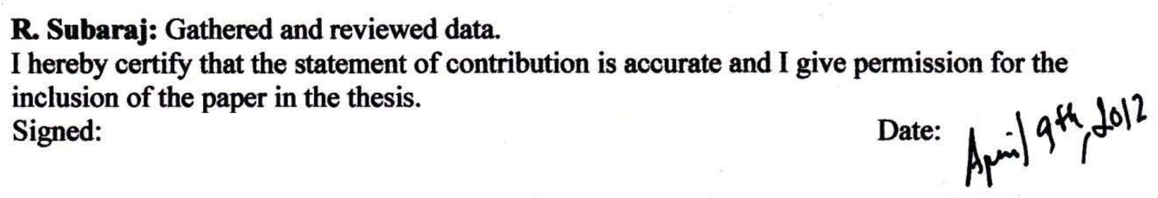
Signed: Date: 22 March 2012



R. Subaraj: Gathered and reviewed data.
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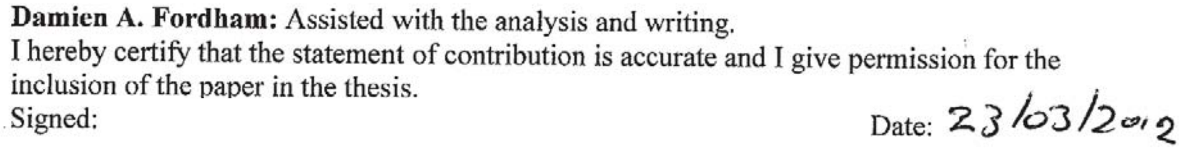
Signed: **Date:** April 9th, 2012



Damien A. Fordham: Assisted with the analysis and writing.
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Navjot S. Sodhi (deceased): Conceived the idea.

Chapter 4 - Delay in autumn arrival date of migratory waders and raptors, but not passerines, in the Southeast Asian tropics.

Abstract

Climate-change-induced phenological changes in migratory birds are predicted from ecological theory and have been well-documented in temperate-zone breeding areas. By contrast, changes in arrival date on the tropical wintering grounds have not been reported. To address this gap, we analysed birdwatchers' records of first arrival dates of 36 species of migratory birds (comprising five orders) in Singapore from 1987–2009. We compared the relative influence of year and population trend (declining vs. stable/increasing) on arrival date, and controlled for observer effort by including it as a covariate in all models. There was evidence for an arrival delay of 1.1 days/year for waders and 0.85 days/year for raptors, but no change in passerines. Five species, all long-distance migrants, showed delays of 1.8–2.1 days/year (*Accipiter gularis*, *Tringa glareola*, *Calidris ferruginea*, *Xenus cinereus*, and *Gallinago gallinago*). *Hirundo rustica* advanced arrival by 0.6 days/year. Population trend had small effects compared to year. During this period, mean summer temperature warmed across East Asia by 0.7 ˚C. Our results suggest that climate change is causing a perceptible shift in avian migration in Southeast Asia. A mechanism for the delay in long-distance migrants may be that warmer temperatures enable species to remain on northern breeding grounds longer. Arrival timing on the wintering grounds may have cascading effects on a migratory species' annual cycle, which underscores the need for further work on climate change impacts on migratory species in the tropics.

Introduction

Changes in phenology are one of the best-documented and most consistently observed impacts of climate change on animals (Lehikoinen and Sparks 2010). For migratory birds, it is well established that spring arrival date on the European and North American breeding grounds is advancing (reviewed in Knudsen et al. 2011; Lehikoinen and Sparks 2010). Long-distance migrants are often thought to have endogenous control of migration timing because they are unaware of weather conditions where they are headed (Gwinner 1996), while short-distance migrants may be more flexible in their capacity to alter migration timing based on their perception of regional weather conditions, especially if they migrate slowly (Hötker 2002;

Hurlbert and Liang 2012). Nonetheless, a recent review found no consistent differences in spring arrival changes between short- and long-distance migrants (Knudsen et al. 2011).

Changes in autumn departure/passage are less studied than spring arrival, and no clear trend of advancing or delaying has emerged (e.g. Thorup et al. 2007). Two comprehensive autumn passage studies from the north-temperate zone found that long-distance species advanced their autumn departure while short-distance migrants delayed departure (Jenni and Kéry 2003; Van Buskirk et al. 2009). One study provided evidence that warmer weather allowed short-distance migrants to remain on the breeding grounds longer, especially for species that could lay multiple clutches (Jenni and Kéry 2003). Most autumn passage studies have focused on passerines, but climate change may act differently on non-passerine groups (Adamík and Pietruszkova 2008; Filippi-Codaccioni et al. 2010).

Even less is known about how changes in autumn departure/passage in the northern hemisphere translate into changes in arrival on the wintering grounds. The only two southern hemisphere analyses found significant advances in arrival of three Siberian breeders in south-eastern Australia (Beaumont et al. 2006), but no significant changes in *Hirundo rustica* (barn swallow) arrival timing in South Africa (Altwegg et al. 2011). Changes in arrival date on the tropical wintering grounds and passage through the tropics are apparently unstudied (Gordo 2007; Lehikoinen and Sparks 2010), likely resulting from the paucity of long-term tropical datasets. Yet analyses from the tropics are urgently needed because hundreds of species make these journeys, and changes in timing can impact other stages in the annual cycle (Marra et al. 1998). For example, late arrival on the wintering grounds may have negative consequences if species compete for non-breeding territories (Faaborg et al. 2010), and birds that occupy poor wintering territories have been shown to arrive later on the breeding grounds which could force them into lower quality territories, or to expend energy competing with earlier arrivals (Norris et al. 2004).

We studied changes in first arrival date of 36 species, comprising passerines (Passeriformes), waders (Charadriiformes), raptors (Falconiformes), and other species, from 1987–2009 in Singapore, a natural bottleneck in the East Asian flyway with diverse habitats and a long history of birdwatching. Given the findings of Jenni and Kéry (2003) and Van Buskirk et al. (2009), we hypothesised: (1) long-distance species would arrive earlier, (2) short-distance species would arrive later, and (3) the taxonomic groups would show different changes.

Methods

First arrival dates came from birdwatchers' records that were verified by local experts and published monthly in the Singapore Bird Group's newsletter (Lim and Subaraj 1987-1990, 1992, 1997-1998, 2000-2003, 2006, 2008-2009). The 23 year span from 1987–2009 should be sufficient to detect a migration shift from climate change (Lehikoinen and Sparks 2010). Full arrival distribution data are preferable to first arrival dates (Lehikoinen and Sparks 2010; Van Buskirk et al. 2009), but first arrival dates are often the only sources available, especially from poorly studied regions (Beaumont et al. 2006).

The study species are common generalists (Lim and Lim 2009; Wells 1999, 2007) that should be weakly affected by habitat loss, allowing a climate signal to be detected (Table S4.1). Species were characterised as short-distance migrants if they breed south of c. 30° N, and long-distance otherwise. All waders were long-distance migrants and three of four raptors were short-distance migrants. The relatively even division in passerines (seven and ten short- and long-distance, respectively) allowed these groups to be analysed separately.

Arrival date anomaly was the response variable in all analyses. The anomaly is the difference in days between arrival date and the rounded mean arrival date from the middle few years of each species' series. Based on the number of parameters in the models, we only analysed cases with at least seven years of verified first arrival dates. The number of middle years in each species' series used to calculate the mean arrival date ranged from 2–4 years (a mean of 28.2% of the data was used to calculate the average date).

General linear models were used to compare the importance of year, population trend, and observer effort on arrival date in R v2.12.1 (R Development Core Team 2010). We accounted for population trend because changes in population size can influence detection probability (Tryjanowski and Sparks 2001), and abundance may also respond to climate change. Birdwatching effort and reporting in Singapore have varied over time (Wee 2006), which could potentially confound our analyses. We accounted for this in three ways: (1) Singapore bird experts among the co-authors (DLY and RS) removed records of post-breeding dispersal and very late "first arrival" records that were due to incomplete sampling, (2) only well-sampled years were analysed (when a reliable arrival date was recorded for > 15 of the 36 study species, leaving 14 years from the 1987–2009 span for the analysis), and (3) observer effort (measured by the proportion of study species seen that year) was included as a covariate in all models (Fig. 4.1).

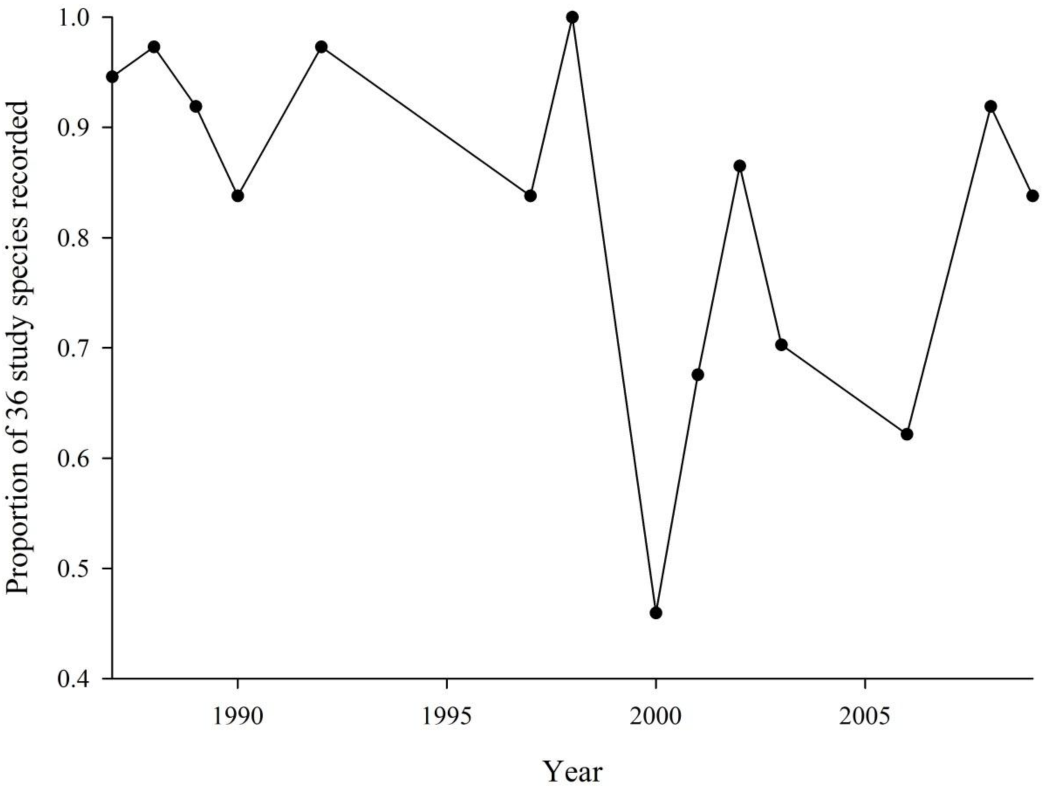

Fig. 4.1. Observer effort, measured by the proportion of 36 study species observed that year, during the study period.

Given the limited time series, we wished to avoid overfitting the general linear models, and thus included a maximum of four parameters in the taxonomic group comparisons (Burnham and Andersen 2002). Sample sizes did not permit testing the effects of population trend or migration distance in raptors. Including observer effort as a covariate in the species-specific models would risk overfitting because of small sample sizes (n = 8–14). Therefore we used the following candidate model set in the species-specific analyses: **arrival date ~ year**, **arrival date ~ observer effort**, **arrival date ~ 1**. We tested for correlations among covariates with a Spearman correlation matrix and found that all variables had Spearman coefficients < 0.55.

Mixed-effects models could have been appropriate for our repeated-measures dataset. Following Zuur et al. (2009), we evaluated the support for using mixed-effect models by comparing global models fit with generalised least squares regression, random intercept (species as random effect), and random slope (year | species) in the nlme package (Pinheiro et al. 2010) in R. We compared the models with restricted likelihood ratio tests in the RLRsim package (Scheipl 2010) and AIC calculated with restricted likelihood. These tests indicated that mixed-effects models were suboptimal in all groups except long-distance passerines. Therefore we present general linear model results for all groups and mixed-effects models for long-distance passerines.

We present diagnostic plots that show the relationship between the fitted values and residuals, the quantiles in the data against theoretical normal quantiles, and the relationship between leverage and standardised residuals (Crawley 2007). For the taxonomic groups we present diagnostic plots for the top-ranked and global models. Ee present diagnostic plots for the top model: **arrival date ~ year** for species-specific analyses. Bootstrapping (10,000 samples with replacement) was used to generate confidence intervals around slope estimates for the **arrival date ~ year** relationship in all taxonomic groups and species.

We tested for effects of the Southern Oscillation Index (a measure of El Niño-related climate) and the number of broods a species lays each year, on arrival date, and found no effects (see supplementary material for more details). Given our limited sample size and that number of broods is unknown for seven species, we did not include these covariates in further analyses.

We used the MAGICC/SCENGEN global climate emulation software (Fordham et al. 2012a) to judge if any shifts in migration coincided with summer temperature change. In MAGICC/SCENGEN we estimated June to August mean temperature change from 1990–2010 in East Asia where our study species migrate (60–178 ˚E, 6–80 ˚N). We used an ensemble of all models except those with known problems (FGOALS1G, GISS IH and GISS ER; Wigley 2008) to estimate temperature change at a 5˚ resolution. We verified that the ensemble results were broadly similar to predictions from three models that were skillful at representing historical global climate data (MICROCMED, MRI232A, UKHADCM3; Fordham et al. 2012a) projected temperature changes of -0.1 to +0.75 ˚C in the study area).

Results

Most waders and raptors showed a delayed arrival date from 1987–2009 that was linearly related to time (Fig. 4.2). Waders showed a stronger effect size compared to raptors (delay of 1.1 days/year ± 0.23 SE, 0.85 days/year ± 0.24 SE, respectively) and stronger evidence for a year effect (Tables 4.1, 4.2). In contrast to waders and raptors, neither long- nor short-distance passerines showed a consistent trend in arrival date over time. The mixed-effect model rankings for long-distance passerines were the same as general linear model rankings (Table S4.2). Population trend was only a statistically supported predictor of arrival date in long-distance passerines, where there was a weak trend of declining species arriving later. The collective trend shown in the raptors (three of which are short-distance migrants) was heavily influenced by the strong delay in the long-distance migrant *Accipiter gularis* (Table S4.3).

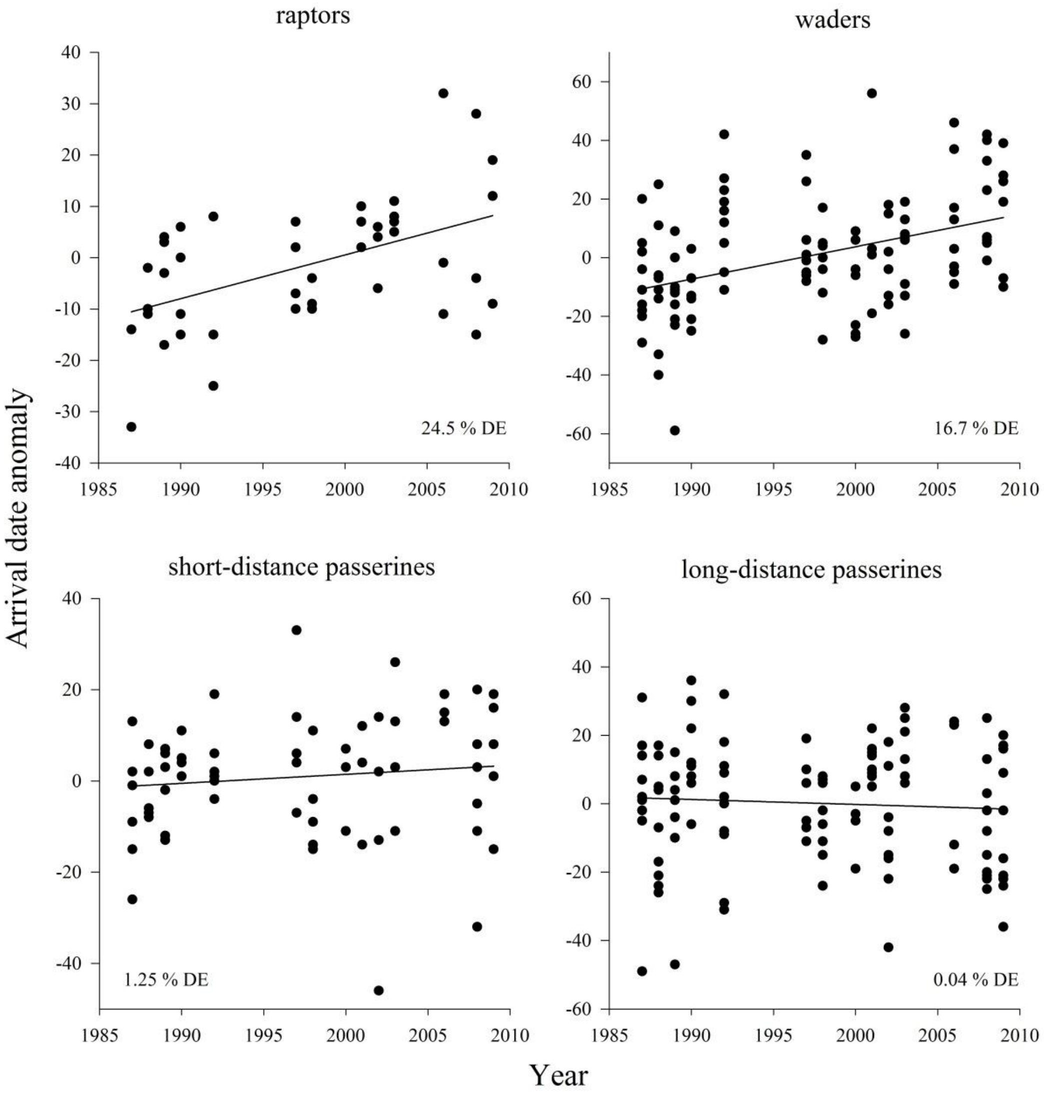

Fig. 4.2. Regression plots of change in arrival date anomaly over time for raptors, waders, and passerines.

Table 4.1. General linear model results for arrival date anomaly in four bird groups.

Model	% DE	evidence ratio	ΔAIC_c	w_i	k
Raptors					
year + observer effort	29.7		0	0.798	4
observer effort	20.4	4	2.7	0.202	3
Waders					
year + observer effort	19.6		0	1	4
population trend + observer effort	3.6	30172	20.6	0	4
observer effort	0.2	74555	22.4	0	3
Short-distance passerines					
observer effort	4.7		0	0.458	3
population trend + observer effort	7.4	1.2	0.3	0.391	4
year + observer effort	4.8	3	2.2	0.151	4
Long-distance passerines					
population trend + observer effort	8.4		0	0.698	4
year + observer effort	6.5	3.5	2.5	0.197	4
observer effort	3.8	6.6	3.8	0.105	3

k indicates the number of parameters; ΔAIC_c shows the difference between the model AIC_c (Akaike's Information Criterion corrected for small sample sizes) and the minimum AIC_c in the set of models; AIC_c weights (w_i) show the relative likelihood of model i; % DE is percent deviance explained by the model; an evidence ratio ($w_{top\ model}$ / w_i) of 5 indicates that the top-ranked model is 5 times better supported by the data than the reference model.

Table 4.2. Slope of relationship between year and arrival date for four bird groups and individual species (ranked by slope). Confidence intervals are based on 10,000 bootstrapped resamples. Bold indicates evidence for change in arrival date over time (year model top-ranked).

	Groups		
	lower CI	slope (days/year)	upper CI
raptors	0.32	0.85	1.41
waders	0.64	1.1	1.56
long-distance passerines	-0.58	-0.15	0.31
short-distance passerines	-0.24	0.2	0.58
	Species		
	lower CI	slope (days/year)	upper CI
Ficedula zanthopygia	-2.06	-0.97	0.27
Dendronanthus indicus	-2.05	-0.81	-0.01
Hirundo rustica	-1.33	-0.6	-0.18
Phylloscopus coronatus	-2.04	-0.49	1.44
Lanius tigrinus	-1.57	-0.38	0.49
Agropsar sturninus	-1.01	-0.35	0.77
Terpsiphone paradisi	-2.42	-0.33	2.51
Charadrius mongolus	-2.29	-0.25	0.76
Aviceda leuphotes	-0.83	-0.23	0.5
Actitis hypoleucos	-0.63	-0.09	0.5

Alcedo atthis	-0.73	-0.02	0.68
Luscinia cyane	-0.9	0.15	1.12
Dicrurus annectans	-1.1	0.22	1.27
Tringa stagnatilis	-1.3	0.23	1.26
Arenaria interpres	-1.21	0.25	1.38
Motacilla tschutschensis	-0.5	0.3	0.96
Muscicapa dauurica	-1.59	0.32	2.32
Phylloscopus borealis	-0.74	0.35	1.8
Pericrocotus divaricatus	-0.4	0.37	1.68
Lanius cristatus	-0.22	0.39	0.9
Cecropis daurica	-0.05	0.48	0.86
Pernis ptilorhyncus	-0.23	0.5	1.59
Halcyon pileata	-0.37	0.55	1.24
Turdus obscurus	-0.58	0.56	1.3
Accipiter soloensis	-0.05	0.85	1.57
Cuculus micropterus	0.05	1.16	2.35
Apus pacificus	-0.13	1.18	2.87
Muscicapa sibirica	-0.8	1.21	2.34
Chlidonias leucopterus	-0.77	1.46	4.79
Calidris ferruginea	0.88	1.77	2.54
Gallinago stenura	-0.32	1.8	4.99
Xenus cinereus	-0.02	1.86	3.49
Tringa glareola	0.5	1.89	2.79
Charadrius dubius	-0.18	1.96	3.77
Accipiter gularis	1.07	1.96	2.92
Gallinago gallinago	0.07	2.09	3.49

The species-specific analyses identified six species with statistical support for change in arrival date over time (Tables 4.2, 4.3; Fig. 4.3). Five long-distance migrants (*Accipiter gularis* (Japanese sparrowhawk), *Tringa glareola* (wood sandpiper), *Calidris ferruginea* (curlew sandpiper), *Xenus cinereus* (terek sandpiper), and *Gallinago gallinago* (common snipe)) showed delays of 1.8–2.1 days/year. *Hirundo rustica* (barn swallow) advanced arrival by 0.6 days/year. Model diagnostics show the data generally met the necessary assumptions for Gaussian-identity link models (Fig. S4.1). Nonetheless, trends in the residuals for *Hirundo rustica*, *Tringa glareola*, and *Gallinago gallinago*, and minor departure from normality in short-distance passerines are reasons for caution in interpretation (Fig. S4.1).

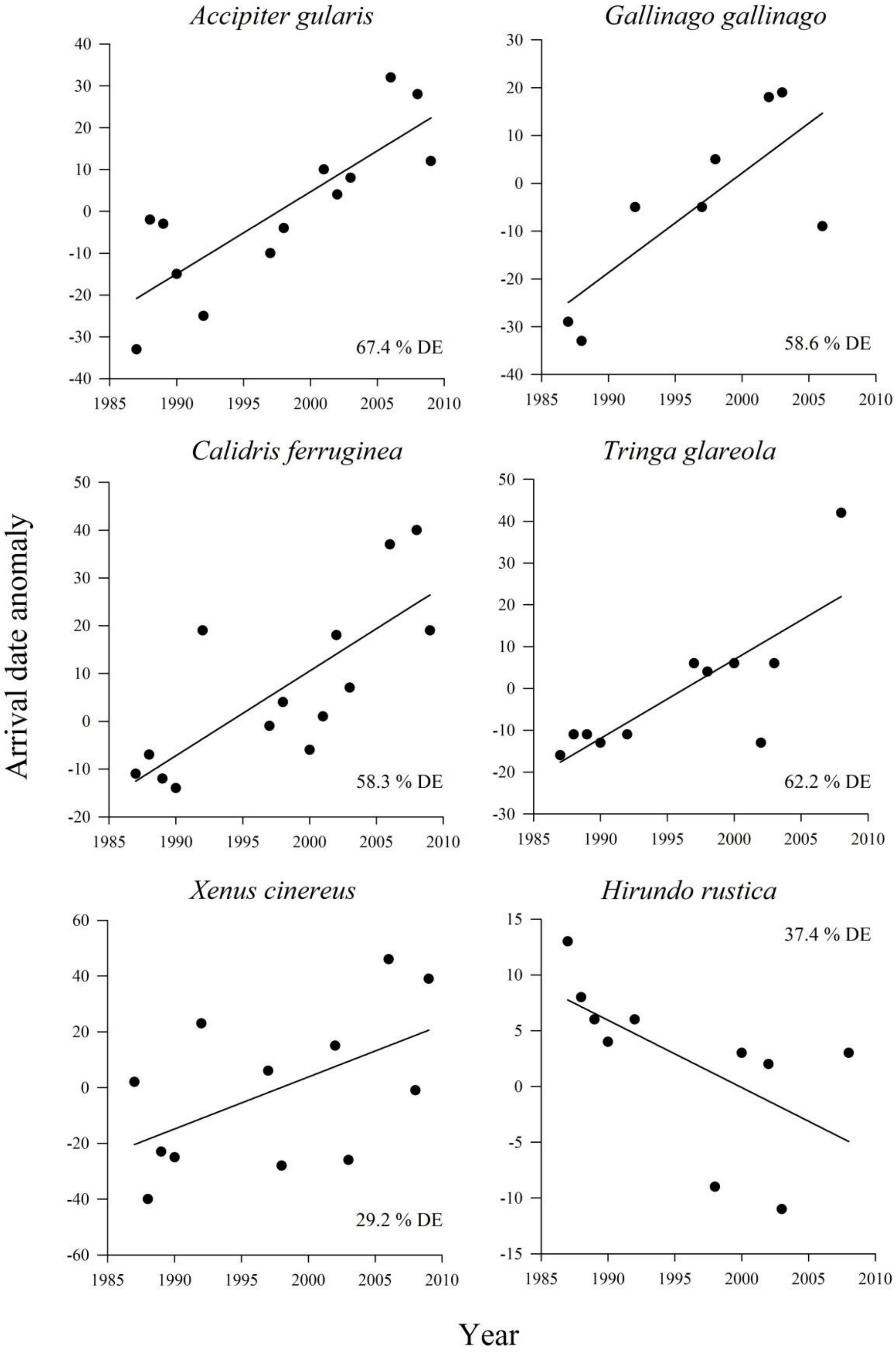

Fig. 4.3. Regression plots of change in arrival date anomaly over time for six species with the best support for an **arrival date ~ year** relationship.

Table 4.3. General linear model results for six species with evidence of change in arrival date over time.

Model	% DE	evidence ratio	ΔAIC_c	w_i	k
Accipiter gularis					
year	67.4		0	0.988	3
observer effort	32.0	120.0	9.6	0.008	3
null	0	260.2	11.1	0.004	2
Tringa glareola					
year	62.2		0	0.962	3
null	0	29.7	6.8	0.032	2
observer effort	3.3	176.7	10.3	0.005	3
Calidris ferruginea					
year	58.3		0	0.986	3
null	0	86.9	8.9	0.011	2
observer effort	0.3	445.6	12.2	0.002	3
Xenus cinereus					
year	29.2		0	0.462	3
null	0	1.3	0.5	0.365	2
observer effort	16.5	2.7	2.0	0.173	3
Gallinago gallinago					
year	58.6		0	0.653	3
null	0	2.1	1.5	0.315	2
observer effort	12.3	20.1	6.0	0.032	3
Hirundo rustica					
year	37.4		0	0.514	3
null	0	1.2	0.4	0.422	2
observer effort	5.0	8.0	4.2	0.064	3

The MAGICC/SCENGEN results represent a change in summer temperature across East Asia by -0.1 to +0.68 ˚C from 1990–2010. Cooling was restricted to a small area of eastern India and Bangladesh.

Discussion

Our results indicate that climate change is causing a perceptible shift in avian migration in the Asian tropics, predominantly towards later arrival dates. This is our favoured explanation because the study species are common generalists that should not be strongly affected by habitat loss, and the region has warmed significantly during the study period. Nonetheless, while the results indicate that many species' arrival in the tropics is being progressively postponed, first arrival date studies do not give information on population wide-changes and can show stronger (although often concordant) trends compared to full arrival distribution studies (Mills 2005; Thorup et al. 2007).

The clear pattern of delay in long-distance migrant waders and *Accipiter gularis* (Japanese sparrowhawk) may be related to warming temperatures enabling species to remain in northern breeding or passage areas later in the year. While the possible mechanism for this pattern is unknown, warmer temperatures could lengthen the growing season when prey would be active, or decrease the energetic cost of birds remaining in northern latitudes (Bradshaw and Holzapfel 2006). *Accipiter* hawks have markedly diets, habitat preferences, and migration strategies than the waders we studied, which suggests different mechanisms could be behind the delays we observed. For example, *Accipiter* migration is not confined to the coast and waders tend to migrate at night (Richardson 1979). Furthermore, *Gallinago gallinago* (common snipe) requires marshes, while the other waders we studied are mudflat species, so changes in diet or passage times through stopovers could differ among these species. Interestingly, Beaumont et al. (2006) found advances in winter arrival for some long-distance species in Australia, including *Calidris ferruginea*, which showed a strong delay in our study. These contradictory results may be related to changes in the rate of migration in between sampling sites (*sensu* Stutchbury et al. 2011), but further investigation is required.

It is unclear why passerines did not change their migration timing, but this lack of response is consistent with the mixed results (including no changes) shown in fall departure/passage studies (Mills 2005; Thorup et al. 2007; Van Buskirk et al. 2009). Differences in resource use and habitat preferences between waders and passerines likely contribute to the observed patterns (Adamík and Pietruszkova 2008).

Changes in arrival timing have conservation implications for species, and potentially, ecosystems. Delayed arrival on the wintering grounds may affect territory acquisition, which can be related to arrival timing on the breeding grounds and, eventually, fitness (Marra et al. 1998). Mistiming can result when species change their phenology at different rates. For example, populations of *Ficedula hypoleuca* (pied flycatcher) that arrive after the peak emergence of their primary food source in Holland are prone to decline (Both et al. 2006). Furthermore, spring oak (*Quercus*) budburst, caterpillar emergence, and hatch dates of *F. hypoleuca* and predatory *Accipiter nisus* (sparrowhawk) are all advancing over time (some not statistically significant), but at different rates (Both et al. 2009). If the changes continue at different rates, trophic interactions may begin to unravel (Brook 2009). These effects of changes in migration timing emphasise the need for further analyses on climate change impacts on migratory species in the tropics.

Chapter 5

Managing the long-term persistence of a rare cockatoo under climate change

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Managing the long-term persistence of a rare cockatoo under climate change.

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J. Berton C. Harris: Applied for funding, performed the analysis, wrote the paper.
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Signed: Date: 2 Apr 2012

Damien A. Fordham: Assisted with funding application, supervised analysis, assisted with writing.
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Patricia A. Mooney: Collected data,provided expert advice on the species.
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David C. Paton: Conceived the idea, provided expert advice on the species, assisted with writing.
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Michael J. Watts: Designed software for results summary and sensitivity analysis.

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Michael G. Stead: Prepared Allocasuarina verticillata data, assisted with writing.

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Chapter 5 - Managing the long-term persistence of a rare cockatoo under climate change

Abstract

1. Linked demographic-bioclimatic models are emerging tools for forecasting climate change impacts on well-studied species, but these methods have been used in few management applications, and species interactions have not been incorporated. We combined population and bioclimatic envelope models to estimate future risks to the viability of a cockatoo population posed by climate change, increased fire frequency, beak-and-feather disease, and reduced management.

2. The South Australian glossy black-cockatoo *Calyptorhynchus lathami halmaturinus* is restricted to Kangaroo Island, Australia, where it numbers 350 birds and is managed intensively. The cockatoo may be at particular risk from climate change because of its insular geographic constraints and specialised diet on a single plant species, *Allocasuarina verticillata*. The cockatoo population model was parameterised with mark-resight-derived estimates of survival and fecundity from 13 years of demographic data. Species interactions were incorporated by using a climate-change-driven bioclimatic model of *Allocasuarina verticillata* as a dynamic driver of habitat suitability. A novel application of Latin Hypercube sampling was used to assess the model's sensitivity to input parameters.

3. Results suggest that unmitigated climate change is likely to be a substantial threat for the cockatoo: all high-CO_2-concentration scenarios had expected minimum abundances of <160 birds. Extinction was virtually certain if management of nest-predating brush-tail possums *Trichosurus vulpecula* was stopped, or adult survival reduced by as little as 5%. In contrast, the population is predicted to increase under low-emissions scenarios.

4. Disease outbreak, increased fire frequency, and reductions in revegetation and management of competitive little corellas *Cacatua sanguinea*, were all predicted to exacerbate decline, but these effects were buffered by the cockatoo population's high fecundity.

5. Spatial correlates of extinction risk, such as range area and total habitat suitability, were non-linearly related to projected population size in the high-CO_2-concentration scenario.

6. *Synthesis and applications*. Mechanistic demographic-bioclimatic simulations that incorporate species interactions can provide more detailed viability analyses than traditional bioclimatic models and be used to rank the cost-effectiveness of management interventions. Our results highlight the importance of managing possum predation and maintaining high adult cockatoo survival. In contrast, corella and revegetation management could be experimentally reduced to save resources.

Introduction

Climate change may be one of the most potent extinction drivers in the future, especially because it can exacerbate existing threats, and there is an urgent need for conservation science to improve tools to predict species’ vulnerability to climate change (Sekercioglu *et al.* 2008). One popular approach is the use of bioclimatic envelope models (BEMs), also known as species distribution models. These models use associations of present-day distributions with climate to forecast changes in species’ bioclimatic envelopes (Pearson & Dawson 2003). BEMs have, in some cases, been used to assess extinction risk for thousands of species under climate change scenarios (e.g. Sekercioglu *et al.* 2008). However, predictions from these models are of constrained value because they: (1) are correlative, and yet typically require extrapolation to environmental space that is beyond the bounds of the statistical fitting (Thuiller *et al.* 2004); (2) use range area type estimates to infer extinction risk rather than measuring threat to population persistence (Fordham *et al.* in press-b); (3) suffer from model selection uncertainty (Araújo & Rahbek 2006); and (4) do not consider biotic interactions (e.g. Araújo & Luoto 2007).

Spatially explicit population-modelling techniques that link demographic models with BEMs are being used to add ecological realism to correlative BEM forecasts (Huntley *et al.* 2010). Combining quantitative population models and BEMs provides a more mechanistic and probabilistic approach compared to modelling distribution alone, because it links demographic parameters to climate and other explanatory variables, and explores a range of uncertain outcomes using stochastic simulation (Brook *et al.* 2009). Several studies have combined habitat and population models to assess population viability (e.g. Akçakaya *et al.* 2004) but few analyses have coupled population and bioclimatic models to estimate extinction risk in the context of climate change (Keith *et al.* 2008; Anderson *et al.* 2009; Fordham *et al.* in press-a), and this methodology has rarely been used in birds (but see Aiello-Lammens *et al.* 2011). Ideal case-study species for this approach are those with long-term estimates of vital rates (and their variance), representative occurrence data over their geographic range, and detailed knowledge of the environmental drivers influencing range and abundance.

The South Australian glossy black-cockatoo *Calyptorhynchus lathami halmaturinus* Temminck (GBC) formerly inhabited mainland South Australia, but now survives only on Kangaroo Island (located off the southern coast of central Australia), and is considered ‘endangered’ by the Australian government (DEH 2000; Fig. 5.1). When the GBC Recovery Program began in 1995, the cockatoo population comprised c. 200 individuals. From 1998 to the present, the intensively-managed population has increased gradually to the current estimate of c. 350 birds (Pedler & Sobey 2008). The GBC’s specialised habitat requirements and slow life history make it inherently vulnerable to decline (Cameron 2006), and its small population size and insular geographic constraints (single location) put it at high risk from population-wide catastrophes such as fire and disease (Pepper 1997). High-quality *Allocasuarina verticillata* (Lam.) L.A.S. Johnson (drooping she-oak) woodlands provide food and cover that are critical to the survival of the GBC; indeed, *A. verticillata* seeds make up 98% of the GBC’s diet (Chapman & Paton 2006). Hollow-bearing eucalypts (primarily *Eucalyptus cladocalyx* F. Muell and *E. leucoxylon* F. Muell), which take many decades to mature and may be vulnerable to fire, are required for nesting (Crowley *et al.* 1998a).

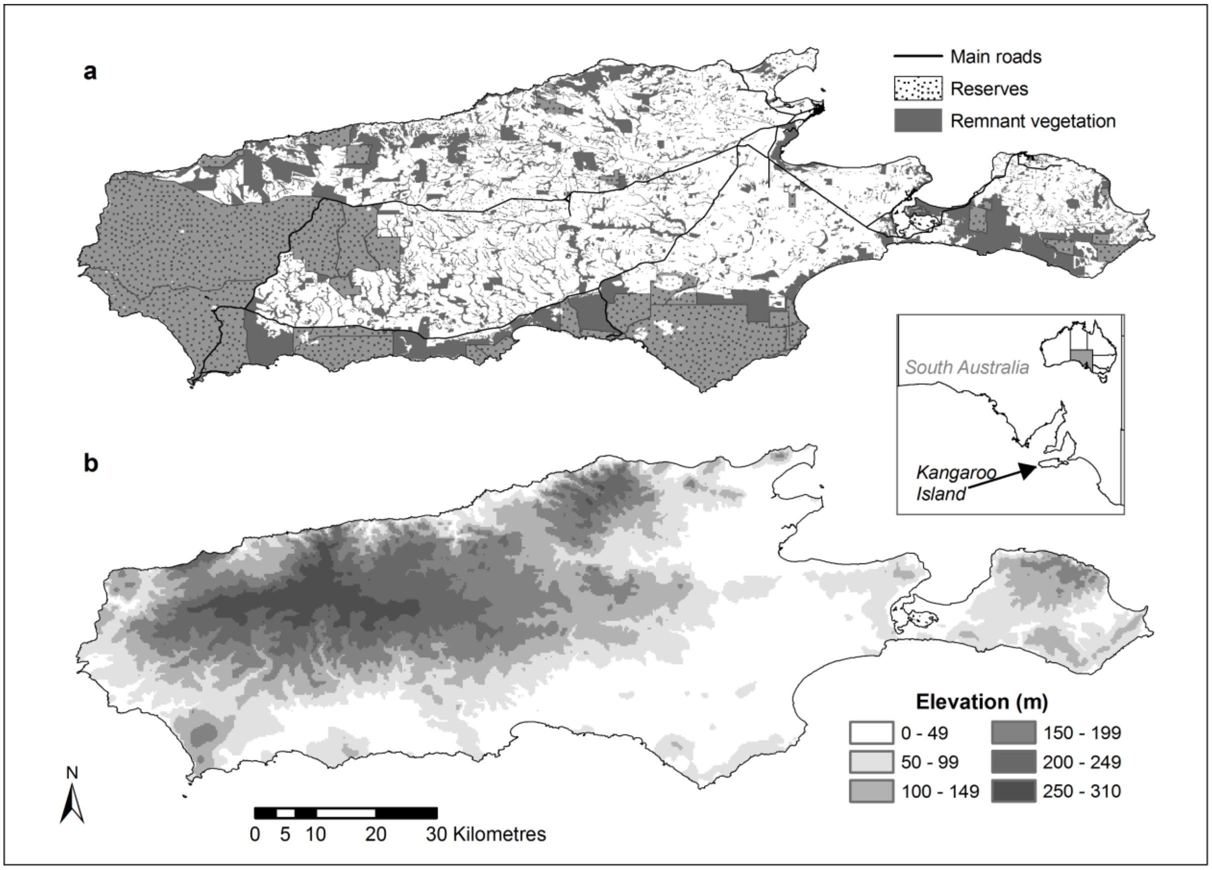

Figure 5.1. The South Australian glossy black-cockatoo *Calyptorhynchus lathami halmaturinus* is restricted to Kangaroo Island, South Australia. Maps showing (a) remnant native vegetation and protected areas, and (b) elevation.

The GBC faces an interacting set of current and future threats including nest competition and predation, wildfire, climate change, and disease (Mooney & Pedler 2005). GBC recruitment can be severely impaired by nest predation from arboreal brush-tail possums *Trichosurus vulpecula* Kerr. Protecting nest trees from possum predation by fitting metal collars and pruning adjacent tree crowns increased nest success from 23 to 42% (Garnett, Pedler & Crowley 1999). Approximately 45% of nests are now placed in artificial hollows fitted by managers. Little corellas *Cacatua sanguinea* Gould and honeybees *Apis mellifera* L. are nest competitors that are also managed (Mooney & Pedler 2005). Wildfires are another threat that can kill nestlings and destroy large areas of habitat (Sobey & Pedler 2008). Kangaroo Island is expected to warm by 0.3–1.5 ºC and receive 0–20% less rainfall by 2050 compared to 1990 levels, under a mid-range greenhouse-gas emissions scenario (CSIRO 2007). Climate change is likely to threaten the GBC by causing *A. verticillata*'s climatic niche to shift and compress southwards toward the southern ocean boundary (Stead 2008), causing heat- and drought-induced mortality (Cameron 2008), and an increased frequency of extreme events, such as fire and drought (Dunlop & Brown 2008). In addition, *A. verticillata* cone production may decrease as conditions become warmer and drier (DCP pers. obs.), limiting the GBC's food supply. Lastly, psittacine beak-and-feather disease, although not yet reported in Kangaroo Island GBCs, could potentially cause substantial declines in the population if an outbreak occurred (DEH 2005; see supplementary material).

Here we develop a detailed spatial population viability model for the GBC by building a demographic model, linking the demographic model to landscape and climate variables, and testing scenarios in a population viability analysis. The analysis is based on a comprehensive location-specific dataset and incorporates climate change and its interaction with fire, disease, and management. Two earlier attempts at modelling the GBC used non-spatial simulations to investigate extinction risk (Pepper 1996; Southgate 2002), but both were limited in scope and made simplifying assumptions. For instance, in contrast to known population increases, Pepper (1996) predicted a rapid decline to extinction, and Southgate (2002) suggested the population would decline by 10% annually (see supplementary material). These studies were hampered by the limited data available when the analyses were done, and did not consider fire, disease, climate change or the positive influence of management. By contrast, we use a detailed data set collected by the GBC recovery program since 1995, consisting of 13 years of mark-resight and reproductive data and extensive documentation of catastrophes and management intervention, to parameterise our models. Few parrots have such complete demographic data available (Snyder *et al.* 2004).

Our approach incorporates a critical biotic interaction between the GBC and its primary food source, *A. verticillata*, by incorporating projected changes in the plant's range in the spatially-explicit cockatoo model to provide direct measures of extinction threat (e.g. expected minimum abundance) as well as implied measures calculated from changes in habitat suitability and range size (Fordham *et al.* in press-b). Similar approximations of species interactions have been used with BEMs (e.g. Araújo & Luoto 2007; Barbet-Massin & Jiguet 2011), but never in combination with a demographic model. Specifically, we sought to: (1) model the population trajectory and extinction risk of the GBC up to the year 2100; (2) determine the possible future effects of current and emerging threats to the subspecies; (3) assess the impact of choosing different management strategies on GBC population trends; and (4) evaluate the relative importance of demography and anthropogenic extinction drivers on the GBC's population viability.

Materials and methods

Population model

For the demographic component of the model, we used 13 years of mark-resight surveys to estimate survival rates using Program MARK v.5.1 (Cooch & White 2008). Birds are marked with numbered bands as nestlings at several sites across the island (some areas are better sampled than others) and telescopes are used to re-sight marked birds during the annual post-breeding census. The mark-resight analysis was used to test the importance of management and environmental variables on survival rates of juvenile (<1 year old) and sub-adult/adult GBCs (Table S5.1). Fecundity was calculated as the number of fledglings of each sex produced per female of breeding age from 1996–2008 (see supplementary material for details on the mark-resight analysis, fecundity calculations, and standard deviations used in the population model). Survival and fecundity estimates were combined with other life-history information, such as age of first breeding, to build a stage- and sex-structured, stochastic population model of the GBC (Table 5.1). We used RAMAS GIS (Akçakaya & Root 2005) to create a spatially-explicit metapopulation model that links the subspecies' demography to landscape data, comprising dynamic bioclimatic maps for *Allocasuarina verticillata* (the GBC's primary food source), and raster layers of native vegetation, substrate, and slope (see below).

Table 5.1. Stage matrices used in the model with stable age distribution (SAD) of each age class. The top row in each matrix represents fecundities, and the subdiagonal and diagonal in the bottom right elements represent survival rates. The first stage (age 0) for both sexes is the sub-adult stage. The final stages (female, age 2+; male, age 4+) are the adult stages. The intermediate stages are pre-breeding sub-adult stages. The proportional sensitivities of the finite rate of increase to small changes in each of the non-zero elements of the female matrix (elasticities) are in parentheses

Female

	Age 0	Age 1	Age 2+	SAD
Age 0	0	0	0.2324 (0.0951)	7.3%
Age 1	0.612 (0.0951)	0	0	4.3%
Age 2+	0	0.913 (0.0951)	0.913 (0.7148)	32.4%

Male

	Age 0	Age 1	Age 2	Age 3	Age 4+	SAD
Age 0	0	0	0	0	0*	9.3%
Age 1	0.612	0	0	0	0	5.5%
Age 2	0	0.913	0	0	0	4.9%
Age 3	0	0	0.913	0	0	4.3%
Age 4+	0	0	0	0.913	0.913	32.0%

*In RAMAS, we specified fecundity values of 0.2324 and 0.296 for females and males, respectively (supplementary material).

Bioclimatic suitability maps for Allocasuarina verticillata

Climate change was incorporated by modelling the potential distribution of *Allocasuarina verticillata*, as a function of three key climate variables that influence the species' distribution (annual rainfall, January temperature, and July temperature; Stead 2008). We used meteorological data to estimate long term average annual rainfall and mean monthly January and July temperature (1980–1999) for Australia (Fordham et al. 2012a). We used thin-plate splines and a digital elevation model to interpolate between weather stations (Hutchinson 1995; supplementary material). An annual time series of climate change layers was generated for each climate variable based on two emission scenarios: a high-CO_2-concentration stabilisation reference scenario, WRE750, and a strong greenhouse gas mitigation policy scenario, LEV1 (Wigley *et al.* 2009). WRE750 assumes that atmospheric CO_2 will stabilize at about 750 parts per million (ppm), while under the LEV1 intervention scenario CO_2 concentration stabilizes at about 450 ppm. Future climate layers were created by first generating climate anomalies from an ensemble of nine general circulation models, and then downscaling the anomalies to an ecologically relevant scale (approximately 1 km^2 grid cells) (Fordham et al. 2012a,b; supplementary material). Averages from multiple climate models tend to agree better with observed climate compared to single climate models, at least at global scales (Fordham et al. 2012a).

Occurrence records for *A. verticillata* (n = 572) came from cleaned records from the South Australian biological survey. An equal number of pseudoabsences were generated randomly within the study region (see supplementary material). Although our focus was on Kangaroo Island, we modelled the distribution of the species across South Australia (325,608 grid cells) to better capture its regional niche (see Barbet-Massin, Thuiller & Jiguet 2010). We modelled the potential current and future climatic suitability of the landscape for *A. verticillata* with an ensemble of seven bioclimatic modelling techniques, including simple surface-range envelope models and more complex machine learning approaches, in BIOENSEMBLES software (Diniz-Filho *et al.* 2009; supplementary material). Ensemble modelling generates consensus projections that circumvent some of the problems of relying on single-model projections of climate change impacts on species' potential distributions (Araújo & New 2007). We used BIOENSEMBLES models to forecast annually for 90 years (i.e. climate suitability maps for each year were created from 2010 to 2100). Nonetheless, our model assumed that the *A. verticillata*-GBC relationship would remain strong and we were unable to consider other species interactions.

Integrating the population model and spatial information

Binomial generalised linear models (GLMs) were used to relate GBC occurrence records to *A. verticillata* present-day climate suitability (above) and three landscape variables that are known to influence the distributions of the GBC and *A. verticillata*: substrate (Raymond & Retter 2010), native vegetation cover (http://www.environment.gov.au/erin/nvis/index.html), and slope (http://www.ga.gov.au/meta/ANZCW0703011541.html; supplementary material). Verified GBC occurrence records (n = 349) consist of presences only. Pseudoabsences were generated by down-weighting cells close to a known sighting (see supplementary material). The analysis was done with package MuMIn (Bartoń 2012) in R (v. 2.12.1; R Development Core Team, http://www.R-project.org). The best model (determined by AIC_c) from this analysis was used to parameterise the habitat suitability function in RAMAS (see supplementary material).

RAMAS uses the habitat suitability function to assign a habitat suitability value to each grid cell of the study area based on values of the input rasters (in this case *A. verticillata* climatic suitability, substrate, native vegetation, and slope). Every grid cell above the habitat-suitability threshold is considered suitable, and suitable cells are aggregated based on neighbourhood distance (the spatial distance at which the species can be assumed to be panmictic; Akçakaya & Root 2005). The habitat suitability threshold (0.83) and neighbourhood distance (four cells) values were derived iteratively to match the well-known current extent of suitable habitat for the GBC on the island (Mooney & Pedler 2005).

The initial population size in all scenarios was 350 birds, in accordance with recent estimates (Pedler & Sobey 2008). The island's current carrying capacity was estimated at 653 birds by combining feeding habitat requirements (Chapman & Paton 2002) with data on *A. verticillata* area (see supplementary material). Dispersal estimates came from data on movements of marked individuals (Fig. S5.1). A ceiling model of density dependence was used to approximate the GBC's intraspecific competition for nest hollows and feeding habitat (Mooney & Pedler 2005). Population dynamics were linked to habitat via the density dependence function: habitat determines carrying capacity which conditions demographic rates (survival and fecundity) in each year, as a function of population size and carrying capacity in that year (Akçakaya & Root 2005). Each simulation incorporated environmental and demographic stochasticity and was run 10,000 times (Akçakaya *et al.* 2004).

Our main measures of population viability were expected minimum abundance (EMA) and mean final population size of persisting runs. EMA, which is equivalent to the area under the quasi-extinction risk curve (McCarthy 1996), provides a better (continuous, unbounded) representation of extinction risk than probability of extinction or quasi-extinction (McCarthy & Thompson 2001). We calculated EMA by taking the smallest population size observed in each iteration and averaging these minima.

We also calculated three spatial measures that are commonly used to infer extinction likelihood: change in total habitat suitability (from RAMAS), occupied range area (area of cells greater than habitat suitability threshold), and average cockatoo density (see Fordham *et al.* in press-b for details). Density was calculated by relating the population size at each time step to habitat suitability values per grid cell in suitable patches.

Model scenarios

We generated RAMAS models for three climate scenarios: WRE750, LEV1, and a control scenario with no climate change. For each climate scenario we assessed GBC population viability given changes in fire frequency, disease outbreak, and changes in management from funding constraints. We modelled severe fires as reducing GBC fecundity by 10% and adult and sub-adult survival by 3%, based on responses measured in 2007 (Sobey & Pedler 2008; PAM pers. comm.). Wildfire frequency was modelled as increasing with building fuel loads. Baseline scenarios include an annual probability of severe fire of 6.8% (see supplementary material). We modelled 5%, 25%, and 220% (i.e., 2.2-fold) increases in fire frequency under climate change (Lucas *et al.* 2007). It was not realistic to model any fire increases for the no climate change scenario or the 25% or 220% increase for the mitigation LEV1 scenario (see supplementary material). Psittacine beak-and-feather-disease outbreaks were modelled as reducing sub-adult survival by 50%, with an annual probability of an outbreak of 5% (DEH 2005; supplementary material). We modelled ending brush-tail possum, little corella, and revegetation management as causing 44%, 7%, and 3% reductions in fecundity, respectively (Mooney & Pedler 2005).

Sensitivity analysis

We used a Latin Hypercube sensitivity analysis to assess the impact of varying the values of six key input parameters (adult survival, varied by ± 5%; sub-adult survival, ± 10%; fecundity, ± 10%; carrying capacity, ± 20%; and proportion of population dispersing annually, ± 20%) on GBC mean final population size (Iman, Helson & Campbell 1981). Latin Hypercube sampling, which simultaneously varies the values of the input parameters and then estimates sensitivity by fitting a spline regression model, is arguably preferable to other Monte Carlo techniques because it requires many fewer iterations to sample the parameter space whilst allowing for co-variation in parameter choices (McKay, Beckman & Conover 1979). We fit a Poisson GLM with all six predictors (a segmented linear model was used for adult survival; segmented package in R; supplementary material), and calculated standardised regression coefficients (fitted slopes divided by their standard errors) to rank the importance of the input parameters (Conroy & Brook 2003). We also tested the model's sensitivity to parameterisation of disease outbreaks by doubling the frequency of simulated outbreaks, increasing the impact to a 75% reduction in survival, and combining these parameterisations.

Results

Demography

The best-supported mark-resight survival model was stage-structured and time invariant (Table S5.2). There was also statistical support for the next eight models ($\Delta \text{AIC}_c < 2$), yet the majority of model structural deviance was explained by the most parsimonious model (88% compared to 99%). The annual survival estimates so derived were 0.612 ± 0.0388 SE for juveniles and 0.913 ± 0.0123 SE for adults. All of the top-ranked 10 survival models incorporated stage structure with two age classes. There was little evidence for differences in survival between the sexes over the study period from the mark-resight data. Models including environmental covariates were suboptimal regardless of stage structure. All covariate models with no stage structure had $w\text{AIC}_c$ <0.01.

We used a mean annual fecundity estimate of 0.232 ± 0.0053 SE female nestlings produced per female of breeding age, and 0.296 ± 0.0068 SE male nestlings produced per female of breeding age, from 1996–2008, such that the finite rate of increase of the resultant matrix model was 1.0345, indicating a population increasing deterministically by 3.5% per year (Table 5.1; supplementary material). The elasticities suggest that the rate of increase is most sensitive to adult survival.

Spatial results

There was considerable overlap between *Allocasuarina verticillata* patches and GBC presences. Approximately 32% of GBC presences (feeding, nesting, and band observations) were inside an *A. verticillata* patch, and 79% of presences were within 1 km of an *A. verticillata* patch (only 19% of the island is within 1 km of a patch).

The bioclimatic envelope modelling predicts that most of *A. verticillata*'s range (and consequently the GBC's habitat) will remain intact under the reduced emissions (LEV1) scenario, while the range is likely to contract substantially under the high-CO_2-concentration scenario (WRE750) (Fig. 5.2). The majority of suitable habitat that is predicted to remain at the end of the century under the WRE750 emissions scenario is on the island's higher-elevation western plateau (Figs. 5.1, 5.2). By 2100, total habitat suitability declined substantially (decreasing by 12%) in the WRE750 scenario, whereas suitability decreased by just 1% under LEV1 (Fig. 5.3). Range area was inversely related to average cockatoo density per cell (Fig. 5.3). This was especially evident for WRE750, where range area contracted by 77% and predicted density increased by 57% by 2100. Range area declined by only 6% in the LEV1 scenario (Fig. 5.3).

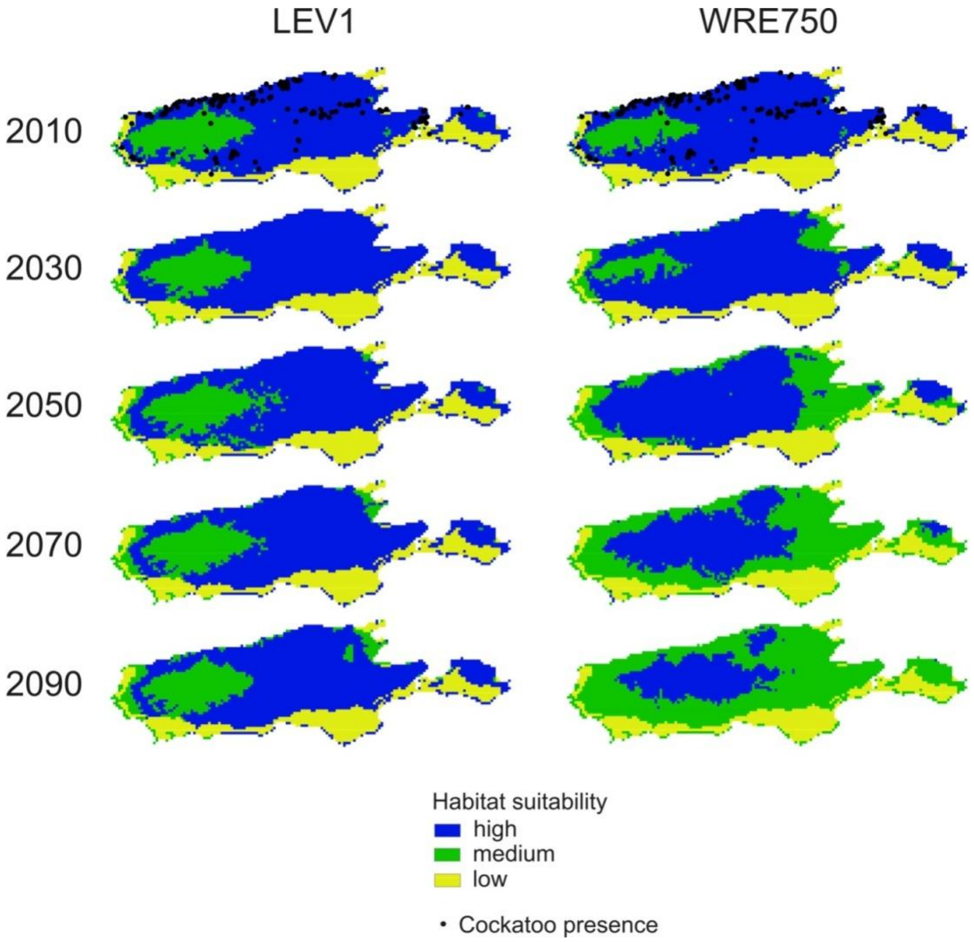

Figure 5.2. Climate-change-driven maps of habitat suitability for *Calyptorhynchus lathami halmaturinus* according to a greenhouse gas mitigation policy scenario (LEV1), and a high-CO_2-concentration stabilisation reference scenario (WRE 750). Recent cockatoo presences are shown on the 2010 maps. Habitat suitability is classified from a continuous variable into three categories to aid visual interpretation: high (above the habitat suitability threshold), medium (below threshold), and low (unsuitable substrate for *A. verticillata*) suitability.

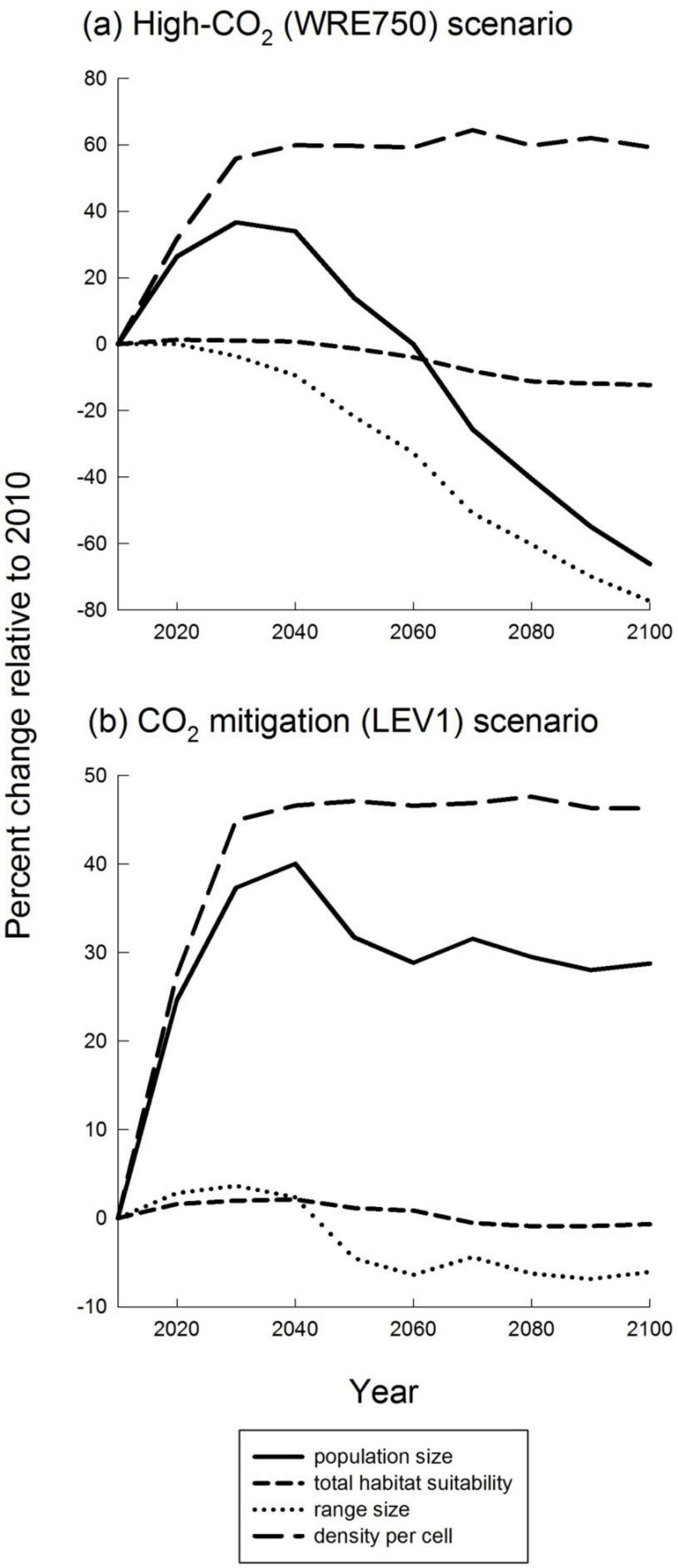

Figure 5.3. Percent changes in total habitat suitability (output from RAMAS GIS), range size (area of suitable habitat), cockatoo density per cell, and population size according to two climate change scenarios: (a) high-CO_2-concentration stabilisation reference scenario (WRE750), (b) greenhouse gas mitigation policy scenario (LEV1).

Population viability

Habitat changes caused by unmitigated climate change had a strong effect on population viability, with simulated final population size and expected minimum abundance always <160 birds, which is roughly equivalent to a return to the population bottleneck of the 1980s (Figs. 5.4, S5.2). In contrast, all simulations in the no climate change (control) case had final population sizes >635, and EMA >350, unless brush-tail possum management ceased. The strong mitigation (LEV1) simulations had slightly lower final population sizes than the no climate change case, but still had all final populations sizes >595 unless there was no possum management. The simulations predicted that stopping possum management would have a serious effect on the population with all EMAs below 90 birds. Scenarios that ceased possum management were the only cases when the population did not stay close to carrying capacity. Unlike all other scenarios, possum scenarios had considerable probabilities of quasi-extinction (falling below 50 individuals): 10% for no climate change, 11% for LEV1, and 36% for WRE750. Stopping all management actions caused severe declines, with EMAs <26 birds for each scenario. The other catastrophes and changes in management had much more minor effects compared to possum management, although they did impact the population in the hypothesised directions (e.g. increased fire management caused slightly higher population sizes in LEV1 and no climate change). In this group of scenarios, beak-and-feather disease outbreak had the strongest effects, but still only resulted in final population size reductions of 13, 12 and one bird compared to the baseline for no climate change, LEV1, and WRE750, respectively.

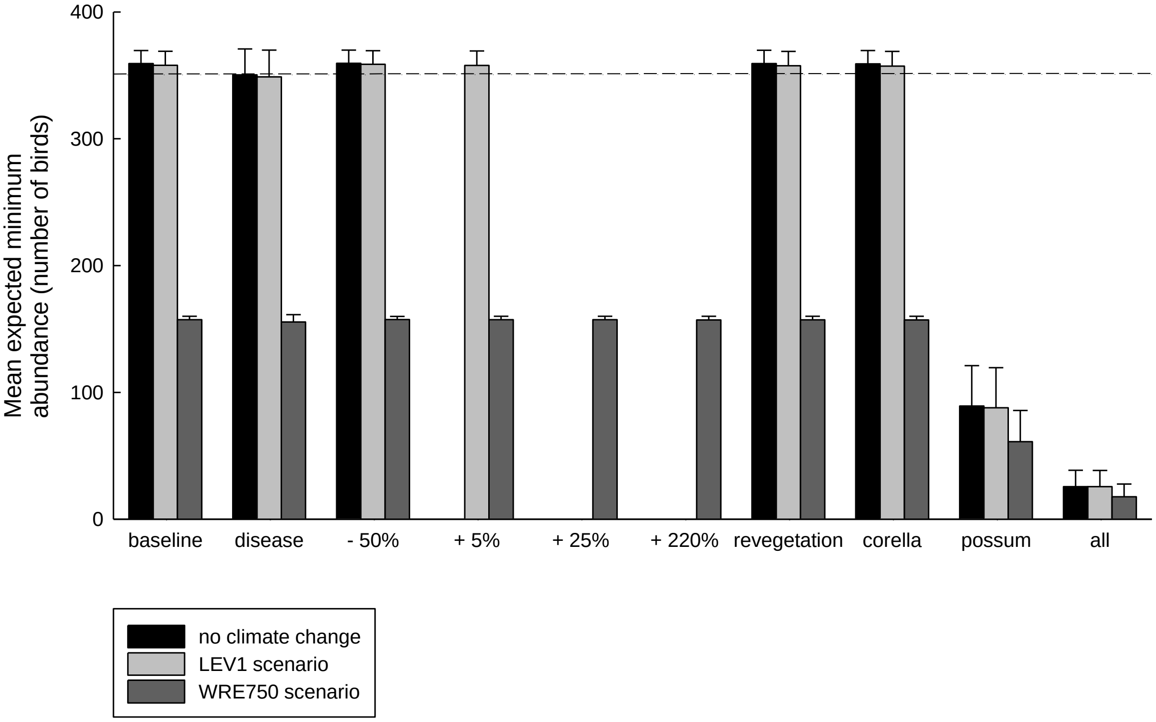

Figure 5.4. Mean expected minimum abundance (± SD) of *Calyptorhynchus lathami halmaturinus* under no climate change, a greenhouse gas mitigation policy scenario (LEV1), and a high-CO_2-concentration stabilisation reference scenario (WRE750). The initial population size was 350 individuals (dashed line). Baseline = baseline scenario that includes observed fire frequency and ongoing use of current population management methods; disease = beak-and-feather disease outbreak; - 50% indicates 50% reduction in fire frequency from increased management; +5%, +25%, and +220% (i.e., 2.2-fold increase) indicate increasing fire frequency from climate change. It was not realistic to model some fire increases for the no climate change or LEV1 scenarios. The last four groups of bars show the effects of ceasing management. "Revegetation", "corella", and "possum" indicate stopping revegetation, little corella *Cacatua sanguinea*, and brush-tail possum *Trichosurus vulpecula* management, respectively. "All" indicates stopping all management actions.

Sensitivity analysis

The Latin Hypercube sensitivity analysis indicated that model results were most heavily influenced by parameterisation of adult survival (top-ranked in each climate scenario) and carrying capacity (ranked second in each scenario; Fig. 5.5; Table S5.4). The standardised regression coefficients show that adult survival (low + high values from the segmented model) accounted for 35% (WRE750) to 52% (no climate change) of total sensitivity, while carrying capacity accounted for 21 to 32% of total sensitivity, respectively (Table S5.4). Decreased adult survival resulted in severe declines in GBC final population size, while increased adult survival had only slight or moderate effects because the modelled population, with the current survival estimate of 0.913, tracks carrying capacity with a positive population growth rate. Accordingly, varying carrying capacity also had substantial effects on final population size, especially for the WRE750 scenario where range area declines sharply. The other input parameters had small effects with sub-adult survival, fecundity, and dispersal listed in order of decreasing importance. The additional disease outbreak sensitivity analysis indicated that increasing disease frequency or impact did not have substantially different effects on the population unless they were combined in the same scenario (Table S5.5).

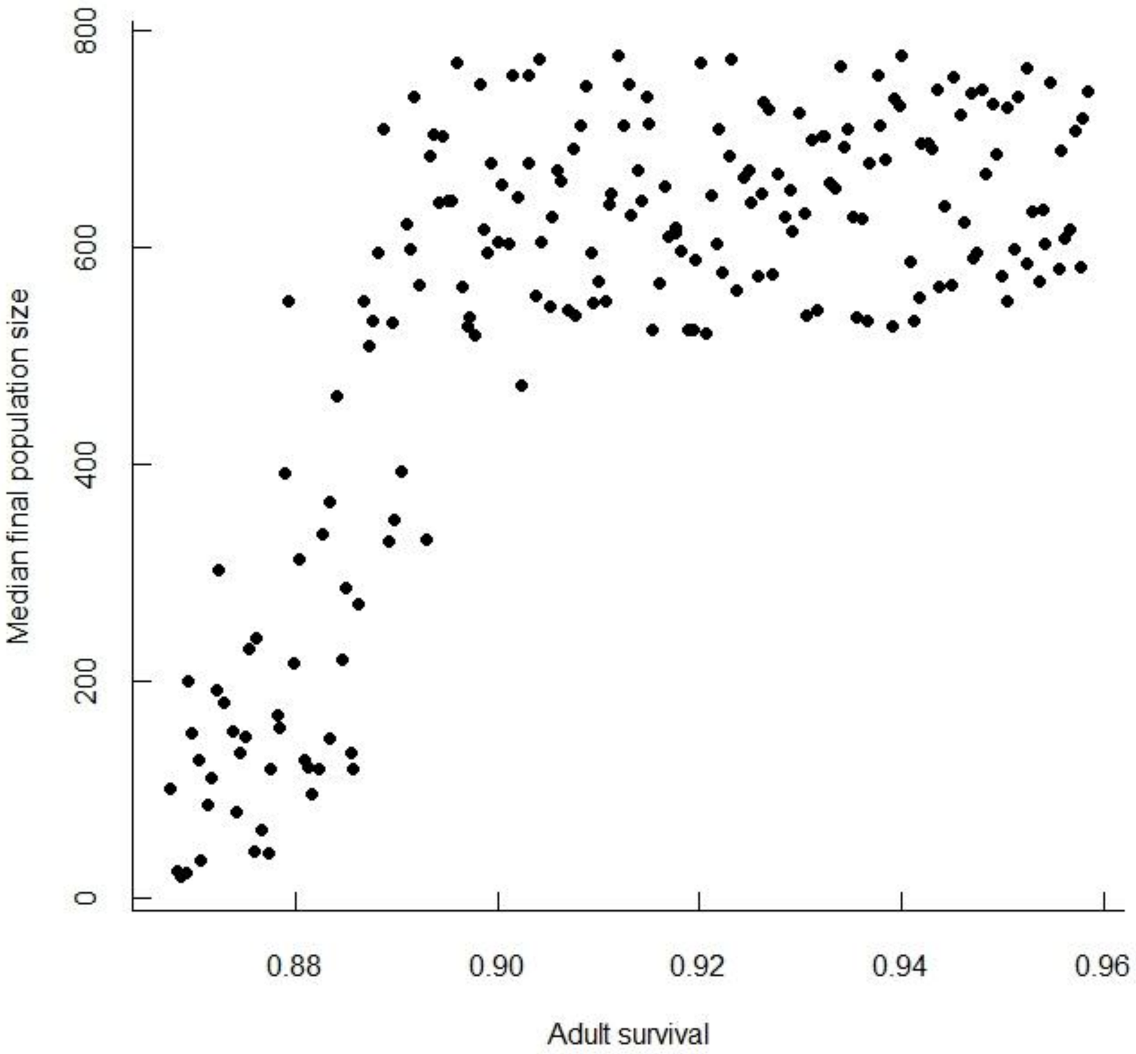

Figure 5.5. Relationship between uncertainty in adult survival and median final population size in a Latin Hypercube sensitivity analysis for the no climate change scenario. The breakpoint for the segmented generalised linear model was 0.89 and the slopes were 78.9 and 0.76 for the low and high parameters, respectively. The mean estimate for adult survival from the mark-resight analysis is 0.913 (95% confidence interval from 0.88 to 0.93).

Discussion

The population viability analysis for the South Australian glossy black-cockatoo illustrates the type of applied management questions that can be addressed using coupled demographic-bioclimatic approaches, as well as a method for incorporating dynamic vegetation-driven habitat change into animal population forecasts. The modelling indicates that the outlook for this small population depends strongly on continuous funding for management and global efforts to mitigate CO_2 emissions. The simulations suggest that GBC population size will increase under a low emissions future even if disease outbreaks were to occur, most management actions were reduced, and fire frequency were to increase. The gradual increase in the population over the last 15 years, combined with the large stands of underutilised *Allocasuarina verticillata* on the island, show the potential for continued population growth. In contrast, a failure to mitigate CO_2 emissions could severely reduce GBC range area, critically threatening long term population viability. Regardless of emissions scenario, our predictions indicate that the GBC's insular geographic constraints and low population size, which is well below estimates of minimum viable estimates for most species (Traill *et al.* 2010), may leave the species vulnerable to decline.

Climate change under high CO_2 emissions (WRE750) caused a large reduction in range area, and contraction to the cooler and wetter western plateau, while habitat changes under low emissions (LEV1) were minimal, with range area decreasing modestly and habitat suitability remaining almost constant. Under high emissions, population size did not decrease as rapidly as range area because habitat suitability and cockatoo density initially increased in the remaining habitat (Fig. 5.3). These results indicate that range area is unlikely to be linearly related to GBC abundance. Habitat differences translated into much lower expected minimum abundance (EMA) for all high emissions scenarios compared to low emissions and no climate change. A population of 150 animals is inherently at risk of extinction from stochastic small-population processes (Traill *et al.* 2010). We did not run simulations beyond 2100 because of uncertainty in climate projections, but such small population sizes at the end of the century do not bode well for the GBC's persistence under a high-CO_2-concentration scenario.

Simulating reduced brush-tail possum management had a profound impact on GBC EMA, while reduction in little corella management was almost negligible because of the resilient GBC population. The absence of a strong response to corella management indicates that culling could be experimentally stopped in some areas in an adaptive management framework to save resources. Simulated psittacine beak-and-feather disease outbreaks also had only slight effects on the GBC population. If mortality rates become higher and outbreak frequency is increased, disease could become a potent threat (Table S5.5). We suggest that continued vigilance and communication with organisations involved with disease management in other threatened parrots (e.g. *Neophema chrysogaster* Latham) is needed.

Our results indicate that revegetation is only having small effects on the population at present, but altered spatial patterns of *A. verticillata* abundance from climate change and the carrying capacity of 653 individuals will likely necessitate revegetation in the future. Our model assumed full dispersal and establishment of habitat trees (with implicit instantaneous seed production), which may overestimate *A. verticillata*'s ability to colonise new areas. Given the strong likelihood that emissions will exceed LEV1 levels (IPCC 2007) and that *A. verticillata* recruitment is limited by herbivores such as *Macropus eugenii* Desmarest, managers will likely need to revegetate to maintain *A. verticillata* and GBC populations. Although revegation effort could be reduced over the short term, key model assumptions (full dispersal and unlimitted recruitment of *A. verticillata*) and model sensitivity to variation in carrying capacity (driven by climate related changes in *A. verticillata*) mean that managers should be ready for intensive revegetation in the future.

Management and monitoring should focus on maintaining adult survival and fecundity at their current levels. The acute sensitivity of the model to lower (but still plausible) values of adult survival in the range of 85–90% emphasises the importance of monitoring adult survival over time. Predation from raptors such as *Aquila audax* Latham, climate variation, fire frequency, and food availability may be important drivers of adult survival (Mooney & Pedler 2005), but there was no evidence of changing survival during the study period, and these relationships are incompletely known. Threats to the GBC may change over time and the effects of climate variation on survival can be difficult to detect without monitoring datasets that span decades (Grosbois *et al.* 2008). Therefore we suggest that mark-resight and reproductive data should continue to be collected to build this unique dataset and allow ongoing analysis of the drivers of adult survival.

In addition to collecting data on the GBC, studies of *A. verticillata* are needed to improve forecasts of the GBC's extinction risk. In particular, studies on the effects of drought, warmer temperatures, and fire on *A. verticillata* survival, recruitment, and seed production are needed, especially given that climate change is likely to cause more extreme environmental events that would affect the life cycle of this food plant. New data could then be integrated with analyses that combine demographic models of both *A. verticillata* and the GBC.

Our approach minimised uncertainty by combining a comprehensive demographic dataset with rigorous methods, including mark-resight estimation of survival and ensemble bioclimatic and global climate modelling, yet the model's assumptions should be considered when interpreting our results. The projected range contraction of *Allocasuarina verticillata* under the high emissions scenario assumes that the species' distribution-climate relationship remains the same as today and that climate is the main driver of range changes (species interactions are not considered for this plant). In addition, our model assumes that the relationship between *A. verticillata* and the GBC will remain strong in the future.

In conclusion, the results of our coupled demographic-BEM simulations suggest that the GBC is likely to continue its population increase over time until carrying capacity is reached, provided the climate remains similar to today and intensive possum control continues. However, should unmitigated climate change or reduced adult survival occur, severe declines are probable. We recommend continued intensive life-history monitoring on the GBC, possum management, and research on *A. verticillata*, to promote the persistence of the GBC. The methods illustrated here demonstrate how species interactions can be included in coupled demographic-bioclimatic modelling approaches to add realism to forecasts of population viability under climate change for well-studied species of conservation concern. Furthermore, our analysis shows how coupled models can provide practical management advice in the face of broader issues and uncertainties such as global emissions mitigation.

Chapter 6

Conserving imperiled species: A comparison of the IUCN Red List and US Endangered Species Act

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STATEMENT OF AUTHORSHIP-CHAPTER 6

Conserving imperiled species: a comparison of the IUCN Red List and U.S. Endangered Species Act.

Conservation Letters – 2012, 5, 64-72.

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Signed: Date: 2 Apr 2012

J. Leighton Reid: Collected data, assisted with writing.
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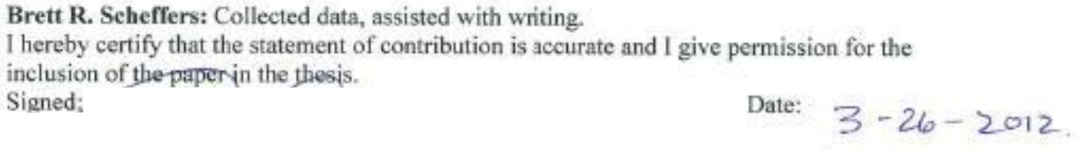

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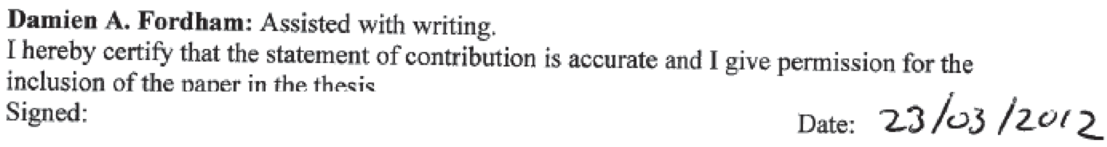

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Chapter 6 - Conserving imperiled species: A comparison of the IUCN Red List and US Endangered Species Act

Abstract

The United States conserves imperiled species with the Endangered Species Act (ESA). No studies have evaluated the ESA's coverage of species on the International Union for Conservation of Nature (IUCN) Red List, which is an accepted standard for imperiled species classification. We assessed the ESA's coverage of IUCN-listed birds, mammals, amphibians, gastropods, crustaceans, and insects, and studied the listing histories of three bird species and Pacific salmonids in more detail. We found that 40.3% of IUCN-listed US birds are not listed by the ESA, and most other groups are under-recognized by > 80%. Species with higher IUCN threat levels are more frequently recognized by the ESA. Our avian case studies highlight differences in the objectives, constraints, and listing protocols of the two institutions, and the salmonids example shows an alternative situation where agencies were effective in evaluating and listing multiple (related) species. Vague definitions of *endangered* and *threatened*, an inadequate ESA budget, and the existence of the *warranted but precluded* category likely contribute to the classification gap we observed.

Introduction

Imperiled species lists have a variety of important uses that include classifying species' conservation status, setting conservation priorities, and directing management (de Grammont & Cuarón 2006). While some imperiled species lists have been criticized because of their qualitative nature and application to multiple objectives (Possingham *et al.* 2002), the lists are firmly established as valuable tools for biological conservation (Lamoreux *et al.* 2003; Miller *et al.* 2007; Mace *et al.* 2008). The IUCN Red List is the most widely used global imperiled species list (e.g. Rodrigues *et al.* 2006; Schipper *et al.* 2008; BLI 2010), and its classifications are correlated with other leading systems such as NatureServe (O'Grady *et al.* 2004; Regan *et al.* 2005). The Red List classifies species as imperiled (*Critically Endangered*, *Endangered*, or *Vulnerable*), not imperiled (*Near Threatened* or *Least Concern*), extinct (*Extinct*, *Extinct in the*

Wild), or *Data Deficient* (IUCN 2001, 2009). If species meet quantitative thresholds of any of the following criteria they will be added to the Red List: (A) decline in population size, (B) small geographic range, (C) small population size plus decline, (D) very small population size, or (E) quantitative analysis. For example, if a species had an estimated population size of < 2 500 mature individuals, and had undergone a continuing decline of ≥ 20% over the last five years, it would be classified as *Endangered*. The IUCN Red List, like any categorical imperiled species classification, must make normative decisions that include risk tolerance in the designation of category boundaries; see IUCN (2001) for more details, and Mace *et al.* (2008) for the development and justification of Red List methods.

In addition to global imperiled species lists, many countries produce national red lists (local or regional imperiled species lists). These lists serve five major functions: (1) classifying the status of species at the local level where they are usually managed, (2) evaluating locally-imperiled species and imperiled subspecies, (3) informing local conservation prioritization, (4) providing data to the global Red List, especially for species not yet evaluated by the IUCN, and (5) in some cases, legally protecting species (Miller *et al.* 2007; Rodríguez 2008; Zamin *et al.* 2010). See http://www.nationalredlist.org/ for an up-to-date listing of countries with national red lists and the methods they employ.

One of the most prominent and legislatively important national red lists is the US Endangered Species Act (ESA). The ESA, passed in 1973 and administered by the US Fish and Wildlife Service (USFWS) and National Marine Fisheries Service (NMFS), classifies an at-risk species (including subspecies and distinct populations) as *endangered* if it is “in danger of extinction throughout all or a significant portion of its range” or *threatened* if it is “likely to become endangered in the foreseeable future throughout all or a significant portion of its range” (USFWS 2009a; Fig. S6.1; see supporting information). The USFWS is responsible for listing terrestrial and some marine species, while the NMFS lists marine species. Once a species is listed, the agencies work towards legally prohibiting “take” (killing, capturing, etc.), protecting critical habitat, and developing and implementing recovery plans for listed species (Schwartz 2008). Take of *endangered* animals is unconditionally prohibited, but for plants, only if they are on federal land. The agencies may develop a 4(d) rule to apply take prohibitions to *threatened* species. Designation of critical habitat and implementation of recovery plans are complicated processes that are not automatically applied by the USFWS (Schwartz 2008). The ESA has the power to stop development that will impact imperiled species. Hence there are more consequences and political obstacles to listing species under the ESA compared to lists that are not legally binding.

In short, the ESA is arguably the world's most effective biodiversity protection law. The act has succeeded in improving the conservation status of most listed species over time, and may have prevented 227 extinctions (Taylor *et al.* 2005; Schwartz 2008). Nonetheless, the US government's implementation of the ESA has been problematic, including poor coverage of imperiled species (Wilcove & Master 2005), inadequate funding (Miller *et al.* 2002; Stokstad 2005), and political intervention (Ando 1999; Greenwald *et al.* 2006; Stokstad 2007). Despite the existence of the ESA, an extinction crisis continues in the US (Elphick *et al.* 2010; Fig. S6.2). For instance, 29 species and 13 subspecies went extinct while being considered for listing from 1973–1995 (Suckling *et al.* 2004). Most of these species already had very small population sizes when listing was proposed (*sensu* McMillan & Wilcove 1994), but several species, such as Curtus's pearly mussel (*Pleurobema curtum*), likely could have been conserved had they been listed rapidly (Suckling *et al.* 2004).

Studies have analyzed the ESA's coverage of species on the NatureServe list, a leading classification of imperiled species in the US (http://www.natureserve.org; Stokstad 2005; Wilcove & Master 2005; Greenwald *et al.* 2006), but, to our knowledge, no previous work has evaluated the ESA's coverage of IUCN-listed species. In the most comprehensive NatureServe comparison, Wilcove and Master (2005) investigated the ESA's coverage of plants, fungi, and animals considered imperiled on NatureServe's (2005) list. Wilcove and Master (2005) estimated that at least 90% of the country's imperiled species are not covered by the ESA. Given that the Red List is becoming the benchmark for global imperiled species classifications (e.g. Mace *et al.* 2008), an evaluation of the ESA's coverage of IUCN-listed species is needed. We refined previous work by focusing on birds, which are one of the best-known animal groups, and for which classification patterns might approximate a best case scenario. Then we looked in detail at three IUCN-listed birds that are not ESA-listed and, more generally, Pacific salmonids as case studies of classification under the ESA. We also compared classifications of insects, crustaceans, gastropods, amphibians, and mammals to evaluate if similar patterns existed to the previous NatureServe comparisons. Considering Wilcove and Master's (2005) results, we hypothesized that many US IUCN-listed species would not be recognized by the ESA, and that poorly-studied and lower risk species (*Vulnerable* compared to *Critically Endangered*) would more likely be overlooked.

Methods

Our evaluation of the ESA's coverage of IUCN-listed species was not intended to evaluate extinction risk, but to provide a general indication of the breadth of coverage of the ESA compared to the Red List. The Red List – based on proxy measures of risk – is imperfect, but it is the most widely used, and among the most encompassing systems for global and national red lists (Lamoreux *et al.* 2003; de Grammont & Cuarón 2006; Rodrigues *et al.* 2006; Miller *et al.* 2007; Mace *et al.* 2008).

We compared classifications for all IUCN-listed birds known to be resident or fairly common visitors in the US including Hawaii and Alaska (Pyle 2002; Dunn & Alderfer 2006). IUCN classification data came from BirdLife International's website (BLI 2010); ESA classifications came from the ESA website (USFWS 2009b). We followed the taxonomy of Chesser *et al.* (2010). If the ESA listed a single subspecies or a single population of an IUCN-listed species we considered the species to be covered by the ESA. We also collated data on *Extinct*, *Extinct in the Wild*, and *Possibly Extinct* birds (BLI 2010) and plotted these over time. Our extinction data were collected independently but are complimentary to Elphick *et al.*'s (2010) analysis which focused on estimating extinction dates.

For the case studies we examined IUCN-listed birds in Table 6.1 that were evaluated by the ESA, yet still not ESA-listed. We selected three species with adequate conservation status information and well-documented listing histories: Kittlitz's murrelet (*Brachyramphus brevirostris*), ashy storm-petrel (*Oceanodroma homochroa*), and cerulean warbler (*Dendroica cerulea*). We reviewed the peer-reviewed and gray literature for each species to examine the species's conservation status and IUCN and ESA listing history. While all three species have large or relatively large ranges, each has undergone population declines and been listed as imperiled by the IUCN since 2004. Given that these species were not selected randomly, we do not mean to imply that their cases can be generalized to all imperiled birds in the US; rather, the case studies are examples of what can happen when declining, IUCN-listed species are considered for ESA listing. We also present the case of Pacific salmonids (Salmonidae: *Oncorhynchus*) as an example where US agencies were successful at evaluating and listing multiple species proactively.

To evaluate if patterns found in previous NatureServe comparisons were evident in IUCN data (IUCN 2009), we compared classifications for all insects, crustaceans, gastropods, amphibians, and mammals evaluated by the IUCN in the US. We studied classifications in animals because the IUCN has evaluated many more animals than plants or fungi, and we selected the six animal groups because they represent a broad sample of taxonomy, distribution, and habitats. The IUCN has not yet evaluated all US resident insects, crustaceans, or gastropods, so our comparisons for these groups are not as representative as for birds, mammals, or amphibians. Nonetheless, the IUCN has evaluated more US species of these groups than the ESA (IUCN 2009; USFWS 2009b), and our comparison gives baseline coverage of each group which should complement previous NatureServe comparisons.

Results

Birds

Of the 62 IUCN-listed birds in the US, 25 species (1 *Critically Endangered*, 6 *Endangered*, 18 *Vulnerable*; 40.3% of the total) are not listed by the ESA (Table 6.1). Ten of the 25 species not listed by the ESA are endemic to the US (40%). Species in IUCN categories of lower risk are more likely to be unrecognized: 5.3% of *Critically Endangered*, 42.9% of *Endangered*, and 62.1% of *Vulnerable* birds are not recognized by the ESA. Conversely, 23 bird species (29 total taxa including subspecies and populations) are ESA-listed as imperiled but not considered by the IUCN to be globally imperiled (6 *Near Threatened* and 17 *Least Concern*; Table S6.1).

Twenty-three US-resident bird species have gone extinct since 1825 (including one species, *Corvus hawaiiensis*, which survives only in captivity) (Fig. 6.1). In addition, seven species are *Possibly Extinct* with the last confirmed sightings ranging from 1937 to 2004. Plotting the last confirmed sightings of *Extinct*, *Extinct in the Wild*, and *Possibly Extinct* birds by decade shows extinction peaks in the 1890s and 1980s (Fig. S6.2). Of the 23 extinct species, 21 were endemic to Hawaii (as well as 5 of the 7 *Possibly Extinct* species). Two species have been declared *Extinct* (*Moho braccatus* and *Myadestes myadestinus*), one *Extinct in the Wild* (*C. hawaiiensis*), and six *Possibly Extinct* (*Numenius borealis*, *Myadestes lanaiensis*, *Psittirostra* *psittacea*, *Hemignathus lucidus*, *Paroreomyza maculata*, and *Melamprosops phaeosoma*) since the passage of the ESA. *Vermivora bachmanii* was probably extinct when the ESA was passed, and the other species already had very small population sizes (with the possible exceptions of *Myadestes myadestinus* and *Melamprosops phaeosoma*).

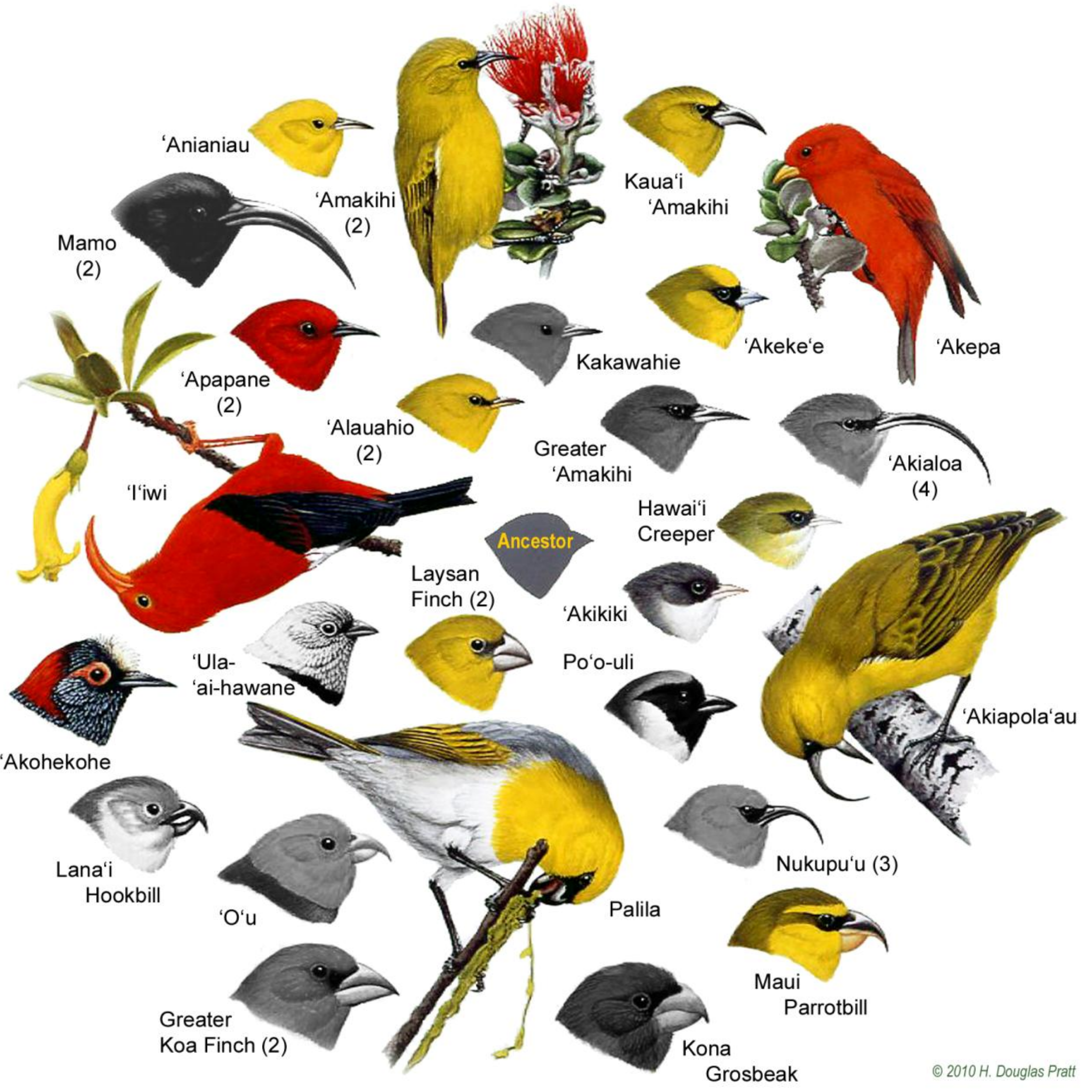

Figure 6.1. Hawaiian honeycreepers in peril. Extant species are in color; extinct and possibly extinct species are in grayscale. Five of the extant species shown (alauahio, kauai amakihi, anianiau, and iiwi) are IUCN-listed species that are unrecognized by the ESA. Numbers in parentheses specify how many species appear similar to the illustration. Note that akikiki is extant. Paintings and labels © H. Douglas Pratt, revised from Pratt (2005, Plate 7), used by permission.

Table 6.1. Endangered Species Act status (*endangered* (E), *threatened* (T), or not listed) of IUCN-listed extant and possibly extinct birds in the United States organized by IUCN category. Twenty-five of the 62 IUCN-listed imperiled birds in the United States are not listed by the Endangered Species Act (IUCN 2009; USFWS 2009b; BLI 2010).

Species and IUCN classification	ESA classification
Critically Endangered	
Laysan duck (*Anas laysanensis*)	E
California condor (*Gymnogyps californianus*)	E
Eskimo curlew (*Numenius borealis*)*[†]	E
Kittlitz's murrelet (*Brachyramphus brevirostris*)*	not listed
ivory-billed woodpecker (*Campephilus principalis*)*	E
millerbird (*Acrocephalus familiaris*)	E
olomao (*Myadestes lanaiensis*)[†]	E
puaiohi (*Myadestes palmeri*)	E
nihoa finch (*Telespiza ultima*)	E
ou (*Psittirostra psittacea*)[†]	E
palila (*Loxioides bailleui*)	E
Maui parrotbill (*Pseudonestor xanthophrys*)	E
nukupuu (*Hemignathus lucidus*)[†]	E
akikiki (*Oreomystis bairdi*)	E
Oahu alauahio (*Paroreomyza maculata*)[†]	E
akekee (*Loxops caeruleirostris*)	E
akohekohe (*Palmeria dolei*)	E
poo-uli (*Melamprosops phaeosoma*)[†]	E
Bachman's warbler (*Vermivora bachmanii*)*[†]	E
Endangered	
Gunnison sage-grouse (*Centrocercus minimus*)	not listed
Hawaiian duck (*Anas wyvilliana*)	E

black-footed albatross (*Phoebastria nigripes*)*	not listed
black-capped petrel (*Pterodroma hasitata*)*	not listed
Newell's shearwater (*Puffinus newelli*)	T
ashy storm-petrel (*Oceanodroma homochroa*)*	not listed
whooping crane (*Grus americana*)*	E
marbled murrelet (*Brachyramphus marmoratus*)*	T
akiapolaau (*Hemignathus munroi*)	E
Hawaii creeper (*Oreomystis mana*)	E
Maui alauahio (*Paroreomyza montana*)	not listed
akepa (*Loxops coccineus*)	E
golden-cheeked warbler (*Dendroica chrysoparia*)*	E
tricolored blackbird (*Agelaius tricolor*)*	not listed

Vulnerable

Hawaiian goose (*Branta sandvicensis*)	E
Steller's eider (*Polysticta stelleri*)*	T
greater prairie-chicken (*Tympanuchus cupido*)	E[‡]
lesser prairie-chicken (*Tympanuchus pallidicinctus*)	not listed
short-tailed albatross (*Phoebastria albatrus*)*	E
Hawaiian petrel (*Pterodroma sandwichensis*)*	E
pink-footed shearwater (*Puffinus creatopus*)*	not listed
buller's shearwater (*Puffinus bulleri*)*	not listed
Hawaiian coot (*Fulica alai*)	E
bristle-thighed curlew (*Numenius tahitiensis*)*	not listed
red-legged kittiwake (*Rissa brevirostris*)*	not listed
Xantus's murrelet (*Synthliboramphus hypoleucus*)*	not listed
red-cockaded woodpecker (*Picoides borealis*)	E
black-capped vireo (*Vireo atricapilla*)*	E
elepaio (*Chasiempis sandwichensis*)	E
Florida scrub-jay (*Aphelocoma coerulescens*)	T
pinyon jay (*Gymnorhinus cyanocephalus*)	not listed
bendire's thrasher (*Toxostoma bendirei*)*	not listed
omao (*Myadestes obscurus*)	not listed
bicknell's thrush (*Catharus bicknelli*)*	not listed

sprague's pipit (*Anthus spragueii*)*	not listed
Laysan finch (*Telespiza cantans*)	E
Kauai amakihi (*Hemignathus kauaiensis*)	not listed
Oahu amakihi (*Hemignathus flavus*)	not listed
anianiau (*Magumma parva*)	not listed
iiwi (*Vestiaria coccinea*)	not listed
cerulean warbler (*Dendroica cerulea*)*	not listed
rusty blackbird (*Euphagus carolinus*)*	not listed
saltmarsh sparrow (*Ammodramus caudacutus*)	not listed

*Not endemic to the United States.

[†] Possibly extinct (IUCN 2009).

[‡] Attwater’s race (*Tympanuchus cupido attwateri*).

Other animal groups

Our evaluation of the ESA’s coverage of IUCN-listed insects, crustaceans, gastropods, amphibians, and mammals indicates that under-recognition of IUCN-listed species is not restricted to birds. We found 50% under-recognition for mammals, 80% under-recognition for amphibians, and 88.9–95.2% under-recognition for the invertebrates, which contributed to a mean of 74.1% under-recognition overall (Table 6.2). *Vulnerable* species (IUCN classification) were more often unrecognized (mean of 83.2%) compared to *Critically Endangered* (67.3%) or *Endangered* (64.9%) (Table 6.2).

Table 6.2. Coverage of IUCN-listed animals (IUCN 2009) by the US Endangered Species Act (USFWS 2009b). IUCN categories: CR = *Critically Endangered*, EN = *Endangered*, VU = *Vulnerable*. Percent of species that are unrecognized by the ESA are given in parentheses. For across-group totals, the mean percent of species unrecognized (± SE) is given.

	Number of CR species	CR species not recognized	Number of EN species	EN species not recognized	Number of VU species	VU species not recognized	Number of species evaluated by IUCN	Total IUCN-listed species	Total un-recognized
Amphibians	2	2 (100)	17	13 (76.5)	36	29 (80.6)	272	55	44 (80)
Birds	19	1 (5.3)	14	6 (42.9)	29	18 (62.1)	888	62	25 (40.3)
Mammals	4	2 (50)	20	7 (35)	12	9 (75)	451	36	18 (50)
Gastropods	62	57 (91.9)	30	27 (90)	103	92 (89.3)	458	195	176 (90.3)
Insects	10	8 (80)	12	10 (83.3)	83	82 (98.8)	207	105	100 (95.2)
Crustaceans	17	13 (76.5)	37	23 (62.2)	135	132 (97.8)	203	189	168 (88.9)
Total	114	83 (67.3 ± 14.2)	130	86 (64.9 ± 9.1)	398	362 (83.2 ± 5.8)	2479	642	531 (74.1 ± 0.09)

Discussion

Our data indicate that 40.3% of the US's IUCN-listed birds and more than 80% of lesser-known taxa have not been placed on the ESA list of *endangered* and *threatened* species. This under-recognition of species on one of the leading global lists suggests that the US system is failing to keep pace with global listing assessments of imperiled species. It is unlikely that this classification gap can be attributed to species being stable in the US but imperiled in their range outside the country. All unrecognized non-endemic birds (Table 6.1) have substantial proportions of their breeding and/or non-breeding range in the US. Possible exceptions are *Pterodroma hasitata*, *Puffinus creatopus*, and *P. bulleri*, but these three species are fairly common to common non-breeding visitors to waters off the US coast and therefore are eligible for listing even though they are not US breeders. The ESA includes other non-breeding species (e.g. *Numenius borealis*).

The ESA list includes 23 species of birds that are *Near Threatened* or *Least Concern* globally (Table S6.1). Nineteen of these species have only some populations or subspecies listed, which shows the ESA is protecting some regionally-imperiled species. The remaining species, *Somateria fischeri*, *Buteo solitarius*, *Charadrius melodus*, and *Dendroica kirtlandii*, are ESA-listed in their entire range, but not by the IUCN, probably as a result of differences in listing criteria between the ESA and IUCN.

Bird species considered less-imperiled on the IUCN scale are more likely to not be listed under the ESA. Along these lines, Scott *et al.* (2006) found that nearly 80% of species listed by the ESA are *endangered* rather than *threatened*. There are several potential explanations for these patterns that are not mutually exclusive. The USFWS may: (1) list severely-imperiled species first, due to an inability to consider all species at once, (2) primarily list species as a result of pressure from citizen petitions, which could focus on highly imperiled species, or (3) accept a higher risk of extinction compared to the IUCN. Risk prioritization seems to occur. Wilcove *et al.* (1993) found very small population sizes at the time of listing for 1,075 vertebrates and 999 invertebrates listed from 1985–1991, suggesting that species are not listed until they are highly imperiled. Outside pressure is also likely to be important. Petitions and/or lawsuits were involved with 71% of listings from 1974–2003 and have become even more important in recent years (Greenwald *et al.* 2006). In fact, the USFWS is so occupied with petitions and lawsuits from citizen groups that its ability to advance its own listing priorities is hampered (Stokstad 2005), and it requested a sub-cap to limit funding used to address petitions (USFWS 2011). Differences in risk tolerance may also contribute to classification differences between the IUCN and ESA.

The ESA might be expected to list only highly-imperiled species because listing results in legal protection, unlike the IUCN which has no legal enforcement ability in the US.

This pattern of delaying listing until species are critically imperiled could be interpreted optimistically; at least the majority of species facing the greatest threat are protected. Unfortunately, chances of recovery are much reduced for highly-imperiled species (Traill *et al.* 2010). The recent cases of two Hawaiian birds, akikiki *Oreomystis bairdi* and akekee *Loxops caeruleirostris*, are prime examples (Fig. 6.1). Both were long known to be in serious trouble (listed by the IUCN as *Endangered* in 1994 and *Critically Endangered* in 2004 and 2008, respectively), but neither was listed by the ESA until 2010, while the akekee population continued to decline steeply (ABC 2008). Listing species before they reach critical imperilment would reduce extinctions and probably costs. It would be interesting for a future study to quantify the USFWS's savings from protecting species under the ESA when they are *Vulnerable* compared to *Critically Endangered*.

Our avian case studies (supporting information) exemplify USFWS decisions to not list declining, IUCN-listed species, and illustrate problems associated with vague categories, inadequate funding, and the *warranted but precluded* category. All three cases would have been more straightforward to resolve if clear, quantitative thresholds were included in the definitions of *threatened* and *endangered*. The effects of funding constraints were especially clear in the cerulean warbler's case where the USFWS took six years to reach a decision. The Kittlitz's murrelet case highlights the paradox of the *warranted but precluded* category; it seems unlikely that funds are so limited, or the *Critically Endangered* murrelet's priority is so low, that it should not be listed. While the USFWS is required to make a decision in 12 months, all three case study species experienced protracted listing times of 22 months to six years. These listing times are actually shorter than average; Greenwald *et al.* (2006) found the mean listing time for all species from 1974–2003 was >10 years.

In contrast to the avian case studies, the salmon case shows how the agencies can objectively and proactively list large groups of species by advancing their own listing priorities (supporting information). In the 1990s the NMFS coordinated teams of scientists to evaluate salmonids in Washington, Idaho, Oregon, and California. By 1999, the NMFS had listed 21 evolutionary significant units of salmonids as *threatened* and five as *endangered*. This case is an example of how science can be effectively translated to ESA policy. Public awareness of the value of salmonids for food and fishing likely contributed to the NMFS's comprehensive actions. Therefore, it seems reasonable that listing of other groups, such as unlisted birds in Table 6.1, could be accelerated if public interest in imperiled species increased (Schwartz 2008).

The multi-taxa results suggest that under-recognition of IUCN-listed birds and mammals is less severe than in other, lesser-known groups (Table 6.2). This pattern could be explained if the USFWS accepts variable levels of extinction risk among taxa or if poorly-known groups tend to be neglected (Wilcove & Master 2005). Wilcove and Master (2005) estimated that approximately 90% of the US's imperiled species (including animals, fungi, and plants) are not included on the ESA list. Given that Wilcove and Master's (2005) estimate was an extrapolation based on a few well-known groups, it is difficult to compare our results. Nonetheless, our finding of 74.1% under-recognition of IUCN-listed animals suggests the ESA covers more IUCN-listed species than NatureServe-listed species.

Our data indicate that a nearly 10-fold increase in listing would be required for the ESA to protect the gamut of IUCN-listed species. Considering the history and objectives of the two institutions, it is not surprising that the ESA covers fewer species. The Red List is intended to identify all imperiled species and has no regulatory apparatus. The ESA, however, legally protects species, so adding a species bears significant cost and responsibility to the agencies (funding per species is greater for the NMFS compared to the USFWS). The ESA is additionally influenced by politics because listing can have profound economic consequences (Ando 1999). If protecting all IUCN-listed species under the ESA is an unattainable endpoint, then triage could play a role in dictating listing decisions once all species are evaluated with objective and thorough procedures. A critical question under triage would be how to prioritize species based on endangerment, recovery likelihood, taxonomic uniqueness, and cost (Bottrill *et al.* 2008). We hold that listing a full complement of imperiled species under the ESA is not an insurmountable task.

Vague definitions of the *threatened* and *endangered* categories may also contribute to a lack of congruence between the ESA and IUCN lists (see Introduction for definitions). The ESA has been in place since 1973, but there is still ample room for debate on the meaning of these two key terms (Greenwald 2009; D'Elia & McCarthy 2010). There is a division between science and policy in ESA implementation by design, where science informs, but does not dictate, listing policy (Laband & Nieswiadomy 2006). In the case of the ashy storm-petrel, a lack of consensus when science informed policy delayed the listing decision and led to an outcome that is still contested by citizen groups and will likely incur further litigation costs to the USFWS. Such consequences from vague categories might be avoided if precedent quantitative thresholds were in place to guide decision-making when science is translated to policy. The IUCN uses unambiguous criteria, objective categories that measure probability of extinction, and a dynamic system that quantifies uncertainty in assessments (de Grammont & Cuarón 2006). Incorporating similarly quantitative attributes in the ESA decision-making framework would improve credibility of listing decisions and could reduce replication of effort between the USFWS and non-governmental institutions such as the IUCN and NatureServe (Arroyo *et al.* 2009). Further, if ESA classifications eventually became more similar to IUCN methods, ESA data would be more useful for informing the Red List (Rodríguez 2008), which is an important function of national red lists to which the ESA does not currently contribute (Miller *et al.* 2007). Countries such as Singapore that use IUCN methods are able to evaluate hundreds of species in a few years (Davison *et al.* 2008); such rapid assessments could help reduce the backlog of ESA candidate species.

An increase to the ESA listing budget could speed the closing of the classification gap. External and internal observers agree that budgetary constraints are a primary barrier to listing species in a timely manner (GAO 1979; Stokstad 2005; USFWS 2006; Greenwald *et al.* 2006; Schwartz 2008). The protracted decision making in our avian case studies supports this conclusion.

Finally, we find that the *warranted but precluded* category compounds the classification gap by excluding imperiled species from the ESA. *Warranted but precluded* was created in 1982 to designate species that should be listed, but for which listing is currently precluded because of funding constraints (supporting information). While w*arranted but precluded* findings can occasionally stimulate conservation efforts to prevent species from declining further (WGA 2011), this category has often been used by the USFWS as a loophole to slow listing (Greenwald *et al.* 2006). Given that citizen groups are unlikely to reduce pressure following *warranted but precluded* decisions, this category may be more likely to increase, rather than decrease long-term conservation costs.

In conclusion, our research agrees with previous findings that most of the United States' imperiled species are not yet listed under the ESA. Our data indicate that less-imperiled (but at-risk) species are most likely to be overlooked, which does not bode well for the ESA's ability to mitigate declines before species become critically imperiled. Our avian case studies exemplify how a lack of consensus on key definitions, funding constraints, and the *warranted but precluded* category likely contribute to the classification gap between IUCN and ESA lists. By contrast, the salmonids case study shows how the agencies can proactively evaluate and list large groups of (albeit closely-related) species.

Conclusion

In summary, chapter 2 (the first data chapter of the PhD thesis) presents the first field measurements of widespread avian range shifts from climate change in Southeast Asia. These results, along with Peh's (2007) findings, indicate that Southeast Asian birds are shifting their ranges in a manner similar to Neotropical birds (Pounds et al. 2005; Forero-Medina et al. 2011a), and managers will need to plan for and react to climate-change-induced range changes in the region. Chapter 3's results indicate the severity future deforestation and climate change impacts on tropical birds will at least partially depend on the width and location of their elevational range. In our study, middle-elevation species were more threatened by deforestation, while high-elevation species were vulnerable to climate change. Chapter 4 shows, for the first time, that tropical birds are changing their migratory phenology in response to climate change, and in an unexpected fashion, with long-distance migrants delaying autumn arrival.

Taken together, the results of the Southeast Asian chapters indicate that birds in this region are already responding to climate change and many species appear to be threatened by climate change in the future. These results agree with findings from a growing body of studies (e.g. Jetz et al. 2007; Sekercioglu et al. 2008) that suggest extinction risk of upland tropical birds is substantially underestimated by the current IUCN Red List rules, which have no obvious means to incorporate this risk directly. More studies are sorely needed to clarify our understanding of climate-change impacts on tropical species, and refine threatened species assessments (chapter 1). Almost no studies have been done to evaluate the dynamics of novel communities created by climate-induced range shifts in the tropics, or of the synergistic (reinforcing) feedbacks that may result from the interactions of climate change, habitat loss, invasive species, disease emergence, and over hunting. For example, we found that the brood parasitic dark hawk-cuckoo *Hierococcyx bocki* is colonising higher elevations on Mt. Kinabalu (chapter 2), but no studies have evaluated the impacts of dark hawk-cuckoos on highland bird communities. In addition to the impacts of colonising brood parasites and predators, lowland colonists may carry diseases and parasites, or the pathogens themselves may shift upwards

(Harvell et al. 2002). Furthermore, colonising lowland generalists may outcompete highland endemics, but this has only been evaluated by one study (Jankowski et al. 2010). This area of research is ripe for further investigation, but the lack of studies should not be an excuse for reduced vigilance. Few recent extinctions have been documented as being directly attributable to climate change (Pounds et al. 2006), but it is likely that disturbance caused by climate change will cause avian declines, especially when combined with other factors such as habitat loss. It should be a priority of the IUCN to work towards formally incorporating climate change impacts (including predictions) in their assessments.

Chapter 5 found that the glossy black-cockatoo in southern (temperate) Australia is likely to be threatened by high-emissions-driven climate change or reduced brush-tail possum management, but other less critical conservation management initiatives could be phased out experimentally, to save resources. This chapter demonstrates how coupled demographic-distribution models make predictions made more realistic, and test management scenarios, while considering broader issues and uncertainties such as global climate change.

Chapter 6 focused on the IUCN Red List and showed that one of the world's best-known national red lists, the US Endangered Species Act, is overlooking 40% of the country's IUCN-listed birds. Furthermore, the results indicate that the ESA tends to postpone listing until species are critically imperilled. While the ESA has had many successes, our findings indicate there is much room for improvement.

The determinants of avian range boundaries are poorly understood. As I discussed in chapter 1, it is likely that climate, competition, and habitat are all important range determinants (Terborgh and Weske 1975; Ghalambor et al. 2006; Price and Kirkpatrick 2009; Jankowski et al. 2010; Gifford and Kozak 2011; chapter 5). But, at this stage so little is known of the relative effects of these processes on bird ranges that it was impossible to include these complex effects in chapters 2–4.

As in animals, the impacts of climate change on plants are better studied in the temperate zone compared to the tropics. Long-term studies have revealed that warming temperatures are driving upslope range shifts in many temperate (Lenoir et al. 2008; Pauli et al. 2012) and subtropical (Jump et al. 2012) plants, as long as there is adequate precipitation for the shifting species (Crimmins et al. 2011; Fajardo and McIntire 2012). Only two studies have measured changes in tropical plant distributions (Feeley et al. 2011; Feeley 2012). Both studies found that

South American plant distributions are shifting upslope, but more slowly than animals. Feeley et al. (2011) found that plant range midpoints are shifting upslope, while Feeley (2012) found evidence for upper, but not lower, range margins shifting upslope. These findings agree with theoretical predictions of plant responses to climate change where dispersal-limited plants do not migrate rapidly, but are more productive at the upper range margin, and die back at the lower range margin (Breshears et al. 2008; Corlett 2009).

Animals are also shifting upward, in accordance with warming temperatures. Several tropical studies have found evidence for climate-related upward range shifts in invertebrates (Chen et al. 2009, 2011), ectothermic vertebrates (Seimon et al. 2007; Raxworthy et al. 2008), and endothermic vertebrates (Pounds et al. 1999, 2005; Forero-Medina et al. 2011). The animal studies include insects on Mt. Kinabalu which suggests that some avian prey items are shifting upslope. The South American plant studies suggest that plants are becoming more productive at their upper range margins, and slowly shifting upward, which could provide suitable bird habitat.

The lack of geographical overlap between the floral and faunal studies, combined with the lack of research on competitive avian interactions (see discussion in chapter 2), makes it difficult to attribute mechanisms to the range changes we observed (chapter 2) and modelled (chapter 3). We hypothesise that habitat shifts, competitive interactions, and physiological responses to warming temperatures all contribute to avian range shifts on tropical mountains. Disentangling the relative impacts of these three variables is a research avenue of great potential. Physiological experiments have succeeded in attributing the relative importance of these drivers in ectotherms (Gifford and Kozak 2011), but no such studies have been done on birds, and these are urgently needed (La Sorte and Jetz 2010b).

In conclusion, my results indicate that climate change will be one of the most potent extinction drivers for tropical and temperate birds over the next century. Birds are one of the best-known groups of organisms, but study of the effects of climate change on birds is in its infancy. Future field work should focus on abundance surveys along elevational gradients and long-term studies that monitor changing community ecologies. Predictive models of climate-change-biodiversity impacts can be made more realistic by including dynamic land cover information, species interactions, demography, physiology, and adaptive potential. To date, scientists have focused on predicting the effects of climate change on birds. Empirical measurements of climate change impacts have lagged behind and should be prioritised over predictions, at least in the short term.

Appendices

Appendix 1- Supplementary Material for Chapter 2

Online Appendix: Range characterisations for 317 bird species on Mt. Kinabalu, Borneo. See http://www.adelaide.edu.au/directory/bert.harris for access to this 52 page appendix.

Table S2.1. Location and elevation of JBCH's point counts. Note that the point ID numbers shown in Fig. 2.2 were for display purposes only.

Point ID	Elevation	Coordinates
K 42	516 m	6.04826˚ N, 116.70244˚ E
K 41	523 m	6.0462˚ N, 116.70332˚ E
K 43	540 m	6.0504˚ N, 116.70179˚ E
K 44	614 m	6.05208˚ N, 116.70027˚ E
K 45	700 m	6.05322˚ N, 116.69832˚ E
K 46	748 m	6.05553˚ N, 116.69812˚ E
K 47	808 m	6.05687˚ N, 116.69636˚ E
K 48	893 m	6.05883˚ N, 116.69525˚ E
K 50	920 m	6.06189˚ N, 116.69195˚ E
K 49	927 m	6.06031˚ N, 116.69357˚ E
K 51	961 m	6.0625˚ N, 116.68982˚ E
K 52	1003 m	6.06355˚ N, 116.68782˚ E
K 1	1465 m	6.00705˚ N, 116.5495˚ E
K 2	1504 m	6.00859˚ N, 116.54781˚ E
K 3	1509 m	6.01056˚ N, 116.54663˚ E
K 4	1531 m	6.01096˚ N, 116.54433˚ E
K 5	1547 m	6.01318˚ N, 116.54479˚ E
K 6	1564 m	6.01489˚ N, 116.54639˚ E

K 7	1594 m	6.01711˚ N, 116.54631˚ E
K 8	1620 m	6.01879˚ N, 116.54779˚ E
K 9	1648 m	6.02109˚ N, 116.54813˚ E
K 10	1688 m	6.02301˚ N, 116.54936˚ E
K 12	1779 m	6.02742˚ N, 116.54959˚ E
K 11	1780 m	6.02519˚ N, 116.54997˚ E
K 13	1789 m	6.0294˚ N, 116.5486˚ E
K 14	1859 m	6.03108˚ N, 116.54717˚ E
K 15	1921 m	6.03065˚ N, 116.54941˚ E
K 16	2023 m	6.03297˚ N, 116.5495˚ E
K 17	2052 m	6.03504˚ N, 116.5503˚ E
K 18	2117 m	6.03731˚ N, 116.55009˚ E
K 19	2200 m	6.03958˚ N, 116.55034˚ E
K 20	2268 m	6.04147˚ N, 116.55157˚ E
K 21	2322 m	6.0413˚ N, 116.55377˚ E
K 22	2446 m	6.04164˚ N, 116.556˚ E
K 23	2556 m	6.04191˚ N, 116.55824˚ E
K 24	2629 m	6.04334˚ N, 116.55996˚ E
K 25	2703 m	6.04558˚ N, 116.56007˚ E
K 26	2806 m	6.04738˚ N, 116.56137˚ E
K 27	2895 m	6.04898˚ N, 116.56301˚ E
K 28	2948 m	6.05113˚ N, 116.5636˚ E
K 29	3036 m	6.0532˚ N, 116.56442˚ E
K 30	3115 m	6.05527˚ N, 116.56525˚ E
K 31	3221 m	6.05745˚ N, 116.56579˚ E
K 32	3294 m	6.05967˚ N, 116.56623˚ E
K 33	3410 m	6.06181˚ N, 116.56715˚ E
K 34	3555 m	6.06403˚ N, 116.56703˚ E
K 35	3697 m	6.06557˚ N, 116.56529˚ E
K 36	3799 m	6.06604˚ N, 116.56302˚ E
K 37	3859 m	6.06781˚ N, 116.56165˚ E
K 38	3946 m	6.07˚ N, 116.56101˚ E
K 39	3976 m	6.07214˚ N, 116.56021˚ E
K 40	4022 m	6.07389˚ N, 116.55877˚ E

Appendix 2-Supplementary Material for Chapter 3

Supplementary Methods

Zero-inflated abundance modeling

Following Zeileis et al. (2008), we used AIC to compare support for Poisson generalized linear models, zero-inflated regression, and hurdle regression for capturing relationships between elevation, aspect and bird abundance in the `pscl` package (Jackman 2011) in `R` (R Development Core Team 2011). The sum of counts from all three sampling sessions at each point count was used as the response variable. For each species we compared linear and second order polynomial parameterizations for elevation to test for a non-linear relationship between elevation and abundance. The residual deviance divided by the degrees of freedom from the top-ranked Poisson model for each species (**abundance ~ poly(elevation,2)**) was close to one (0.61-1.36 for the four study species). This result indicated our data were not substantially overdispersed (Crawley 2007), and Poisson errors were preferable over negative binomial (Potts & Elith 2006). Zero-inflated regression uses mixture models made up of a count component and a point mass at zero (Zeileis et al. 2008). Our hurdle models used a binomial component to model presence versus absence and a Poisson component to model non-zero counts (Mellin et al. 2012).

Calculating the adiabatic lapse rate

Musser (1982) collected temperature data at two sites (Mt. Nokilalaki summit [2279 m] and at 2061 m) continuously from 4 March to 2 May 1975. He also collected temperature data at Tomado, near Lake Lindu (1061 m; c. 15 km from Mt. Nokilalaki) from 16 September to 2 November 1974. The mean minimum temperatures over these periods were 10.6, 12.6, and 19.1 °C for 2279 m, 2061 m, and 1061 m, respectively, which yields a slope of 6.8 °C per 1,000 m (99.6 % deviance explained in an ordinary least squares regression). Whitten et al. (2002; pers. comm.) calculated the lapse rate from Mt. Rantemario (c. 200 km from Mt. Nokilalaki) from minimum temperature measurements at three elevations (c. 3200 m, 2000, and 900 m) over approximately five days.

Supplementary Tables

Table S3.1. Results of hurdle models comparing elevation and aspect as drivers of bird abundance in Lore Lindu National Park.

Model	*w*AIC	Δ AIC	degrees of freedom	% DE
Rhipidura teysmanni				
elevation polynomial	0.768	0	6	5.2
elevation polynomial + aspect	0.196	2.7	8	5.6
null	0.014	8.0	2	0
elevation	0.009	8.9	4	1.0
aspect	0.008	9.1	4	0.9
elevation + aspect	0.004	10.5	6	1.8
Pachycephala sulfuriventer				
elevation polynomial	0.816	0	6	6.4
elevation polynomial + aspect	0.180	3.0	8	6.7
null	0.002	12.6	2	0
elevation	0.001	12.7	4	1.2
elevation + aspect	0.001	14.8	6	1.8
aspect	0	15.1	4	0.4
Phylloscopus sarasinorum				
elevation polynomial + aspect	0.623	0	8	21.5
elevation polynomial	0.367	1.1	6	19.9
elevation + aspect	0.007	9.1	6	17.4
elevation	0.003	10.6	4	15.6
aspect	0	54.1	4	1.8
null	0	55.8	2	0
Myza sarasinorum				
elevation	0.672	0	4	37.9
elevation polynomial	0.165	2.8	6	38.3

elevation + aspect	0.129	3.3	6	38.1
elevation polynomial + aspect	0.033	6.0	8	38.7
null	0	89.3	2	0
aspect	0	90.6	4	1.1

Table S3.2. Land cover classification errors in the CRISP dataset at our 149 sampling points. There were 19 errors (87% accuracy).

Type of error	classified as forest; should have been non-forest	classified as non-forest; should have been forest	classified as agriculture; should be regrowth	classified as regrowth; should be agriculture
Number of point counts	7	9	1	2

Table S3.3. Reductions in population size index (number of birds in the study area) for high-elevation (*Myza sarasinorum*, *Phylloscopus sarasinorum*) and middle-elevation (*Rhipidura teysmanni*, *Pachycephala sulfuriventer*) study species under climate change and land-use scenarios.

Species	Current population	Climate change (no deforestation)	Halved deforestation rate	Observed deforestation rate	Climate change + halved deforestation	Climate change + observed deforestation
Myza sarasinorum (high-elevation)	4732	2603	4475	4436	2344	2335
Phylloscopus sarasinorum (high-elevation)	12599	8838	12016	11729	8368	8194

Rhipidura teysmanni (middle-elevation)	19790	17665	17323	16229	15869	15047
Pachycephala sulfuriventer (middle-elevation)	22035	19499	19557	18435	17505	16541

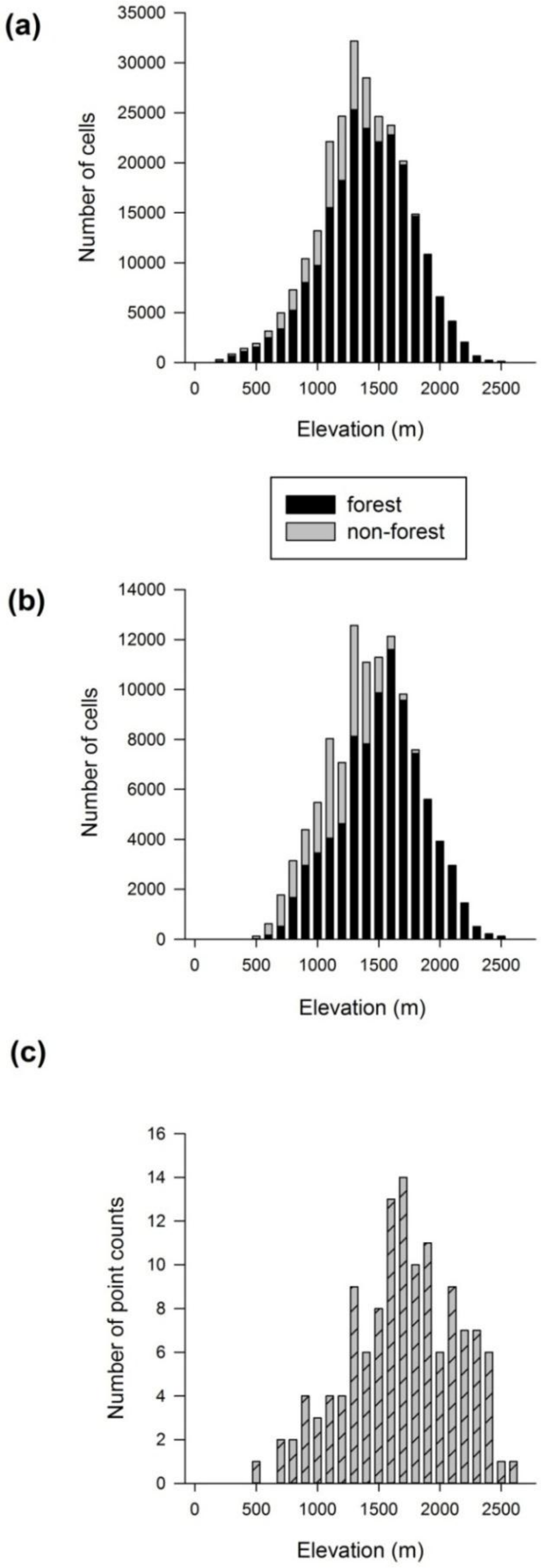

Figure S3.1. Elevation and 2010 forest cover of **(a)** Lore Lindu National Park and **(b)** the study area (within 10 km of sampling points). Cells are approximately 0.85 ha; forest cover data come from Miettinen et al. (2011). **(c)** Sampling effort by elevation within the study area (one sampling session; hatched bars).

Appendix 3.1. Point count coordinates, elevation, and land cover. Forested points inside the elevational ranges of the study species (n=118) were used in the analysis (shown in bold).

Point	Easting	Northing	Elevation (m)	Field notes on land cover	Correct CRISP classification
Pakuli 1	829494	9863670	174	mixed agriculture	open/mosaic
Pakuli 2	829748	9863606	204	scrubby secondary growth with bamboo	open/mosaic
Pakuli 3	830009	9863596	292	disturbed secondary forest with some tall trees	plantation/regrowth
Pakuli 4	830160	9863389	417	cacao patch surrounded by tall secondary forest	open/mosaic
Pakuli 5	830230	9863136	502	edge of tall secondary forest above cacao	forest
Pakuli 6	830378	9862921	618	tall secondary forest with some agrofrestry	forest
Pakuli 7	830639	9862897	786	primary forest	forest
Dali 1	184023	9811929	1659	riparian, wet, tall forest like at Danau Tambing	forest
Dali 2	183794	9811837	1681	riparian, wet, tall forest like at Danau Tambing	forest
Dali 3	183555	9811717	1713	riparian, wet, tall forest like at Danau Tambing	forest
Dali 4	183328	9811629	1772	forest, foot of drier ridge	forest
Dali 5	183084	9811707	1884	forest, drier ridge, low elevation	forest
Dali 6	182864	9811811	1959	forest, drier ridge, low elevation	forest
Dali 7	182653	9811655	1996	many oaks, higher elevation, still on ridge	forest

Dali 8	182419	9811555	2077	many oaks, higher elevation, still on ridge	forest
Dali 9	182218	9811412	2200	high mountain forest, very mossy	forest
Dali 10	182145	9811164	2229	high mountain forest, very mossy	forest
Dali 11	182202	9810915	2228	high mountain forest, very mossy	forest
Dali 12	182322	9810689	2245	high mountain forest, very mossy	forest
Dali 13	184220	9812093	1632	forest, foot of drier ridge	forest
Dali 14	184477	9812073	1689	forest, foot of drier ridge with much leaf litter	forest
Dali 15	184623	9812272	1650	forest, foot of drier ridge with much leaf litter	forest
Dali 16	184853	9812398	1626	last primary forest point before entering disturbed area	forest
Dali 17	185098	9812440	1597	tall secondary forest	forest
Dali 18	185352	9812486	1567	tall secondary forest	forest
Dali 19	185596	9812535	1532	tall secondary forest	forest
Dali 20	185836	9812437	1483	tall secondary forest	forest
Dali 21	186080	9812335	1433	tall secondary forest	forest
Dali 22	186338	9812345	1357	edge of field (grassy)	open/mosaic
Dali 23	186563	9812220	1350	in forest patch surrounded by field	forest
Dali 24[1]	186826	9812217	1357	grass	open/mosaic
Dali 25	187080	9812179	1350	grass	open/mosaic
Dali 26	187327	9812098	1348	grass	open/mosaic
Dali 27	187582	9812036	1327	grass	open/mosaic
Dali 28	187838	9812011	1295	grass	open/mosaic
Nokilalaki 1	184603	9866234	823	cacao	open/mosaic
Nokilalaki 2	184372	9866133	854	mixed agriculture	open/mosaic

Nokilalaki 3	184183	9865973	886	mixed agriculture	open/mosaic
Nokilalaki 4	184114	9865733	915	mixed agriculture	open/mosaic
Nokilalaki 5	184102	9865485	943	mixed agriculture, a few remnant trees in riparian corridor	open/mosaic
Nokilalaki 6	184158	9865244	973	mixed agriculture	open/mosaic
Nokilalaki 7	184235	9865006	1003	mixed agricuture and grass	open/mosaic
Nokilalaki 8	184256	9864757	1032	second growth (small patch)	plantation/regrowth
Nokilalaki 9	184037	9864644	1063	primary forest next to edge	forest
Nokilalaki 10	183897	9864424	1110	forest	forest
Nokilalaki 11	183656	9864340	1178	forest	forest
Nokilalaki 12	183476	9864187	1210	forest	forest
Nokilalaki 13	183338	9863999	1277	forest	forest
Nokilalaki 14	183233	9863780	1378	forest	forest
Nokilalaki 15	183117	9863563	1486	forest	forest
Nokilalaki 16	183063	9863314	1544	forest	forest
Nokilalaki 17	182975	9863083	1611	forest	forest
Nokilalaki 18	182966	9862831	1674	forest	forest
Nokilalaki 19	183047	9862597	1736	forest	forest
Nokilalaki 20	183060	9862354	1835	forest	forest
Nokilalaki 21	183306	9862303	1915	forest	forest
Nokilalaki 22	183540	9862213	2024	forest	forest
Nokilalaki 23	183685	9862014	2060	forest	forest
Nokilalaki 24	183873	9861849	2052	forest	forest
Nokilalaki 25	184087	9861723	2171	forest	forest
Nokilalaki 26	184199	9861502	2215	forest	forest
Nokilalaki 27	184353	9861304	2278	forest	forest
Nokilalaki 28	184524	9861124	2340	forest	forest
Nokilalaki 29	184722	9860969	2362	forest	forest
Rorekatimbu 1	199662	9853794	1695	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 2	199683	9854041	1761	tall secondary forest along trail with older forest off	forest

				trail	
Rorekatimbu 3	199939	9854082	1803	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 4	200115	9854272	1855	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 5	200349	9854366	1883	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 6	200471	9854581	1921	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 7	200430	9854828	1984	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 8	200483	9855076	2027	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 9	200696	9855221	2040	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 10	200597	9855449	2038	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 11	200487	9855675	2072	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 12	200349	9855887	2055	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 13	200226	9856114	2108	tall secondary forest along trail with older forest off	forest

				trail	
Rorekatimbu 14	200111	9856345	2140	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 15	200223	9856565	2160	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 16	200229	9856816	2158	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 17	200363	9857029	2170	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 18	200519	9857229	2224	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 19	200664	9857430	2245	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 20	200643	9857713	2311	tall secondary forest along trail with older forest off trail	forest
Rorekatimbu 21	200614	9857967	2366	mossy primary forest	forest
Rorekatimbu 22	200546	9858202	2369	mossy primary forest	forest
Rorekatimbu 23	200568	9858455	2399	mossy primary forest	forest
Rorekatimbu 24	200638	9858697	2485	mossy primary forest	forest
Rorekatimbu 25	200486	9858895	2512	mossy primary forest	forest
Rorekatimbu 26	199420	9853870	1671	tall old forest, probably secondary	forest
Rorekatimbu	199219	9854033	1632	forest	forest

27					
Rorekatimbu 28	198959	9854013	1585	forest	forest
Rorekatimbu 29	198799	9854204	1564	scrubby forest	plantation/regrowth
Rorekatimbu 30	198554	9854277	1539	secondary scrub, younger than R29	plantation/regrowth
Rorekatimbu 31	198272	9854222	1531	forest	forest
Rorekatimbu 32	198059	9854410	1535	forest	forest
Rorekatimbu 33	197953	9854644	1494	tall secondary forest	forest
Rorekatimbu 34	197789	9854842	1458	tall secondary forest, forest in better shape than at R20 and R30	forest
Rorekatimbu 35	197605	9855051	1430	slightly more disturbed than R34	forest
Rorekatimbu 36	197491	9855285	1361	tall secondary forest	forest
Rorekatimbu 37	197285	9855443	1343	tall secondary forest	forest
Rorekatimbu 38	197050	9855551	1309	tall secondary forest	forest
Rorekatimbu 39	196822	9855674	1296	disturbed secondary forest	plantation/regrowth
Rorekatimbu 40	196636	9855891	1264	secondary, next to first farmer's field	plantation/regrowth
Rano Rano 1	184505	9814624	1498	tall forest like at Danau Tambing, but lower elevation	forest
Rano Rano 2	184238	9814575	1503	tall forest like at Danau Tambing, but lower elevation	forest
Rano Rano 3	183977	9814585	1581	ridge forest	forest

Rano Rano 4	183721	9814629	1618	ridge forest	forest
Rano Rano 5	183486	9814742	1646	forest	forest
Rano Rano 6	183294	9814914	1715	forest	forest
Rano Rano 7	183054	9815020	1771	forest	forest
Rano Rano 8	182790	9814963	1844	forest	forest
Rano Rano 9	182538	9814907	1894	forest	forest
Rano Rano 10	182280	9814878	1919	forest	forest
Rano Rano 16	179997	9817864	1898	forest	forest
Rano Rano 17	179765	9817963	1892	forest	forest
Rano Rano 18	179511	9818012	1860	forest	forest
Rano Rano 19	179273	9818114	1812	forest	forest
Rano Rano 20	179036	9818213	1764	taller, more tropical forest	forest
Rano Rano 21	178790	9818153	1749	forest	forest
Rano Rano 22	178544	9818229	1722	forest	forest
Rano Rano 23	178330	9818369	1709	forest	forest
Rano Rano 24	178161	9818569	1620	forest	forest
Rano Rano 25	177971	9818749	1570	forest	forest
Rano Rano 26	177791	9818918	1516	forest	forest
Rano Rano 27	177593	9819091	1459	forest	forest
Rano Rano 28	177410	9819272	1403	secondary forest, edge of regenerating field	plantation/regrowth
Rano Rano 29	177269	9819487	1354	forest	forest
Rano Rano 30	177170	9819721	1282	return to primary forest	forest
Rano Rano 31	177065	9819953	1283	forest	forest
Rano Rano 32	176971	9820191	1252	forest	forest
Rano Rano 33	176887	9820438	1206	forest	forest
Rano Rano 34	173323	9821909	480	bamboo, scrubby woodland above river	open/mosaic
Rano Rano 35	173449	9821678	616	young secondary forest	open/mosaic
Rano Rano 36	173688	9821560	684	secondary forest	plantation/regrowth
Rano Rano 37	173867	9821377	716	a field	open/mosaic
Rano Rano 38	174075	9821218	768	0.18 km from RR 39 to RR 38 lightly disturbed primary forest	forest
Rano Rano 39	174268	9821046	838	primary forest	forest

Rano Rano 40	174464	9820878	874	becoming disturbed, but still tall forest; rattan trails	forest
Rano Rano 41	174694	9820755	876	primary forest nearby; some rattan collection	forest
Rano Rano 42	174944	9820684	884	primary forest with bamboo (continues until RR 41)	forest
Rano Rano 43	175194	9820614	917	scruby area near forest	plantation/regrowth
Rano Rano 44	175400	9820445	979	primary forest	forest
Rano Rano 45	175658	9820423	993	primary forest	forest
Rano Rano 46	175798	9820644	1034	primary forest	forest
Rano Rano 47	176023	9820778	1042	forest	forest
Rano Rano 48	176283	9820802	1108	forest	forest
Rano Rano 49	176544	9820765	1159	forest	forest
Rano Rano 50	176702	9820588	1220	forest	forest

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[1] Points Dali 24-28, Rorekatimbu 21-25 are outside of the national park.

Appendix 3-Supplementary Material for Chapter 4

Supplementary Methods: Additional Covariates

The large range of latitudes where our 36 study species breed (c. 5-80° N) made it unfeasible to include local temperature as a covariate. Instead, we opted to use the Southern Oscillation Index (Bureau of Meteorology 2011) as a measure of El Niño-related changes in regional climate. El Niño/Southern Oscillation has been shown to have profound effects on climate in the Asia-Pacific region (e.g. Wang et al. 2001), and has correlated with changes in avian migration timing in other studies (Lehikoinen and Sparks 2010). Initial tests indicated the index had only weak effects on arrival date, and the index was negatively correlated with observer effort (Spearman correlations ranged from -0.37 to -0.48 depending on the taxonomic group). Hence there was little support for including Southern Oscillation Index in the final analyses, especially when considering the small sample sizes.

Given the possible relationship between a species' ability to produce > 1 brood and autumn departure (Jenni and Kéry 2003), we tested for the influence of number of broods on arrival date. Information on number of broods was not available in any single source, and is apparently unknown for seven of our study species (Table S4.1). Trial models indicated that there was no relationship between the number of broods and arrival date (null model selected above brood model). The lack of an effect, combined with the absence of brood information for seven species, made it sensible to not include brood as a variable in further analyses.

Supplementary Tables

Table S4.1. Study species. Apparent global population trend comes from Bamford et al. (2008), BirdLife International (2011), and Lim and Lim (2009); migration distance from del Hoyo et al. (1992-2009) and Wells (1999, 2007); number of broods from del Hoyo et al. (1992-2009), Kynstautas (1993), Nettleship (2000), Planet of Birds (2011), Robinson (2005), and Rogacheva (1992); and Singapore status from Lim and Lim (2009) and Lim (2009). Taxonomy follows the International Ornithologists' Union (Gill and Donsker 2011).

Common name	Scientific name	Apparent population trend[1]	Migration distance	Number of broods	Status in Singapore

black baza	*Aviceda leuphotes*	declining	short	no information	uncommon WV^2 and PM
crested honey buzzard	*Pernis ptilorhyncus*	stable	short	one	common WV and PM (*P. p. orientalis*) and uncommon WV (*P. p. torquatus*)
Chinese sparrowhawk	*Accipiter soloensis*	stable	short	one	uncommon WV and PM
Japanese sparrowhawk	*Accipiter gularis*	stable	long	one	common WV and PM
little ringed plover	*Charadrius dubius*	stable	long	greater than one	common WV and PM
lesser sand plover	*Charadrius mongolus*	declining	long	one	common WV and PM
pin-tailed snipe	*Gallinago stenura*	stable	long	one	common WV and possible migrant
common snipe	*Gallinago gallinago*	declining	long	one	common WV and PM
marsh sandpiper	*Tringa stagnatilis*	declining	long	one	very common WV and PM
wood sandpiper	*Tringa glareola*	stable	long	one	common WV and PM
terek sandpiper	*Xenus cinereus*	stable	long	one	uncommon WV and PM
common sandpiper	*Actitis hypoleucos*	declining	long	one	common WV and PM

ruddy turnstone	*Arenaria interpres*	declining	long	one	uncommon WV and PM
curlew sandpiper	*Calidris ferruginea*	declining	long	one	fairly common WV and PM
white-winged tern	*Chlidonias leucopterus*	stable	long	one	uncommon WV and PM
Pacific swift	*Apus pacificus*	stable	short	one	common WV and PM
Indian cuckoo	*Cuculus micropterus*	stable	short	not applicable	uncommon WV and PM
black-capped kingfisher	*Halcyon pileata*	declining	short	no information	fairly common WV and PM
common kingfisher	*Alcedo atthis*	declining	long	greater than one	common WV and PM
ashy minivet	*Pericrocotus divaricatus*	stable	long	one	uncommon WV and PM
tiger shrike	*Lanius tigrinus*	declining	short	one	common WV and PM
brown shrike	*Lanius cristatus*	declining	short	one	common WV and PM
crow-billed drongo	*Dicrurus annectans*	stable	short	no information	uncommon WV and PM
Asian paradise flycatcher	*Terpsiphone paradisi*	stable	short	greater than one	common PM and uncommon WV
barn swallow	*Hirundo rustica*	declining	short	greater than one	very common WV and PM
red-rumped swallow	*Cecropis daurica*	increasing	short	greater than one	common PM and

					uncommon WV
Arctic warbler	*Phylloscopus borealis*	stable	long	greater than one	common WV and PM
eastern crowned warbler	*Phylloscopus coronatus*	stable	long	no information	uncommon WV and PM
Daurian starling	*Agropsar sturninus*	stable	long	no information	common WV and PM
eyebrowed thrush	*Turdus obscurus*	declining	long	greater than one	uncommon PM and scarce WV
Siberian blue robin	*Luscinia cyane*	declining	long	no information	fairly common PM and uncommon WV
dark-sided flycatcher	*Muscicapa sibirica*	stable	short	one	common WV and PM
Asian brown flycatcher	*Muscicapa dauurica*	stable	long	one	common WV and PM
yellow-rumped flycatcher	*Ficedula zanthopygia*	stable	long	one	common PM and uncommon WV
forest wagtail	*Dendronanthus indicus*	stable	long	no information	fairly common WV and PM
eastern yellow	*Motacilla tschutschensis*	declining	long	greater than one	common WV and PM

wagtail

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[1] Global population trend information was unavailable for *Charadrius mongolus*, *Gallinago stenura*, *Dicrurus annectans*, and *Agropsar sturninus*. Trends for these species were approximated based on Singapore trend data in Lim and Lim (2009). In contrast to information from BirdLife International (2011), data from the Asian-Australasian flyway indicate *Calidris ferruginea* is declining (Bamford et al. 2008). No trend data were available for *Turdus obscurus*. We assumed this species was declining based on the common pattern of temperate Asian forest bird decline from habitat loss (Kurosawa and Askins 2003).

[2] WV indicates winter visitor, PM indicates passage migrant.

Table S4.2. Gaussian mixed-effects model results for long-distance passerines.

Model	% DE	evidence ratio	ΔAIC_c	w_i	k
population trend + observer effort + (1|species)	2.3		0	0.846	5
year + observer effort + (1|species)	1.8	9.5	4.5	0.089	5
observer effort + (1|species)	1.5	13.2	5.2	0.064	4
1 + (1|null)	0	>10,000	18.5	0	3

Table S4.3. General linear model results from a follow-up test where *Accipiter gularis* was removed from the raptor dataset. For the remaining three species (*Aviceda leuphotes*, *Pernis ptilorhyncus*, and *Accipiter soloensis*), there is no longer strong evidence for a relationship between year and arrival date.

Model	% DE	evidence ratio	ΔAIC_c	w_i	k
observer effort	16.2		0	0.788	3
year + observer effort	16.4	3.7	2.6	0.212	4

Supplementary Figures

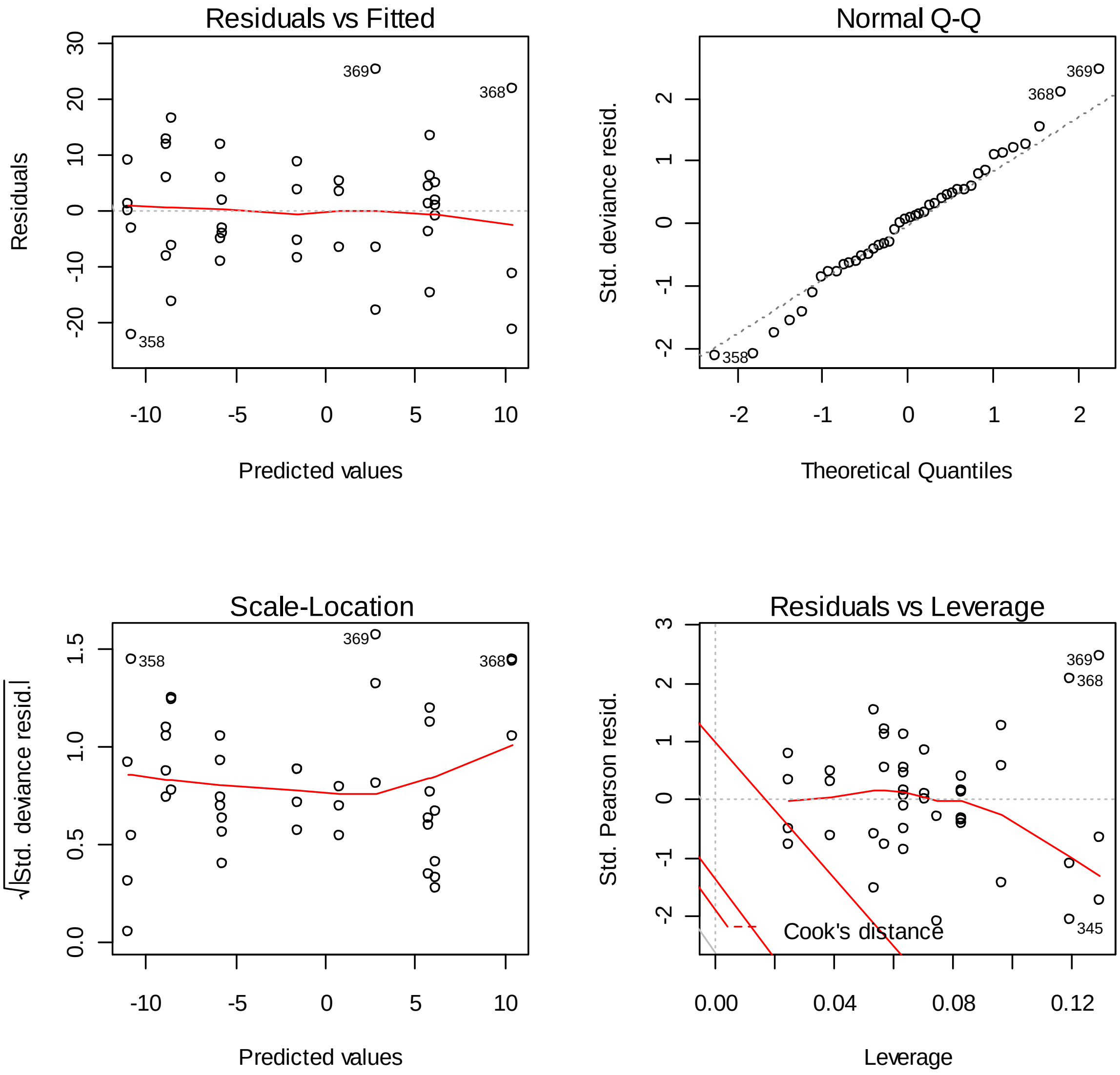

Fig S4.1A. Diagnostic plots from arrival date ~ year + observer effort model (top and global model) for raptors.

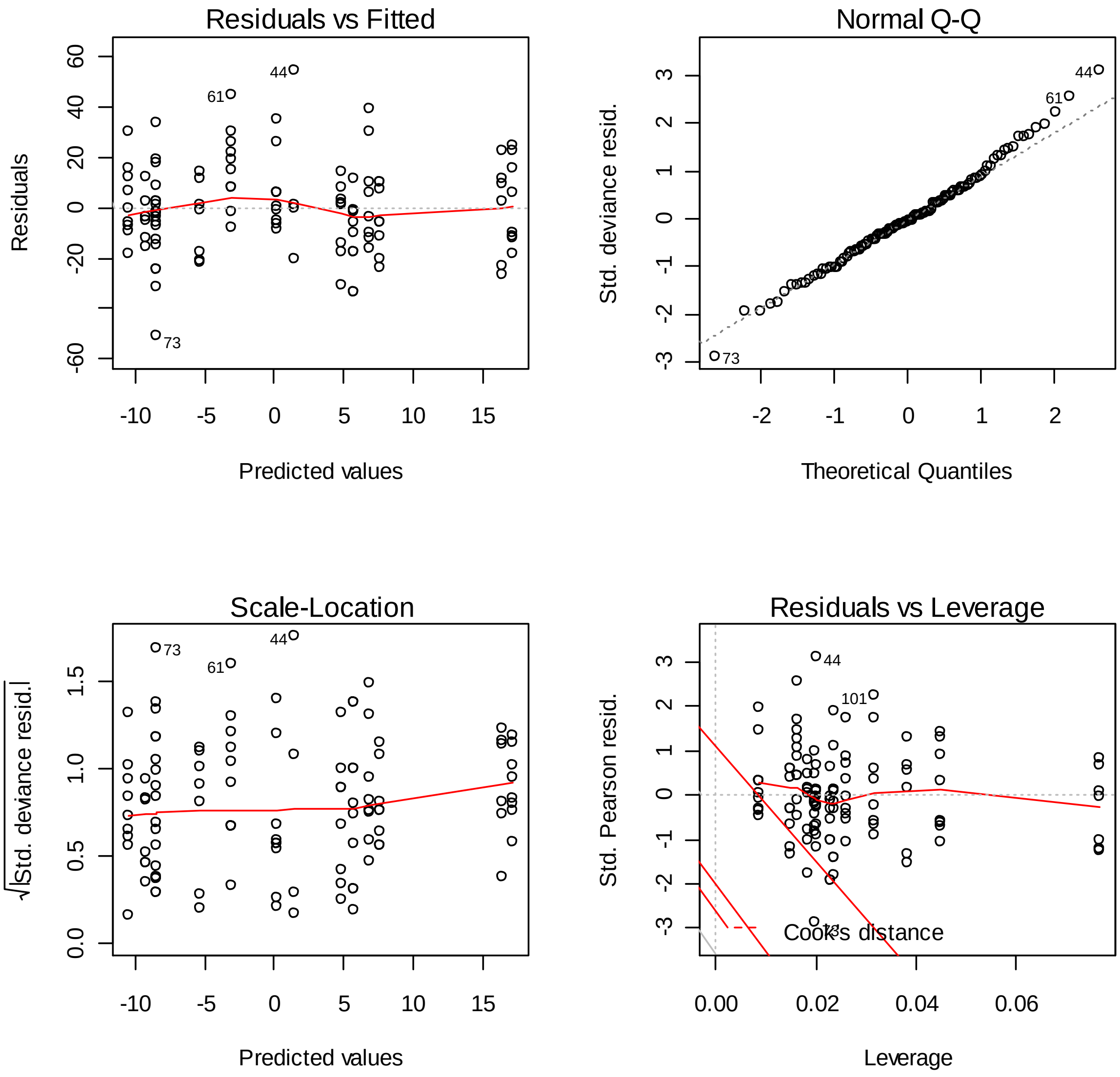

Fig S4.1B. Diagnostic plots from arrival date ~ year + observer effort model (top and global model) for waders.

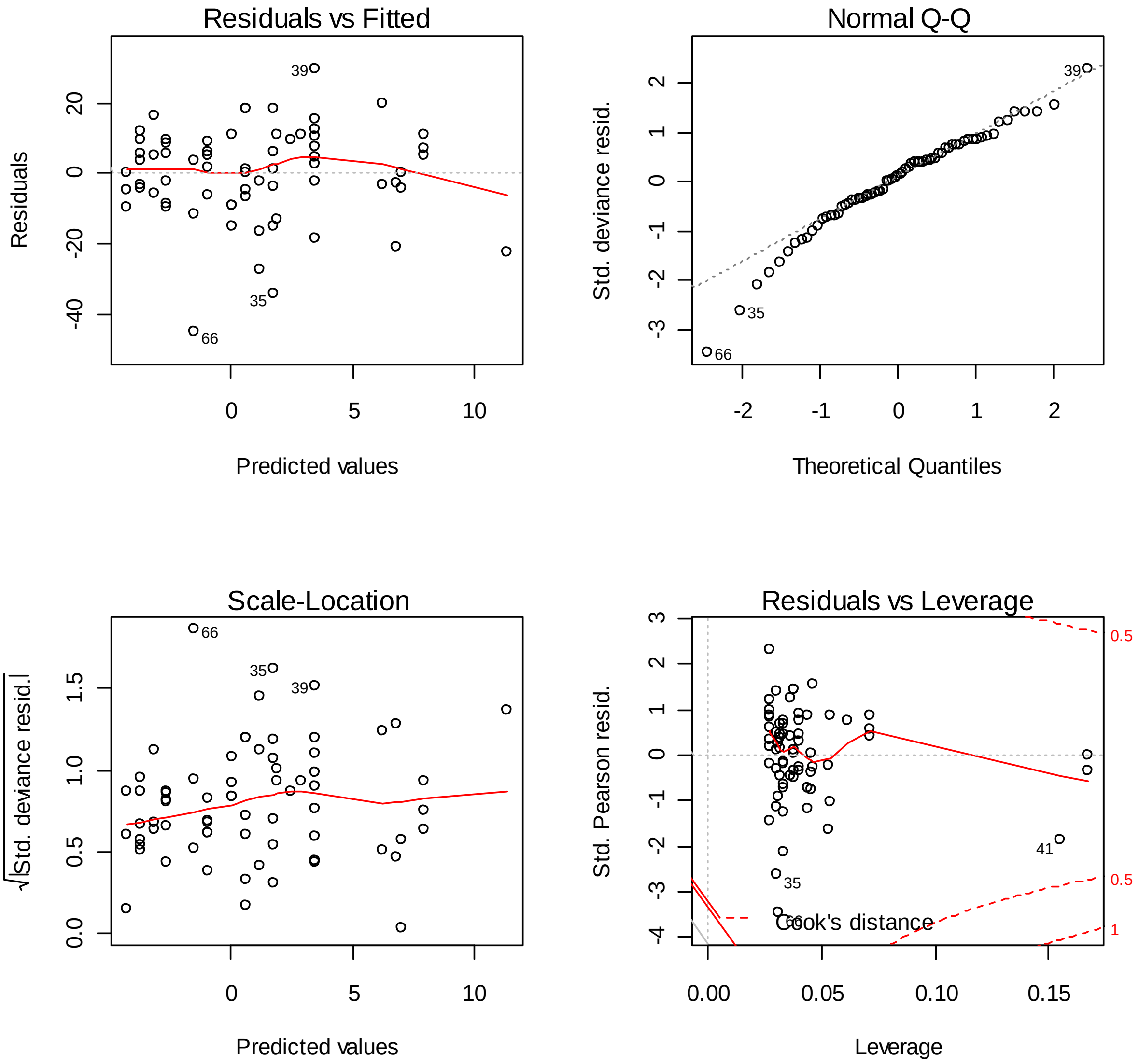

Fig S4.1C. Diagnostic plots from arrival date ~ population trend + observer effort (global model) for short-distance passerines.

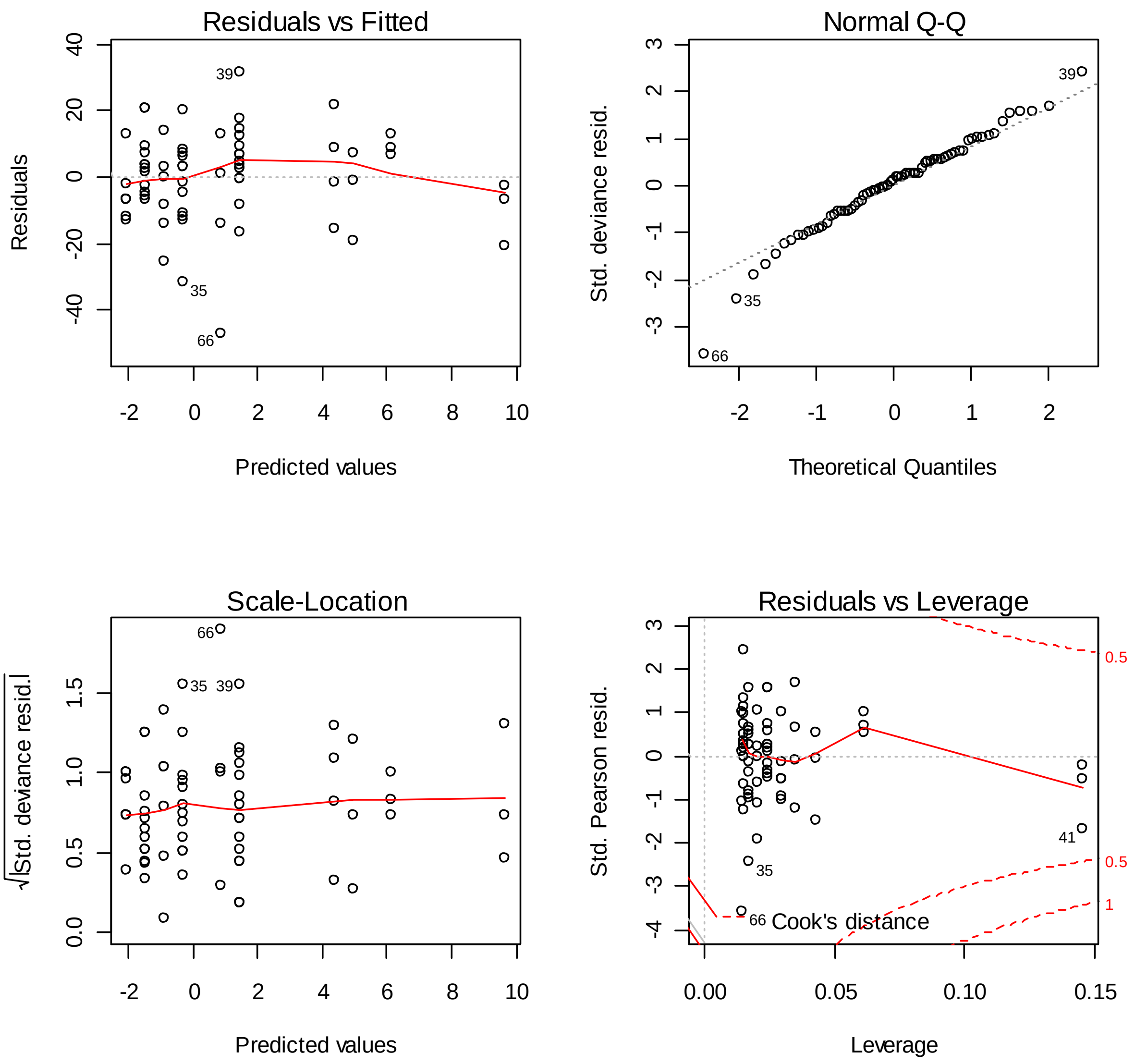

Fig S4.1D. Diagnostic plots from arrival date ~ observer effort (top model) for short-distance passerines.

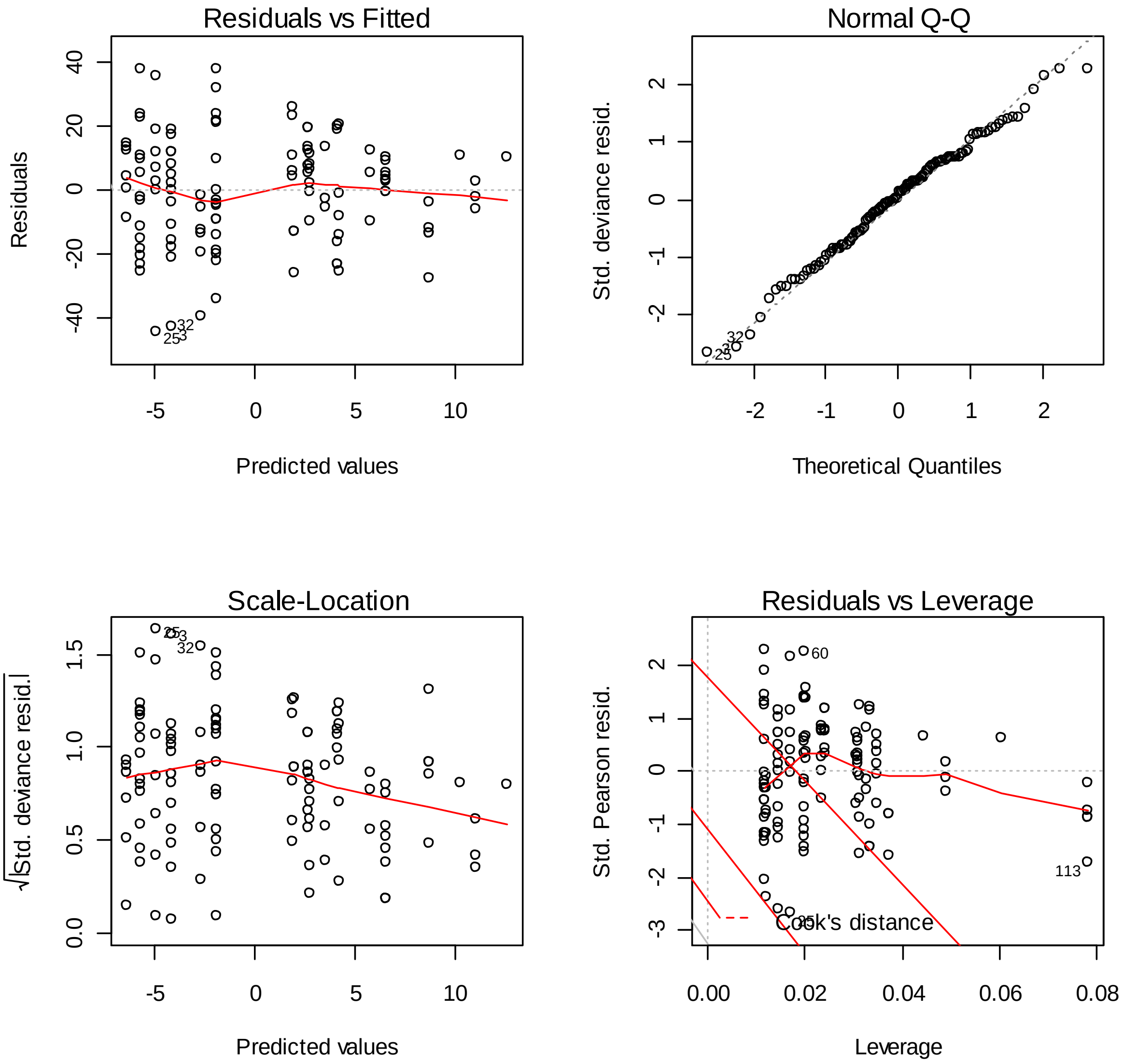

Fig S4.1E. Diagnostic plots from arrival date ~ population trend + observer effort model (top and global model) for long-distance passerines.

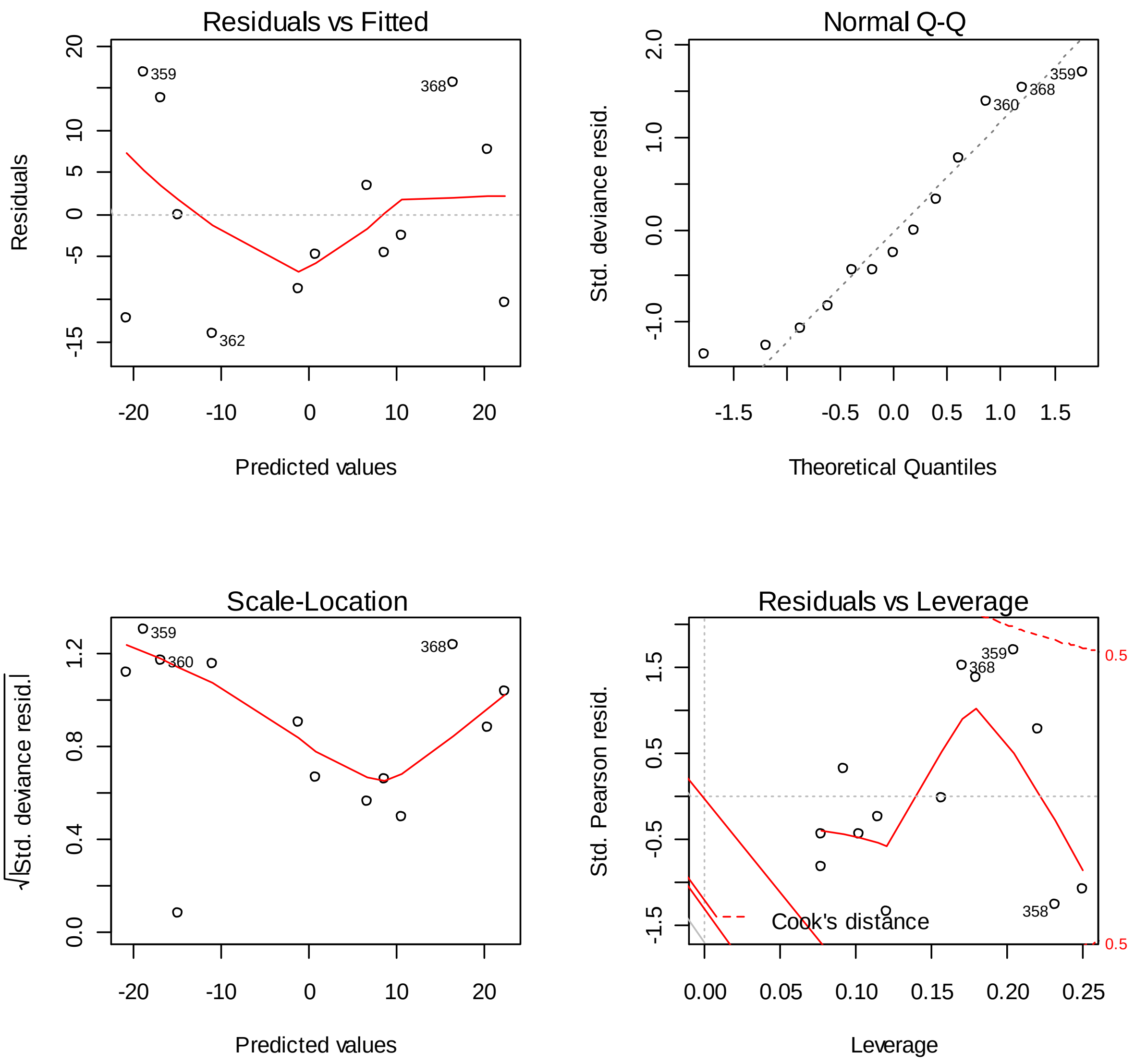

Fig S4.1F. Diagnostic plots from arrival date ~ year model for *Accipier gularis*.

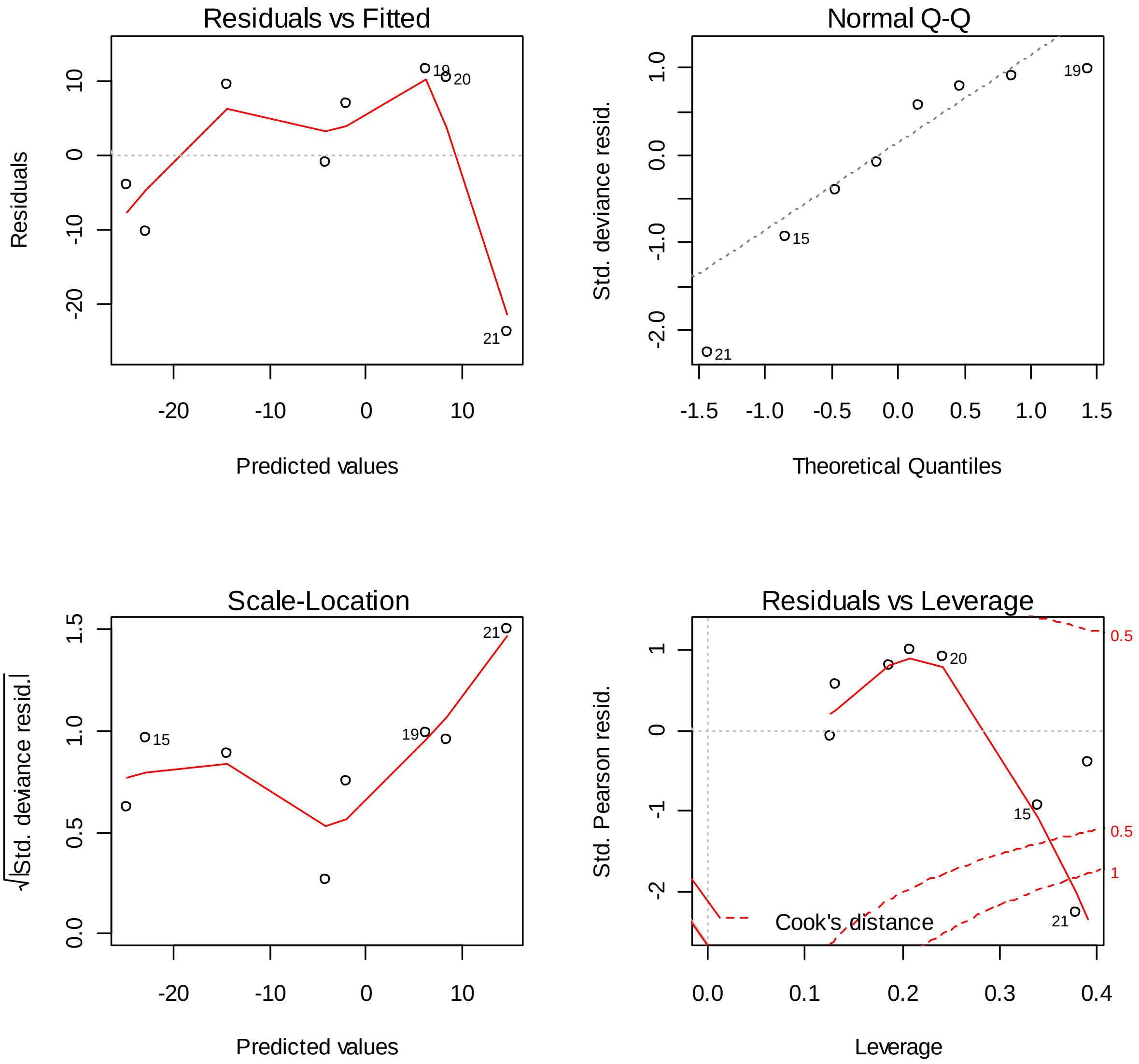

Fig S4.1G. Diagnostic plots from arrival date ~ year model for *Gallinago gallinago*.

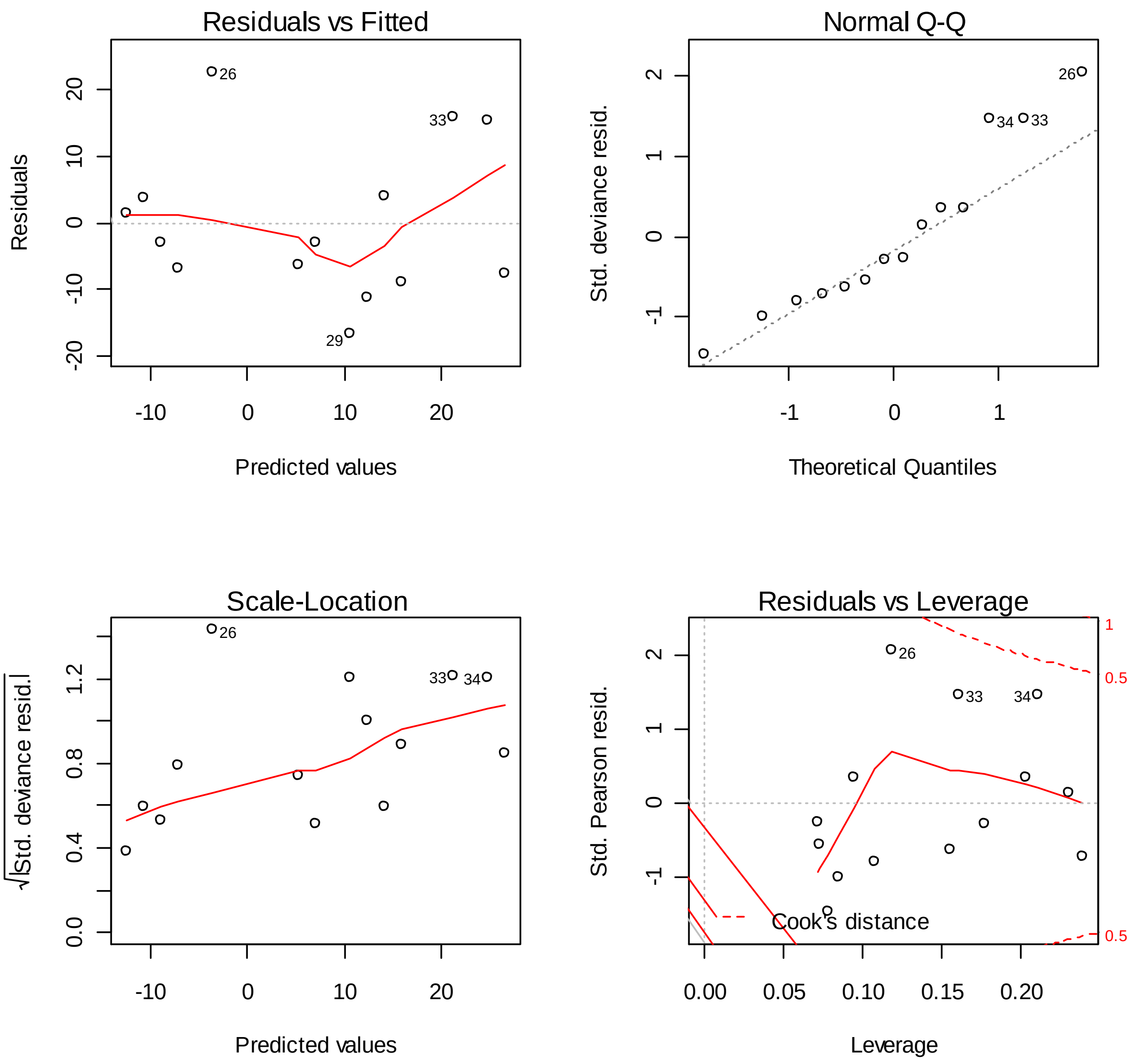

Fig S4.1H. Diagnostic plots from arrival date ~ year model for *Calidris ferruginea*.

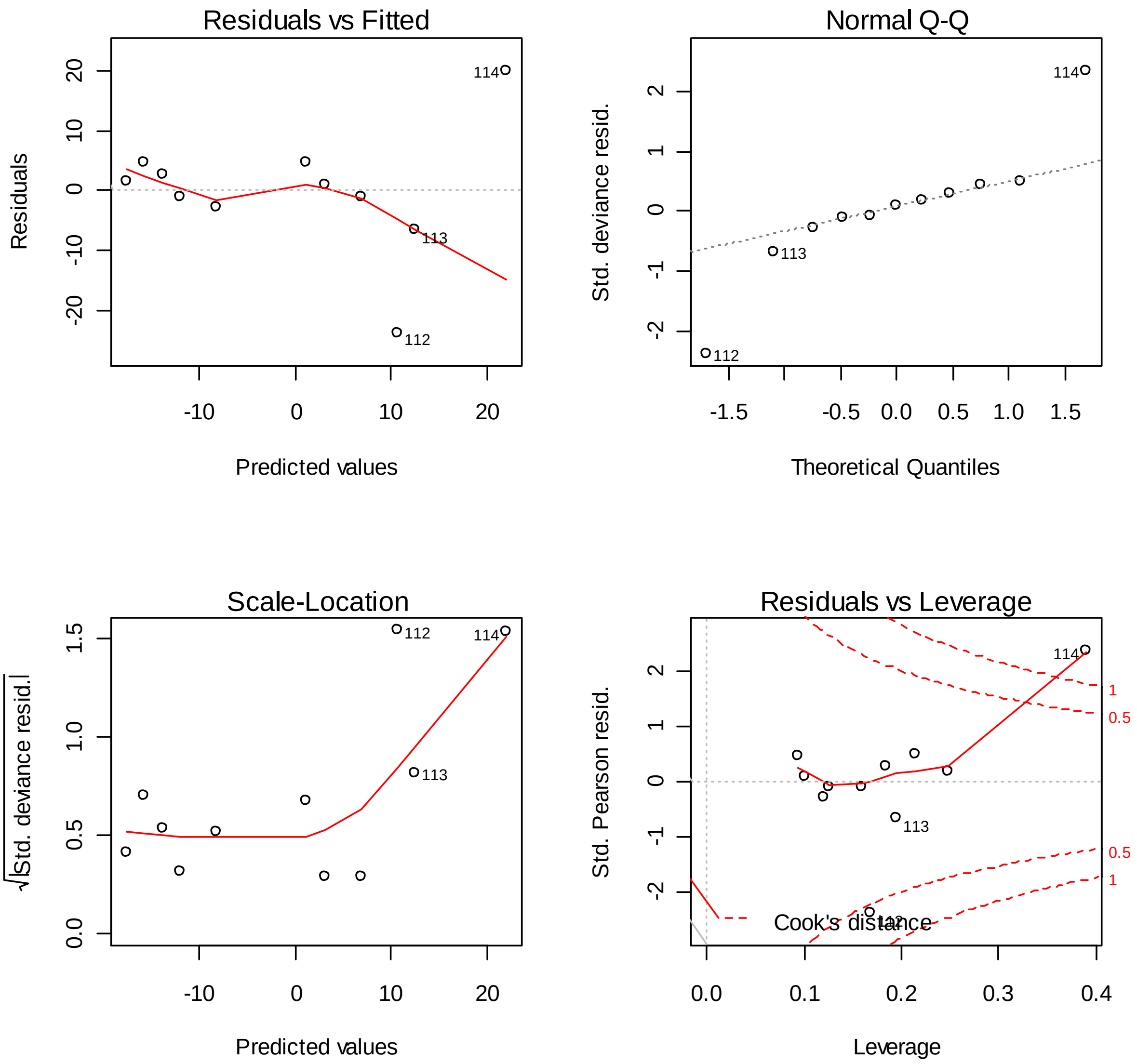

Fig S4.1I. Diagnostic plots from arrival date ~ year model for *Tringa glareola*.

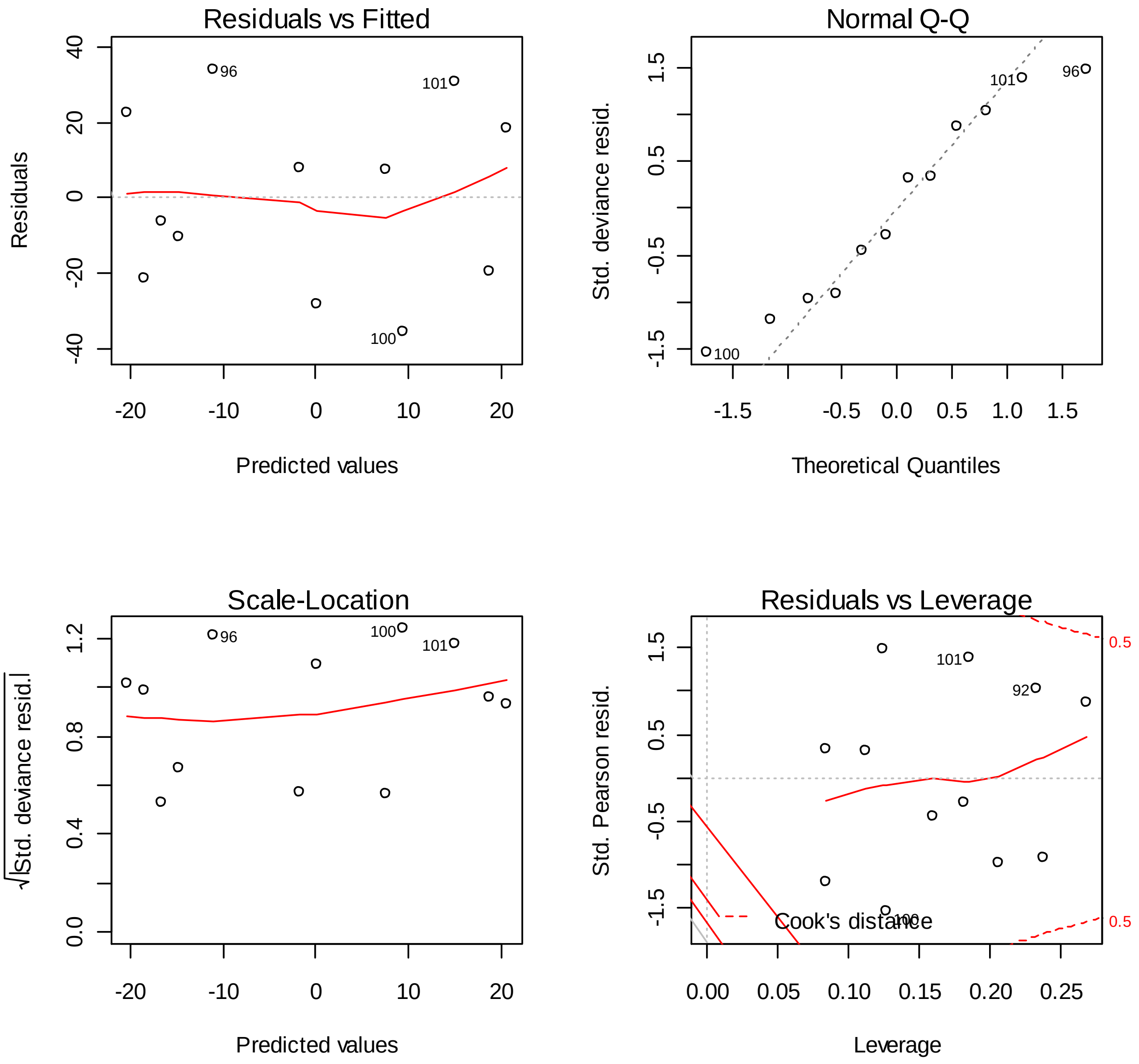

Fig S4.1J. Diagnostic plots from arrival date ~ year model for *Xenus cinereus*.

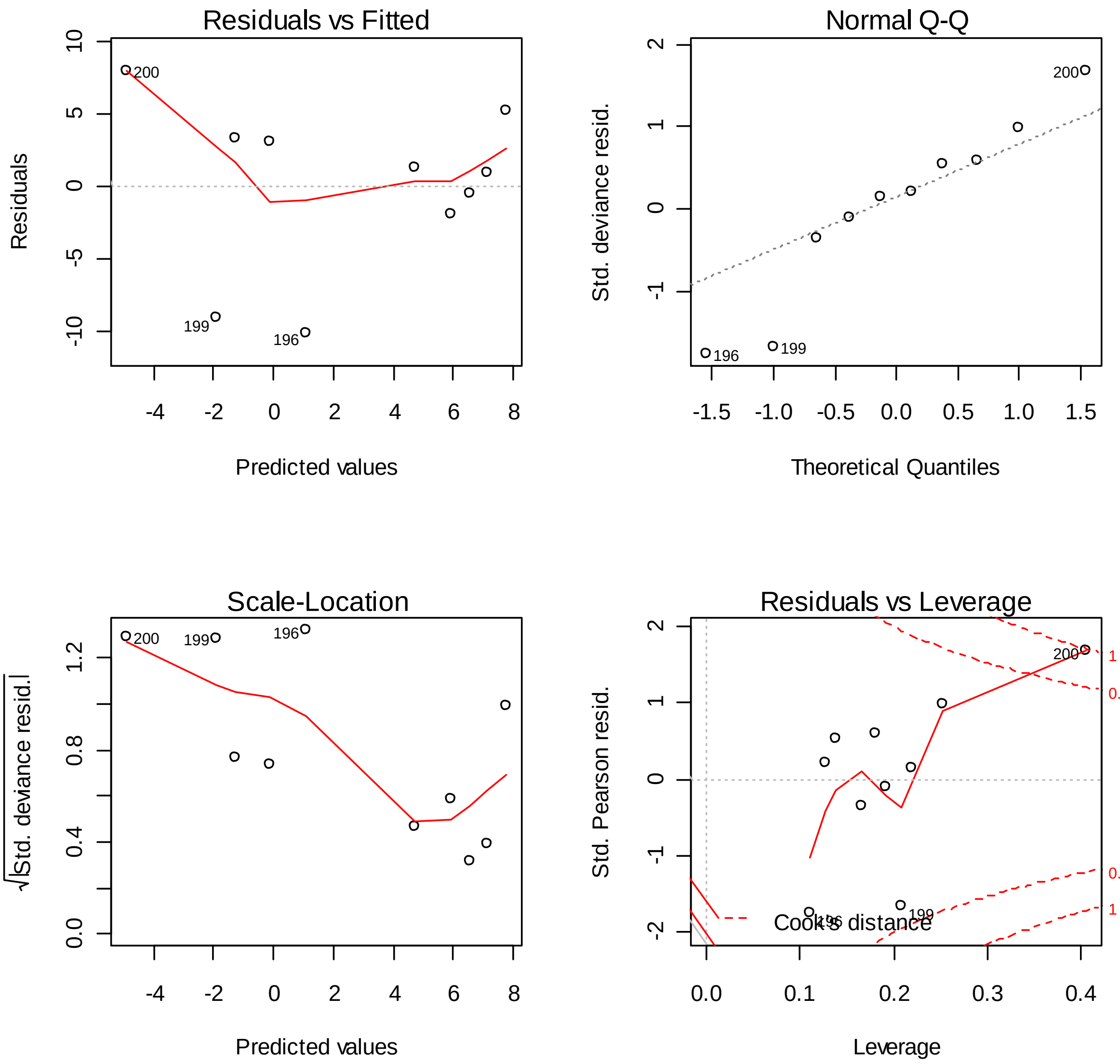

Fig S4.1K. Diagnostic plots from arrival date ~ year model for *Hirundo rustica*.

Appendix 4- Supplementary Material for Chapter 5

Previous modelling studies on the Kangaroo Island GBC

Two previous studies used population models to estimate the viability of the GBC population, although neither considered climate change. Pepper (1996) used survival estimates from Carnaby's black-cockatoo (*C. latirostris*) and fecundity data from the little reproductive research that had been done on Kangaroo Island by that time. Using VORTEX software (Lacy 1993), Pepper (1996) calculated a mean time to extinction of 5.8 years. Pepper (1996) doubted the results and suggested that the assumptions of the model were incorrect. Southgate (2002) used mark-recapture data from 1996–2001 to estimate survival, without explicitly modelling recapture probability. He calculated survival to be 0.296 for egg to age 1, 0.77 for age 1 to 2, 0.83 for age 2 to 3, and c.0.85 for age 3+. Southgate (2002) used data on sex ratio, clutch size, and percent of females breeding to estimate fecundity to be equal to 0.4 for female nestlings. Southgate (2002) used the software ALEX (Possingham & Davies 1995) to estimate that the GBC population was declining by 10% a year. This finding conflicted with census data which showed the population was increasing by c. 4% annually. Southgate (2002) attributed the discrepancy to inaccurate survival data.

Detailed population modelling methods

Demographic structure

We used life history data and expert knowledge from the GBC recovery program to parameterise the model (Crowder *et al.* 1994; Table 5.1). Breeding age for females is three years and for males is five years (LPP, pers. obs.; Mooney & Pedler 2005), and the species forms permanent or semi-permanent monogamous pairs (Garnett *et al.* 2000). Black-cockatoos probably show minimal reproductive senescence (Heinsohn *et al.* 2009). Thus, we developed a stage- and sex-structured model with composite age classes for breeding female (3+) and male age (5+) classes. Changes in mortality related to senescence are unknown in *Calyptorhynchus lathami* but we simulated the possible effects of senescence by adding a senescent stage (age 20+), whereby mortality in this oldest stage was doubled. We found that the growth rate (lambda) was reduced from 1.035 to 1.011.

Survival estimates

We estimated survival from 950 observations of 317 individuals marked between 1996–2008, using the Cormack-Jolly-Seber model for live recaptures in Program MARK (Cooch & White 2008). We used a two-stage modelling approach for mark-recapture data, whereby recaptures were initially modelled in combination with the most parameterised survival model, so as to retain as much power as possible for testing likely drivers of survival parameters (see Pardon *et al.* 2003 for justification). After the optimal recapture model was selected, a parsimonious survival model was sought.

Initially, we were interested in testing the effects of 13 covariates on annual cockatoo survival. We tested for correlations among covariates with a Spearman correlation matrix and excluded five correlated variables (all remaining variables had all Spearman coefficients <0.65; most were <0.3). The final analysis tested the effects of eight covariates on survival (Table S5.1). The covariates for extreme events (drought, river flow, and repeated fire) were best represented by thresholds in order to model GBC tolerance to low levels of these variables. Therefore we converted these covariates into a binary format–ones or zeros if the values were above or below the median, respectively. Models were tested from an *a priori* candidate set of 27 ecologically plausible models, which were developed based on our experience with the species in the field. We used a hierarchical approach when testing for the optimal survival model (using likelihood) (Cooch & White 2008). We first tested for a cohort effect but found no evidence for this. Then we tested different stage structures (two, three, or four age classes) and found two stages was optimal. As the final step we compared models with no stage structure to those with two stages. Both classes of models included constant, time-variant, and environmental covariate models. The only difference was that models with no stage structure compared eight covariates (Table S5.1), while stage-structured models compared the three covariates (available protected hollows, number of hollows treated for bees, and number of little corellas *Cacatua sanguinea* culled) that were likely to have a stronger effect on sub-adults than adults (Mooney & Pedler 2005). Models with *w*AIC <0.01 are not included in Table S5.2.

We used parametric bootstrapping to estimate goodness-of-fit in the mark-recapture data (White 2002). We calculated $\hat{c} = 1.08$ by dividing the observed deviance for the most parameterised model by the mean deviance from 1,000 bootstrap simulations. This low value suggests little overdispersion and requires no adjustment (White, Burnham & Anderson 2001).

For model comparisons, we report -2*log(likelihood) as the measure of deviance. We calculated an R^2 statistic from an analysis of deviance based on the following formula from Le Bohec *et al*. (2008): R^2 = (DEV(constant model) - DEV(covariate model)) / (DEV(constant model) - DEV(time-dependent model)), where DEV is deviance. The advantage of this method is that it assesses the relative effects of covariates on survival and recapture rates. We used MARK to calculate weighted averages of the parameter estimates from the Akaike weights (Burnham & Andersen 2002). Mark-resight data area continually collected by the recovery program. Researchers wishing to use GBC survival estimates should contact the recovery program for the latest figures.

Table S5.1. Covariates and their data sources for the mark-recapture survival analysis of *Calyptorhynchus lathami halmaturinus* on Kangaroo Island. **availprot** = available protected hollows (artificial + natural); **bee** = number of hollows with honeybee *Apis mellifera* deterrent inserted; **corella** = number of little corellas *Cacatua sanguinea* culled; **drought** = drought index (total rainfall in previous five years); **heat** = number of summer days ≥ 35 ºC; **flow** = flow in Rocky River; **revegetation** = area revegetated with *A. verticillata* (with a six year delay because *A. verticillata* cones require a minimum of six years to mature; PAM pers. obs.); **fire** = repeated fire index (area burned in previous 5 years)

Covariate	Source	Possible effect on cockatoos
availprot	GBCRP data*	Nest predation by possums
bee	GBCRP data	Hollow competition
corella	GBCRP data	Hollow competition/nest predation
drought (threshold)	BOM, mean of 7 stations†	*A. verticillata* seed production and drinking water
heat	BOM, mean of 3 stations	Heat stress on adults‡
flow (threshold)	DWLBC¶	Proxy for available surface water for cockatoo drinking

revegetation	GBCRP data	*A. verticillata* seed production
fire (threshold)	GBCRP/DENR data	Reduction of nesting and feeding habitat

*Glossy black-cockatoo recovery program. See Mooney & Pedler (2005) for details.

†Bureau of Meteorology. We used data from weather stations with the most complete collection histories: stations 22800, 22801/23, 22803, 22817, 22835, 22836, & 22839 for rain; stations 22801/23, 22803, & 22841 for temperature. http://www.bom.gov.au

‡Summer is defined as December of the previous year and January and February of the current year. See Cameron (2008), Saunders, Mawson & Dawson (2011) for information on heat stress in *Calyptorhynchus*.

¶Department of Water, Land, and Biodiversity Conservation. Flow of Rocky River at gorge falls, site A5130501. http://e-nrims.dwlbc.sa.gov.au/swa/.

Table S5.2. Comparison of survival model results from Cormack-Jolly-Seber models in program MARK. The optimal recapture model was stage-structured and time-dependent.

Model	Δ AIC$_c$	w_i	k	LL	R^2
subad(.) ad(.)	0	0.20	15	2601.1	0.88
subad(corella) ad(.)	0.2	0.18	16	2599.2	0.90
subad(bee) ad(bee)	1.0	0.12	16	2600.0	0.89
subad(availprot) ad(.)	1.5	0.09	16	2600.5	0.88
subad(.) ad(.) + sex	1.6	0.09	16	2600.6	0.88
subad(availprot + corella) ad(.)	1.7	0.09	17	2598.6	0.90
subad(availprot) ad(availprot)	1.7	0.08	16	2600.7	0.88
subad(corella) ad(corella)	1.8	0.08	16	2600.8	0.88
subad(bee) ad(.)	2.0	0.07	16	2601.0	0.88
subad(*t*) ad(*t*) + sex	10.4	0	27	2586.6	1
constant	103.4	0	14	2706.5	0
t	104.4	0	25	2684.7	0.18
sex + *t*	105.5	0	26	2683.8	0.19

t represents time. subad represents sub-adults, ad represents adults. Explanatory variables (Table S5.1) are availprot = available protected hollows, bee = hollows treated for bees, corella = number of corellas culled, repfire = repeated fires in the last five years. k indicates the number of parameters, AIC_c is Akaike's Information Criterion corrected for small samples sizes, $\Delta\ AIC_c$ shows the difference between the model AIC and the minimum AIC in the set of models, AIC weights (w_i) show the relative likelihood of model i and % DE is percent deviance explained by the model.

Fecundity

We used the number of known fledglings in the population from 1996–2008 to measure reproductive output in the population. This number is calculated each year by summing the number of large nestlings seen at the nest up to a week before fledging, and additional fledglings noted during the census. Sex ratio of fledglings and adults is 1.3 and 1.5 males to females, respectively (GBC recovery program data, 1996–2008). Fecundity was calculated thus (Brook & Whitehead 2005):

$$\text{Number of nestlings of one sex produced per pair in year } i =$$

$$x * \frac{\text{Number of known fledglings in year } i}{\text{population estimate in year } i * \text{proportion of females in breeding age class}}$$

The denominator represents the number of pairs alive in year i which is defined by the number of breeding females in the population because females are limiting; the proportion of females of breeding age (0.31) comes from the stable age distribution. x, the fledgling sex proportion, is equal to 0.4 and 0.6 to estimate the number of females and males produced per breeding female, respectively (LPP pers. obs.). We then multiplied the number of fledglings per female with adult survival to calculate fecundity based on a post-breeding census. This resulted in a lambda < 1, whereas the observed population change indicated an annual rate of increase (R) of 1.035. We thus adjusted the fecundities so that the eigenvalue of the stage matrix is 1.035.

Environmental stochasticity

RAMAS GIS simulates environmental stochasticity by sampling distributions as specified by the mean and standard deviation of each stage matrix element (Akçakaya & Root 2005). To estimate standard deviation of fecundity we followed Akçakaya's (2002) approach of subtracting the weighted average of demographic variance from the total variance. These methods are commonly used to separate demographic and environmental variability for population viability analyses (Lambert *et al.* 2006, Zeigler *et al.* 2010, Aiello-Lammens *et al.* 2011). For the standard deviation of survival estimates, we used the square root of the process error (sigma) reported by MARK (White, Burnham & Anderson 2001).

Climate change forecasts and bioclimatic envelope modelling

Climate change forecasts

Spatial layers describing present day climate (0.01º x 0.01º latitude/longitude) were created by interpolating between weather station records sourced from the Queensland Government SILO patched point data base (Jeffrey *et al.* 2001), following the approach described in detail by Fordham *et al.* (in press-b).

We used MAGICC/SCENGEN v5.3 (http://www.cgd.ucar.edu/cas/wigley/magicc), a coupled gas cycle/aerosol/climate model used in the IPCC Fourth Assessment Report (IPCC 2007), to generate an annual time series of future climate anomalies for (2000–2100) for annual, austral winter and summer precipitation and temperature (0.5º x 0.5º latitude/longitude; annual rainfall, January temperature, and July temperature in this study). Projections were based on two emission scenarios: a high-CO_2-concentration stabilisation reference scenario, WRE750, and a policy scenario that assumed substantive intervention in CO_2 emissions, LEV1 (Wigley, Richels & Edmonds 1996; Wigley *et al.* 2009). Models were chosen using an assessment of model convergence and skill in predicting seasonal precipitation and temperature (see Fordham *et al.* in press-b for details). The nine skilful GCMs used to generate the multi- climate model ensemble average forecasts were GFDL-CM2.1, MIROC3.2(hires), ECHAM5/MPI-OM, CCSM3, ECHO-G, MRI-CGCM2.3.2, UKMO-HadCM3, GFDL-CM2.1, MIROC3.2 (medres) (model terminology follows the CMIP3 model database; http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php). Although there is no standard procedure for assessing the skill of GCMs (Fordham et al. 2012a), by using an ensemble model set of greater than five GCMs, the influence of model choice on model prediction skill is lessened (Murphy *et al.* 2004; Pierce *et al.* 2009).

We downscaled the climate anomalies to an ecologically relevant spatial scale (0.01 x 0.01° longitude/latitude), using the "change factor" method, whereby the low-resolution change from a GCM is added directly to a high-resolution baseline observed climatology (Hulme, Raper & Wigley 1995). One advantage of this method is that, by using only GCM change data, it avoids possible errors due to biases in the GCMs' baseline (present-day) climate (Fordham et al. 2012a,b).

Bioclimatic envelope modelling

Allocasuarina verticillata *presence data*

We modelled the bioclimatic envelope of *Allocasuarina verticillata* (drooping she-oak) because it provides the primary habitat and 98% of the diet of the GBC. *A. verticillata* presences came from Department of the Environment and Natural Resources (DENR) biological survey records across South Australia (http://www.environment.sa.gov.au/Knowledge_Bank/Information_and_data/Biological_databases_of_South_Australia). The presences were carefully cleaned before inclusion; only records with an accuracy of 1 km or better were retained, duplicate and erroneous records were removed, and no opportunistic records were included, which left 572 presences for the analysis. Much of *A. verticillata*'s range has been cleared, which may influence our ability to model the species's distribution. Using presences from across the species's South Australian range and requesting validation from local plant ecologists helped address this issue. An equal number of pseudoabsences were generated randomly within the study region; random pseudoabsences were appropriate in this case because of the difficulty of intensively sampling the study area (South Australia) (Wisz & Guisan 2009). Plant ecologists identified three climate variables as having the greatest general influence on *A. verticillata* survival and recruitment: mean annual rainfall, mean January temperature, and mean July temperature (Stead 2008).

Ensemble forecasting

The potential distribution of *A. verticillata* was modelled with an ensemble forecasting approach (Araújo & New 2007) based on seven BEM techniques: BIOCLIM (Busby 1991), Euclidian and Mahalanobis distances (Farber & Kadmon 2003), generalised linear models (GLMs; McCullagh & Nelder 1989); Random Forest (Breiman 2001), Genetic Algorithm for Rule Set Production (Stockwell & Noble 1992), and Maximum Entropy (Phillips & Dudík 2008) in BIOENSEMBLES software (Diniz-Filho *et al.* 2009). Internal evaluation of the models was performed with a data split procedure, whereby 70% of the occurrence data were randomly split and used for calibration of the models, and the remaining 30% were used for cross-evaluation of the models. This procedure was repeated 10 times, thus generating a 10-fold cross-validation of model results. The observed prevalence of species was maintained in each partition, and for each partition we obtained alternative models by projecting ranges after performing a full factorial combination of the environmental variables used as predictors. The fitting and projection of alternative models using data partition and multiple combinations of variables was used to account for uncertainties arising from the initial conditions and model parameterization (sensu Araújo & New 2007). Model accuracy was measured using the average True Skill Statistic (Allouche, Tsoar & Kadmon 2006). This analysis was performed to check if a grossly implausible projection was being made (i.e. TSS < 0.3). However, because measures of accuracy on non-independent data do not provide a reliable benchmark for evaluation of projections of species distributional changes under climate change (Araújo *et al.* 2005), we instead used an unweighted consensus of the seven modelling techniques. The resulting map of the current distribution was validated by an expert botanist (P. Lang, DENR). We then ran the distribution models with the climate layers for 2011–2100 (described above) to create a combined time series of 91 climatic suitability maps for each year from 2010 to 2100.

The climate projected for 2100 on Kangaroo Island was within the range of variation in the training data for 2010. This was true for all three climate variables in both emissions scenarios. Therefore the bioclimatic model did not extrapolate to novel climates, which reduces uncertainty in projections (Pearson & Dawson 2003).

Integrating population and distribution models

Calculating the habitat suitability function

The *A. verticillata* probability of occurrence maps for 2010−2100 (hereafter ‘AVS’) were added to edaphic spatial layers (substrate, slope, and native vegetation) to mask out unsuitable areas and delineate more suitable areas for *A. verticillata* and the GBC (Pearson, Dawson & Liu 2004). Substrate and slope are specific to *A. verticillata*, while native vegetation affects *A. verticillata* and the GBC.

Substrate, or geology, strongly influences soil type and is an important predictor of *A. verticillata* presence (Specht & Perry 1948; Green 1994). We collapsed category classes in the

Surface Geology of Australia dataset (1:1 million scale; Raymond & Retter 2010) into 17 classes in South Australia. Expert knowledge was used to define which substrate classes are unsuitable for *A. verticillata* (mainly Holocene sands, and floodplain alluvium; P. Lang unpubl. data). We treated areas with native vegetation (National Vegetation Information System; http://www.environment.gov.au/erin/nvis/index.html) as having twice the suitability of areas without native vegetation (Crowley et al. 1998b). Because *A. verticillata* prefers to grow on steep, rocky slopes (Crowley *et al.* 1998a,b), we created a slope layer from a digital elevation model (DEM-9S, http://www.ga.gov.au/meta/ANZCW0703011541.html) in Arc GIS v9.3 (Arc GIS, Environmental Systems Research Institute, Redlands, CA, USA).

We used binomial GLMs to relate the spatial layers to cockatoo presences and generate the habitat suitability function. Presence data for the GBC (349 points) came from active nest locations (n = 157; GBC recovery program data), band observations (n = 100; GBC recovery program data), known feeding sites (n = 18; GBC recovery program data), and the South Australian Biological Survey (n = 74). No reliable absence points were available for the GBC, so we were forced to generate psuedoabsences. Considering that the island has been well surveyed for GBCs, and that we wanted the model to focus on the factors determining its distribution within the landscapes in which one might reasonably expect to survey, we generated pseudoabsences using a positive distance weighting function that favours areas away from presences when creating pseudoabsences (Phillips *et al.* 2009; Wisz & Guisan 2009). We tested models from an *a priori* candidate model set generated using our knowledge of probable factors limiting the occurrence of GBCs. We primarily relied on Akaike's Information Criterion corrected for small sample sizes (AIC_c) for model selection (Burnham & Andersen 2002), but we also calculated the Bayesian Information Criterion (BIC) because it is more conservative (tends to fit fewer tapering effects) and requires substantially better fit before selecting a more complex model (Bolker 2008).

Habitat suitability function

Our selected covariates adequately predict GBC occurrence, explaining 38.5% of the variance (Table S5.3). The best model (**habitat suitability ~ substrate*slope + vegetation*AVS**; *w*AIC of 0.954) became the habitat suitability function for the RAMAS model. Thus, habitat suitability is defined as:

habitat suitability = ((4.61*[substrate] + 1.49*(thr([slope],0.01366)) - 2.11*[vegetation] - 0.454*(thr([AVS],0.399)) - 0.8818*[substrate]*(thr([slope],0.01366)) + 3.784*[vegetation]*(thr([AVS],0.399)))*[substrate]) / 5.34375

The coefficients were estimated from the binomial model. The entire equation is multiplied by substrate in order to mask out areas with unsuitable substrate, and then divided by 5.34375 to scale habitat suitability from 0 to 1 in each grid cell. We applied thresholds (thr) to slope and AVS such that this part of the equation was equal to zero unless the grid cell's value was greater than the lower fifth percentile of the variable where GBCs occur. Thresholds used in this manner better capture species' responses to continuous spatial variables in metapopulation models (DAF unpubl. data).

We used a threshold to determine a lower habitat suitability limit below which we would not expect an occurrence. Threshold selection affects range area predictions, and the choice of a threshold depends on the goals of the modelling exercise (Liu *et al.* 2005). The GBC population on Kangaroo Island has been carefully censused so we had high confidence that the distribution was well-represented by the point locality data. We aimed to characterise the current extent of medium to high quality habitat and predict the potential distribution of suitable habitat patches in the future which we did by selecting cells with a HS value higher than the value recorded for the lowest 5% of GBC presences. We used our knowledge of the species in the field to validate the resulting habitat suitability maps.

Table S5.3. Results of binomial GLMs relating spatial variables to *Calyptorhynchus lathami halmaturinus* presences on Kangaroo Island. AVS stands for climatic suitability of *Allocasuarina verticillata* (the cockatoo's food plant). The global model had the strongest AIC$_c$ and BIC support, explaining 38.5% of model structural deviance. Of the single term models, slope had greatest support explaining 26.5% of model deviance. Models in bold had *w*AIC >0.01.

Model	% DE	*w*AIC$_c$	Δ AIC$_c$	*w*BIC	Δ BIC	*k*
substrate*slope + vegetation*AVS	38.5	0.954	0	0.497	0	7
substrate*slope + vegetation + AVS	35.9	0.022	7.5	0.065	4.1	6

substrate + vegetation + slope + AVS	35.1	0.015	8.4	0.245	1.4	5
substrate*slope + AVS	34.9	0.010	9.2	0.161	2.3	5
substrate*slope	31.4	0	20.0	0.004	9.5	4
substrate + slope	30.8	0	20.0	0.024	6.1	3
substrate + vegetation + slope	31.0	0	21.7	0.002	11.3	4
AVS*slope	30.8	0	22.1	0.001	11.6	4
slope	26.5	0	34.1	0	16.6	2
vegetation*slope	27.3	0	35.4	0	25.0	4
substrate + vegetation*AVS	20.0	0	64.6	0	57.6	5
substrate	10.8	0	92.6	0	75.1	2
vegetation*AVS	6.7	0	111.9	0	101.5	4
AVS	3.3	0	120.2	0	102.7	2
null	0	0	130.5	0	109.5	1
vegetation	0.04	0	132.4	0	114.9	2

Carrying capacity

Estimates of carrying capacity were based on previous research on *A. verticillata* productivity and extent on Kangaroo Island, and known density of GBCs in *A. verticillata* stands. One hectare of moderate quality she-oak habitat (334,000 cones) supports approximately 7.5 birds (Crowley, Garnett & Pedler 1997; Chapman & Paton 2002). The current area of *A. verticillata* on Kangaroo Island is 4,900 ha (SA DENR data), so the approximate carrying capacity of the island is 653 birds. This is a maximum estimate of current carrying capacity given that GBCs only feed on c. 10% of available *A. verticillata* (Chapman & Paton 2005). In RAMAS we used a scaling constant (0.233) to relate the known carrying capacity to the number of suitable cells (noc). We applied a threshold to the equation to eliminate very small unviable patches with carrying capacity <10 birds:

K = thr(0.233*noc,10)

Initial abundance

Initial abundance was calculated in a similar way. Annual censuses of the population estimated the current population size at c. 350 individuals, so we used a lower scaling constant to approximate this:

$$\mathbf{N_{initial} = thr(0.125*noc,10)}$$

We ran trial scenarios with initial abundances of 100 and 200 birds and found that the population showed the same general responses as with 350 birds. These trials, combined with the carrying capacity of 653 under ceiling density dependence, suggest that the model was not very sensitive to initial population size.

Dispersal

Data on movements of marked birds were used to estimate annual dispersal. Available information suggests that approximately 73% of birds leave the general natal area annually and 23% of these leave the wider flock region, so c. 17% of birds disperse annually (Southgate 2002; Mooney & Pedler 2005). Dispersers moved an average of 44 km and up to 78 km (Southgate 2002). This high rate of dispersal supports our use of mark-recapture- derived survival estimates even though only a portion of the island is covered by the mark-recapture surveys. Our dispersal function had 17% of birds dispersing ≥28 km annually and 1% of the population (4 birds) dispersing 78 km annually (Fig. S5.1). We modelled dispersal as a function of the distance between the centres of suitable habitat patches.

dispersal ~ a = 0.8, b = 16.5, c = 1

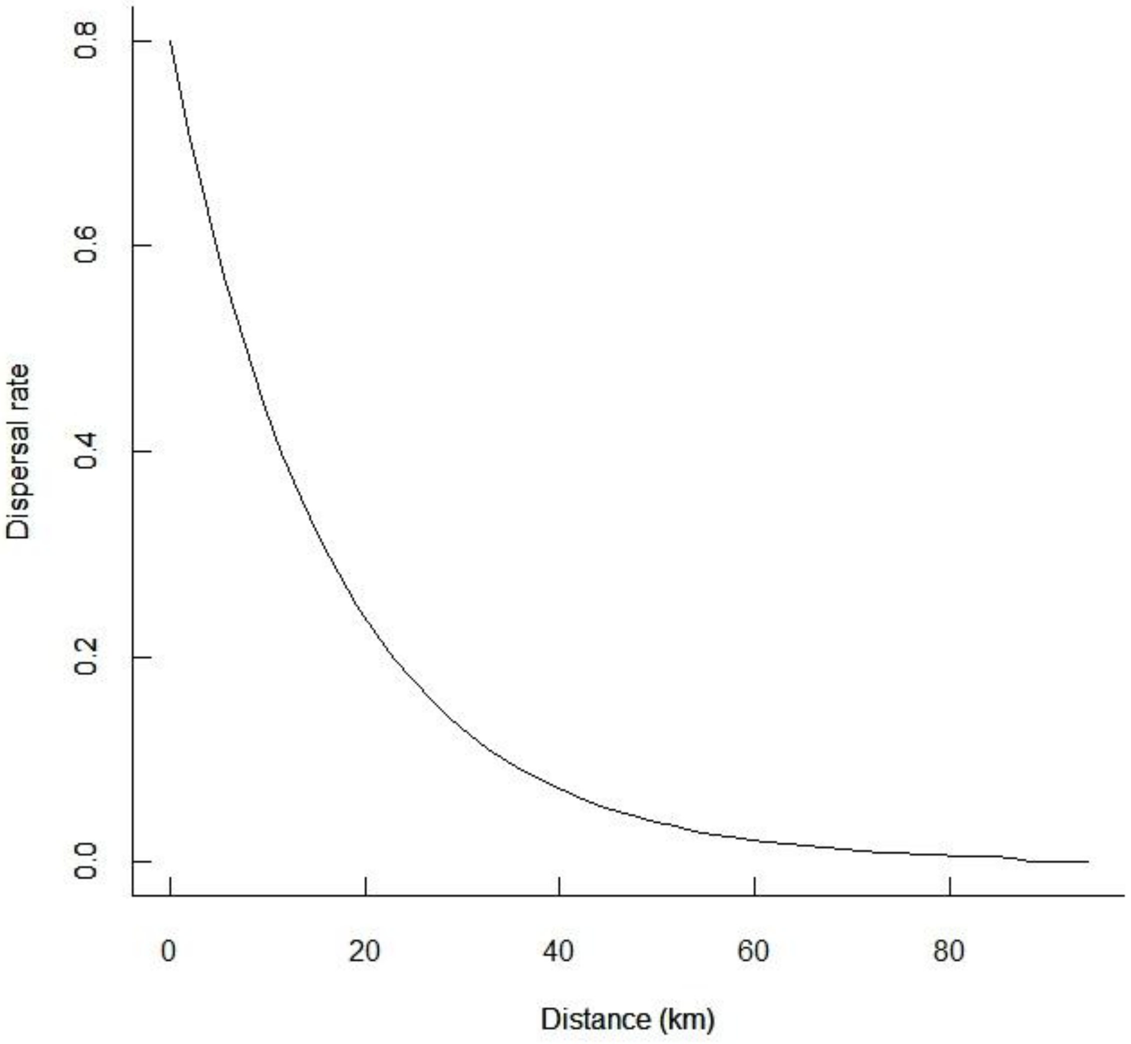

Figure S5.1. Annual dispersal-distance curve for the *Calyptorhynchus lathami halmaturinus* population on Kangaroo Island.

Correlation among grid cells

Environmental variability was set to be correlated between populations depending on their spatial separation. Pairwise correlations were calculated using an exponential function, P = a.exp($D^{c/b}$), where D is the distance between centroids of habitat patches and a, b and c are constants. Following Keith et al. (2008), we used regional variation in year-to-year annual rainfall across South Australia to approximate environmental variability (a = 0.79, b = 1266, c = 1).

RAMAS scenarios and sensitivity analysis

Fire

Baseline fire frequency

Four fires burned >10% of Kangaroo Island from 1950−2008, which yields an annual probability of severe fire of 6.8% (GBC recovery program data). Our vital rates estimates included the effects of past severe fires so we included observed fire frequency in the baseline scenarios. We modelled fire probability as being the lowest after a fire (0.1% probability) and then increasing with mounting fuel loads until the maximum probability (6.8%) is reached after seven years (Keith *et al.* 2008). To maintain structural simplicity of the model, it was assumed that fires burnt entire patches (i.e. no fire heterogeneity within patches)

Impacts of fire on the GBC

The best data on the effects of a severe fire on the GBC come from 2007 when fires burned 85,920 ha (19.5% of the island), destroying five known nest sites and 425 ha of *A. verticillata* feeding habitat (Sobey & Pedler 2008). Based on nesting data from 1997−2003, if five nests are lost, fecundity is reduced by 8−12%. Therefore we modelled the effects of a severe fire as having a 10% reduction in fecundity. Reduction in feeding habitat from severe fires is expected to have a minor, delayed impact on survival (DCP pers. obs.), so we modelled this effect by reducing sub-adult and adult survival by 3% after a severe fire.

Climate change and increased fire management

Climate change is predicted to cause a substantial increase in the number of days with very high to extreme fire danger on the Fleurieu Peninsula (Lucas *et al.* 2007). These predictions suggest that severe fire danger will increase by 5% or 25% by 2050 for low and high emissions scenarios, respectively. We interpreted these changes as percent increases in base probability of fire on Kangaroo Island and used the 2050 estimates as guidelines. Making the conservative assumption that there is a linear correlation between fire frequency and fire days, increases of 5% and 25% would yield annual fire probabilities of 7.1% and 8.5% on Kangaroo Island. We also considered a nonlinear example where a 2.2-fold increase in fire frequency yielded a 15% annual fire probability on Kangaroo Island (approximately doubling the current probability). We also investigated the impact of increasing fire management to reduce the annual probability of severe fire by half to 3.4%.

Disease

Psittacine beak-and-feather disease typically kills juvenile parrots only (DEH 2005). Virulence of the disease varies; major epidemics with high mortality can occur in isolated parrot populations with little immunity, while populations with previous exposure to the disease are more resilient (DEH 2005; Khalesi 2007). There have been no recorded cases of beak-and-feather disease on Kangaroo Island (LPP pers. obs.), so we assumed low immunity and high mortality. Little corellas regularly cross from the mainland to Kangaroo Island (Mooney & Pedler 2005) and could serve as vectors of the disease (DEH 2005). We modelled a possible outbreak by reducing survival of zero year olds and one year olds by 50%. We set the annual probability of an outbreak at 5% and the probability of an infected dispersing bird transmitting the disease at 75%. While the values of these parameters are poorly known in the wild (Khalesi 2007) an expert on beak-and-feather disease confirmed that our parameterisation was realistic (M. Holdsworth, pers. comm.).

Active management

Brushtail possum management

The GBC recovery team manages nest-predating brush-tail possums *Trichosurus vulpecula* by placing metal collars around the trunks of GBC nest trees and pruning overlapping tree crowns to prevent access to nest trees (Mooney & Pedler 2005). Possum management can increase fecundity by 78% (the probability of an egg producing a fledgling increases from 23% to 41%; Garnett, Pedler & Crowley 1999). If possum management were stopped, fecundity would decrease by approximately 44%. We assumed a linear decrease in fecundity after stopping management in 2010. By 2025 (15 years after stopping management) all benefits from protected hollows are modelled as being lost (no new hollows protected, tree crowns overlap, and metal collars rust and fall off trees; LPP pers. obs.) and fecundity is 44% lower.

Corrella management

The little corella *Cacatua sanguinea* population on Kangaroo Island has increased substantially over time, probably as a result of land clearance and grain cropping (Garnett *et al.* 2000). Corellas compete with GBCs for nests and kill GBC nestlings. As a result, corellas found near GBC nests have been culled since 1998. If corella management were stopped, it has been estimated that approximately two GBC nestlings would be lost per year (Garnett, Pedler & Crowley 1999; PAM pers. obs.), so we modelled stopping corella management as causing a 7% drop in fecundity. We simulated stopping management in 2010 and assumed a linear decrease in fecundity that took five years to reach the 7% reduction.

Revegetation

Volunteers and the GBC recovery team have planted *A. verticillata* on Kangaroo Island since 1988 in an effort to augment GBC food sources. From 1996−2007, 39.3 ha were revegetated which amounts to 3.5 ha per year on average. Most revegetation is now done near traditional nesting areas where remnant *Allocasuarina verticillata* has been reduced considerably by clearing. Consequently, the current revegetation rate can be approximated as boosting fecundity by approximately 3% annually (PAM pers. obs.). We modelled stopping revegetation as causing a linear decline in fecundity that lead to a 3% drop in five years.

We also simulated the effects of stopping all management actions (possum, corella, and revegetation in 2010). This lead to a 24.7% decrease in fecundity in five years and a 54% drop in 15 years.

Sensitivity analysis

For the Latin Hypercube sensitivity analysis we took samples from 200 equal-width strata (following the method described in Brook, Griffiths & Puckey 2002) along the following ranges of parameter values relative to the value used in the RAMAS models: adult survival (± 5 %), sub-adult survival (± 10 %), fecundity (± 10 %), carrying capacity (± 20 %), and annual dispersal (± 20 %) (Brook, Griffiths & Puckey 2002). The range for fecundity is equivalent to the standard error around the parameter estimate. The ranges for survival needed to be larger than the standard errors to evaluate the model's sensitivity over a plausible range. We used large ranges for carrying capacity and dispersal for the same reason.

Standardised regression coefficients, calculated by dividing the coefficient of each parameter by its standard error, and then weighting the resulting coefficients to sum to 1 (Conroy & Brook 2003), were used to assess the sensitivity of the model to the input parameters. The coefficients were estimated by fitting a quasiPoisson GLM (to correct for overdispersion) with all of the sensitivity analysis parameters (adult survival, sub-adult survival, fecundity, carrying capacity, and annual dispersal). The non-linear, near-threshold relationship between adult survival and final population size was broken into two parts and was best dealt with by fitting a segmented model (Fig. 5.5; Muggeo 2012). Therefore, the GLM included a segmented fit for adult survival which resulted in two parameters, one above and one below the breakpoint. The breakpoints were estimated at 0.893 ± 0.00081 SE for no climate change (6 iterations to reach convergence), 0.895 ± 0.0011 SE for LEV1 (8 iterations), and 0.886 ± 0.0010 SE for WRE750 (4 iterations). Bootstrapping with 10,000 samples was used to estimate the 95% confidence intervals for the parameter estimates.

Table S5.4. Latin Hypercube sensitivity analysis results. Standardised regression coefficients were calculated from generalised linear models to rank six sensitivity parameters in order of their importance on *Calyptorhynchus lathami halmaturinus* mean final population size. "adult survival-low" is the parameter below the break point in the segmented model and "adult survival-high" is the above the break point.

	standardised coefficient	coefficient	lower CI	upper CI
no climate change				
adult survival-low	0.485	78.9	65.8	103.4
carrying capacity	0.211	0.0011	0.0009	0.0014
juvenile survival	0.110	1.26	0.76	1.86
fecundity, daughters	0.087	2.63	1.15	4.37

dispersal	0.041	-0.18	-0.39	0.01
fecundity, sons	0.033	0.79	-0.22	1.88
adult survival-high	0.033	0.76	0.27	1.78
LEV1				
adult survival-low	0.412	64.4	50.5	152.8
carrying capacity	0.246	0.96	0.75	1.14
sub-adult survival	0.154	1.98	1.24	2.77
fecundity, daughters	0.093	3.10	1.41	5.04
fecundity, sons	0.060	1.58	0.18	2.86
dispersal	0.022	0.11	-0.11	0.34
adult survival-high	0.013	0.35	-0.49	4.26
WRE750				
adult survival-low	0.327	67.7	45.2	131.4
carrying capacity	0.319	1.05	0.90	1.19
sub-adult survival	0.141	1.50	0.85	2.18
fecundity, sons	0.076	1.69	0.43	3.16
fecundity, daughters	0.071	1.99	0.51	3.59
dispersal	0.039	-0.16	-0.39	0.07
adult survival-high	0.026	0.49	-0.31	1.81

Table S5.5. Sensitivity of results to parameterisation of disease outbreaks.

Scenario	Mean final population size ± SD
baseline	649.66 ± 1.9
disease outbreak, 5% annual probability, sub-adult survival reduced by 50%[1]	636.79 ± 29.1
disease outbreak, 10% annual probability, sub-adult survival reduced by 50%	605.35 ± 65.3
disease outbreak, 5% annual probability, sub-adult survival reduced by 75%	607.02 ± 69.6
disease outbreak, 10% annual probability, sub-adult survival reduced by 75%	449.25 ± 164.6

[1] This is the parameterisation used in the present study (see above).

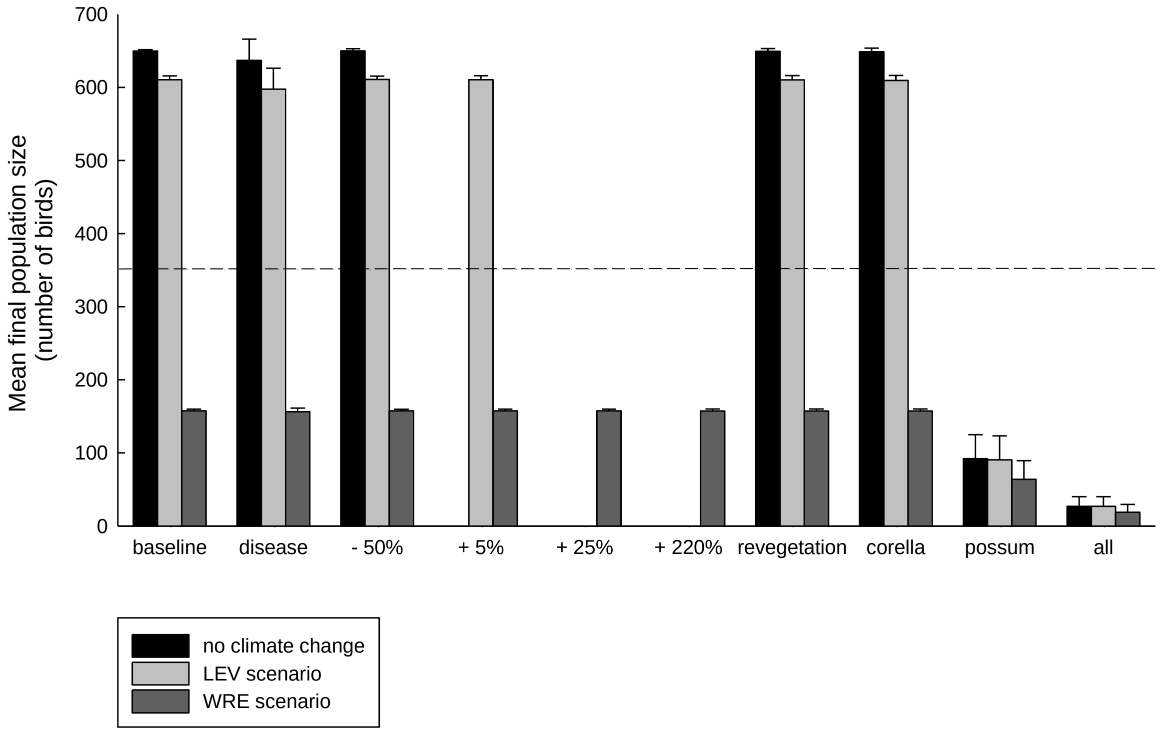

Figure S5.2. Mean final population size of persisting runs (± SD) of *Calyptorhynchus lathami halmaturinus* under no climate change, a greenhouse gas mitigation policy scenario (LEV1), and a high-CO$_2$-concentration stabilisation reference scenario (WRE750). The initial population size was 350 individuals (dashed line). Baseline = baseline scenario that includes observed fire frequency; disease = beak-and-feather disease outbreak; - 50% indicates 50% reduction in fire frequency from increased management; +5%, +25%, and +220% (i.e., 2.2-fold increase) indicate increasing fire frequency from climate change. The last four groups of bars show the effects of ceasing management. “Revegetation”, “corella”, and “possum” indicate stopping revegetation, little corella *Cacatua sanguinea*, and brush-tail possum *Trichosurus vulpecula* management, respectively. “All” indicates stopping all management actions.

Appendix 5 - Supplementary Material for Chapter 6

Supplementary methods: ESA listing procedures

Proposals for listing new species under the ESA are initiated in two ways: on the USFWS’s own accord (discretionary path), or by way of a petition from a member of the public (USFWS 2009a; Figure S6.1). The status of species on the candidate list is evaluated annually until it is listed, or listing is determined to be unwarranted. If a species is petitioned, the USFWS undertakes a 90-day finding, and if there is substantial information that listing may be warranted, the USFWS conducts a scientific status review to determine if the species should be listed. In the “12 month finding” due 12 months after the USFWS receives the petition, the USFWS decides if listing is *not warranted*, *warranted*, or *warranted but precluded* (the latter if sufficient information is available to warrant listing but listing is precluded by higher listing actions, and the species is placed on the candidate list) (US Congress 1982; USFWS 2009a).

Case studies

Ashy storm-petrel (*Oceanodroma homochroa*)

The ashy storm-petrel is a smoky-gray seabird that feeds on small fish, squid, and crustaceans in the California current (Fig. S6.3A). The species nests on islands off California and Baja California (Mexico) and disperses along the California coast during the non-breeding season, but does not migrate long distances (BLI 2010). The current global population estimate is 5,200–10,000 breeding birds (BLI 2010). At the species’ main breeding colony on southeast Farallon Island, the population declined by 42 % from 1972–1992 (Sydeman *et al.* 1998), and there is evidence of continuing recent declines across its range (BLI 2010; Ainley & Hyrenbach 2010). These declines led to the species being listed by the IUCN as *Endangered* in 2004 (criteria A2ce+3ce+4ce; IUCN 2009). The storm-petrel is threatened by pesticide pollution, climate change (changes in ocean currents and upwelling; Ainley & Hyrenbach 2010), squid fishing (lights may increase nest predation), and nest predation from expanding western gull (*Larus occidentalis*) and burrowing owl (*Athene cunicularia*) populations (BLI 2010).

The Center for Biological Diversity (CBD) filed a petition to list the storm-petrel under the ESA in October 2007 (CBD 2010). In response to the USFWS repeatedly missing deadlines to decide whether or not to list the species, the CBD filed two intents to sue (March 2008 and January 2009) and finally sued the USFWS for delaying its decision (April 2009) (CBD 2010). On 18 August 2009, nearly 10 months after the deadline required by the ESA, the USFWS decided to not list the species (USFWS 2009c). Initially the USFWS decided listing was *warranted but precluded*, but the USFWS's regional office revised the decision to *not warranted* (Vespa 2010). A USFWS biologist disputed the revision because it contained "inaccuracies" and made questionable interpretations on the species' population trend from an unpublished report produced by the Point Reyes Bird Observatory (Warzybok & Bradley 2007; Vespa 2010). After the CBD filed an intent to sue based on these scientific inaccuracies, the USFWS agreed to revise its 2009 finding (USFWS 2010). The revised finding is still pending.

Kittlitz's murrelet (*Brachyramphus brevirostris*)

The Kittlitz's murrelet has the highest IUCN threat level of any bird in the US that is not protected by the ESA (Table 6.1). The murrelet is a small, poorly-known seabird that is endemic to Alaska and Russia where it forages for fish and macrozooplankton in glacial meltwater near the coast (Fig. S6.3B). The species nests on glaciated mountaintops and upland habitats on islands (BLI 2010). The current global population estimate is 20,000–49,999, with 70 % of the population found in Alaska (BLI 2010). Several independent datasets suggest the murrelet has undergone a steep decline of 59–90 % in the last 15 years across most of its range (Kuletz *et al.* 2003; Kissling *et al.* 2007; BLI 2010), which led to it being listed as *Critically Endangered* by the IUCN in 2004 (criterion A4bcde; IUCN 2009). Kittlitz's murrelet is threatened by glacial recession, oil spills, disturbance from tour boat traffic, and entanglement in salmon fishing nets (Kuletz *et al.* 2003; BLI 2010). In 2008 the US government leased large portions of the Chukchi Sea shelf to oil and gas companies for offshore development, where oil spills could dramatically impact Kittlitz's murrelets (BLI 2008).

Kittlitz’s murrelet was first petitioned for listing under the ESA by environmental groups in May 2001 (CBD 2009). In May 2004 the USFWS decided not to list the species and classified it as a candidate with a listing priority of 5 (facing non-imminent threats of high magnitude) (USFWS 2004). The USFWS (2004) stated:

> “…we believe that glacial retreat and oceanic regime shifts are the factors that are most likely causing population-level declines in this species. Existing regulatory mechanisms appear inadequate to stop or reverse population declines or to reduce the threats to this species.”

Presumably, this statement refers to difficulty in addressing climate change as a threat. In November 2005 the CBD (2009) filed suit against the USFWS for delaying ESA protection of species on the candidate list, including the murrelet. In December 2007 the species moved up to priority 2 due to imminent threats of high magnitude (USFWS 2007). In March 2009 the CBD petitioned the Alaska Game & Fish Department to protect the species under the Alaska State ESA, but Alaska denied the petition in April, and the species remains at listing priority 2 (USFWS 2009d).

Cerulean warbler (*Dendroica cerulea*)

The cerulean warbler is a migratory insectivorous songbird that breeds in mature hardwood forests in the US and Canada, and winters in the foothills of the Andes from Venezuela to Bolivia (Hamel 2000; Fig. S6.3C). The global population estimate of 560,000 individuals (BLI 2010) is much larger than the other case study species, but Breeding Bird Survey data indicate that the species declined by 26 % per decade from 1980–2002 (Sauer *et al.* 2003 in BLI 2010) which contributed to an 82 % overall decline in the last 40 years (BLI 2006). The species was labeled the “fastest declining wood warbler in the US” (BLI 2006) and listed as *Vulnerable* in 2004 (criteria A2c+3c+4c; IUCN 2009). The warbler is threatened by habitat loss throughout its range (BLI 2010). Important contributors to habitat loss on the breeding grounds include mountaintop removal coal mining, logging, and urban development; cattle ranching and coffee farming are important factors on the wintering grounds (Wood *et al.* 2006; BLI 2010).

The warbler was petitioned for listing by 28 environmental groups in 2000. After two years (*c.f.* the 90 day deadline; Fig. S6.1), the USFWS decided that the petition had merit and started a 12-month finding (Bies 2007). After conservation organizations sued the USFWS for repeatedly missing deadlines (Bies 2007), the USFWS finally decided that listing was *not warranted* for the species in 2006 (USFWS 2006). The USFWS used Breeding Bird Survey data to estimate an annual decline of 3 % and concluded that the species would still number in the tens of thousands by 2100 (USFWS 2006). The listing decision caused uproar in the environmental community because it downplayed the decline of the species and took just over six years to be announced (e.g. BLI 2006). The USFWS (2006) cited funding constraints for the long delays in reaching a decision.

Pacific salmonids

The National Marine Fisheries Service's actions to evaluate and list Pacific salmonids offer an example of how the ESA can be effectively applied to multiple species. Anadromous salmonids (*Oncorhynchus* sp.), which hatch in fresh water, migrate to the ocean, and then return to their natal waterways to breed, are threatened primarily by habitat loss from dams and overfishing (SOS 2011). In the 1990s, the NMFS initially responded to petitions to list individual populations of salmonids, but the NMFS eventually began a proactive effort to evaluate all populations of anadromous salmon and steelhead in Washington, Idaho, Oregon, and California (NMFS 2011). The NMFS first had to determine which populations should be considered distinct population segments, and subsequently defined 52 evolutionary significant units (ESUs) based on reproductive isolation and evolutionary distinctiveness. From 1994 to 1999 the NMFS, using teams of salmon experts to incorporate relevant scientific information, decided to list 21 ESUs as *threatened* and 5 as *endangered* (NMFS 2011). In a 2005 status review, the NMFS maintained all earlier listings and added an additional ESU to the list (NMFS 2005; Good *et al.* 2005). Only one species of *Oncorhynchus* found in the region reviewed by the NMFS, sockeye salmon (*O. nerka*; Fig. S6.2D), has been evaluated by the IUCN. The IUCN assessment identified 1 threatened subpopulation of the species in the region: Redfish Lake (Columbia River) sockeye (*Critically Endangered*) (Rand 2008). The NMFS listed the Snake River population (equivalent to Redfish Lake) as *endangered* and the Ozette Lake, Washington population as *threatened* (NMFS 2011). In this four state region the NMFS has undertaken a much more comprehensive review of the status of salmonid populations compared to the IUCN, although the IUCN Salmonid Specialist Group is working to evaluate the other species (SOS 2011). The NMFS's action on Pacific salmonids is an example of a US agency making ample use of science to proactively evaluate a large group of species.

Table S6.1. Twenty-three bird species are listed as imperiled by the ESA (USFWS 2009b) but not the IUCN (IUCN 2009). ESA categories are *endangered* (E) or *threatened* (T); IUCN categories are *Least Concern* (LC) and *Near Threatened* (NT). Taxonomy for the 'species' column follows Chesser *et al.* (2010).

species	IUCN status	taxon listed by ESA (if different)	ESA status	where listed
northern bobwhite (*Colinus virginianus*)	NT	masked bobwhite (*Colinus virginianus ridgwayi*)	E	entire range
spectacled eider (*Somateria fischeri*)	LC		T	entire range
wood stork (*Mycteria americana*)	LC		E	U.S.A. (AL, FL, GA, SC)
crested caracara (*Caracara cheriway*)	LC	Audubon's crested caracara (*Polyborus plancus audubonii*)	T	U.S.A. (FL)
aplomado falcon (*Falco femoralis*)	LC	northern aplomado falcon (*Falco femoralis septentrionalis*)	E	entire range, except where listed as an experimental population
snail kite (*Rostrhamus sociabilis*)	LC	Everglade snail kite (*Rostrhamus sociabilis plumbeus*)	E	U.S.A. (FL)
Hawaiian hawk (*Buteo solitarius*)	NT		E	entire range
clapper rail (*Rallus longirostris*)	LC	California clapper rail (*Rallus longirostris obsoletus*)	E	entire range
		light-footed clapper rail (*Rallus longirostris levipes*)	E	U.S.A. only
		Yuma clapper rail (*Rallus longirostris yumanensis*)	E	U.S.A. only
sandhill crane (*Grus canadensis*)	LC	Mississippi sandhill crane (*Grus canadensis pulla*)	E	entire range

black-necked stilt (*Himantopus mexicanus*)	LC	Hawaiian stilt (*Himantopus mexicanus knudseni*)	E	entire range
piping plover (*Charadrius melodus*)	NT		E	Great Lakes watershed in States of IL, IN, MI, MN, NY, OH, PA, and WI and Canada (Ont.)
			T	Entire, except those areas where listed as endangered above
snowy plover (*Charadrius alexandrinus*)	LC	western snowy plover (*Charadrius alexandrinus nivosus*)	T	U.S.A. (CA, OR, WA), Mexico (within 50 miles of Pacific coast)
roseate tern (*Sterna dougallii*)	LC	roseate tern (*Sterna dougallii dougallii*)	E	U.S.A. (Atlantic Coast south to NC), Canada (Newf., N.S, Que.), Bermuda
		roseate tern (*Sterna dougallii dougallii*)	T	Western Hemisphere and adjacent oceans, incl. U.S.A. (FL, PR, VI), where not listed as endangered
least tern (*Sternula antillarum*)	LC		T	U.S.A. (AR, CO, IA, IL, IN, KS, KY, LA_Miss. R. and tribs. N of Baton Rouge, MS_Miss. R., MO, MT, ND, NE, NM, OK, SD, TN, TX_except within 50 miles of coast)
		California least tern (*Sterna antillarum browni*)	E	entire range
spotted owl (*Strix occidentalis*)	NT	Mexican spotted owl (*Strix occidentalis lucida*)	T	entire range
		northern spotted owl (*Strix occidentalis caurina*)	T	entire range
willow flycatcher (*Empidonax traillii*)	LC	southwestern willow flycatcher (*Empidonax traillii extimus*)	E	entire range
loggerhead shrike (*Lanius ludovicianus*)	LC	San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*)	E	entire range
Bell's vireo (*Vireo*	NT	least Bell's vireo (*Vireo*	E	entire range

bellii)		*bellii pusillus*)		
California gnatcatcher (*Polioptila californica*)	LC	coastal California gnatcatcher (*Polioptila californica californica*)	T	entire range
Kirtland's warbler (*Dendroica kirtlandii*)	NT		E	entire range
grasshopper sparrow (*Ammodramus savannarum*)	LC	Florida grasshopper sparrow (*Ammodramus savannarum floridanus*)	E	entire range
sage sparrow (*Amphispiza belli*)	LC	San Clemente sage sparrow (*Amphispiza belli clementeae*)	T	entire range
California towhee (*Melozone crissalis*)	LC	Inyo California towhee (*Pipilo crissalis eremophilus*)	T	entire range

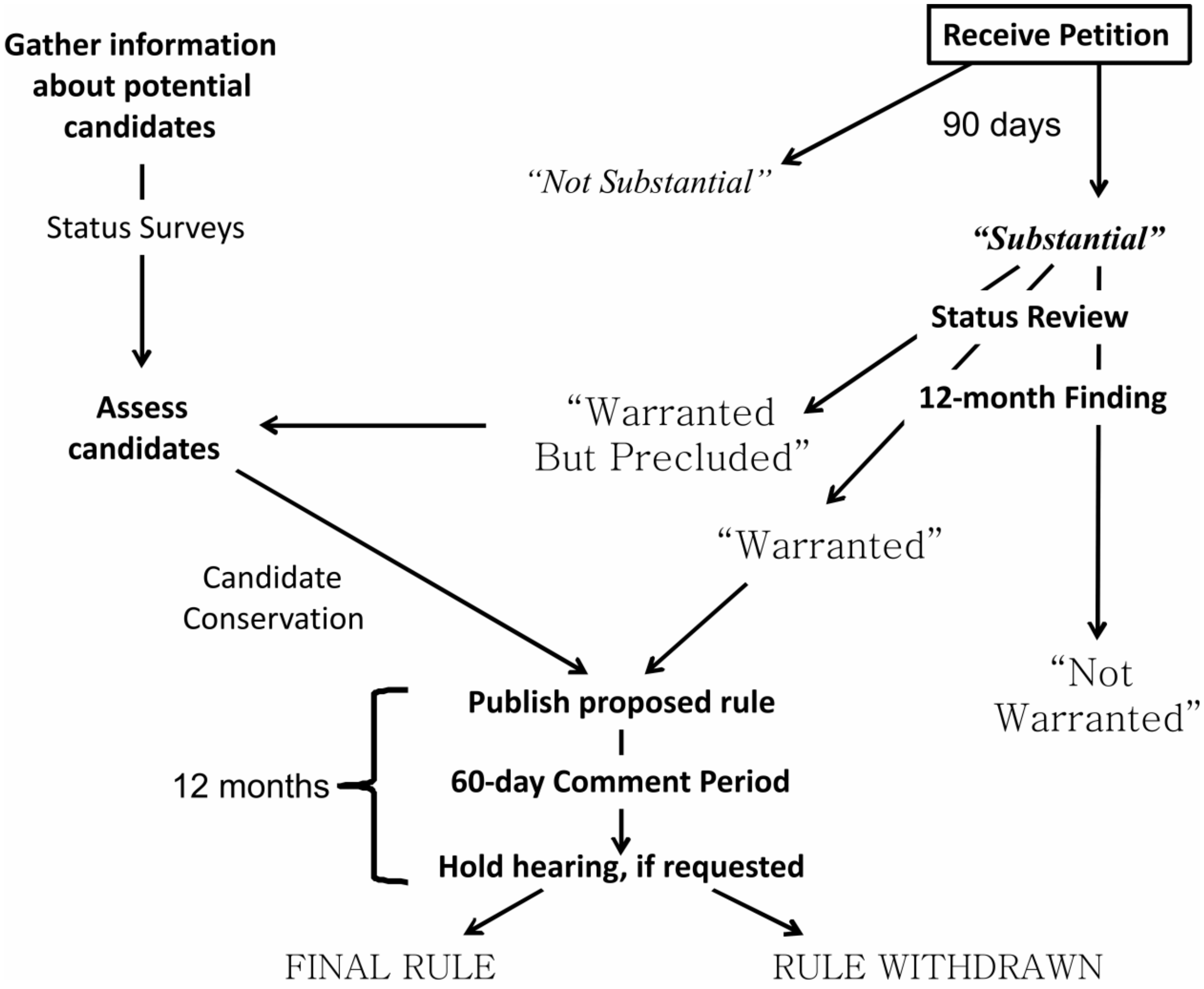

Figure S6.1. Species can be added to the ESA on the USFWS's own accord (discretionary pathway, left) or by way of petitions from parties outside the service (right). Figure adapted from USFWS (2009a).

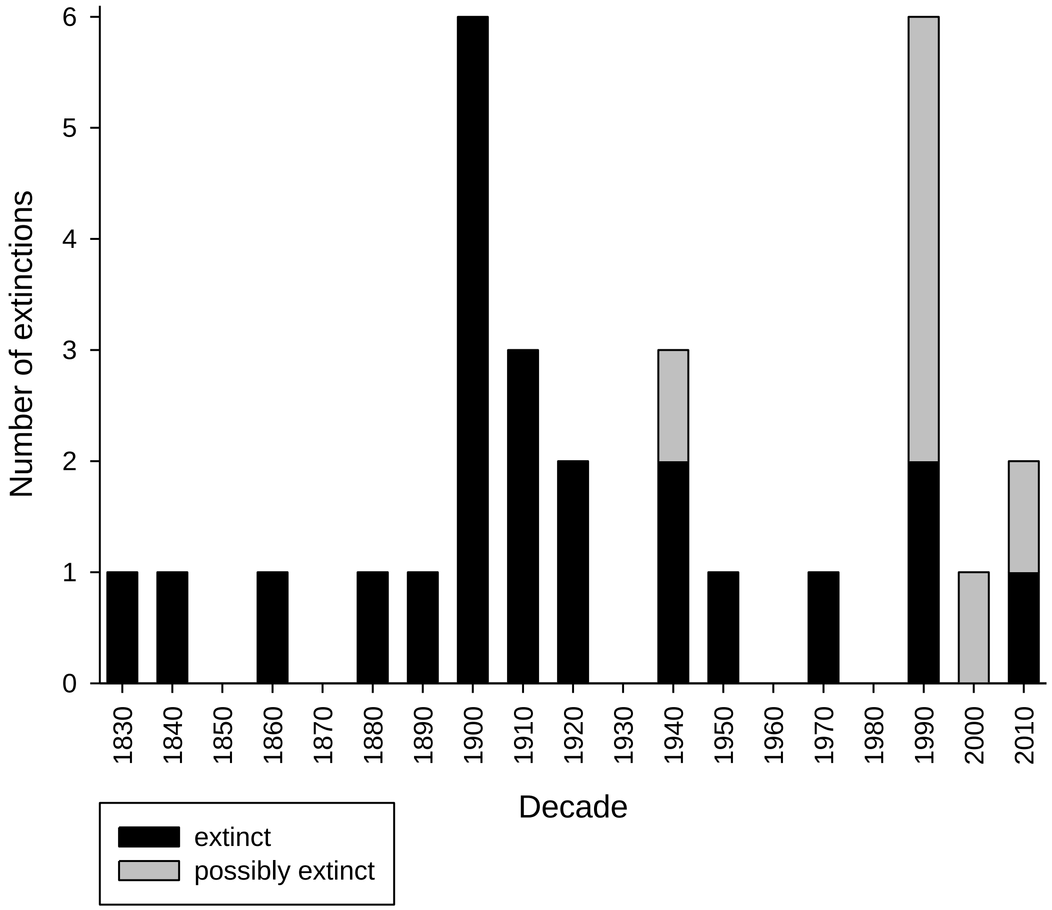

Figure S6.2. Bird extinctions by decade in the United States. Confirmed extinctions are shown in black; species classified as possibly extinct shown in gray. Extinction date is when species was last seen in the wild (data from IUCN 2009, BLI 2010). Twenty-five of the 30 *Extinct* and *Possibly Extinct* birds from the United States were endemic to Hawaii. Note the “extinction” in the 2000s was Hawaiian crow *Corvus hawaiiensis*, which was declared *Extinct in the Wild* in 2004.

Figure S6.3. Case study species. A. ashy storm-petrel (*Oceanodroma homochroa*), B. Kittlitz’s murrelet (*Brachyramphus brevirostris*), C. cerulean warbler (*Dendroica cerulea*), D. sockeye salmon (*Onycorhynchus nerka*). Photographs by D. Pereksta, R. H. Day, L. Hays, and P. Colla, respectively; used with permission.

Appendix 6 - Selected Media Coverage for Chapter 6

SCIENTIFIC AMERICAN™

Permanent Address: http://www.scientificamerican.com/article.cfm?id=us-exempts-species-classified-as-endangered

U.S. Exempts Species Classified as Endangered in the Rest of the World

Kittlitz's Murrelet: The Kittlitz's murrelet is the most endangered species that appears on the IUCN list and not the ESA list. Murrelets live in Alaska and Russia, where they eat fish and large plankton from the water that melts off glaciers. There are less than 50,000 left in the world, and their population has declined as much as 90 percent in the last fifteen years. In 2004 the United States Fish and Wildlife (USFWS) service decided not to list the murrelet as endangered. [Less] [Link to this slide] *U.S. Fish and Wildlife Service*

By Rose Eveleth | Wednesday, December 14, 2011 | 6

A comparison of the U.S. list of endangered species with the world standard finds many species are left unprotected

In the last few months the Western black rhino and the South Florida Rainbow Snake have gone extinct, as far as official recordkeepers are concerned. Less than 3,200 tigers remain as human development, pollution and climate change impinge on ever narrowing habitats.

Tracking these events is not easy. The worldwide arbiter—The International Union for Conservation of Nature (IUCN) —maintains a Red List of endangered species that has become the accepted standard. In the United States, the Endangered Species Act (ESA) establishes protections for animals on the brink. Or does it?

A recent study by scientists at the University of Adelaide and the Center for Biological Diversity (CBD) looked at which American animals made the ESA list, and which didn't. About 40 percent of the bird species listed by the IUCN didn't make the ESA list, and over 80 percent of other groups like fish, amphibians and insects. In total, 531 species that live in the United States and are listed by the IUCN didn't make the ESA cut.

See some of them here.

Being on the IUCN list isn't worth much, since it's simply informational. The ESA list, on the other hand, affords species government backed protection from things like development and hunting. The U.S. Fish and Wildlife Service, that maintains the ESA list, is often steeped in politics, which make listing species very difficult. There are hundreds of species under review by the agency, and those reviews are often delayed many years.

THE CONVERSATION

5 January 2012, 6.49am AEST

Three-quarters of America's threatened species aren't being protected

Author: Bert Harris, PhD Scholar at University of Adelaide

The US has information about its threatened species, but isn't acting on it. photommo/Flickr

We know very little about the world's biodiversity. A recent study suggests that, despite 250 years of taxonomic effort, a mere 14% of the world's species are recognised by scientists.

Worryingly, anthropogenic effects, including habitat loss, climate change, and invasive species, threaten to exterminate thousands of species before they are even described. In this race against time, scientists are working to describe new species and characterise the extinction risk of known species so they can plan actions to reduce extinctions.

The International Union for the Conservation of Nature (IUCN) has been working since 1994 to identify which species are at greatest risk of immediate extinction and place them on the Red List of threatened species.

The IUCN uses quantitative and objective criteria (such as population size, rate of decline, and range size) to classify species as imperilled (Vulnerable, Endangered, or Critically Endangered), Near Threatened, or Least Concern. Through the collaboration of many scientists, and regular refinement of the categories and criteria, the IUCN Red List has emerged as the leading global threatened species list.

Many countries use national "red lists" to protect locally threatened species and evaluate species at the local level where they are managed. One of the best known national lists is the United States Endangered Species Act (ESA), which legally protects species. It is arguably the world's most effective conservation law.

The ESA classifies a species as endangered if it is “in danger of extinction throughout all or a significant portion of its range”. It is threatened if it is “likely to become endangered in the foreseeable future”. If sufficient information is available to warrant listing but listing is “precluded by higher listing actions”, species are considered “warranted but precluded" and not listed. This means that species deemed to be at greater risk of extinction are often listed before “warranted but precluded” species.

ESA listing decisions often become political because listings have the power to stop development projects that impact listed species.

The ESA has succeeded in improving the conservation status of most listed species over time and may have prevented 227 extinctions. Nonetheless, the US government’s implementation of the ESA has been problematic, including political intervention and protracted listing times.

For example, the listing rate varies greatly depending on who is president. The mean listing time from 1974–2003 was greater than 10 years (in contrast to stated maximum of one year). Partly as a result of these shortcomings, at least 42 species or subspecies have gone extinct while awaiting ESA listing.

Given the ESA’s status as one of the world’s most prominent national lists, its track record at conserving species is of international interest. A previous study found that the ESA does not recognise at least 90% of the United States’ imperilled species listed by NatureServe. But no studies have analysed the ESA’s coverage of species listed as globally imperiled by the IUCN.

We undertook the first comparison of IUCN and ESA listings of US birds, mammals, amphibians, gastropods, crustaceans, and insects. We studied the listing histories of three bird species and Pacific salmon in more detail. We found that 40% of IUCN-listed birds, 50% of mammals, and 80–95% of species in the other groups were not recognised by the ESA as imperilled.

Our research suggests that a nearly 10-fold increase in listing would be required if the ESA were to protect the gamut of IUCN-listed species. Our data indicate that less imperilled (but at-risk) species are most likely to be overlooked. This does not bode well for the ESA’s ability to mitigate declines before species become critically imperilled.

The bird case studies exemplify how rapidly declining species can be carefully evaluated by the ESA but still not listed. By contrast, the salmon example shows an alternative situation: agencies were effective in evaluating and listing multiple (closely-related) species.

Lack of funding, vague definitions of the ESA’s threatened and endangered categories, and the existence of the “warranted but precluded" category likely contribute to the ESA’s under-recognition of imperiled species.

The ESA is a powerful environmental law, but its impact is limited because most imperilled species (measured by the IUCN Red List) are not ESA-listed. The case of the ESA illustrates a tradeoff between strong species protection and poor coverage of threatened species caused by the substantial implications of listing. The successes and failures of the ESA provide rich lessons in threatened species conservation stategies that should inform managers in other countries.

Appendix 7 – Cover of *Journal Applied Ecology* featuring chapter 5

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