Predicting and detecting the impacts of climate change on montane fauna in Australian tropical rainforests

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Statement of originality

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Luke P. Shoo

April 2005
Plate 1. Thornton Peak (1375 m) rising steeply from the coastal lowlands of the Daintree (top). Macleay’s Honeyeater (*Xanthotis macleayana*), an endemic rainforest bird of the Wet Tropics biogeographic region (bottom).
Abstract

Global climates are changing rapidly and biological responses are becoming increasingly apparent. Some models indicate that climate warming impacts will largely consist of latitudinal and altitudinal shifts in potential species’ distributions while others suggest that the complete disappearance of critical climate types and dependent species are possible. While early investigations have focused on high latitudes where warming has been most pronounced, there is an increasing recognition of the need to understand impacts in biodiverse tropical regions that support many spatially and climatically restricted species.

The vertebrate fauna of the Wet Tropics biogeographic region of north-eastern Australia provides a unique opportunity to address this deficiency. First, endemic species are typically associated with cool, wet and relatively aseasonal upland environments; characteristics considered to have predisposed the fauna to being particularly vulnerable to future global climate change. Second, recent projections of species responses to future climate scenarios suggest strong systematic change in the extent and location of species’ distributions with even small amounts of warming. Altitude is effectively a surrogate for turnover in temperature in the region and impacts of increasing temperature are expected to be most noticeable along this gradient. Focusing on two ecologically disparate taxa (i.e. rainforest birds and microhylid frogs) empirical abundance patterns across altitudinal gradients and predicted altitudinal range shifts are used to: (1) predict changes in total population size; (2) estimate change in total population size relative to distribution area; and (3) quantify the sensitivity and bias of widely used measures for assessing contemporary range shifts along altitudinal gradients.

According to the most conservative model scenario, 41 of 55 (74%) rainforest birds and 6 of 6 (100%) microhylid frogs examined are predicted to become threatened as a result of projected mid-range warming expected within the next 100 years. Extinction risk varied according to where along the altitudinal gradient a species was most abundant. Upland species were most affected and are likely to be immediately threatened by even small increases in temperature. In contrast, there is a capacity for the population size of lowland species to increase, at least in the short term.

In the context of climate warming impacts, a documented decline in distribution area will not necessarily reflect the extent of change in total population size. For 9 out
of 12 species of regionally-endemic birds and 5 out of 6 species of microhylid frogs, total population size is expected to decline more rapidly than distribution area with increasing temperature. For both groups combined, only 4 species (22%) showed either a comparable or slower decline in population size with change in distribution area. The disproportional loss in population size suggests that extinction risk associated with climate change can be more severe than that expected from decline in distribution area alone.

Detection and measurement of climate induced change is crucial if we are to improve predictions of future change and attempt to mitigate impacts to biodiversity. Randomisations of available data suggest that the mean position of presence records allows for a smaller minimum detectable range shift than change measured at upper or lower range boundaries. For a moderate survey effort of 96 surveys, measurements of change in the mean altitude of 34 rainforest birds has the capacity to provide strong inference for mean altitudinal range shifts as small as 40 m across the species assemblage. Randomizations also demonstrate that range shifts measured at range boundaries can be potentially misleading when differences in sampling effort between contemporary and historical data sets are not taken into account.

In conclusion, abundance data collected across climatic gradients will be fundamental to gaining an understanding of population size change associated with climate warming. Complex spatial variability in species’ abundance along with area constraints of mountain systems undermine the ability of documented change in distribution area to predict important change in population size. There is therefore an urgent need to not only track changes in location and extent of distribution area but also spatial patterns in the relative abundance of species within current and future distributions. Randomisations suggest that change in the mean altitude of species will allow for the detection of smaller range shifts than change measured at range boundaries. As detection limit is dependent on sampling effort, analyses of statistical power should be considered an integral first step in designing future monitoring programs.
To my parents for their constant support and making everything seem possible
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1 The Wet Tropics biogeographic region as a case study for advancing our understanding of the impacts of global warming on montane fauna
Abstract
This review synthesises recent literature pertaining to: (1) trends in global climate change in the past two centuries; (2) projections of future climate change; and, (3) approaches used to measure ecological consequences of climate change with particular emphasis on predicted shifts in the distribution and abundance of species along climatic gradients. Global average surface temperature has risen ca. 0.6 °C in the period 1901-2000 and modelled projections of future temperature change suggest a further 1.4-5.8 °C warming by 2100. As temperatures become less favourable, species are predicted to move either poleward or upwards in altitude to occupy areas within their metabolic temperature tolerances. A number of different approaches have been used to document range shifts of species in response to contemporary warming. In some cases range shifts have been inferred indirectly from change within local communities while, in others, range shifts have been measured directly from change in the position of species tracked along climatic gradients over time. The collective evidence suggests a pervasive climate change response across a wide range of taxa. To date, however, evidence has been predominately derived from European, British and North American examples and there is a noticeable lack of information on biodiverse tropical regions and the Southern Hemisphere in general where severe impacts have been predicted. Finally, some of the most important limitations of current range shift analyses are considered and the vertebrate fauna of the Wet Tropics biogeographic region of north-eastern Australia is proposed as a model system for advancing our understanding of the impacts of global warming on montane fauna.

Introduction
In 1979 the first world climate conference organized by the World Meteorological Organization (WMO) expressed concern that human activities may cause significant regional or even global changes to climate (IPCC 2004). Today, initial concerns have evolved into international policy to reduce global greenhouse gas emissions (ie. Kyoto Protocol) and the broader establishment of international working groups such as the Intergovernmental Panel on Climate Change (a joint collaboration between the WMO and the United Nations Environment Program, UNEP) dedicated to synthesizing scientific information on climate change including environmental and socioeconomic impacts. This review focuses primarily on climate change induced shifts in the distribution and abundance of species. Supportive evidence for a contemporary climate
change response among species is considered along with approaches used to predict and detect change. Important limitations in our current understanding of climate change induced range shifts are identified and the vertebrate fauna of the Wet Tropics biogeographic region of north-eastern Australia is proposed as a model system to address some of these deficiencies. For a more general treatment of biological consequences of contemporary climate warming the reader is referred to other recent reviews (Hughes 2000; Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003).

To provide a context to the current review, a summary of trends in both global climate change in the past two centuries and projections of climate change in the future is also provided. The climate summary encompasses some of the major findings of the Third Assessment Report of the International Panel on Climate Change (Houghton et al. 2001) and is supplemented with recent contributions to the climate change literature that have subsequently become available.

**A changing climate**

Reconstructions of Northern Hemisphere temperature during the past millennium from indirect or ‘proxy’ indicators, such as tree-ring data, corals and ice cores, suggest small amplitude variations in temperature followed by a clear warming trend in the past two centuries (Jones et al. 1998; Mann et al. 1998, 1999; Briffa 2000; Crowley & Lowery 2000; Folland et al. 2001; Esper et al. 2002; Mann & Jones 2003; Jones & Mann 2004). The abrupt, rapid increase in temperature since the pre-industrial period is largely attributed to an increase in radiative forcing resulting from anthropogenic production of well-mixed greenhouse gases (ie. CO₂, CH₄, N₂O, and hydrocarbons) (Ramaswamy et al. 2001). There is an increasing appreciation, however, that centennial variability in temperature has been underestimated by tree-ring and other proxies produced with regression based calibration methods, suggesting that past variation may have been at least a factor of two larger than indicated by empirical reconstructions (von Storch et al. 2004). Large multicentenial variability greater than most previous multi-proxy reconstructions is supported by a recent analytical approach combining high resolution proxies preserved in tree-rings with low-resolution proxies retained in lake and ocean sediments (Moberg et al. 2005) and is consistent with temperatures reconstructed from borehole measurements (Pollack & Smerdon 2004) where physical laws rather than statistical relations are used to estimate temperature trends (Moberg et al. 2005).

Importantly, however, model experiments that use natural-only forcings fail to
reproduce global warming observed in recent decades (Stott et al. 2000; Folland et al. 2001; Bertrand et al. 2002; Widmann and Tett 2003). Rather than negating an anthropogenic explanation for recent climate change, then, the increasing recognition of past climate variability raises the possibility that predicted anthropogenic climate change will be either amplified or attenuated by natural forcings (Moberg et al. 2005).

Reconstructions of temperature for the last two millennia provide no evidence for warmer conditions than observed during the post-1990 period (Jones et al. 1998; Mann et al. 1998, 1999; Crowley & Lowery 2000; Mann & Jones 2003; Moberg et al. 2005). Direct instrumental measurements indicate that global average surface temperature has risen ca. 0.6 °C in the period 1901-2000 (Folland et al. 2001). The increase in mean surface air temperature is due, at least in part, to differential changes in daily maximum and minimum temperatures (Karl et al. 1991; Karl et al. 1993; Easterling et al. 1997; Sperling et al. 2004). Minimum temperatures have increased more rapidly than maximum temperatures resulting in a narrowing of the diurnal temperature range. Modelled projections of future temperature change suggest 1.4-5.8 °C warming by 2100 combined with large increases in CO₂ concentrations (Cubasch et al. 2001). The full range of possible responses of climate to rising greenhouse gas levels is potentially greater where equilibrium responses of global mean temperature to doubling levels of atmospheric carbon dioxide, beyond those currently seen in general circulation models, are considered (Stainforth et al. 2005). While most projections of temperature increase cluster around a mid-range scenario of 3.4 °C, there is a potential for warming to range from less than 2 °C to more than 11 °C (Stainforth et al. 2005) - a range more than twice that found in the general circulation models used in the Third Assessment Report of the International Panel on Climate Change (Cubasch et al. 2001).

An increase in global temperature is expected to be coupled with change in other climatic factors. While predictions pertaining to rainfall are less certain, significant changes in rainfall patterns are likely with an increase in rainfall variability and dry season severity (Walsh & Ryan 2000) possibly combined with increased frequency of disturbance events such as flooding and cyclones (Easterling et al. 2000; Walsh & Ryan 2000; Milley et al. 2002; Palmer & Raianen 2002). Simulations of global climate under a scenario of doubled atmospheric carbon dioxide concentration also suggest that the relative humidity surface and consequently the height of cloud formation will be shifted upwards by hundreds of meters (Still et al. 1999). Change in the basal height of orographic cloud, combined with an increase in evapo-transpiration is expected to
drastically alter climatic conditions particularly in montane cloud forests (Still et al. 1999). Thermal expansion and loss of mass from glaciers and icecaps is expected to raise global mean sea level by 0.09 to 0.88 m between 1990 and 2100 (Church et al. 2001).

**Ecological consequences of global warming**

Sala et al. (2000) examined global biodiversity scenarios for the year 2100 and concluded that habitat destruction followed by climate change is likely to be the most important driver of biodiversity change in the future. Recent analyses emphasise the importance of climate suggesting that “anthropogenic warming at least ranks alongside other recognized threats to global biodiversity” and is “likely to be the greatest threat in many if not most regions” (Thomas et al. 2004a). There is accumulating evidence that climate warming is already having a measurable impact on species’ traits and the subject has been the focus of numerous recent reviews (Hughes 2000; Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003). Major types of change in species’ traits include, among others: shifts in distribution and abundance (e.g. Grabherr et al. 1994; Parmesan 1996; Parmesan et al. 1999; Thomas & Lennon 1999; Roy et al. 2001; Hill et al. 2002; McLaughlin et al. 2002; Konvicka et al. 2003; Brommer 2004), microevolutionary change (e.g. Rodriguez-Trelles & Rodriguez 1998; Bradshaw & Holzapfel 2002) and change in behaviour (Thomas et al. 2001), morphology (de Jong and Brakefield 1998; Thomas et al. 2001), and timing of events (phenology) such as egg-laying (e.g. McCleery et al. 1998; Crick & Sparks 1999) or migration (Lehikoinen et al. 2004).

In 1985, drawing upon evidence of species responses to historical climate change, Peters and Darling considered the potential for future warming to alter the distribution and abundance of species and ultimately diminish biological diversity encompassed within reserve systems. The paper is significant in that it highlighted at-risk species and pre-empted many of the general trends in species response to climate change that have only more recently found support with empirical field data. The following is a synthesis of what has been learnt since Peters and Darling’s (1985) early review.

**Climate related shifts in distribution and abundance of species**

Some models indicate that climate change impacts will largely consist of latitudinal and altitudinal shifts in potential species’ distributions (Peterson et al. 2002) while others
suggest that the complete disappearance of critical climate types and dependent species are possible (Williams et al. 2003; Hilbert et al. 2004; Thomas et al. 2004a). Potential shifts in distribution will mean that, in many instances, no part or only a small portion of current ranges will be contained within future distributions (Beaumont & Hughes 2002) necessitating dramatic spatial movements in order for species to track preferred climates (Peterson 2003).

Climate related range shifts are expected to manifest in a number of ways. The density of species may change at specific locations as climates become more or less favourable and the position of species along climatic gradients may change with species moving either poleward or upwards in altitude to occupy areas within their metabolic temperature tolerances (Root et al. 2003). While often treated en masse, the analyses from which evidence is derived differ greatly in the way in which change has been measured or inferred. Range shifts may be inferred indirectly from change within local communities or measured directly from change in the position of species tracked along climatic gradients over time (Root et al. 2003) – hereafter referred to as ‘indirect’ and ‘direct’ studies respectively.

For indirect studies, a single or small number of permanent sampling plots are typically established at a select position along the climatic gradient. Change within the narrow observation window is then interpreted, in relation to range shift predictions, using additional knowledge of the distribution of species along the climatic gradient outside the census area. Examples include increased abundance and species richness of premontane birds in a long term montane census plot (Pounds et al. 1999), increased species richness in summit floras (Grabbherr et al. 1994) and increased shrub abundance in the arctic (Sturm et al. 2001). For indirect studies, range shifts have been inferred from documented change in species richness and composition (eg. Grabherr et al. 1994; Beaugrand et al. 2002; van Herk et al. 2002), relative abundance (eg. Smith 1994; Sagarin et al. 1999; Strum et al. 2001), extent of occurrence (eg. van Herk et al. 2002) or some combination of these parameters (Pounds et al. 1999).

In contrast, in the case of direct studies, sampling occurs at multiple points along the climatic gradient and change is measured by tracking the estimated position of a species through time. Examples include uphill shifts in the mean position of butterfly records in the Czech Republic (Konvicka et al. 2003) and extension of the northern range boundary of British (Thomas & Lennon 1999) and Finnish birds (Brommer 2004). Range shifts, then, have been quantified by documented change in the position of

The obvious difference between indirect and direct studies is the scale at which change is observed. A major limitation of indirect studies is that they assume that change at one point can be “unambiguously interpreted as range shifts, rather than as merely local density changes, range expansions or contractions” (Parmesan 1996). In direct studies observations of change are more widely distributed and therefore allow coherent patterns of change to be investigated throughout the range of the sample species. In addition, direct studies enable researchers to extract important, spatially explicit, details of change. For example: how quickly do range shifts proceed (Thomas & Lennon 1999; Parmesan et al. 1999; Hill et al. 2002; Konvicka et al. 2003; Brommer 2004; Hickling et al. 2005); do range shifts keep pace with or lag behind climatic change (Archaux 2004); and, are range shifts accompanied by expansion or contraction in the distribution area of species (Thomas & Lennon 1999; Hill et al. 2002; Brommer 2004; Hickling et al. 2005)?

**Potential biases and limitations**

Altitudinal and latitudinal shifts measured at single range boundaries can result from overall population expansions or contractions and do not necessarily imply a systematic change in the position of a species’ range along a climatic gradient (Thomas & Lennon 1999). It is therefore necessary to control for change in distribution area when estimating change at range boundaries. Thomas and Lennon (1999) estimated the mean shift in range of British birds with no overall change in distribution area as the $\chi = 0$ intercept of a regression of changes in species’ range margins against changes in their distribution area. The same approach has subsequently been adopted in analyses of British butterflies (Hill et al. 2002) and Finnish birds (Brommer 2004).

Increased sampling effort is expected to improve the probability of detecting a species beyond its currently documented range boundary. Temporal bias in recorder effort toward particular species or locations therefore has the potential to confound interpretation of observed patterns of change at range margins. In an analysis of climate related range shifts, Hill et al. (2002) sub-sampled individual surveys from a pool of available survey data to equalise sampling effort between time periods. Although this approach offers a practical tool to retrospectively calibrate sampling effort among
datasets it is apparent that such techniques are rarely applied and the importance of recorder effort is often overlooked.

A lack of evidence for range shifts in some studies may be in part attributable to an absence of suitable habitat for species to colonize at expanding range boundaries. For example, in the case of British butterflies, loss or degradation of breeding habitat has outweighed the expected positive response of climate warming and documented evidence of range shifts has largely been confined to the most mobile, generalist species (Warren et al. 2001). For the Speckled Wood Butterfly (Pararge aegeria), habitat availability is likely to constrain range expansion (Hill et al. 1999) with rates of expansion slower in areas where habitat is less available (Hill et al. 2001). The importance of mobility is further exemplified by the larger estimated latitudinal range shift documented in birds than butterflies across Britain (Thomas & Lennon 1999; Hill et al. 2002). The difference is likely to be attributable to the greater dispersal ability of birds and their capacity to colonize isolated patches of suitable habitat beyond previous range boundaries (Hill et al. 2002).

Latitudinal shifts in species’ range may be masked by altitudinal shifts in regions of high topographic diversity. A number of studies of European (Parmesan et al. 1999) and British taxa (Thomas & Lennon 1999; Hickling et al. 2005) have shown that northern range boundaries have expanded more than southern range boundaries have contracted. While this has led some authors to conclude that “cool margins of temperate species might be more immediately responsive than warm margins to the direct effects of thermal variation” (Thomas & Lennon 1999), others have commented that many species reach their southern limits in mountainous regions which offer a broad range of microclimates conducive to tracking climate warming (Parmesan et al. 1999; Hill et al. 2002). The lack of observed range shifts in these areas, then, “may be due to species moving to higher elevations, rather than higher latitudes, which might not be detected on a coarse grid map” (Hill et al. 2002). Thus, finer resolution data are required to detect confounding effects of altitude when examining latitudinal range shifts (Hill et al. 2002).

Predictions and contemporary evidence of range shifts have largely been concerned with estimating change in the position of species along climatic gradients with impacts inferred from the resulting change in distribution area. Few studies have examined broad spatial patterns of abundance within range boundaries and how this may change with climate warming. Mehlman (1997) documented abundance changes in
three North American bird species following a harsh winter providing some insight into how species may respond to global climate change. Population declines were accompanied by a contraction toward core areas of the range that formerly had the highest abundance. A greater proportional change in abundance and a preponderance of extinctions and colonization events was documented at sites closest to range boundaries resulting in a roughening of the range boundary with abundance decrease and a smoothing of the range boundary with abundance increase. The extent to which spatial patterns of abundance are likely to change within shifting ranges, however, is largely unknown. Parmesan (1996) revisited historical population localities of Edith’s checkerspot butterfly (*Euphydryas editha*) throughout its range and found significant latitudinal and altitudinal clines in population extinctions consistent with that expected to result from polar and upwards shifts in the species’ range. Similarly, for British butterflies, Hill et al. (2002) compared the mean altitude of continuously occupied grid cells with newly occupied or vacated grid cells and documented a preponderance of extinctions and colonizations at low and high altitudes respectively. Documented spatial patterns of extinction, colonization and change in abundance along climatic gradients have the potential to enhance our understanding of change occurring within range boundaries but, as yet, remain poorly explored.

Finally, documented evidence of climate-associated change has predominantly been derived from North America and Europe (Hughes 2003). The paucity of examples from Australia and the Southern Hemisphere in general is unlikely to reflect an absence of impacts, but rather a lack of long-term data sets with which to detect change (Westoby 1991; Hughes 2003). The deficiency of available information is recognised by the Australian ‘National Biodiversity and Climate Change Action Plan’ (Natural Resource Management Ministerial Council 2004) and specific actions have been developed in recognition of the problem. Some of the most relevant actions in the context of climate change induced range shifts include: identification of limitations in the current modelling of climate change impacts on biodiversity (Action 1.2.4); improvement of the capacity of models to predict climate change impacts on biodiversity (Action 1.2.1); identification of information requirements and priorities for long-term monitoring of climate change impacts on biodiversity (Action 1.3.1); and, implementation of high priority monitoring programs (Action 1.3.3).
The Wet Tropics as a case study

The Wet Tropics biogeographic region is a listed World Heritage Area that encompasses a narrow band of disjunct mountain ranges extending from Cooktown in the north to Townsville in the south (approximately 15 and 19° S respectively) along the north-eastern coast of Australia. Although the area of rainforest within the region is small on a global scale (ca. 10,000 km²), there are 79 species of rainforest vertebrates that are regionally endemic, most of which are cool adapted upland species (Nix 1991). The region itself has been described as a ‘mesotherm archipelago’ comprising a “chain of temperate mountain and tableland ‘islands’ that rises from the shallow ‘sea’ of tropical and subtropical lowlands, separating the major mesotherm source areas of southern Australia from those of montane New Guinea” (Nix 1991). While early commentaries emphasised the importance of rainfall regime as the principle determinant of archipelago-like disjunctions in rainforest habitat and associated fauna (Herbert 1967) more recent analyses have stressed the importance of lowlands as significant thermal barriers to mesotherm elements (Nix 1991). Microclimatic diversity is heightened by the regions complex topography (ranging from sea level to 1615 m, Bartle-Frere South Peak) producing steep gradients in temperature. Coldest month mean minimum temperatures remain above 17 °C in the coastal lowlands but decline to about 7 °C in the uplands where temperature may even fall below 0 °C (Nix 1991).

The preponderance of regionally endemic vertebrates restricted to upland environments within the Wet Tropics is thought to be an artefact of an extinction filter imposed by contraction of rainforest to cool, moist upland refugia during historical climate fluctuations (Williams & Pearson 1997). Impacts of historical climate change are supported by molecular data combined with paleodistribution models (Joseph et al. 1995; Schneider et al. 1998; Hugall et al. 2002). Paleodistribution models predict the location and size of refugia and patterns of extinction and colonization of species as a function of historical climate and provide the most parsimonious explanation for current observed patterns of molecular phylogeography. While the collective characteristics of the endemic fauna (ie. association with cool, wet and relatively aseasonal environments) have no doubt been important in promoting persistence through historical climate fluctuations, recent concern has been raised that the same characteristics may well predispose the fauna to being particularly vulnerable to future global climate warming.

Average surface temperatures in the Southern Hemisphere have increased by approximately 0.52 ± 0.13 °C in the period 1901 to 2000 (Folland et al. 2001). Regional
models of projected climate change for Queensland (Walsh et al. 2002) predict a further increase in temperature of 0.3 to 2.0 °C by 2030 or a larger 0.8-6.0 °C by 2070, relative to the year 1990. In general minimal change in rainfall is expected, though disagreement continues to exist between projections derived from different climate models (Walsh et al. 2002). For rainforest vertebrates of the Wet Tropics, even small amounts of contemporary climate warming are expected to result in strong systematic change in the extent and location of species distributions (Williams et al. 2003; Hilbert et al. 2004). Altitude is effectively a surrogate for turnover in temperature in the region and impacts of increasing temperature are expected to be most noticeable along this gradient (Williams et al. 2003).

Clearly, there is an urgent need to establish suitable monitoring programs to document ecological change within the Wet Tropics biogeographic region. In addition to providing valuable data to inform local and regional management practices, an effective monitoring program established within the Wet Tropics region is expected to provide more general insights into change occurring in tropical mountain regions that have, to date, been largely neglected from comprehensive analyses. Some distinct advantages of the Wet Tropics as a model system include: a species rich assemblage of rainforest vertebrates with a highly resolved, relatively stable taxonomy; an already comprehensive understanding of regional occurrence of species (Nix & Switzer 1991; Williams et al. 1996) and, in some instances, altitudinal patterns of abundance (ie. arboreal mammals, Trenerry, 1993 and Kanowski et al. 2001; microhyloid frogs, Shoo & Williams 2004); and, ready access to detailed models of distributional change predicted under future climate change (Williams et al. 2003; Hilbert et al. 2004). Further, the high level of protection afforded to rainforests habitats within the region offers a unique opportunity to examine altitudinal range shifts in an ecological system with minimal confounding influence from anthropogenic disturbance.
Objectives of the current study
The overall goal of the current dissertation was to enhance capacity to predict and detect the impacts of climate change on montane fauna within the Wet Tropics region whilst attempting to address some of the most important limitations of current range shift analyses. The objectives of the thesis, within this context, were fourfold:

1) to establish high resolution baseline data for detecting biological responses to future climate change along altitudinal gradients (Chapters 2 and 3);
2) to estimate extinction risk from predicted change in total population size as a consequence of climate warming (Chapter 4);
3) to determine how well documented change in distribution area is likely to describe change in population size of montane species (Chapter 5); and
4) to evaluate the most suitable method and statistical power of analyses for detecting climate induced range shifts along altitudinal gradients (Chapter 6).

Why rainforest birds and microhylid frogs?
Differential patterns of change observed among ecologically disparate taxa have previously provided valuable corroborative evidence for potential mechanisms (e.g. relative dispersal ability) limiting the capacity of species to track climate change (Hill et al. 2002). Within the Wet Tropics region, rainforest birds and microhylid frogs are two taxa that characterise the ecological breadth present within the vertebrate fauna and are expected to be suitable model taxa for monitoring climate responses for a number of reasons. First, leaf-litter frogs of the family Microhylidae are recognised as being among the most geographically restricted endemic vertebrates of the region immediately threatened by loss of core habitable environment (Williams & Hilbert in press). The high vulnerability of the group is supported by recent evidence of population crashes of ecologically similar, terrestrial-breeding rain frogs (Eleutherodactylus diastema) in highland forests of Monteverde, Costa Rica (Pounds et al. 1999). Second, the high mobility of birds is expected to promote a rapid, detectable response to climate change that may not be apparent in other taxa (Hill et al. 2002). Third, birds are well represented in analyses of range shifts elsewhere though, importantly, climate related responses have been observed at some (Thomas & Lennon 1999; Pounds et al. 1999; Brommer 2004) but not all (Archaux 2004) locations. Additional data from ecologically disparate taxa occurring in geographical regions currently underrepresented in climate.
change analyses is expected to contribute to our understanding of the generality of observed change and also provide correlative evidence for causative mechanisms underlying the differential response of species in relation to contemporary climate change.

Comments on the structure and content of the thesis

All thesis chapters have been prepared as stand alone manuscripts suitable for submission for publication in the form of journal papers. For consistency, a single style of text formatting has been applied throughout. In order to avoid undue repetition of text, a single combined reference list has been provided at the end of the thesis. At the time of writing, Chapters 2, 4, 5 and 6 have been submitted and/or accepted for publication. All manuscripts have been prepared and written by the author of the thesis and, where co-authors have contributed to the content of a submitted manuscript, due acknowledgement is given at the beginning of the relevant chapter. The location and status of each manuscript at the time of writing in regard to publishing is also indicated. A series of Boxes have been appended to Chapters 4 and 5 to extend the scope of analyses published therein to include comparable data on microhylid frogs. Analyses of rainforest birds (Chapters 3, 4, 5 and 6) were based on field data collected within the rainforest macroecology and climate change project lead by Steve Williams and funded by the Rainforest-CRC, Australian Research Council, Earthwatch Institute and James Cook University. Standardised abundance surveys were initiated in 1996 and continue to present. Intensive contributions of field data on the part of the thesis author were primarily for the period 2002-2004 though active contribution to the database is ongoing.
2 Altitudinal distribution and abundance of microhylid frogs (Cophixalus and Austrochaperina) of north-eastern Australia: baseline data for detecting biological responses to future climate change

Article type: Full Length Article:
Abstract
Extensive abundance surveys of microhylid frogs across altitudinal gradients within the Wet Tropics rainforests of north-eastern Australia were undertaken. Detailed patterns of abundance were resolved for nine microhylid species exhibiting differing associations with the altitudinal gradient. The position of altitudinal range boundaries was found to be largely consistent with previous accounts in the literature, providing confidence in established limits to species’ distributions. Microhylid frogs, in particular those species restricted to mountaintops, are considered among other endemic rainforest vertebrates within the region to be one of the groups most immediately threatened by climate change. The combined results establish important baseline data for assessing the impacts of climate change, including altitudinal shifts in distribution and localised declines in abundance, on microhylid frogs in the region.

2.1 INTRODUCTION
Global climates are changing rapidly (Houghton et al. 2001) and biological responses are becoming increasingly apparent (Hughes 2000; Walther et al. 2002). Species are expected to shift up mountains and away from the equator in response to warmer temperatures associated with climate change (Peters & Darling 1985). Although many instances of recent climate related shifts in distribution have been documented (Parmesan & Yohe 2003; Root et al. 2003), to date evidence has predominantly been derived from North America and Europe and examples from Australian biota are notoriously lacking (Hughes 2003). The discrepancy is unlikely to reflect an absence of impacts in Australia, but rather a lack of long-term data sets with which to detect change (Westoby 1991; Hughes 2003). There is, therefore, an urgent need to identify species whose biology suggests that they might be sensitive indicators of climate change and to establish suitable monitoring programs for such species (Hughes 2003).

The endemic rainforest vertebrate fauna of the Wet Tropics region of north-eastern Australia provides a unique opportunity to address this deficiency. First, endemic species are typically associated with cool, wet and relatively aseasonal upland environments; these are characteristics that have predisposed the fauna to being particularly vulnerable to future global climate change (Williams et al. 2003). The preponderance of upland endemic species has been attributed to an ‘extinction filter’ imposed by Pleistocene contractions in rainforest area to cool, moist upland refugia (Williams & Pearson 1997; Schneider et al. 1998). Second, detailed projections of
species responses to future climate scenarios suggest strong systematic change in the extent and location of species’ distributions with even small amounts of warming (Williams et al. 2003). Climate warming of the magnitude predicted within the century is expected to manifest in a decline in endemic species richness across the lowlands and mid-altitudinal areas and, for many mountain-top species within the region, the complete disappearance of core habitable environment (Williams et al. 2003). Altitude is effectively a surrogate for turnover in temperature in the region and impacts of increasing temperature are expected to be most noticeable along this gradient (Williams et al. 2003).

Leaf-litter frogs of the family Microhylidae are recognised as being among the most geographically restricted endemic vertebrates of the region immediately threatened by loss of core habitable environment (Williams et al. 2003). Recent molecular analysis and an assessment of museum specimens (Hoskin 2004) has clarified taxonomic uncertainty within the group and, with the redescription of *C. concinnus*, has increased the number of species known to be restricted to a single isolated mountain range only (ie. *Cophixalus concinnus, C. exigus, C. hosmeri, C. mcdonaldi, C. monticola* and *C. saxatilis*). Significant phylogenetic structuring has also been reported for subpopulations of species distributed across disjunct mountain ranges (ie. *C. aenigma* and *C. neglectus*) (Hoskin 2004).

The quantification of altitudinal range boundaries has played an important role in refining details of the distribution of microhylid species and has been well recognised by previous authors in species descriptions and reviews (Zweifel 1985; McDonald 1992; Richards et al. 1994; Hoskin 2004). No attempt has yet been made to quantify the relative abundance of species within established altitudinal range boundaries. Absence of this information has implications for interpreting recognised threats of climate change in the region (Williams et al. 2003) and is expected to impede future efforts to detect and quantify predicted impacts such as change in population size and range shifts across the altitudinal gradient. Hoskin (2004) suggested that priority should be given to monitoring geographically restricted mountain-top species most immediately threatened by loss of core environment and possible extinction following climate change. In the present study we use extensive systematic sampling of abundance along the altitudinal gradient and provide baseline data on four restricted mountain-top species along with five other species of the family within the region.
2.2 METHODS

Fourteen species of microhylid (3 *Austrochaperina* and 11 *Cophixalus* spp.) are recognized within the Wet Tropics region of north-eastern Australia accounting for 54% of the rainforest-restricted frog fauna (Hoskin 2004). Species richness of the group within the region is negatively correlated with temperature and is limited by low rainfall in the dry season (Williams & Hero 2001). These relationships are driven by a preponderance of species restricted to high altitudes (Williams & Hero 2001). Males call from a range of positions, including leaves and axils of palms, leaf-litter, fallen epiphytes and among boulders or rocky scree (Richards et al. 1994; Hoskin 2004). All breeding records describe eggs laid in terrestrial situations followed by direct development into fully formed froglets (Zweifel 1985; Hoskin 2004).

Abundance data for microhylid species was collected from standardized field surveys throughout the region (325 surveys at separate locations). Each survey consisted of a slow-paced walk (~10 min duration) along a 50 m transect through rainforest. Calls were identified to species and counts of the number of individuals within 10 m either side of each transect were recorded. Mountain ranges and associated lowlands were sampled, covering much of the latitudinal range within the region (16°15’ - 18°15’S) including Kirrama Uplands (KU), Atherton Uplands (AU), Bellenden-Ker/Bartle-Frere (BK), Lamb Uplands (LU), Cairns-Cardwell Lowlands (CC), Carbine Uplands (CU), Windsor Uplands (WU) and Mossman Lowlands (ML) (Table 2.1: see Williams et al. 1996 for subregional boundaries).

Survey locations were visited on one occasion only. While calling activity is expected to be non-uniform in space and time, a definitive estimate of presence and/or abundance at any one site was not necessary. Our objective was to document patterns of relative abundance over the altitudinal gradient. False negatives (ie. a zero count when the species is actually present), however, have the potential to confound the interpretation of abundance patterns where a systematic bias in their prevalence correlates with the gradient being investigated. We addressed this issue in two ways. First, we minimised the occurrence of false negatives in the dataset. Because detection was dependent on encountering calling males, surveys were timed to coincide with known months of breeding and surveys were conducted only on wet, humid nights (>80% relative humidity (RH)); these conditions were expected to be conducive to calling activity. In all, 25 of the 27 dated breeding records compiled for 13 species of microhylid in the region are attributable to the spring/summer wet season between
October and February (Hoskin 2004). We define the breeding season in accordance with the available information. Second, we ensured that regional and altitudinal sampling of mountain ranges was interspersed over the 21 nights of survey through years 2001-04. On each night, a chosen access route within a mountain range was stratified by altitude using topographic maps and surveys were undertaken at ~50, 100 or 200 m altitudinal intervals to maximise the coverage of the gradient. All mountain ranges, excepting Kirrama Range, and all species were surveyed on multiple nights.

Although the study area covers a narrow latitudinal range, variation in climate at equivalent altitudes through the extent of the region has the potential to confound interpretation of abundance patterns and range boundaries for a subset of broadly distributed species. Therefore, we reduced the latitudinal spread of survey locations by dividing the region along the Black Mountain Corridor and reporting data from the central and northern parts of the region separately (central region: KU, AU, BK, LU and CC; northern region: CU, WU and ML). In doing so, we spatially partitioned some of the variability in counts and accommodated potential geographic patterns of abundance and range boundaries for the relevant species. Three species are known to occur in both central and northern parts of the region (ie. *A. fryi*, *A. pluvialis* and *C. ornatus*).

Some species were encountered more readily than others. An index of relative encounter (RE) was derived for each species by examining count data and dividing the number of surveys in which a species was recorded present by the total number of surveys undertaken within the altitudinal range and regional distribution of a given species as defined by McDonald (1992) and Hoskin (2004).

### 2.3 RESULTS

Although all three *Austrochaperina* species have been widely recorded across altitudinal gradients in the region, *A. robusta* was noticeably more conspicuous, being both frequently encountered on surveys (Table 2.2) and regularly recorded at densities greater than five individuals per transect (Fig. 2.1). *Austrochaperina robusta* was commonly recorded in conjunction with the broadly distributed *C. ornatus*, with both species reaching highest densities at ~ 700 m, within the middle of the altitudinal gradient (Fig. 2.1, Table 2.2). The most extreme high densities of *C. ornatus* (ie. 39-59 individuals on a single transect), for instance, were encountered along Tully Falls Road in the vicinity of Koombooloomba (17°50'S, 145°33'E) and on the wet slopes of the Kirrama Range (18°12'S, 145°45'E) between 600 and 800 m altitude (Fig. 2.1).
Of the nine species examined, four (ie. *C. aenigma*, *C. hosmeri*, *C. monticola* and *C. neglectus*) showed restricted distributions in association with upland rainforest. Each of these species was recorded at moderate to high densities within their narrow altitudinal ranges (Fig. 2.1; Tables 2.2, 2.3). On the upper slopes of the Carbine Tablelands *C. monticola* was encountered less frequently on surveys (ie. lower RE) than sympatric *C. aenigma* and *C. hosmeri* (Table 2.3). The low RE of *C. neglectus* was attributable to an apparent absence of the species in the lower part of its previously documented altitudinal range (McDonald 1992).

Of the three species known to occur in both central and northern parts of the region, *C. ornatus* showed the strongest differences in altitudinal abundance pattern in respective parts of its range. Both RE and density of *C. ornatus* were lower in the northern region (Fig. 2.1; Tables 2.2, 2.3).

Altitudinal range boundaries were largely consistent with limits previously established by McDonald (1992) and Hoskin (2004) and support the extremely restricted altitudinal range for *C. monticola*, a species endemic to the Carbine Tablelands (Tables 2.2, 2.3). The most noticeable discrepancies were apparent for *A. fryi*, *A. pluvialis* and *C. neglectus*. *Austrochaperina fryi* and *A. pluvialis* lacked records from low and high altitudes respectively. Despite previous accounts of *C. neglectus* as low as 900 m (Zweifel 1985), we were unable to locate the species below 1200 m.

### 2.4 DISCUSSION

Our ability to detect altitudinal range shifts and population change is likely to be dependent on how readily a species is encountered on surveys and the magnitude of the abundance response to the altitudinal gradient. The four high priority, geographically restricted, upland species recorded in this study (*Cophixalus aenigma*, *C. hosmeri*, *C. monticola* and *C. neglectus*) all occurred at moderate-to-high densities in at least some part of their altitudinal range and two species (*Cophixalus aenigma* and *C. hosmeri*) were among the most frequently encountered species within their known distribution. The combined characteristics suggest that upland species are suitable candidates for long-term monitoring, although the low RE of *C. monticola* and *C. neglectus* requires further clarification.

Richards et al. (1994) noted previously that *C. monticola* appeared less uniformly distributed throughout the forest floor than other sympatric species. The availability of select microhabitats, such as areas of rainforest where the understorey is dominated by
Linospadix palms (Richards et al. 1994), might be an important determinant of localised distribution in this species. For *C. neglectus*, the low reported RE is attributable to an apparent absence of the species in part of its previously documented altitudinal range, a point that we return to later.

Of the nine species examined, *A. pluvialis* and *C. infacetus* were encountered least frequently throughout their known range. A low RE is expected to arise from either a poor ability to detect the species, resulting in false negatives (ie. a zero count when the species is actually present) or a ‘patchy’ occurrence of a species within the broad confines of rainforest. *Austrochaperina pluvialis* was originally considered to be patchily distributed throughout its range (Zweifel 1985), but increased explorations have since shown that the species is more geographically widespread than previously thought (Hoskin 2004). The slow accumulation of records, combined with the low reported counts of the species, is suggestive of low detectability rather than a patchy occurrence. *Cophixalus infacetus* has been described as “patchily distributed along the eastern escarpment of the Atherton Tableland and Kirrama Range, often associated with rocky substrate” (Hoskin 2004). The availability of select microhabitats may well explain the apparent patchy distribution of this species in the field. Further research is needed to differentiate between microhabitat associations and sampling error (ie. false negatives) in these species.

Much of what is known about the position of altitudinal range boundaries for microhylid frogs within the Wet Tropics can be attributed to a few sources (Zweifel 1985; McDonald 1992; Richards et al. 1994). A revised taxonomy and additional data on species distribution has further clarified altitudinal range boundaries particularly for those species occurring in the northern mountains of the region (Hoskin 2004). The most notable revisions include: (1) the redescription of *C. concinnus*, now considered to be restricted to a very small high-altitude area (above 1100 m) around the summit of Thornton Peak; (2) the description of *C. aenigma* (formerly referred to as *C. concinnus*) restricted to higher altitudes (generally above 750 m) on the Carbine Tableland, Thornton Uplands, Finnigan Uplands and Bakers Blue Mountain; and (3) recognition of *C. bombiens* outside the Windsor Tablelands, extending the distribution of the species to lowland areas surrounding the Thornton and Finnigan Uplands.

Taxonomic revision has the potential to confound the interpretation of differences between recent and historically reported range boundaries. Historical datasets are potentially made up of a conglomerate of records comprising two or more sympatric
species not recognised at the time. We expect that misidentification of species would result in two major types of error. That is, the distribution of a newly described species would be underestimated (i.e. only a fraction of potential records of a new species are verified and are available to delineate the proposed distribution), or the distribution of a long-established species would be overestimated (i.e. records of an established species are supplemented erroneously by records of a previously unrecognised species).

Although the altitudinal ranges reported here for the most recently described species (i.e. \textit{C. aenigma} and \textit{C. monticola}) are largely consistent with previous accounts, this is not the case for some of the long-established species (i.e. \textit{A. fryi}, \textit{A. pluvialis} and \textit{C. neglectus}) where considerable discrepancies are apparent. Although all Australian species formally recognized as belonging to the genus \textit{Sphenophryne} (Parker 1934; Zweifel 1965, 1985) have recently been referred back to \textit{Austrochaperina} (Zweifel 2000) no new species have been described from the region since the designation of \textit{Sphenophryne pluvialis} (Zweifel 1965) almost 40 years before present. Similarly, \textit{C. neglectus} has long been recognized (Zweifel 1962) and, by virtue of its distribution, has been exempt from the taxonomic confusion that has surrounded species of \textit{Cophixalus} in the northern part of the region. Relevant literature and most specimens utilized by McDonald (1992) were collected after 1970. Therefore, the altitudinal ranges reported for each of the three species are unlikely to be attributable to taxonomic confusion.

There are a number of possible reasons for the observed discrepancies. First, the differences may be artificial. \textit{Austrochaperina fryi}, \textit{A. pluvialis} and \textit{C. neglectus} may be genuinely patchy and/or at low abundance in parts of their range where they were not encountered in this study. Kanowski et al. (2001) demonstrated that, even within continuous rainforest of the region, areas of high density of folivorous marsupial species are restricted to a small subset of altitudes from which species are known to occur. If the same applies for microhylid species, then the likelihood of encountering individuals outside of areas of high density might be greatly reduced and the position of the boundary will be underestimated. The probability of not detecting the species, even though it is present, is likely to be compounded for \textit{A. fryi}, because of a deficiency of surveys in the northern lowlands. Similarly, for \textit{A. pluvialis} the probability of not being detected is probably compounded by an already low RE rate, even in those parts of the range where the species was recorded.

Second, the observed differences in altitudinal ranges might be real. The ramifications of a decline in range are expected to be most severe for the already
restricted mountain-top species *C. neglectus*. Zweifel (1985) reported the lower altitudinal range boundary of *C. neglectus* to be 900 m. It is of interest that extensive altitudinal surveys by Hoskin (2004) on Mt Bartle-Frere in 2000 and 2001 failed to record the species below 1150 m. During subsequent sampling in the present study, comprising a night of systematic altitudinal surveys on each of Mt Bellenden-Ker and Mt Bartle-Frere, we were unable to locate the species below 1200 m and 1340 m on the respective mountain ranges. The lower range boundary was underestimated even though surveys were undertaken on wet nights that coincided with regular showers of rain, where the species was frequently encountered calling at higher altitudes. Further, numerous additional traverses of the eastern and western slopes of Mt. Bartle-Frere during 2002-04 (L. P. Shoo, unpublished data) provide no contemporary evidence of *C. neglectus* at its formerly recognized range boundary. Given the available information, we are reluctant to defer to methodological constraints to account for the observed discrepancy for this species. Continued systematic effort to document change in abundance and the position of the lower altitudinal range boundary should, therefore, be regarded as a high priority for *C. neglectus* on isolated mountaintops within its distribution.

Hoskin (2004) considered a record of *C. aenigma* from Mt Finlay (15°48'S, 145°21'E) to be of interest as it was from considerably lower altitude (580 m) than all other records for the species. Surveys undertaken in the vicinity of the Carbine Tablelands during the present study failed to record the species below 850 m, further supporting the notion that this specimen might be a misidentified *C. exigus* (Hoskin 2004). Further work is required to quantify the altitudinal abundance of *C. bombiens*, *C. exigus*, *C. saxatilis* and, most importantly, the high-altitude-restricted species *C. concinnus* and *C. mcdonaldi*. Attempts were made to sample populations of these species; however, dry conditions at the time of survey prevented adequate estimates of abundance.

Three microhylid species are known from both central and northern parts of the region. Baseline data suggest that *C. ornatus* is more restricted or occurs at lower densities in the northern part of the region. *Cophixalus ornatus* was less frequently encountered, recorded at lower abundance and, consistent with previous accounts (Williams et al. 1996), was absent from the Mossman Lowlands despite being recorded on the adjacent Carbine Tablelands. The RE of the remaining two species (*A. fryi* and *A. pluvialis*) was similar in both northern and central parts of the region and though
anomalies in range boundaries were observed, differences were attributable to a few
records only (Tables 2.2, 2.3).

2.4.1 Implications
Species are expected to undergo upslope shifts in distribution along altitudinal
gradients in response to increased temperatures associated with climate change (Parmesan &
Yohe 2003). Shifts in ranges will lead to population declines and extinctions where
climatically suitable environments are no longer available or cannot be reached.
Immediate detection of biological responses to climate change is vital if we are to
improve predictions and attempt to mitigate impacts to biodiversity. In the present study
we have provided baseline data on the abundance and distribution of nine microhylid
species across altitudinal gradients within the Wet Tropics. This will provide
conservation managers with comparative data with which to detect and quantify
ecological impacts of climate change and other threatening processes.
Table 2.1: Regional distribution of survey effort (no. of surveys) for microhylid species across central and northern altitudinal gradients. AU, Atherton Uplands; BK, Bellenden-Ker/Bartle-Frere; CC, Cairns-Cardwell Lowlands; CU, Carbine Uplands; KU, Kirrama Uplands; LU, Lamb Uplands; ML, Mossman Lowlands; WU, Windsor Uplands.

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Table 2.2: Mean estimates of abundance (including zero counts) and relative encounter rate of microhylid species across the altitudinal gradient, central region. Numbers in parentheses are a ratio between the number of surveys for which a species was recorded present and the total number of surveys undertaken at a given altitude within the regional distribution of a species. AU, Atherton Uplands; BK, Bellenden-Ker/Bartle-Frere; CC, Cairns-Cardwell Lowlands; CU, Carbine Uplands; KU, Kirrama Uplands; LU, Lamb Uplands; ML, Mossman Lowlands; WU, Windsor Uplands; RE, relative encounter.

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<tr>
<td>(KU, BK, AU, LU, CC)</td>
<td>(3:14)</td>
<td>(4:27)</td>
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<td>A. robusta</td>
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<tr>
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<td>(5:27)</td>
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<tr>
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<td>0.00</td>
</tr>
<tr>
<td>(BK)</td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>C. ornatus</td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>(KU, BK, AU, LU, CC)</td>
<td>(0:14)</td>
<td>(4:27)</td>
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</tbody>
</table>

^A Altitudinal ranges that were established previously (McDonald 1992; Hoskin 2004).
^B Altitudinal ranges that were established in the present study.
Table 2.3: Mean estimates of abundance (including zero counts) and relative encounter rate of microhylid species across the altitudinal gradient, northern region. Numbers in parentheses are a ratio between the number of surveys for which a species was recorded present and the total number of surveys undertaken at a given altitude within the regional distribution of a species. AU, Atherton Uplands; BK, Bellenden-Ker/Bartle-Frere; CC, Cairns-Cardwell Lowlands; CU, Carbine Uplands; KU, Kirrama Uplands; LU, Lamb Uplands; ML, Mossman Lowlands; WU, Windsor Uplands; RE, relative encounter.

Altitudinal ranges that were established previously (McDonald 1992; Hoskin 2004).

Altitudinal ranges that were established in the present study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Altitude (m)</th>
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<td>0-99</td>
<td>100-199</td>
</tr>
<tr>
<td>A. fryi (CU, WU, ML)</td>
<td>0.00&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.00&lt;sup&gt;A&lt;/sup&gt;</td>
</tr>
<tr>
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<td>0.50&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.25&lt;sup&gt;B&lt;/sup&gt;</td>
</tr>
<tr>
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<td>-</td>
</tr>
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<td>C. hosmeri (CU)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>C. montocola (CU)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>C. ornatus (CU)</td>
<td>-&lt;sup&gt;A&lt;/sup&gt;</td>
<td>-&lt;sup&gt;A&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
**Fig. 2.1.** Distribution and abundance of microhylid species across the altitudinal gradient in central (C) and northern (N) parts of the region. Vertical lines indicate actual counts and bold lines represent mean abundance (including zero counts) within 100 m altitudinal intervals across mountain ranges in which a species occurs (sample sizes are reported in Tables 2.2 and 2.3). Note that the scale of number of individuals on the $\gamma$-axis varies for each species. The grey line below the $\chi$-axis denotes established altitudinal range of species, derived from McDonald (1992) and Hoskin (2004).
A. pluvialis (N)

A. pluvialis (C)

C. ornatus (N)

C. ornatus (C)

A. fryi (N)

A. fryi (C)

C. ornatus (C)

C. ornatus (C)

C. hosmeri (N)

C. neglectus (C)

C. infacetus (C)

C. infacetus (C)

A. fryi (N)

C. ornatus (C)

A. fryi (C)

C. neglectus (C)

C. ornatus (C)

C. hosmeri (N)

C. neglectus (C)

C. ornatus (C)

C. infacetus (C)

C. infacetus (C)

C. monticola (C)

C. monticola (N)

Altitude (m)

Altitude (m)

Number of calling males per transect

Number of calling males per transect
3 Altitudinal distribution and abundance of rainforest birds of north-eastern Australia: baseline data for detecting biological responses to future climate change
Abstract
Extensive abundance surveys of 76 rainforest birds across altitudinal gradients within the Wet Tropics rainforests of north-eastern Australia were undertaken. High-resolution data from transect surveys highlight differences among species in their association with the altitudinal gradient and quantify variable patterns of abundance within altitudinal ranges. Collated data for 12 endemic species demonstrate that, while the mean altitude of presence records is consistent with available published information, the position of altitudinal range boundaries for some species appears to have been previously underestimated. The combined results establish important baseline data for assessing the impacts of climate change, including altitudinal shifts in distribution and localized declines in abundance, on rainforest birds in the region. Some important deficiencies in knowledge remain, however, and targeted surveys to quantify the effect of season and latitude on the altitudinal occurrence of rainforest birds is suggested.

3.1 INTRODUCTION
Recent reviews have greatly improved our understanding of the broad distribution of rainforest birds within the Wet Tropics biogeographic region of north-eastern Australia (Crome & Nix 1991; Williams et al. 1996). Crome and Nix (1991) collated data from museum collections, field observations by vertebrate specialists and published material and provided detailed point locality records for thirteen endemic species along with maps of potential distribution generated from BIOCLIM models (Busby 1986; Nix 1986). Williams et al. (1996) subsequently summarized distribution information for all vertebrate species across disjunct mountain ranges and associated lowlands within the region.

While broad distribution data has proved a useful resource for conservation and management of vertebrate species within the region, detailed information on the distribution of species is currently lacking and continues to impede ecological analyses at finer levels of resolution (Williams et al. 1996). At the time of their review, Williams et al. (1996) acknowledged the importance of clarifying altitudinal associations of species and identified two major shortcomings in the available data. First, a general paucity of information at mid-altitudes (300-600 m) and second, an absence of detailed information on the variable abundances patterns of species throughout the region.
Crome and Nix (1991) reported minimum, maximum and mean altitude of point localities for endemic species however, for the wider bird fauna, detailed knowledge of altitudinal distributions was not adequate to allow a meaningful analysis based on point locality data (Williams et al. 1996). Attempts have been made to expand knowledge on the altitudinal distribution of species however, to date, data has been restricted to individual species (Wieneke 1992) or select mountain ranges within the region (Gill 1970; Boles & Longmore 1989). In lieu of better information Williams et al. (1996) deferred to larger geographic zones primarily defined by biogeographically distinct upland mountain ranges utilising the 300 m contour to delineate between upland and lowland occurrences.

Information on the altitudinal occurrence and abundance of species has implications for understanding patterns of assemblage structure and environmental correlations with patterns of diversity within the region (Williams et al. 1996) as well as interpreting and documenting recognised threats of climate change (Shoo & Williams 2004). Projections of species responses to future climate scenarios suggest strong systematic change in the extent and location of species distributions with even small amounts of warming (Williams et al. 2003; Hilbert et al. 2004). Altitude is effectively a surrogate for turnover in temperature in the region and impacts of increasing temperature such as shifts in distribution are expected to be most noticeable along this gradient (Williams et al. 2003).

Here replicated, standardized surveys of rainforest birds are used to estimate the occurrence and relative abundance of species along altitudinal gradients within the Wet Tropics region. Altitudinal records for endemic species are then compared with available data previously compiled by Crome and Nix (1991) whilst drawing additional support from the literature (Gill 1970; Storr 1984; Boles & Longmore 1989; Wieneke 1992). Such data is expected to greatly improve knowledge of patterns of assemblage structure and enhance future efforts to detect and quantify predicted impacts of climate warming such as change in population size and range shifts along the altitudinal gradient.

3.2 METHODS

3.2.1 Abundance estimates
Abundance data for rainforest bird fauna were collated from standardized field surveys throughout the region (723 surveys at 362 separate locations, years 1996-2003). Surveys
were compiled with the expressed purpose of comprehensively sampling rainforest spatially throughout the region whilst endeavouring to sample the representative range of available environmental conditions. Consequently, sampling effort varied across the gradient with effort generally greatest at mid-altitudes where rainforest is most extensive and least toward the highest peaks where rainforest is much more restricted. Each survey consisted of a 30 minute, 150 m transect through rainforest using both visual observations and calls to identify species. Five major mountain ranges and associated lowlands were sampled covering much of the latitudinal range within the region (16°15’ - 19°00’S) including the Spec Uplands, Kirrama Uplands, Atherton Uplands, Bellenden-Ker/Bartle-Frere Range, Carbine Uplands and Cairns-Cardwell and Mossman Lowlands (Table 3.1: see Williams et al. 1996 for sub-regional boundaries).

The objective was to document broad patterns of relative abundance of individual species across the altitudinal gradient. Spatial and temporal differences in detectability have the potential to confound estimates of relative abundance (Rosenstock et al. 2002) and, as such, specific efforts were made to address this issue. First, standardized sampling protocols were adopted to reduce the influence of confounding environmental factors. Surveys were conducted between 0600 and 0830 hours to coincide with peak calling activity and only employed on clear mornings under low wind conditions where detection probability was high, thereby allowing best possible estimates of abundance to be made. Second, regional and altitudinal sampling of mountain ranges was interspersed through time. The vast majority of surveys were undertaken in summer with no seasonal bias in altitudinal sampling. Third, all surveys were undertaken within rainforest habitat. More than 90% of detections during surveys were auditory and, as such, detections were expected to be robust to minor variation in vegetation structure and density across the altitudinal gradient.

### 3.2.2 Comparison with existing data set

Crome and Nix (1991) collated data from museum collections, field observations by vertebrate specialists and published material and provided a summary of minimum, maximum and mean altitude of records for thirteen endemic species. Similar comparative data was derived from the current study although one species, the Lesser Sooty Owl (*Tyto multipunctata*), was excluded as the diurnal nature of sampling prevented a meaningful assessment of the abundance and distribution for this species. While it should be acknowledged that sampling effort was not evenly distributed across
the altitudinal gradient, spatial bias in sampling effort was nevertheless similar in both studies (ie. percentage of records in altitudinal zones: Crome and Nix (1991), 0-399 m = 14%, 400-799 m = 35%, 800-1199 m = 49% and ≥1200 m = 2%; current study, 0-399 m = 14%, 400-799 m = 36%, 800-1199 m = 45% and ≥1200 m = 5%, see Table 3.1). The major difference between the two data sets then, was the lower sample size available to Crome and Nix (1991) (Table 3.2).

### 3.3 RESULTS

Seventy six species of birds that predominantly occur in rainforest within the region were recorded during systematic surveys (Appendix A, Fig. 3.1). However, of these, 15 species were encountered on fewer than 30 surveys (Fig. 3.1). The 12 endemic species examined (see Table 3.2) showed a range of associations with the altitudinal gradient (Fig. 3.1). Peak mean abundance of one species was recorded in the lowlands (< 300 m), seven species at mid-altitudes (300 – 1199 m) and four species in the uplands (> 1200 m) indicating high levels of endemism in mountainous parts of the region.

The greatest disparity between the current study and the data set of Crome and Nix (1991) related to the altitudinal position of range boundaries (Table 3.2). For the majority of species, altitudinal ranges reported by Crome and Nix (1991) appear conservative. Species were recorded at lower altitudes in this study (eight out of 12 species, Paired *t*-test, *t* = -2.334, 11 d.f., *p* = 0.040, Table 3.2) with large differences between range boundaries apparent for some species (ie. 500 and 566 m extension in the lower altitudinal boundary for the Bridled Honeyeater *Lichenostomus frenatus* and Bower’s Shrike-Thrush *Colluricincla boweri* respectively). Similarly, species were recorded at higher altitudes (10 out of 12 species, Paired *t*-test, *t* = 4.393, 11 d.f., *p* = 0.001, Table 3.2) with range extensions exceeding 300 m altitude in some instances (ie. Mountain Thornbill *Acanthiza katherina*, Grey-headed Robin *Heteromyias albispecularis*, Golden Bowerbird *Prionodura newtoniana*). A comparison of mean altitude of records between the two studies however, suggests no difference in the estimated altitudinal position of species (Paired *t*-test, *t* = 0.984, 11 d.f., *p* = 0.346, Table 3.2, Fig. 3.2).

### 3.4 DISCUSSION

Altitude-abundance data was collated for 76 bird species that predominately occur in rainforest environments within the region. This represents 68% of the 112 species
previously recorded from closed forest habitats and 24% of the 311 species known to occur in the Wet Tropics as a whole (Williams et al. 1996). The data reiterate the importance of cool, moist, mountainous parts of the region for endemic bird fauna (Crome & Nix 1991; Williams et al. 1996). Of the 12 endemic species examined, Macleay’s Honeyeater (*Xanthotis macleayana*) was the only species to be recorded at greatest mean abundance in the lowlands (ie. < 300 m). The importance of mountainous environments is further substantiated when consideration is given to those species that reach high abundance at mid and upper altitudes and whose range is in a large part encompassed by the Wet Tropics (ie. Spotted Catbird *Ailuroedus melanotis* or have a recognised race endemic to the region (Eastern Whipbird *Psophades olivaceus lateralis*, Satin Bowerbird *Ptilonorhynchus violaceus minor*, Pizzey & Knight 2003).

Crome and Nix (1991) examined minimum, maximum and mean altitude of collated records and concluded that, of the 13 endemic species, eight were restricted to the uplands with the remaining five being widespread. An examination of the altitude-abundance pattern of species shows that there is considerable variability among species in altitudinal affinities within these groupings. For example, within the upland restricted species group, the position of peak mean abundance ranged from 700-799 m (Bower’s Shrike-Thrush *Colluricincla boweri*) to 1400-1499 m (Golden Bowerbird *Prionodura newtoniana*, Atherton Scrubwren *Sericornis keri*). These data highlight the variable abundance of species within established distributions and support the previous assertion that analyses based on presence/absence data alone are likely to result in an overly simplistic and potentially misleading impression of change in assemblage composition across the altitudinal gradient (Williams et al. 1996).

Data collated in this study indicate that the altitudinal ranges of endemic species reported by Crome and Nix (1991) are conservative. Apparent discrepancies between the datasets, however, are most likely to be attributable to artefacts of sampling rather than a temporal change in the altitudinal occurrence of species for a number of reasons. First, no difference was apparent between studies in the mean altitude of records suggesting that no systematic shift in the range of species has occurred. Second, Crome and Nix (1991) were restricted to much lower sample sizes and it is expected that increased survey effort would increase the probability of detecting species at distribution edges resulting in an extension in the estimated position of range boundaries. Indeed, numerous other studies attest to a wider altitudinal distribution for endemic birds (Gill 1970; Storr 1984; Boles & Longmore 1989).
Kikkawa (1982) highlighted major discontinuities in the composition of bird communities between, lowlands, highlands and a mountaintop sampling location. With the benefit of additional information, however, Boles and Longmore (1989) considered the pattern to be “more apparent than real” with differences in species composition being accentuated by a lack of sampling at intervening altitudes. Boles and Longmore (1989) therefore concluded that the transition in species composition occurs in a more gradual, less abrupt manner than previously thought. Data from this study further support the assertion with species exhibiting not only a range of associations with the altitudinal gradient but also variable patterns of abundance within those ranges.

Systematic surveys were predominantly, but not exclusively, undertaken during spring-summer months. While no quantitative data are currently available on altitudinal migration among seasons, a number of species are considered to breed in highland forests of the Great Dividing Range in spring-summer and move to lower altitudes in autumn-winter. These include Australian King Parrot (*Alisterus scapularis*), Crimson Rosella (*Platycercus elegans*), Noisy Pitta (*Pitta versicolor*), Lewin’s Honeyeater (*Meliphaga lewinii*), Golden Whistler (*Pachycephala pectoralis*), Grey Fantail (*Rhipidura fuliginosa*), Pied Currawong (*Strepera graculina*), Satin Bowerbird (*Ptilonorhynchus violaceus*) and Bassian Thrush (*Zoothera lunulate*) (Pizzey & Knight 2003). Seasonal variability in altitudinal occurrence has the potential to confound altitudinal-abundance patterns and complicate comparisons between data sets with different seasonal bias in sampling. Consequently there is a real need to clarify seasonal altitudinal movements of species within the region.

If temperature is a major factor limiting the distribution and abundance of species, it is expected that species would show clines in altitudinal position across their latitudinal range. Boles and Longmore (1989) considered that several species restricted to highland rainforests in the region were capable of occupying lower altitudes in southern parts of their range. The Crimson Rosella *Platycercus elegans*, for example, has a lower altitudinal limit of 600 m in the Wet Tropics (Boles & Longmore 1989; Fig. 3.1, Appendix A), but further south in the Border Ranges has been recorded as low as 450 m (Storr 1984) and even reaches the coast in parts of New South Wales (Morris et al. 1981). Similarly, Wieneke (1992) recorded the Grey-headed Robin *Heteromyias albispecularis* no more than 50 m above sea level (see also Table 3.2) despite further to the north in mountains of New Guinea the species being known only from between 1900 – 2400 m altitude (Beehler et al. 1986). While these observations suggest clinal
variation in altitudinal range does exist for at least some widespread species, the pervasiveness of such a pattern is currently unknown. Quantitative support in the form of systematic surveys across mountain ranges in rainforest isolates to the north and south is therefore needed to elucidate geographic variability in species altitudinal distributions and is likely to contribute to our understanding of factors potentially limiting the distribution and abundance of species.

3.4.1 Implications

Increasingly, fine-scale information on distribution and abundance has led to a re-evaluation of perceived ecological associations of species within the Wet Tropics biogeographic region. In the present study, extensive baseline data has been provided for 76 rainforest birds distributed across the altitudinal gradient - the most important gradient affecting assemblage composition in all subsets of the terrestrial vertebrate fauna in the region (Williams et al. 1996). This will provide conservation managers with comparative data with which to detect and quantify ecological impacts of contemporary anthropogenic climate change and other threatening processes. Nevertheless, large gaps in our knowledge remain. Of particular interest are the effects of season and latitude on the altitudinal distribution and abundance of rainforest birds across mountainous areas of rainforest within the Wet Tropics and eastern Australia generally.
Table 3.1: Regional distribution of survey effort (no. of surveys) for rainforest birds across altitudinal gradients. AU, Atherton Uplands; BK, Bellenden-Ker/Bartle-Frere; CC, Cairns-Cardwell Lowlands; CU, Carbine Uplands; KU, Kirrama Uplands; ML, Mossman Lowlands; SU, Spec Uplands; TV, Townsville Lowlands.

<table>
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Table 3.2: Altitudinal position of 12 endemic rainforest birds derived from presence records. Estimates from Crome and Nix (1991) are shown in brackets for comparison. Taxonomy and common names follow Christidis and Boles (1994).

<table>
<thead>
<tr>
<th>Common name</th>
<th>Species</th>
<th>n</th>
<th>min</th>
<th>max</th>
<th>mean</th>
<th>sd</th>
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</thead>
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<td>Femwren</td>
<td><em>Oreoscopus gutturalis</em></td>
<td>214 (50)</td>
<td>340 (600)</td>
<td>1509 (1520)</td>
<td>877.7 (960)</td>
<td>192.2 (190)</td>
</tr>
<tr>
<td>Atherton Scrubwren</td>
<td><em>Sericornis keri</em></td>
<td>34 (40)</td>
<td>440 (680)</td>
<td>1509 (1260)</td>
<td>1003.9 (960)</td>
<td>261.2 (180)</td>
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<td>Mountain Thornbill</td>
<td><em>Acanthiza katherina</em></td>
<td>158 (48)</td>
<td>600 (640)</td>
<td>1579 (1260)</td>
<td>1016.1 (950)</td>
<td>219.3 (170)</td>
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<td>Macleay’s Honeyeater</td>
<td><em>Xanthotis macleayana</em></td>
<td>231 (63)</td>
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<td>361 (52)</td>
<td>110 (610)</td>
<td>1579 (1540)</td>
<td>870.1 (925)</td>
<td>196.0 (180)</td>
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<td><em>Heteromyias albispecularis</em></td>
<td>571 (41)</td>
<td>40 (430)</td>
<td>1579 (1260)</td>
<td>830.7 (840)</td>
<td>226.5 (200)</td>
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<td>Chowchilla</td>
<td><em>Orthonyx spaldingii</em></td>
<td>359 (63)</td>
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<td>Bower’s Shrike-Thrush</td>
<td><em>Colluricincla boweri</em></td>
<td>326 (49)</td>
<td>74 (640)</td>
<td>1540 (1260)</td>
<td>849.1 (950)</td>
<td>159.9 (170)</td>
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<td><em>Arses kaupi</em></td>
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<td>106 (10)</td>
<td>1111 (1180)</td>
<td>718.0 (530)</td>
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<td>Victoria’s Riflebird</td>
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<td>396 (71)</td>
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<td>1360 (1200)</td>
<td>741.3 (630)</td>
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<td><em>Scenopoetes dentirostris</em></td>
<td>263 (53)</td>
<td>600 (600)</td>
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<td>153.2 (170)</td>
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<td>Golden Bowerbird</td>
<td><em>Prionodura newtoniana</em></td>
<td>84 (42)</td>
<td>636 (680)</td>
<td>1579 (1260)</td>
<td>998.6 (960)</td>
<td>198.1 (170)</td>
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</tbody>
</table>
**Fig. 3.1.** Distribution and abundance of 76 rainforest birds across the altitudinal gradient. Taxonomy and common names follow Christidis and Boles (1994).
Fig. 3.2. Comparison of mean altitude of presence records of 12 endemic rainforest birds between Crome and Nix (1991) and this study. Broken line indicates line of equivalency.
4 Climate change and the rainforest fauna of the Australian Wet Tropics: using abundance data as a sensitive predictor of change in total population size*

Article type: Full Length Article:

*For the purposes of the thesis chapter, a series of Boxes have been appended to the submitted manuscript extending the scope of analyses to include data on microhylid frogs.
Abstract
Global average surface temperatures have increased rapidly over the last 100 years and there is accumulating evidence that climate change is already causing shifts in species’ distributions. We use extensive abundance data and expected range shifts across altitudinal gradients to predict changes in total population size of rainforest birds of Australian tropical rainforests in response to climate warming. According to our most conservative model scenario, 74% of rainforest birds of north-eastern Australia are predicted to become threatened (including 26 critically endangered species) as a result of projected mid-range warming expected within the next 100 years. Extinction risk varies according to where along the altitudinal gradient a species is currently most abundant. Upland birds are most affected and are likely to be immediately threatened by even small increases in temperature. In contrast, there is a capacity for the population size of lowland species to increase, at least in the short term. We conclude that abundance data collected across climatic gradients will be fundamental to gaining an understanding of population size change associated with climate warming.

4.1 INTRODUCTION
Recent analyses suggest that climate warming is likely to be a major driver of biodiversity change in the future (Sala et al. 2000; Thomas et al. 2004a) with increasing evidence that measurable impacts on species’ traits may already be apparent (Hughes 2000; Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003). Documented shifts in species’ distributions along climatic gradients (eg. Parmesan et al. 1999; Thomas & Lennon 1999; Hill et al. 2002; Konvicka et al. 2003; Brommer 2004; Hickling et al. 2005) have contributed to evidence for a biological response to contemporary climate change. Estimates of extinction risk following range shifts have largely been derived from modelled projections of “climatic envelopes” where risk has been inferred from predicted change in the relative size of species’ distributions under future climate change (for a recent review see Pearson & Dawson 2003). Such models suggest that large numbers of species will potentially experience dramatic decreases in distribution area under predicted climate change scenarios (eg. Williams et al. 2003; Hilbert et al. 2004; Thomas et al. 2004a). Quantitative estimates of change in population size during range contraction or expansion, however, have been prevented by a lack of data on the spatially variable patterns of abundance within a species’ range. This is despite assertions that population size and trend are the best correlates of extinction risk.
(O’Grady et al. 2004) and the wide application of these measures in determining the conservation status of species (eg. IUCN 2001 criteria). It is imperative that we now go beyond broad distribution modelling and consider the implications of abundance patterns on predicting climate change impacts to population size.

The rainforest vertebrate fauna of the Wet Tropics region of north-eastern Australia provides a unique opportunity to address this deficiency. Rugged topography imposes a high degree of turnover in temperature conditions across a discrete, relatively small area of rainforest (ca. 10 000 km²). The altitudinal gradient dominates the historical biogeography of the region (Nix & Switzer 1991; Williams et al. 1996) and predictions from climate envelope models suggest widespread displacement of species’ distributions along the altitudinal gradient as a result of future climate warming (Williams et al. 2003; Hilbert et al. 2004). Finally, altitudinal variation in abundance has already been documented for a number of rainforest species within the region (Trenerry 1993; Kanowski et al. 2001; Shoo & Williams 2004).

Here we draw upon extensive data describing the altitudinal abundance pattern of 55 rainforest birds (including 12 regional endemics) and demonstrate the potential for such data to be used to quantify change in population size of species as a consequence of climate warming. Specifically, we use expected upslope shifts in species’ distributions with increasing temperature and empirical altitude-abundance patterns to predict change in the relative population size of species under a range of probable future climates. This is a novel analysis that extends projections of species responses to climate change to the population level, enabling us to make explicit predictions about the changes to total population size, a key criteria in estimating IUCN conservation status.

4.2 METHODS

4.2.1 Predicted shifts in distribution
Rainforest predominantly occurs across windward slopes in the Wet Tropics of north-eastern Australia where we would expect temperature to decrease at the saturated adiabatic lapse rate of about 1 °C per 200 m altitude under most conditions. Established lapse rates are supported by field measurements collated from 21 weather stations distributed across the Wet Tropics region (Commonwealth Bureau of Meteorology). A 1 °C decline in temperature corresponds to an upward shift in altitude of between 142 and 250 m, based on minimum and maximum temperatures respectively (mean monthly
maximum temperature = -0.004 meters altitude + 28.587, r² = 0.562, p<0.001; mean monthly minimum temperature = -0.007 meters altitude + 20.152, r² = 0.807, p<0.001). The magnitude of change in temperature from field measurements is essentially equivalent to that expected following a saturated adiabatic lapse rate.

4.2.2 Abundance estimates

Abundance data for rainforest bird fauna were collated from standardized field surveys throughout the region (723 surveys at 362 separate locations, years 1996-2003). Each survey consisted of a 30 minute, 150 m transect through rainforest using both visual observations and calls to identify species. Surveys were conducted between 0600 and 0830 hours to coincide with peak calling activity and only carried out on clear mornings under low wind conditions where detection probability was high, thereby allowing best possible estimates of abundance to be made. Five major mountain ranges and associated lowlands were sampled covering much of the latitudinal range within the region (16°15’ - 19°00’S) including the Spec Uplands, Kirrama Uplands, Atherton Uplands, Bellenden-Ker/Bartle-Frere Range, Carbine Uplands and Cairns-Cardwell and Mossman Lowlands (see Williams et al. 1996 for subregional boundaries).

4.2.3 Population size change

An index of total population size was derived by multiplying the mean abundance of a species across survey transects located within each 100 m altitudinal interval by the total available area of rainforest (km²) within corresponding altitudinal intervals and summing values across the entire gradient. Rainforest area was determined for 100 m altitudinal intervals from a Geographic Information System (GIS) using regional vegetation mapping based on Tracey and Webb (1975) and subsequently updated by the Wet Tropics Management Authority and an 80 m resolution digital elevation model. The altitudinal range and estimates of mean abundance at altitudinal intervals within the range were then shifted upward by increments of 100 m to simulate successive increases of 0.5 °C in temperature (eg. Grey-headed Robin, Fig. 4.1). The index of population size was then recalculated for scenarios ranging from 0 m shift (current, assuming no temperature increase) to 1400 m shift (ie. +7 °C). In doing so, we assume that: (1) species will respond to increasing temperature by shifting along the altitudinal gradient; and (2) the integrity of the altitudinal abundance pattern will be retained as a species shifts along the altitudinal gradient. Change in the index of total population size was
presented as a proportion relative to the current scenario estimate (ie. 0 m shift) for each species.

The estimate of available rainforest area within each 100 m altitudinal interval represents the combined available area summed across multiple disjunct mountain ranges. Within the Wet Tropics region, individual species of the rainforest bird fauna are widespread among rainforest isolates (Williams et al. 1996). With the possible exception of the Atherton Scrubwren (*Sericornis keri*), that is absent from the southern ranges of the Spec and Halifax Uplands, no species are known to exhibit localised, patchy distributions or significant distribution gaps on a broad scale that would render the use of a combined area estimate unreasonable. It is expected, however, that the same considerations are unlikely to apply to all taxa and regions and that finer resolution, sub-regional estimates of available habitat area may be necessary in some applications of the method.

Under climate warming, environmental space currently not available in the region will be created at the lowest altitudes. While it is likely that lowland species will take advantage of the additional climatic habitat, no equivalent environmental space is currently available in the region to measure the response of species. In the absence of quantitative information we examine two potential scenarios. That is, that either: a species is incapable of occupying newly created climatic habitat such that the abundance pattern does not extend beyond the currently observed distribution (Scenario 1); or, that a species is capable of occupying newly created habitat beyond its currently observed distribution (Scenario 2). Assuming that the current distribution represents the full range of climates within the physiological tolerance of a species (Scenario 1), and not just an artefact of a physical barrier, is likely to portray a pessimistic view of the response of lowland species to climatic habitat to which no current analogue exists. Similarly, assuming that abundance continues to increase indefinitely in response to newly created climatic space is likely to be overly optimistic. In the absence of better information, for model Scenario 2 an abundance pattern symmetrically distributed about the abundance maxima was adopted as an intermediate scenario to infer abundance of lowland species (ie. abundance maxima <800 m altitude) in newly created climatic habitat (eg. Graceful Honeyeater, Fig. 4.2).

Seventy six species of birds effectively confined to rainforest in the region were recorded during surveys. For the purpose of analysis, we excluded 15 species that were recorded on fewer than 30 surveys as the level of sampling was considered to be
insufficient to establish a meaningful estimate of the altitude-abundance pattern for these species. To allow a direct comparison of results from both model scenarios we only present data for 55 of the remaining 61 species for which a symmetric abundance pattern could be inferred. That is, those species that displayed an identifiable peak in abundance along the altitudinal gradient (i.e. abundance maxima) that could be used as an inflection point for a symmetric abundance pattern.

4.2.4 Extinction risk
Species were allocated to extinction risk categories within the region according to their projected decline in population size in response to increasing temperature. Species were classified as either “Extinct” (100% decline), “Critically Endangered” ($\geq 80\%$ decline), “Endangered” ($\geq 50\%$ decline), “Vulnerable” ($\geq 30\%$ decline) or “Not Threatened” (all other remaining species). Extinction risk thresholds were consistent with IUCN Red List Categories and Criteria (Criterion A, IUCN 2001) utilising the maximum 100 year timescale to allow for chronic population declines attributable to climate change. Three temperature projections for the year 2100 were discussed recognising the uncertainty in future projections of global climate warming (Cubasch et al. 2001). These were “maximum” (+ 5.8 °C), “mid-range” (+ 3.6 °C) and “minimum” (+ 1.4 °C) scenarios relative to the year 1990. Projections for coastal north-eastern Queensland (Walsh et al. 2002) are essentially equivalent to those produced from global models (Cubasch et al. 2001) with approximately one degree of regional warming predicted per degree of global warming.

4.3 RESULTS
As climate warming proceeds, many of the climate types that support species at high density are expected to shift off extensive areas of rainforest at low and middle altitudes onto limited areas of rainforest distributed across mountaintops within the region (e.g. Grey-headed Robin, Fig. 4.1). At the same time, there is a potential for lowland species to expand into new climatic habitat created at the lowest altitudes (e.g. Graceful Honeyeater, Scenario 2, Fig. 4.2).

We estimated future extinction risk in response to three projections of climate change (and range shifts of corresponding magnitude) for the year 2100 (Cubasch et al. 2001) using two model scenarios (Table 4.1, Fig. 4.3). For our most conservative model scenario (i.e. assuming occupancy of new climates at low altitudes, Scenario 2), under
maximum climate change projections (ie. +5.8 °C) we estimate that 55 (100%) species of rainforest birds will become threatened with 31 (56.4%) species critically endangered and 7 (12.7%) species extinctions. Less severe climate projections (ie. +1.4-3.6 °C) also suggest high levels of threatened species but no extinctions. For the mid-range projections (ie. +3.6 °C), 41 (74.5%) species are expected to become threatened with 26 (47.3%) species reaching critically endangered status. For the minimum projection (ie. +1.4 °C), 29 (52.7%) species are expected to become threatened with 4 (7.3%) species critically endangered. Under the assumption of no occupation of newly created climatic habitat for lowland species (Scenario 1), more species are expected to be listed as threatened following minimum and mid-range climate projections and species are predicted to progress more rapidly through the hierarchy of threat status with increasing temperature (Table 4.1). Regardless, all 55 species are expected to become threatened under both model scenarios using the maximum (ie. +5.8 °C) climate projection.

Projected extinction risk varied according to where along the altitudinal gradient a species was most abundant (ie. position of abundance maxima). We find that the population size of upland species declines rapidly with even a small increase in temperature (Fig. 4.4a,b). This response corresponds to the strong decrease in available rainforest area at high altitude (Fig. 4.1). In contrast, lowland species experience lower levels of threat as population size declines more slowly with increasing temperature. Further, decline in population size for lowland species may be buffered, or even countered in the short term, through the colonization of newly created habitat at the lowest altitudes (Scenario 2, Fig 4.4b).

4.4 DISCUSSION

4.4.1 Climate change impacts on population size

The approach presented here represents a significant advance on previous attempts to estimate extinction risk from climate change that have employed modelled projections of climatic envelopes to predict the relative size of species’ distributions under climate change (Williams et al. 2003; Hilbert et al. 2004; Thomas et al. 2004a). Although the qualitative results are similar and suggest that climate change is a major threatening process for rainforest birds of the north-eastern Australia, they provide quantitative estimates of the impact on the most important conservation threat index, population size (O’Grady et al. 2004). We conclude that montane fauna of the region is likely to be
immediately threatened by projected warming with dramatic crashes in population size predicted with even small amounts of warming.

The projected pattern of change in population size broadly approximates that of range reductions and loss of core environment area predicted by Williams et al. (2003) and Hilbert et al. (2004). Some noticeable discrepancies however exist between the predictions and require explanation. Most notably, we report higher variability among species in the trajectory of change with increasing temperature and we report considerably lower extinction rates.

First, previous analyses were confined to endemic vertebrates that are predominantly restricted to cool upland environments (Nix & Switzer 1991). As we have seen, species restricted to such environments are likely to be disproportionately threatened by climate change. The inclusion of lowland species in our analyses, then, reduces the mean level of threat and inflates the variability among species in population size remaining. Second, unlike the previous multi-species study (Williams et al. 2003), our analysis was confined to birds, a subset of the rainforest vertebrate fauna. In relative terms as a group, birds are under-represented among the extreme geographically restricted vertebrate fauna of the region. This is reflected in the relatively low proportion of endemic birds predicted to lose greater than 50% of their current area of core environment with only 1 ºC increase in temperature (Hilbert & Williams 2003). Third, variability among species in population size change is increased when allowances are made for the colonization of newly created climates under climate change. Previous models have been confined to the projection of climate envelopes whose extent has been delineated by climates available under present conditions only. Finally, the present analysis was based on a temperature response alone and the findings are likely to be conservative where impacts associated with distribution shifts are compounded by other limiting factors such as rainfall.

Predicted range shifts in relation to a changing climate imply that temperature is the primary, overriding mechanism currently limiting the abundance and distribution of species. The capacity for physical change in climate to alter species’ distributions and result in localized extinctions is evidenced by numerous studies documenting range shifts of species along climatic gradients in association with contemporary climate warming (Parmesan et al. 1999; Thomas & Lennon 1999; Hill et al. 2002; Konvicka et al. 2003; Brommer 2004; Hickling et al. 2005; but see also Archaux 2004). The literature suggests a pervasive climate related response with broad congruence in
change observed across a diverse taxonomic and ecological range of species. Within the Wet Tropics, impacts of historical climate change are supported by molecular data (Joseph et al. 1995; Schneider et al. 1998; Hugall et al. 2002). Paleodistribution models that predict the location and size of refugia and patterns of extinction and colonization of species as a function of historical climate provide the most parsimonious explanation for current observed patterns of molecular phylogeography. We recognize, however, that other physical factors, disturbance and interactions with other species (Brown & Lomolino 1998) may also limit the distribution of species. Each of these mechanisms along with evolutionary adaptation (Harte et al. 2004) has the potential to alter the predicted impacts of climate warming on species survival.

4.4.2 Limitations of predictive models
Species interactions, specifically competition, have previously been implicated in limiting the abundance and distribution of species along altitudinal gradients (Diamond 1973; Remsen & Graves 1995; Brown & Lomolino 1998). While case studies suggest that interspecific competition governs the distribution of some species, the pervasiveness of this mechanism is unknown. Terborgh and Weske (1975) provided the only quantitative support for widespread influence of interspecific competition in this context although criticisms of the data set and interpretations suggest that the issue remains unresolved (Graves 1985; Weins 1989; Remsen & Graves 1995).

Although we cannot rule out the possible influence of interspecific competition, it is important to recognize that the mechanism itself does not preclude a response to increasing temperature. If, as Diamond (1973) proposed, altitudinal replacement is governed by underlying, differential adaptations of species to physical conditions that are themselves continuous functions of altitude, it is reasonable to expect that competitive interactions will not prevent but rather be carried through range shifts invoked by increasing temperature. As one species preferentially adapted to cooler temperatures shifts to higher altitude so too will the lower altitude counterpart thereby preserving the enforced segregation but invoking the transition at a new position along the altitudinal gradient. Under this scenario the most likely implication of competitive interaction is the potential for rapid expansion of species where localized extinctions release species from competitive interactions currently preventing species from occupying a wider range of altitudes.
Anthropogenic disturbance has the potential to affect predictions where vegetation clearance or regeneration alters the extent of future available habitat (Warren et al. 2001; Hilbert et al. 2004). Further, models of vegetation responses under climate warming suggest that significant shifts in the extent and spatial distribution of particular rainforest types are likely (Hilbert et al. 2001). Change in the extent of forest area will also be compounded by pervasive alteration in tree and liana communities in response to the rising concentration of atmospheric CO₂ (Phillips et al. 2002; Laurance et al. 2004). For species potentially restricted to specific rainforest types or communities, the rapidity of conversion from one forest type to another will be crucial in determining whether climatic environments within a species physiological tolerance can be reached and successfully occupied. A detailed understanding of the degree of specialization in rainforest birds and the pace at which vegetation change is expected to proceed would therefore be valuable in refining future projections of population size within the region.

Species may shift less than expected along climatic gradients where evolutionary adaptation increases the climate tolerance of species. The potential for genetic adaptation to climate at the population level, however, is not well known (Harte et al. 2004). Available evidence suggests that rainforest species will have a limited potential to evolve in response to rapid climate change (Hoffmann et al. 2003) and others have argued that “long generation times of macroscopic species will probably prevent adaptation rates from keeping pace with anthropogenic climate change” (Harte et al. 2004). The effect of warming on survival or extinction rates will also depend on the extent of existing differential population level adaptation to variable climates within the distribution of species (Harte et al. 2004).

We used a symmetric altitude-abundance pattern to infer the abundance of species within novel climatic space created under climate warming. Our intention was to highlight the potential for lowland species to benefit, at least initially, from increased temperatures by simultaneously invading upland habitats and taking advantage of additional suitable climatic habitat that becomes available at lowest altitudes with climate change. While a symmetric abundance pattern provides a plausible, intermediate scenario, agreement has yet to be reached on the expected shape of species response curves to an environmental gradient (Austin 2002) and, in particular, newly created climatic space. It is important to recognize, however, that the assumption relates primarily to already widespread species and does not affect predictions for mountaintop species that are expected to be most severely impacted by climate induced change.
Lastly, we assume that the integrity of the altitudinal abundance pattern will be retained as a species shifts along the altitudinal gradient. While climate induced change in the position of range boundaries has been documented (Parmesan et al. 1999; Thomas & Lennon 1999; Hill et al. 2002; Konvicka et al. 2003; Brommer 2004; Hickling et al. 2005), it is currently not known how well species track change within their distribution. If, for example, abundance at the lagging range boundary deteriorates more rapidly than abundance at the leading range boundary increases, we would expect the abundance pattern to become skewed or compressed. Similarly, under stressful conditions the overall abundance pattern may be depressed or otherwise take on some different, unanticipated form. Unfortunately, at present, a lack of suitable abundance data in long-term monitoring programs impedes our understanding of change in spatial abundance patterns of species.

4.4.3 Implications
Climate change has already altered the distribution of some species (Parmesan & Yohe 2003; Root et al. 2003) but direct estimates of change in population size are currently lacking. Here we utilize abundance data and provide a novel approach for documenting change in population size associated with range shifts across the altitudinal gradient. Our predictive models show that upslope movements have the potential to translate into dramatic reductions in the population size of mountaintop species. Twelve percent of all species are expected to become extinct eventually as a result of maximum projected climate change for the year 2100 with the vast majority of remaining species being severely threatened with population loss.

While abundance data and the methodological framework proposed herein provide a valuable, practical tool to quantify important change in population size, large gaps remain in our understanding of change in the spatial pattern of abundance of species within shifting distributions. We strongly advocate, therefore, the collection of systematic abundance data across the distribution of species and emphasise the need for sampling effort to be stratified along climatic gradients over which the greatest change is expected to proceed. Unless we start collecting the appropriate abundance data now, important climate change impacts may proceed completely unnoticed and we will forego the opportunity to test model assumptions and enrich our understanding of change in population size associated with range shifts. Information on the spatial pattern of abundance of species will allow us to move beyond broad accounts of change in
range boundaries and distribution area and consider the implication of climate change on the populations themselves.
Table 4.1: Accumulated number of rainforest bird species expected to qualify for threatened status within the region as a consequence of decline in population size with increasing temperature. Thresholds of population decline follow IUCN Red List Categories and Criteria (Criterion A, IUCN 2001). Results from two alternative model scenarios are shown: (a) no occupation of newly created climatic habitat at low altitudes was inferred (Scenario 1, n = 55 species); or (b), an abundance pattern symmetrically distributed about the abundance maxima was adopted to infer abundance of the species in newly created climatic habitat (Scenario 2, n = 55 species).

<table>
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<tr>
<th>Threat category</th>
<th>Model Scenario 1</th>
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<th>Model Scenario 2</th>
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<tr>
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<td>Min (+ 1.4°C)</td>
<td>Mid (+ 3.6°C)</td>
<td>Max (+ 5.8°C)</td>
<td>Min (+ 1.4°C)</td>
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<tr>
<td></td>
<td>no. (%)</td>
<td>no. (%)</td>
<td>no. (%)</td>
<td>no. (%)</td>
</tr>
<tr>
<td>Not Threatened (&lt;30% decline)</td>
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<td>1 (1.8)</td>
<td>0 (0)</td>
<td>26 (47.3)</td>
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<td>Vulnerable (≥ 30% decline)</td>
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<td>0 (0)</td>
<td>9 (16.4)</td>
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<td>Endangered (≥50% decline)</td>
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<td>16 (29.1)</td>
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<tr>
<td>Critically Endangered (≥80% decline)</td>
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<td>33 (60.0)</td>
<td>47 (85.5)</td>
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<td>Extinct (100% decline)</td>
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<td>0 (0)</td>
<td>8 (14.5)</td>
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<td>54 (98.2)</td>
<td>55 (100)</td>
<td>29 (52.7)</td>
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Fig. 4.1. Diagrammatic representation of Scenario 1 altitudinal shifts in the abundance pattern of the upland Grey-headed Robin (*Heteromyias albispecularis*) with increasing temperature against a breakdown of available rainforest area across the altitudinal gradient. 0.5 °C equates to approximately 100 m upward shift in altitude associated with climate warming. We assume that a species is incapable of occupying newly created climatic habitat such that the abundance pattern does not extend beyond the currently observed distribution (Scenario 1). Shaded bars highlight the altitudinal range of rainforest habitat predicted to be occupied with consecutive increases in temperature. Abundance estimates were multiplied by the corresponding area of rainforest at each altitude and summed across the gradient to provide an index of current population size. Altitude-abundance pattern is the mean count of individuals per 150 m survey transect with bars representing 95% confidence intervals of the mean.
Fig. 4.2. Diagrammatic representation of Scenario 2 altitudinal shifts in the abundance pattern of the lowland Graceful Honeyeater (*Meliphaga gracilis*) with increasing temperature against a breakdown of available rainforest area across the altitudinal gradient. 0.5 °C equates to approximately 100 m upward shift in altitude associated with climate warming. An abundance pattern symmetrically distributed about the abundance maxima was adopted to infer abundance of the species in newly created climatic habitat at low altitude (Scenario 2). The altitudinal range of rainforest habitat predicted to be occupied under Scenario 1 (dark shaded bars) is less that that occupied under Scenario 2 (dark and light shaded bars combined) where allowance has been made for the potential colonisation of newly created habitat with consecutive increases in temperature. Abundance estimates were multiplied by the corresponding area of rainforest at each altitude and summed across the gradient to provide an index of current population size. Projected change in population size arising from Scenario 2 is compared to that where no occupation of newly created climatic habitat was inferred (Scenario 1). Altitude-abundance pattern is the mean count of individuals per 150 m survey transect with bars representing 95% confidence intervals of the mean.
Fig. 4.3. Accumulated number of rainforest bird species expected to qualify for threatened status as a consequence of decline in population size with increasing temperature. Thresholds of population decline follow IUCN Red List Categories and Criteria (Criterion A, IUCN 2001) and correspond to the following threat categories: Vulnerable (filled circles), Endangered (open squares), Critically Endangered (filled squares) and Extinct (open circles). Results from two alternative model scenarios are shown: (a) no occupation of newly created climatic habitat at low altitudes was inferred (Scenario 1, solid lines, n = 55 species); or (b), an abundance pattern symmetrically distributed about the abundance maxima was adopted to infer abundance of the species in newly created climatic habitat (Scenario 2, broken lines, n = 55 species).
Fig. 4.4. Across-species mean decline in population size of rainforest birds within the region with increasing temperature under two alternative model scenarios: (a) no occupation of newly created climatic habitat at low altitudes was inferred (Scenario 1, n = 55 species); or (b), an abundance pattern symmetrically distributed about the abundance maxima was adopted to infer abundance of the species in newly created climatic habitat (Scenario 2, n = 55 species). Population size is expressed as a percentage of current population size. Species were classified into altitudinal groups based on the altitudinal position of their abundance maxima: 0-299 m (filled triangles, n = 12); 300-599 m (open circles, n = 12); 600-899 m (filled squares, n = 15), 900-1199 m (open squares, n = 6), 1200-1499 m (filled circles, n = 10). Data points were staggered to reveal overlapping values. Bars represent 95% confidence intervals of the mean.
**Box 4.1:** Accumulated number of microhylid species expected to qualify for threatened status within the region as a consequence of decline in population size with increasing temperature. Thresholds of population decline follow IUCN Red List Categories and Criteria (Criterion A, IUCN 2001). Assuming a symmetric abundance pattern for lowland species (Scenario 2) did not suggest occupation of newly created habitat beyond the currently observed distribution of species. Consequently both alternative model scenarios yielded equivalent predictions and results from both model scenarios for microhylid frogs are considered simultaneously (n = 6 species). Estimates of extinction risk follow methods outlined in 4.2.4 with abundance data derived from Chapter 2.

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<td>0 (0)</td>
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<tr>
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</tr>
<tr>
<td>Critically Endangered (≥ 80% decline)</td>
<td>3 (50.0)</td>
</tr>
<tr>
<td>Extinct (100% decline)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Total Threatened</td>
<td>5 (83.3)</td>
</tr>
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</table>
Box 4.2. Accumulated number of microhylid species expected to qualify for threatened status as a consequence of decline in population size with increasing temperature. Thresholds of population decline follow IUCN Red List Categories and Criteria (Criterion A, IUCN 2001) and correspond to the following threat categories: Vulnerable (filled circles), Endangered (open squares), Critically Endangered (filled squares) and Extinct (open circles). Both alternative model scenarios yielded equivalent predictions for microhylid frogs. Consequently results from both model scenarios are presented simultaneously (n = 6 species). Estimates of extinction risk follow methods outlined in 4.2.4 with abundance data derived from Chapter 2.
Box 4.3. Predicted decline in population size of microhylid species within the region with increasing temperature. Assuming a symmetric abundance pattern for lowland species (Scenario 2) did not suggest occupation of newly created habitat beyond the currently observed distribution of species. Consequently both alternative model scenarios yielded equivalent predictions and results from both model scenarios for microhylid frogs are considered simultaneously (n = 6 species). Population size is expressed as a percentage of current population size. Number labels refer to individual species of microhylid frogs: (1) *Cophixalus monticola*; (2) *C. neglectus*; (3) *C. hosmeri*; (4) *C. aenigma*; (5) *C. ornatus*; (6) *C. infacetus*. Estimates of population size follow methods outlined in 4.2.3 with abundance data derived from Chapter 2.
5 Potential decoupling of trends in distribution area and population size of species with climate change*

Article type: Full Length Article:

*For the purposes of the thesis chapter, a Box has been appended to the submitted manuscript extending the scope of analyses to include data on microhylid frogs.
Abstract
Global climates are changing rapidly and biological responses are becoming increasingly apparent. Here we use empirical abundance patterns across an altitudinal gradient and predicted altitudinal range shifts to estimate change in total population size relative to distribution area in response to climate warming. Adopting this approach we predict that, for nine out of twelve species of regionally-endemic birds, total population size will decline more rapidly than distribution area with increasing temperature. Two species showed comparable loss and one species exhibited a slower decline in population size with change in distribution area. Population size change relative to distribution area was greatest for those species that occurred at highest density in the middle of the gradient. The disproportionally loss in population size reported here suggests that extinction risk associated with climate change can be more severe than that expected from decline in distribution area alone. Therefore, if we are to make accurate predictions of the impacts of climate change on the conservation status of individual species, it is crucial that we consider the spatial patterns of abundance within the distribution and not just the overall range of the species.

5.1 INTRODUCTION
It is accepted that contemporary climate change (Folland et al. 2001) is already causing shifts in species’ distributions (Hughes 2000; Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003) and that there is the potential for these changes to be devastating in the future (Peterson et al. 2002; Thomas et al. 2004a; Thuiller 2004). Previous attempts to estimate extinction risk following range shifts have employed modelled projections of “climate envelopes” to predict the relative extent of potential species’ distributions under climate change (Bakkeness et al. 2002; Erasmus et al. 2002; Thuiller 2003; Pearson & Dawson 2003). Some models indicate that climate change impacts will largely consist of latitudinal and altitudinal shifts in potential species’ distributions (Peterson et al. 2002) while others suggest that the complete disappearance of critical climate types and dependent species are possible (Williams et al. 2003; Hilbert et al. 2004; Thomas et al. 2004a).

Climate envelope models provide valuable insight into the extent and location of a potential species’ distribution under predicted climate scenarios. However, a lack of data on the spatially variable patterns of abundance within a species’ range has prevented estimates of change in population size during range contraction or expansion.
This is despite assertions that population size and trend are the best correlates of extinction risk (O’Grady et al. 2004) and the wide application of these measures in determining the conservation status of species (eg. IUCN 2001 criteria). To date, the implications of abundance patterns remain poorly understood and have not been widely considered in predicting impacts. Predictions of declines in range size are basically assuming that, on average, loss of distribution area results in a loss of population size of similar or equivalent magnitude. But is this realistic? The climate envelope simply represents the full spectrum of climates encountered within the distribution of a species. Most species are expected to exhibit complex variability in abundance within this range due to spatial patterns of climate within their range, topography, biological interactions, biogeographic barriers and disturbance (Brown & Lomolino 1998). Therefore, in order to make more accurate predictions regarding the impacts of climate change, it is critical that we quantify abundance patterns across the most significant environmental gradients within a given species’ distribution and use both distribution area and population size in predictive analyses.

Here we use empirical data describing the altitudinal abundance pattern of 12 endemic rainforest birds of north-eastern Australia to highlight the potential decoupling of trends in population size and distribution area change with increasing global temperature. This is a novel analysis that extends projections of species response to climate change to the population level. Finally, we use the expected change in the altitude abundance pattern to recommend an appropriate sampling strategy that will enable explicit assessments of change to total population size in the future - a key criteria in estimating extinction risk.

5.2 METHODS

5.2.1 Predicted shifts in distribution

Rainforest predominantly occurs across windward slopes in the Wet Tropics of north-eastern Australia where we would expect temperature to decrease at the saturated adiabatic lapse rate of about 1 °C per 200 m altitude under most conditions. Established lapse rates are supported by field measurements collated from 21 weather stations distributed across the Wet Tropics region. A 1 °C decline in temperature corresponds to an upward shift in altitude of between 142 and 250 m, based on minimum and maximum temperatures respectively (mean monthly maximum temperature = -0.004 meters altitude + 28.587, $r^2 = 0.562, p<0.001$; mean monthly minimum temperature = -
0.007 meters altitude + 20.152, \( r^2 = 0.807, \ p<0.001 \). The magnitude of change in temperature from field measurements is essentially equivalent to that expected following a saturated adiabatic lapse rate.

5.2.2 Abundance estimates

Abundance data for rainforest bird fauna were collated from standardized field surveys throughout the region (723 surveys at 362 separate locations, years 1996-2003). Surveys were compiled with the expressed purpose of comprehensively sampling rainforest spatially throughout the region whilst endeavouring to sample the representative range of available environmental conditions. Consequently, sampling effort varied across the gradient with effort generally greatest at mid-altitudes where rainforest is most extensive and least toward the highest peaks where rainforest is much more restricted. Each survey consisted of a 30 minute, 150 m transect through the forest using both visual observations and calls to identify species. Five major mountain ranges and associated lowlands were sampled covering much of the latitudinal range within the region (16°15’ - 19°00’S) including the Spec Uplands, Kirrama Uplands, Atherton Uplands, Bellenden-Ker/Bartle-Frere Range, Carbine Uplands and Cairns-Cardwell and Mossman Lowlands (see Williams et al. 1996 for subregional boundaries).

Our objective was to document broad patterns of relative abundance of individual species across the altitudinal gradient. Differences in detectability have the potential to confound estimates of relative abundance (Rosenstock et al. 2002) and, as such, specific efforts were made to address this issue. First, we adopted standardized sampling protocols to reduce the influence of confounding environmental factors. Surveys were conducted between 0600 and 0830 hours to coincide with peak calling activity and only employed on clear mornings under low wind conditions where detection probability was high, thereby allowing best possible estimates of abundance to be made. Second, we ensured that regional and altitudinal sampling of mountain ranges was interspersed through time. The vast majority of surveys were undertaken in summer with no seasonal bias in altitudinal sampling. Third, all surveys were undertaken within rainforest habitat. More than 90% of detections during surveys were auditory and, as such, detections were expected to be robust to minor variation in vegetation structure and density across the altitudinal gradient.
5.2.3 Population size and distribution area change

The analyses presented here were restricted to 12 regionally-endemic species of bird effectively confined to rainforest in the Wet Tropics biogeographic region. The future prognosis of endemic species is of immediate interest as extinction of these species within the region represents an irreplaceable loss of species level diversity. Distribution area was estimated as the available rainforest area within the altitudinal range of a species within the region. Rainforest area was determined for 100 m altitudinal intervals from GIS using regional vegetation mapping based on Tracey and Webb (1975) and subsequently updated by the Wet Tropics Management Authority and an 80 m resolution digital elevation model. Altitudinal range was determined from the abundance dataset with species’ presence collated into corresponding 100 m altitudinal intervals. An index of total population size was derived by multiplying the mean abundance of a species across survey transects located within each 100 m altitudinal interval by the total available area of rainforest (km²) within corresponding altitudinal intervals and summing values across the entire gradient. The altitudinal range and estimates of mean abundance at altitudinal intervals within the range were then shifted upward by increments of 200 m to simulate successive increases of 1 °C in temperature (eg. Grey-headed Robin, Fig. 5.1). Distribution area and the index of population size were then recalculated for scenarios ranging from 0 m shift (current, assuming no temperature increase) to 1400 m shift (ie. +7 °C). In doing so, we assume that: (1) species will respond to increasing temperature by shifting along the altitudinal gradient; and (2) the integrity of the altitudinal abundance pattern will be retained as a species shifts along the altitudinal gradient. Change in the index of total population size was presented as a proportion relative to the current scenario estimate (ie. 0 m shift) for each species.

5.3 RESULTS

The 12 endemic species examined showed a range of associations with the altitudinal gradient. Peak mean abundance of one species was recorded in the lowlands, 7 species at mid-altitudes and 4 species in the uplands (Fig. 5.2). Lower range boundaries were scattered across the gradient with 5 of the 12 species not recorded below 300 m altitude (Fig. 5.2). As climate warming proceeds, many of the climate types that support species at high density are expected to shift off extensive areas of rainforest at low and middle
altitudes onto limited areas of rainforest distributed across mountaintops within the region (eg. Grey-headed Robin, Fig. 5.1).

We estimated relative change in population size and distribution area in response to altitudinal shifts in range for 12 species (Fig. 5.3). The relationship is linear where population size declines in direct proportion to distribution area and curvilinear where population size declines more rapidly or more slowly than distribution area with increasing temperature. The total population size of 9 out of 12 endemic bird species is predicted to decline with increasing temperature at a faster rate than their distribution area (Fig. 5.3). Population size is predicted to decline at an equivalent rate to distribution area for two species and more slowly for 1 species. Consequently, the extent of change in population size with increasing temperature is expected to be highly variable between species despite a similar reduction in distribution area (Fig. 5.3). A reduction in distribution to 75% of current area corresponded to between 91 and 38% of population size remaining and distribution area reduced to 50% corresponded to between 62 and 8% of population size remaining. Population size change relative to distribution area was greatest for those species that occurred at highest density in the middle of the gradient. Macleay’s Honeyeater *Xanthotis macleayana*, a lowland endemic, was the only species to show a positive bias with distribution area declining more rapidly than population size. Regardless of species, the decoupling of population size and distribution area change became negligible for extreme scenarios where both population size and distribution area were severely reduced.

### 5.4 DISCUSSION

#### 5.4.1 Climate warming and differential change in distribution area and population size

“An understanding of range reduction and accompanying decline in numbers is vital for the preservation of biodiversity, but this understanding does not yet exist” (Channell & Lomolino 2000). In the context of climate warming impacts, we show that a documented decline in distribution area will not necessarily be instructive of the extent of change in total population size. Declines in population size can occur at a much faster rate than that suggested by distribution area alone. In fact, 9 out of 12 endemic birds examined here are expected to suffer disproportionately large losses in population size following an initial reduction in distribution area. These analyses suggest that findings from previous distribution-based studies (Williams et al. 2003; Hilbert et al. 2004;
Thomas et al. 2004a) may themselves be conservative, further reinforcing the notion that climate change is a major threatening process for rainforest birds of north-eastern Australia.

That a severely reduced range should correspond to a depleted population size is not of interest in itself. What we want to know about is the trajectory of change in range and numbers toward extinction (Soulé 1983). Individualistic responses predicted for species here suggests that the detail of the population size-distribution area relationship is likely to be important for estimating extinction risk. A decline in distribution to 75% of current area translates to between 91 and 38% of the population size remaining. A more severe reduction in distribution area to 50% results in a projected reduction of population between 62 and 8% of current size. Documenting differential change in population size between species will be crucial in identifying species at immediate risk of extinction and understanding processes of change affecting future survival.

In general, we would consider endemic species restricted to mountain peaks within the region to be at greatest risk from impacts arising from climate warming (Williams et al. 2003, Hilbert et al. 2004). Our finding that species occurring at highest density in the middle of the gradient, not upper end, are likely to suffer most from a disproportionate decline in population size is unexpected. In our analysis, the deviation from the expected pattern is attributable to the ‘hump shaped’ distribution of rainforest area across the gradient. For mid-altitudinal species, then, initial warming results in the displacement of climatic conditions that support species at high density off extensive areas of rainforest at middle altitudes and onto limited areas of rainforest scattered across mountaintops within the region. While our results do not consider the timing of extinction risk, for mountaintop species the probable loss of distribution area remains immediate and absolute, we conclude that the generalized notion that species occurring in mountaintop areas will be the focus of negative climate change impacts is overly simplistic. Complex topography and localised patterns of habitat occurrence dictate that, in practice, the ‘cone shaped’ model (Peterson 2003) of decreasing habitat area with increasing altitude is not always applicable (eg. Gottfried et al. 1999), and that the interplay between both the altitude-rainforest area pattern and the altitude-abundance pattern will be important in predicting population impacts for montane species.

Many gaps remain in our understanding of how population size will change as a consequence of global warming. We illustrate the potential for the decoupling of trends in population size and distribution area to result in complex, individualistic responses to
climate warming. In turn this is expected to further contribute to previously identified sources of uncertainty associated with predictions of extinction risk (Thomas et al. 2004b; Thuiller et al. 2004). Some of the most important uncertainties that currently limit our ability to predict change in population size using our model are considered herein.

5.4.2 Factors contributing to uncertainty in predictive models
Predicted range shifts in relation to a changing climate imply that temperature is the primary, overriding mechanism currently limiting the abundance and distribution of species. The capacity for physical change in climate to alter species’ distributions and result in localized extinctions is evidenced by numerous studies documenting range shifts of species along climatic gradients (Grabherr et al. 1994; Parmesan 1996; Parmesan et al. 1999; Thomas & Lennon 1999; Hill et al. 2002; Konvicka et al. 2003; Brommer 2004; but see also Archaux 2004) and population fluctuations (McLaughlin et al. 2002) in association with contemporary climate change. The literature suggests a pervasive climate related response with broad congruence in change observed across a diverse taxonomic and ecological range of species. We recognize, however, that other physical factors such as rainfall patterns (Williams 2003) and basal height of cloud inundation (Pounds et al. 1999), as well as disturbance (Warren et al. 2001; Hilbert et al. 2004) and interactions with other species (Diamond 1973; Remsen & Graves 1995; Brown & Lomolino 1998) may also limit the abundance and distribution of species. Each of these mechanisms along with evolutionary adaptation (Harte et al. 2004) has the potential to alter the predicted impacts of climate warming on the altitude-abundance pattern of species.

Further, it is also conceivable that different processes could be limiting distribution and abundance at respective ends of the climatic gradient (Parmesan et al. 1999; Thomas & Lennon 1999; Brommer 2004). If for example, as suggested by Thomas and Lennon (1999), “cool margins of species might be more immediately responsive than warm margins to the direct effects of thermal variation,” we would expect the abundance pattern to become skewed or stretched. Similarly, under stressful conditions the overall abundance pattern may be depressed or otherwise take on some different, unanticipated form. Unfortunately, at present, a lack of suitable abundance data from long-term monitoring programs impedes our understanding of change in patterns of spatial abundance within the distribution of species.
In our analyses, the estimated position of altitudinal range boundaries is used to derive an index of distribution area. For our purposes, we defined the position of range boundaries by the lowest and highest documented presence of a species within 100 m altitudinal intervals. The obvious caveat of this approach is that, in practice, one or a few individuals only are needed to extend the altitudinal range of a species and thereby inflate the estimate of distribution area. The population size index is relatively unaffected as low estimates of abundance effectively down-weight the contribution of additional habitat area at range boundaries. Uncertainty in range boundary estimates are greatest where limits of occurrence are proceeded by a tail of decreasing abundance and most problematic at lower range boundaries where the extent of rainforest area within 100 m altitudinal intervals is comparatively large. Although agreement has yet to be reached on the expected shape of species’ response curves to an environmental gradient (Austin 2002), strong altitudinal patterns of abundance do not appear unique to rainforest birds and decreasing abundance at range boundaries has also been documented for other taxa within the region (ie. arboreal mammals, Trenerry 1993 and Kanowski et al. 2001; microhylid frogs, Shoo & Williams 2004).

Under climate warming, climatic space currently not available in the region will be created at the lowest altitudes. The majority of species included in our analysis have montane distributions and we may infer that the lower range boundary along the climatic gradient represents the extent of “conditions in which a species (normally) shows a positive demographic balance (rarely the absolute physical limits of a species, but the set of conditions under which it survives in at least some multi-species communities)” (Thomas et al. 2004a). For at least one species (*Xanthotis macleayana*), however, the lower boundary is constrained by an imposed barrier (ie. sea level) and the potential for such a species to take advantage of additional climatic habitat is unclear. While no equivalent climatic space is currently available in the region to measure the response of this species, there is a real potential for such lowland species to expand their range and consequently benefit, at least initially, from increased temperatures thereby rendering our predictions overly pessimistic.

The spatial extent of upland forest types in the region is predicted to shrink significantly under expected climate change scenarios (Hilbert et al. 2001). Consequently, in the long term, predictions of population change based on the current distribution of rainforest are likely to be conservative. Not only will species shift off the more extensive areas of forest at low altitudes but will struggle to capitalize on habitats
that are themselves expected to become increasingly scarce, physiologically stressed and more fragmented under climate warming. In the near future most rainforest types are expected to experience climates that are more appropriate to some other rainforest type (Hilbert et al. 2001). While the propensity for ecological change is high, the pace at which vegetation change in the region is expected to proceed is currently unknown.

Finally, the analysis based on species’ abundance data pooled across mountain ranges does not account for potential spatial heterogeneity in temperature conditions at equivalent altitudes or within region variability of future warming. The obvious implication of spatial heterogeneity in temperature, if present, is that it would diminish the capacity of altitude as a surrogate variable to capture small differences in temperature variability throughout the region. Considerable potential exists, therefore, to refine predictive models and increase the capacity of sampling strategies to detect and also predict change by explicitly accommodating spatial variability in climatic conditions.

In the absence of detailed climate information, altitudinal gradients should be selected to encompass secondary gradients such as latitude over which temperature is expected to vary most. The benefits of comprehensive, representative sampling of regional variability in temperature conditions are threefold. Firstly, the sampling design would allow change to be examined along individual altitudinal gradients thereby removing variability resulting from small scale differences in temperature across the region. Secondly, the sampling design would provide necessary data in the future to document and account for flow on impacts of heterogeneous warming in the region should it occur. Thirdly, as high resolution information becomes available, abundance data could be combined with regional climate models to predict differential change among isolated populations resulting from spatial heterogeneity in climate warming.

5.4.3 Implications

Previous attempts to estimate extinction risk have employed modelled projections of “climate envelopes” to predict the relative size of potential species’ distributions under climate change. Typically, extinction risk has then been evaluated in terms of established threat criteria (ie. IUCN Red Data Book criteria) or, in the case of Thomas et al. (2004a), using species-area relationships. Here we have used a novel approach to show that upslope movements will translate into previously unanticipated change in the population size of species. Change in the spatial extent of specific climates that support
high densities of a species are likely to play a decisive role in ameliorating or exacerbating biological impacts of projected climate change. We suggest that critical climate change impacts may be underestimated or proceed unnoticed if, in the pursuit of monitoring range boundaries, we neglect to take notice of the populations that reside within them. There is an urgent need to not only track changes in location and extent of distribution area but also spatial patterns in the relative density of species within current and future distributions.
Fig. 5.1. Diagrammatic representation of altitudinal shifts in the abundance pattern of the Grey-headed Robin (*Heteromyias albispecularis*) with increasing temperature against a breakdown of available rainforest area across the altitudinal gradient. 1 °C equates to approximately 200 m upward shift in altitude. Abundance estimates were multiplied by the corresponding area of rainforest at each altitude and summed across the gradient to provide an index of current population size.
Fig. 5.2. Altitudinal abundance patterns for 12 endemic rainforest birds of north-eastern Australia. Estimated position of upper and lower range boundaries are represented by inverted triangles with the number of surveys a species was recorded present at the range boundary also indicated.
Fig. 5.3. Projected change in the relative population size and distribution area of rainforest birds following altitudinal range shifts associated with climate warming. The relationship is linear where population size declines in direct proportion to distribution area (i.e. dotted grey line) and curvilinear where population size declines more rapidly or more slowly than distribution area with increasing temperature. Number labels refer to individual species of rainforest birds: (1) Macleay’s Honeyeater *Xanthotis macleayana*; (2) Tooth-billed Bowerbird *Scenopoeetes dentirostris*; (3) Pied Monarch *Arses kaupi*; (4) Victoria’s Riflebird *Ptiloris victoriae*; (5) Golden Bowerbird *Prionodura newtoniana*; (6) Chowchilla *Orthonyx spaldingii*; (7) Mountain Thornbill *Acanthiza katherina*; (8) Fernwren *Oreoscopus gutturalis*; (9) Atherton Scrubwren *Sericornis keri*; (10) Bridled Honeyeater *Lichenostomus frenatus*; (11) Grey-headed Robin *Heteromyias albispecularis*; (12) Bower’s Shrike-thrush *Colluricincla boweri*. 
Box 5.1. Projected change in the relative population size and distribution area of microhylid species following altitudinal range shifts associated with climate warming. The relationship is linear where population size declines in direct proportion to distribution area (ie. dotted grey line) and curvilinear where population size declines more rapidly or more slowly than distribution area with increasing temperature. Number labels refer to individual species of microhylid frogs: (1) *Cophixalus hosmeri*; (2) *C. ornatus*; (3) *C. aenigma*; (4) *C. monticola*; (5) *C. neglectus*; (6) *C. infacetus*. Estimates of population size and distribution area change follow methods outlined in 5.2.3 with abundance data derived from Chapter 2.
6 Detecting climate change induced range shifts: where and how should we be looking?

Article type: Full Length Article:

Abstract

Global climate warming is expected to cause systematic shifts in the distribution of species and consequently increase extinction risk. Conservation managers must be able to detect, measure and accurately predict range shifts in order to mitigate impacts to biodiversity. However, important responses to climate change may go unnoticed or be dismissed if we fail to collect sufficient baseline data and apply the most sensitive analytical tests. Here we use randomisations of a contemporary data set on rainforest birds of north-eastern Australia to quantify the sensitivity of three measures for assessing range shifts along altitudinal gradients. We find that smaller range shifts are detectable by analyzing change in the mean altitude of presence records rather than upper or lower range boundaries. For a moderate survey effort of 96 surveys, measurements of change in the mean altitude of 34 species has the capacity to provide strong inference for mean altitudinal range shifts as small as 40 m across the species assemblages. We also show that range shifts measured at range boundaries can be potentially misleading when differences in sampling effort between contemporary and historical data sets are not taken into account.

6.1 INTRODUCTION

Immediate detection of biological responses to contemporary climate change is vital if we are to improve our capacity to predict change and attempt to initiate management strategies in time to counter species loss and mitigate impacts to biodiversity. Upslope and poleward shifts in species’ distributions have regularly been cited as evidence of climate related change (eg. Parmesan & Yohe 2003; Root et al. 2003). To date, however, documentation of upslope shifts has lagged behind that of poleward shifts. This is despite the potential for upslope shifts to mask important poleward shifts (Hill et al. 2002) and the immediate threat of climate warming on mountaintop restricted species (Williams et al. 2003; Hilbert et al. 2004) that by virtue of their distribution are incapable of migrating latitudinally.

In many instances, evidence for altitudinal range shifts has been derived from a single or small number of permanent sampling plots established at a select position along the climatic gradient. Change within the narrow observation window has then been interpreted, in relation to range shift predictions, using additional knowledge of the distribution of species along the altitudinal gradient outside the census area. Examples
include increased abundance and species richness of premontane birds in a long term montane census plot (Pounds et al. 1999) and increased species richness in summit floras (Grabherr et al. 1994). However, these studies assume that change at one point can be “unambiguously interpreted as range shifts, rather than as merely local density changes, range expansions or contractions” (Parmesan 1996).

For poleward shifts, more comprehensive evidence has come from analyses that have utilized atlas data to broaden coverage of sampling effort across the latitudinal gradient (Thomas & Lennon 1999; Hill et al. 2002; Brommer 2004; Hickling et al. 2005). Similar attempts to expand the investigation of range shifts across the altitudinal gradient have struck difficulties (Hill et al. 2002; Konvicka et al. 2003). The course spatial scale of atlas data imposes limits on the detection of trends in vertically diverse grid cells, rendering the method unsuitable for detecting shifts in vertically restricted montane species (Konvicka et al. 2003) – the very species that are of greatest concern (Williams et al. 2003; Hilbert et al. 2004). Further, there is a lack of altitudinal replication of grid squares that precludes the application of important sub-sampling techniques to equalize sampling effort between time periods (Hill et al. 2002). For these reasons, transects or point counts are likely to be more appropriate for investigating altitudinal range shifts in response to contemporary climate warming (Archaux 2004).

Research to date has provided valuable first evidence of altitudinal range shifts (Grabherr et al. 1994; Pounds et al. 1999; Konvicka et al. 2003; Hill et al. 2002; but see Archaux 2004). Most analyses however, have been reliant on the comparison of contemporary data with historical data sets not originally collected with the explicit purpose of investigating range shifts. Therefore an evaluation of baseline data characteristics most likely to promote the detection of range shifts would be both timely and valuable for informing the design of future monitoring programs. Here we use randomisations of a high-resolution data set on rainforest birds of north-eastern Australia, compiled from recent transect surveys, to evaluate the potential for efficient and reliable detection of altitudinal range shifts. Specifically, we determine and compare the effect of sampling effort on the magnitude of minimum detectable range shifts across a species assemblage for three measures of altitudinal position (lower and upper range boundaries: Thomas & Lennon 1999; Hill et al. 2002; Brommer 2004; Hickling et al. 2005; and mean position of presence records: Konvicka et al. 2003; Archaux 2004). Further, we examine the effect of differential sampling effort on estimates of range shift. Knowing what to measure and how much survey effort is
required will greatly improve our capacity to achieve sufficiently strong inference so that important responses to climate change will not go unnoticed in the future.

6.2 METHODS

6.2.1 The data set

Presence data for rainforest bird fauna were collated from standardized abundance surveys along altitudinal gradients throughout the Wet Tropics biogeographic region of north-eastern Queensland, Australia (680 surveys at 397 separate locations, years 2000-2004). Each survey consisted of a 30 minute, 150 m transect through rainforest using both visual observations and calls to identify species. Surveys were conducted between 0600 and 0830 hours to coincide with peak calling activity and only carried out on clear mornings under low wind conditions where detection probability was high. Ten major mountain ranges and associated lowlands were sampled covering much of the latitudinal range within the region (15°40’ - 19°00’S) including the Spec Uplands, Kirrama Uplands, Hinchinbrook Island, Atherton Uplands, Bellenden-Ker/Bartle-Frere Range, Black Mountain Corridor, Carbine Uplands, Windsor Uplands, Thornton Uplands, Mt Finnegan Uplands and Townsville Lowlands, Cairns-Cardwell Lowlands, Mossman Lowlands, Thornton Lowlands and Bloomfield-Helenvale Lowlands (see Williams et al. 1996 for sub-regional boundaries).

6.2.2 Measuring change in altitudinal position of the assemblage

Three measures for determining range shifts along the altitudinal gradient were considered: (1) the lower and (2) the upper position of presence records (ie. range boundaries: Thomas & Lennon 1999; Hill et al. 2002; Brommer 2004; Hickling et al. 2005); and (3) the mean position of presence records (Konvicka et al. 2003; Archaux 2004). Infrequently recorded species are unlikely to be good candidates for investigating systematic range shifts as the addition of a small number of records has the potential to drastically alter estimated position along the gradient. Similarly, range shift measures are unlikely to provide meaningful information where change in the measure is already constrained by the upper or lower limits of the gradient. For example, species currently occupying the highest mountaintops in the region are incapable of colonising higher altitudes and, as a consequence, the upper range boundary does not allow for a test of upslope range shifts. We address both limitations by adopting a two tier selection process to determine which species to include in the analysis for each of the three
measures of altitudinal position. First, for low recording frequency we excluded those species that were not recorded on each of the random sub-samples of the complete data set (see below). Second, species with upper or lower range boundaries that fell within 300 m of either end of the gradient were excluded from analysis for the respective measures. As a result, three, 12 and 34 species were available for analyses of lower, upper and mean position of presence records respectively.

6.2.3 Effect of sampling effort and measure choice on minimum detectable range shifts
Range shift data is amenable to analysis following a paired-sample \( t \)-test design with matched-pairs arising from the desire to quantify temporal change in the estimated position of individual species between two time periods. The analysis is therefore concerned with temporal differences \( (d) \) in the estimated position of species along the gradient and can be calculated directly by subtracting the estimated position of a species at one time period from that of another. If the null hypothesis of no difference is correct, we would expect multiple values of \( d \) derived from the pool of available species, to be distributed about a mean of zero (ie. \( H_0: \overline{d} = 0 \)). The likelihood of rejecting the null hypothesis is then dependent on both the magnitude of the observed mean difference (\( \overline{d} \)), and the standard error of \( \overline{d} \) according to the equation (Zar 1996):

\[
t = \frac{\overline{d}}{s_{\overline{d}}}
\]

For the purpose of the study, we ask how small a difference in \( \overline{d} \) (hereafter referred to as \( \delta \)), can be detected using a paired-sample \( t \)-test with 1 - \( \beta \) power, at an \( \alpha \) level of significance, using a specified number of species, \( n \). The minimum detectable range shift across a species assemblage (\( \delta \)) using a two-tailed paired-sample \( t \)-test can be derived from the following equation (Zar 1996):

\[
\delta = \sqrt{s^2_d/n} (t_{(\alpha/2),v} + t_{(\beta),v})
\]

where \( s^2_d \) is the variance of sample values of \( d \), \( n \) is the number of species and \( v = n - 1 \). For all tests an \( \alpha \) level of 0.05 and \( \beta \) of 0.1 (ie. difference between \( \overline{d} \) and zero that is detectable 90% of the time) was adopted.

We simulated time series comparisons of range shifts using randomized sub-samples of the complete data set. This allowed us to quantify variability in our field
data and estimate change in minimum detectable range shift with increasing sampling effort. In order to retain a broad coverage of sampling across the gradient spanning 0 – 1600 m altitude, one to six surveys were randomly selected from each of consecutive 100 m altitudinal intervals along the gradient resulting in total sampling effort ranging from 16 to 96 surveys. Ten paired random sub-samples of the complete data set (simulated Time 1 and 2) were extracted in this manner and the position of lower, upper and mean presence records determined for each species with successive increases in sampling effort. Differences in the estimated position of individual species (\(d\)) between simulated time periods were determined (eg. see Table 6.1) and the minimum detectable range shift across a species assemblage (\(\delta\)) calculated for each measure of altitudinal position and for intervals of sampling effort.

We expect variance of \(d\) and subsequently the minimum detectable range shift across a species assemblage (\(\delta\)) to decline as more species are included in the analysis. As the number of species available for analysis at lower and upper range boundaries was low, four and 12 species respectively, we performed analyses of the mean position of presence records on subsets of species common to range boundary analyses. This allowed us to control for the effect of number of species when making comparisons between estimates of minimum detectable range shift (\(\delta\)) resulting from analyses of the mean position of presence records and range boundaries. Estimates of minimum detectable range shift (\(\delta\)) were also derived for analyses of the mean position of presence records utilizing the full 34 available species.

6.2.4 Effect of uneven sampling effort on range shift estimates

We also used paired random sub-samples of the complete data set to simulate time series comparisons with uneven sampling effort between time periods. Specifically we examined the potential for disproportionate sampling effort to result in a biased estimate of mean range shift across a species assemblage (\(\bar{d}\)). Instead of increasing sampling effort in both simulated time periods concurrently, then, sampling effort in simulated Time 2 was fixed at 96 surveys (ie. 6 surveys per 100 m altitude) and the sampling effort in simulated Time 1 varied between 16 and 96 surveys (ie. 1 to 6 surveys per 100 m altitude). This allowed us to determine the sensitivity of range shift estimates to the uneven distribution of sampling effort in time series comparisons.
6.3 RESULTS

6.3.1 Effect of sampling effort and measure choice on minimum detectable range shifts

For all three measures, minimum detectable range shift across a species assemblage declined with increasing sampling effort (Fig 6.1a & b). Controlling for differences in the number of species between analyses, mean position of presence records enabled lower minimum detectable range shifts than either lower or upper range boundaries at equivalent sample sizes (Fig 6.1a & b). A larger pool of species was available for analysis using the mean position of presence records than either lower or upper range boundaries. An analysis of the mean position of presence records using the full 34 species further reduced the minimum detectable range shift, ranging from 76-124 m at a sampling effort of 16 surveys to 20-39 m at a sampling effort of 96 surveys (Fig 6.2).

6.3.2 Effect of uneven sampling effort on range shift estimates

Uneven sampling effort between time periods resulted in a systematic bias in range shift estimates at lower and upper range boundaries (Fig. 6.3a & b). A disproportionately large sampling effort in the second time period resulted in the false impression that range boundaries had extended outwards. The sampling artifact diminished as the difference in sampling effort between the two simulated time periods approached zero. The same systematic bias was not apparent for range shift estimates derived from the mean position of presence records (Fig. 6.3a & b) where increased sampling effort simply reduced the variability between range shift estimates.

6.4 DISCUSSION

6.4.1 Detecting climate change induced range shifts along the altitudinal gradient

While it seems intuitive that edges of ranges will be the most sensitive areas to monitor range shifts, to date, there has been no evaluation as to whether range boundaries provide the most effective ‘signal’ with which to identify systematic change. Here we have used randomisations of a high-resolution data set to show that the mean position of presence records consistently allows for a smaller detectable range shift than do range boundary estimates (Fig 6.1a & b). Extensions or contractions of range boundaries are dependent on fewer individuals than change measured at the mean where the entire pool of available records is utilised. Archaux (2004) reasoned previously that change in species mean altitude was more indicative of a population response than change
measured at range boundaries. It is the capacity of the mean to draw upon information from throughout the distribution of a species, that is likely responsible for the lower random variability between simulated time period estimates and consequently the more sensitive detection limit of the measure.

Annual mean temperature for Queensland is projected to increase by 0.3 to 2.0 °C by the year 2030 relative to 1990 with 0.8 to 6.0 °C of warming possible by 2070 (Walsh et al. 2002). Rainforest predominantly occurs across windward slopes in the Wet Tropics where we would expect temperature to decrease at a saturated adiabatic lapse rate of about 1 °C per 200 m altitude under most conditions. The combined information suggests that isotherms under warmer predicted climates for 2030 are likely to be 60 to 400 m higher than in 1990, calibrating to a 15 to 100 m altitudinal shift per decade. Using randomisations of our data set, measuring change in mean altitude of the full 34 species and a sampling effort of 96 surveys, we demonstrate potential to confidently detect altitudinal range shifts as small as 40 m (Fig. 6.2). The detection limit of our data set therefore is expected to allow for a meaningful test of range shifts whose sensitivity is congruent with the magnitude of decadal change predicted as a consequence of contemporary climate warming. In addition, an extrapolation of the trend in declining minimum range shift with increasing sampling effort suggests that there is further potential to reduce the detection limit by sampling in excess of the 96 surveys.

We also show that, unlike estimates of mean altitude, the position of range boundaries is strongly dependent on sampling effort. Low sampling effort generally corresponds to an underestimate of the actual position of the range boundary and, as a consequence, additional sampling results in an extension of the range boundary. While such difficulties can be overcome by sub-sampling data to equalize sampling effort between time periods (Hill et al. 2002), it is important to note that, to date, such techniques have rarely been applied.

For the purpose of hypothesis testing, the implication of a systematic bias in the estimated shift at range boundaries, as an artefact of unequal sampling effort, is twofold. Upper range boundaries will be seen to be expanding more rapidly than is actually the case (ie. Type I error) and lower range boundaries will be seen to be stable or even extending despite a true retraction in the position of boundaries (Type II error). These biases could explain, at least in part, the phenomenon reported for European butterflies (Parmesan et al. 1999), British birds (Thomas & Lennon 1999) and odonates (Hickling
et al. 2005) and Finnish birds (Brommer 2004) where northern range boundaries have expanded more than southern range boundaries have retracted. Such observations have previously led to the conclusion that “cool margins of temperate species might be more immediately responsive than warm margins to the direct effects of thermal variation” (Thomas & Lennon 1999). Our results indicate that similar trends can potentially arise from disproportional sampling effort between time periods. Interestingly, in a recent analysis of British butterflies, Hill et al. (2002) applied sub-sampling techniques to equalize sampling effort between time periods and found no evidence for a systematic shift northwards across all British butterflies.

6.4.2 Potential limitations
Data pooled across multiple mountain ranges do not allow for potential spatial heterogeneity in current and future climatic conditions throughout the region. Although the Wet Tropics region is narrow in latitudinal extent (approximately 400 km north-south), a minor latitudinal cline in temperature at equivalent altitudes is possible. Further, differential patterns of cloud inundation between small isolated mountains and main ridges of major mountain ranges (Grubb 1971) or mountain ranges with differing adjacent land use (Lawton et al. 2001) may also influence small scale variability in the altitudinal distribution of species throughout the region. Pounds et al. (1999) provided correlative evidence for a link between height of cloud inundation and the abundance and altitudinal distribution of premontane birds in highland rainforest of Monteverde, Costa Rica. Considerable opportunity therefore exists to improve the sensitivity of monitoring programs by stratifying sampling across the region to explicitly account for regional climatic variability.

Our analysis was based on a compilation of 680 surveys from 397 separate locations. The approach was necessary to provide comprehensive coverage of the altitudinal gradient and sufficient sample sizes to allow for randomized sub-sampling of a large data set. If temporal variability in survey data is substantially lower within locations than among locations at equivalent altitude, our estimates of minimal detectable range shift may be unduly large. A comparison of repeat surveys both within and among locations would therefore be valuable in quantifying variability in survey data as a function of location and would allow us to properly ascertain the relative merit of resurveying the same location between consecutive time periods.
The capacity of a monitoring program to detect change in species’ distributions in response to contemporary warming is dependent not only on the sensitivity of the analysis but also the rate and magnitude of the range shift response. Although we may predict that, as a consequence of probable warming between 1990 and 2030 (Walsh et al. 2002), species will eventually be displaced 60 to 400 m along the altitudinal gradient, it is not yet known how quickly species will be able to track change in their preferred climatic environment. Konvicka et al. (2003) reported a maximum altitudinal range shift of 148 m for Czech butterflies between 1951-1980 and 1995-2001 but the magnitude of change varied widely between species and altitudinal position even decreased in some cases. While Konvicka et al. (2003) found no consistent habitat affiliations that differentiated displaced from stable species, elsewhere rapid responses have predominately been observed in highly mobile generalist species (Warren et al. 2001; Hill et al. 2002). For the purpose of our analysis, estimates of minimum detectable range shift are dependent on change averaged across multiple species from a range of ecological guilds. Conceivably, therefore, a time lag between shifting climate and distribution in some species will reduce the capacity of the analysis to immediately detect coherent-fauna wide range shifts in response to future warming. Similarly, predicted extinctions related to climate change (Williams et al. 2003; Hilbert et al. 2004) or declines in the population size of species are likely to reduce the number of species available for analysis and consequently the statistical power of future tests.

6.4.3 Implications

Despite accumulating evidence, field biologists have encountered difficulty in convincing other disciplines, policy-makers and the general public that important biological impacts of climate change are already apparent (Parmesan & Yohe 2003). Part of the difficulty is that biologists seek evidence of small systematic trends that may become important in the longer term (Parmesan & Yohe 2003). ‘Noise’ in biological data is inherently problematic for confidently establishing differences where the effect size is small. More recently, in an attempt to establish strong evidence for a coherent ‘fingerprint’ of climate change impacts, some researches have moved away from single case examples and pursued meta-analyses synthesizing correlative evidence from numerous studies (Parmesan & Yohe 2003; Root et al. 2003).

We believe that direct evidence from single study examples of climate related range shifts across altitudinal gradients could be greatly improved if two key analytical
tools were adopted. First, sub-sampling should be used to equalise sampling effort between contemporary and historical data sets when assessing change at range boundaries. It is crucial that ‘real’ change is not clouded by artificial trends arising from comparisons between data sets with different underlying properties. Second, the statistical power of range shift analyses to detect change needs to be ascertained and appropriate steps taken to ensure that researchers are collecting the appropriate data and expending enough sampling effort to detect range shifts of the desired magnitude.

Here we provide a methodological framework, using randomisations, for quantifying the detection limit of range shift analyses and demonstrate high potential for detecting even small amounts of change in the future. We encourage others to report detection limits in published analyses so that we may work toward establishing more general guidelines for baseline monitoring programs that may be applicable for different taxa or in other regions.
Table 6.1. Mean altitude of presence records (Alt) and number of recorded presences (p) for 34 rainforest birds derived from a paired random sub-sample (Simulated Time 1 and 2, 96 surveys or 6 surveys per 100 m altitude) of the complete data set. A sample estimate of minimum detectable range shift (δ) calculated from differences in the measured altitudinal position of species (d) is provided. Taxonomy and common names follow Christidis and Boles (1994).

<table>
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<th>Species</th>
<th>Simulated Time 1</th>
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<th>Alt1</th>
<th>p2</th>
<th>Alt2</th>
<th>d</th>
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</table>

Number of species (n) = 34, \( v = n-1 = 33 \), \( \alpha(2) \) level of 0.05 and \( \beta(1) \) of 0.1

**Minimum detectable range shift across species assemblage** (\( \delta = 19.6 \) m)

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* Regionally endemic species, †Species included in lower range boundary analysis, ‡Species included in upper range boundary analysis
Fig. 6.1. Effect of measure choice on the minimum detectable range shift across a species assemblage. Range shifts measured at the mean altitude of presence records (closed circles, solid line) were compared with range shifts measured at (a) upper range boundaries (open circles, broken line) and (b) lower range boundaries (open triangles, dotted line) using subsets of species common to both measures. Estimates of minimum detectable range shift were derived from ten paired random sub-samples of the complete data set. Sampling effort was adjusted simultaneously for both simulated Time 1 ($T_1$) and simulated Time 2 ($T_2$) and varied between 16 and 96 surveys along the altitudinal gradient. Lines connect mean estimates of minimum detectable range shift at intervals of sampling effort. Note that the scale of minimum detectable range shift on the $y$-axis varies between figures.
Fig. 6.2. Relationship between sampling effort and minimum detectable range shift measured at the mean altitude of presence records across an assemblage of 34 species of rainforest birds.
Fig. 6.3. Effect of measure choice on the mean estimated range shift across a species assemblage when sampling effort is uneven between time periods. Range shifts measured at the mean altitude of presence records (closed circles, solid line) were compared with range shifts measured at (a) upper range boundaries (open circles, broken line) and (b) lower range boundaries (open triangles, dotted line) using subsets of species common to both measures. Estimates of minimum detectable range shift were derived from ten paired random sub-samples of the complete data set. Sampling effort in simulated Time 2 (T₂) was held constant at 96 surveys and sampling effort in simulated Time 1 (T₁) was varied between 16 and 96 surveys along the altitudinal gradient. Lines connect mean estimates of range shift at intervals of sampling effort.
General conclusion

Contribution to knowledge
The National Biodiversity and Climate Change Action Plan (Natural Resource Management Ministerial Council 2004) identifies national priorities for research and monitoring to reduce the impact of climate change on Australian biodiversity. Here the main findings of the thesis are summarized in the context of relevant actions proposed therein.

Identify limitations in the current modelling of climate change impacts on biodiversity (Action 1.2.4); and, improve capacity of models to predict climate change impacts on biodiversity, including regional shifts, at scales relevant to natural resource management programs, reserve design and management programs, and species management and recovery programs (Action 1.2.1)
To date, attempts to predict climate change impacts and estimate extinction risk have been predominately based on modelled change in distribution area (eg. Bakkeness et al. 2002; Erasmus et al. 2002; Thuiller 2003; Williams et al. 2003; Hilbert et al. 2004; Thomas et al. 2004a). Spatial variation in the abundance of species within current and future distributions have been poorly explored and explicit estimates of change in population size are lacking. The combined approach of Chapters 4 and 5 demonstrate that spatial variation in the abundance of species can be incorporated into current models of climate change impacts and used to predict extinction risk resulting directly from change in population size. This advance has been achieved by combining (1) predicted range shifts of species along altitudinal gradients (Chapter 1) with (2) high resolution data on abundance-patterns of species along altitudinal gradients (Chapters 2 & 3) and (3) explicit estimates of the spatial availability of specific temperature conditions under current and future climates (Chapters 4 & 5). In the case of the Wet Tropics, altitudinal gradients most effectively capture spatial turnover in temperature conditions and repeat measurements of local abundance across altitudinal gradients are expected to allow early detection and robust estimates of population size change at a regional scale.
Identify information requirements and priorities for long-term monitoring of climate change impacts on biodiversity (Action 1.3.1)

Chapter 6 used randomisations of standardized transect surveys to assess the effectiveness of three measures for quantifying altitudinal range shifts predicted to occur as a consequence of future climate warming. Smaller range shifts were detectable across an assemblage of rainforest birds by analysing change in the mean altitude of presence records of individual species rather than upper or lower range boundaries. Minimum detectable range shift across a species assemblage declined with increasing sampling effort. The maximum examined sampling effort of 96 surveys was sufficient to confidently detect a mean altitudinal range shift as small as 40 m across an assemblage of 34 rainforest birds when change in the mean altitude of presence records was measured.

Annual mean temperature for Queensland is projected to increase by 0.3 to 2.0 ºC by the year 2030 relative to 1990 (Walsh et al. 2002). Isotherms under warmer predicted climates for 2030 are likely to be 60 to 400 m higher than in 1990, calibrating to a 15 to 100 m altitudinal shift per decade. A repeat of 96 surveys in the future, then, is expected to allow detection of predicted range shifts in response to mid-range or greater warming projected within 10 years and minimum-range or greater warming projected within 20-25 years. Unfortunately, currently low sample sizes at altitudes above 1300 m prevented an assessment of detection limits following larger amounts of sampling effort. However, an extrapolation of the trend in declining minimum detectable range shift with increasing sampling effort suggests that there is further potential to lower the detection limit by sampling in excess of 96 surveys.

Implement high priority monitoring programs (Action 1.3.3)

Chapters 2 and 3 summarized extensive standardized abundance surveys for rainforest birds and microhylid frogs undertaken across altitudinal gradients within the Wet Tropics rainforests of north-eastern Australia. The resulting data provides conservation managers with important baseline information on altitudinal position and altitudinal-abundance patterns of individual species, that can be used to detect future altitudinal range shifts (Chapter 6), quantify change in population size (Chapter 4) and estimate extinction risk (Chapter 4).
**Future directions**

Modeled projections of population size (Chapters 4) suggest that even small amounts of climate warming are likely to substantially increase extinction risk of rainforest species within the Wet Tropics region. While population size models provide a clear indication of the magnitude of potential impacts some important uncertainties remain. The priority now is to begin in earnest to collect the appropriate data to detect climate warming induced change in species’ abundance and distribution and to evaluate the predictive capacity and underlying assumptions of models. Some future priorities for research and data collection include:

*Immediate-term priorities:*

- Additional targeted surveys of rainforest birds above 1300 m altitude to allow expanded analyses of minimum detectable range shift to determine if, and to what extent, the detection limit of the current data set could be improved by further increasing sampling effort beyond 96 surveys.
- Application of power analysis and randomisation techniques (Chapter 6) to data collated for microhylid frogs to evaluate the adequacy of current baseline data for a second taxa and advise on future sampling effort required to confidently detect altitudinal range shifts in response to future climate warming.
- Replication of altitudinal surveys of rainforest birds within rainforest isolates to the north and south of the Wet Tropics to provide an independent test of the limiting effect of temperature on the distribution and abundance of at least some widespread species (eg. FNEQ - McIlwraith Range, Iron Range; MEQ – Clarke Range; SEQ – Conondale Range; SEQ/NENSW – Border Ranges).
- Replication of altitudinal surveys of rainforest birds in both summer and winter months to quantify seasonal altitudinal movements of species within the region.

*Long-term priorities:*

- Replication of altitudinal surveys of rainforest birds (at least 96 surveys or six surveys per 100 m altitude) and microhylid frogs (sampling effort yet to be determined) within the region at 10 year intervals to quantify shifts in distribution and change in population size of species in response to future climate warming.
References


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**Appendix A:** Mean estimates of abundance (including zero counts) for 76 rainforest birds across the altitudinal gradient. Taxonomy and common names follow Christidis and Boles (1994). Species endemic to the region are denoted by an asterisk.

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<thead>
<tr>
<th>Species</th>
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### Species

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### PSITTACIFORMES

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### CUCULIFORMES

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### CORACIIFORMES

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