# Climate change and birds: perspectives and prospects from southern Africa Ostrich

Article · October 2004

6 authors, including:

Some of the authors of this publication are also working on these related projects:

Project   Papuan Harrier conservation View project

Project   African raptor ecology View project

# Climate change and birds: perspectives and prospects from southern Africa

**Robert E Simmons[1]\*, Phoebe Barnard[2], WRJ Dean[1], Guy F Midgley[3], Wilfried Thuiller[3] and Greg Hughes[3]**

[1] DST Centre of Excellence in Birds as Keys to Biodiversity Conservation at the Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7701, Cape Town, South Africa

[2] Global Invasive Species Programme, South African National Biodiversity Institute, Private Bag X7, Claremont 7735, Cape Town, South Africa

[3] Climate Change Research Group, Ecology and Conservation, Kirstenbosch Research Centre, South African National Biodiversity Institute, Private Bag X7, Claremont 7735, Cape Town, South Africa and Centre for Applied Biodiversity Science, Conservation International, 1919 M St, Washington, DC, United States of America

\* Corresponding author, e-mail: harrier@botzoo.uct.ac.za

Global climate warming, now conclusively linked to anthropogenically-increased $CO_2$ levels in the earth's atmosphere, has already had impacts on the earth's biodiversity and is predicted to threaten more than 1 million species with extinction by 2050. Climate change in southern Africa is expected to involve higher temperatures and lower rainfall, with less predictability and a greater frequency of severe storms, fires and El Niño events. The predicted changes to birds in Africa — the continent most at risk from climate change — have hardly been explored, yet birds and many other vertebrates face uncertain futures. Here, in one of the first focused analyses of the correlates of climate change vulnerability in southern African birds, we offer a wide-ranging perspective on which species may be most at risk, and explore which traits may influence the adaptability or extinction risk of bird species.

Our review suggests that small nomadic species with short generation times may be least at risk. While larger-bodied species may be physiologically buffered against environmental change, their longer generation times may make them less able to adapt evolutionarily to climate change. Migrant species, and those with specialised feeding niches such as pollinators, are also predicted to be at risk of population declines, based on low ability to adapt to new environments when introduced there as aliens. Species with small ranges (<50 000km$^2$) restricted to the two southern African biodiversity hotspots most at risk from climate change — the Cape Floral Kingdom and the Succulent Karoo — are ranked according to low, medium or high risk of extinction. Those restricted to mountain slopes, mountain tops or islands, and those occurring mainly at the southern or western extremes of these biomes, are ranked as highest risk. These include endemic sunbirds, warblers and rock-jumpers — none of which are currently recognised Red Data species. Using climate envelopes we modelled the possible range shifts by 2050 of three pairs of species found in habitats considered to be at risk: fynbos, mountain and arid Karoo. All six species lost substantial portions of their range ($\bar{x}$ = 40%), with the montane Drakensberg Rock-jumper *Chaetops aurantius* losing most (69%). Significant reductions of available climate space in all species may interact with life history characteristics to threaten many southern African bird species unable to shift geographic range or adapt to novel resource conditions. We conclude with a list of research priorities and testable hypotheses which may advance our understanding of the complex influence that climate change is likely to have on African, particularly southern African, birds.

## Introduction

Global climate change has been recently recognised as one of humankind's most profound and far-reaching threats to biodiversity (Thomas *et al.* 2004). The earth's atmosphere is expected to become warmer in the next few decades than at any time in the last 40 million years (Overpeck *et al.* 2003). A 0.6°C increase in mean temperature has been recorded over the last century as a result of increasing concentrations of greenhouse gases such as carbon dioxide ($CO_2$) trapping solar energy within the earth's atmosphere (IPCC 2001). While the earth has warmed and cooled significantly at least 20 times in the last 500 000 years, the current warming spell is faster than ever recorded before, and is now conclusively linked to increasing concentrations of $CO_2$ in the atmosphere, mainly from human activity (Houghton *et al.* 2001). Atmospheric $CO_2$ levels are now 30% higher than in the past

420 000 years (Petit *et al.* 1999), and are on track to reach levels by 2100 not seen on the planet in several tens of millions of years. Given that previous climatic change has led to widescale shifts in paleo-species distributions, leading to many extinctions (e.g. Barnosky 1986, Woodward 1987), extant species are also expected to move rapidly in response to moving climatic envelopes. The resultant shifts in species distributions and the likelihood of extinctions as biomes move poleward has given rise to much modelling and a few empirical studies (IPCC 2001, Midgley *et al.* 2001, Thomas *et al.* 2004). But to what extent highly mobile birds or sessile plants can adapt or successfully move in response to changing climates in Africa is poorly known. This information is important for current and future conservation planning.

This paper outlines a framework for the analysis and prediction of climate change impacts on birds in Africa, with a particular focus on southern Africa. Its aims are four-fold:
- to briefly review and summarise information relevant to climate change impacts on African birds, especially those species at high risk of extinction in the next 50 years;
- to provisionally identify demographic and life history variables likely to correlate with vulnerability to climate change;
- to identify sets of species in Africa and individual species in southern Africa most at risk of extinction under climate change scenarios, illustrated with a limited set of examples modelled using bioclimatic niche characteristics derived from SABAP distribution data;
- to generate an initial set of explicit hypotheses for future testing.

Remarkably little research is currently underway on the impacts of climate change on Africa's rich biodiversity, with a few exceptions (see Midgley *et al.* 2001, 2003 for plant diversity, Erasmus *et al.* 2002 for vertebrate diversity in South Africa and Wichmann *et al.* 2003 for a single raptor species). This is despite the rising tide of reports predicting (Thomas *et al.* 2004) or measuring (Pounds *et al.* 1999, Parmesan and Yohe 2003, Root *et al.* 2003) grim effects on the earth's biodiversity. Due to the lack of empirical data from Africa, our perspectives are drawn from similar studies in other parts of the world, and this paper is designed as a prospective basis for future research and testing.

## Africa's vulnerability to climate change

Several important reviews have been undertaken of the potential effects of global warming on biodiversity, and these identify Africa as the most vulnerable of all continents (Hulme 1996, IPCC 2001). This is partly because of Africa's great aridity — in particular the large proportion of its land mass outside the tropics occupied by arid and semi-arid lands — and partly due to its low financial, technical and institutional capacity to mitigate the impacts of such change (IPCC 2001). Understanding the likely effects of climate change on human-altered and natural ecosystems and measuring the speed of change and responses to change are vital for African countries to manage their development efficiently and proactively. In the context of biodiversity conservation, effective bio-regional planning will require a much better understanding than we currently have of how (and whether) species will respond to the intense pressures on them by moving across landscapes (e.g. Cowling *et al.* 2003).

Climate change is only one of an array of environmental pressures facing Africa. Increasing impacts on African ecosystems also arise from other basic drivers of environmental change, which present fundamental challenges to human development. These drivers include rapid human population growth and urbanisation, HIV/AIDS, malaria and other diseases (Rogers and Randolf 2000), low literacy, poverty and political instability in some regions. Collectively, they drive a number of cumulative and related pressures on biodiversity, such as land cover change, desertification, alien species invasion, unsustainable resource use, soil erosion and pollution (Millennium Ecosystem Assessment 2003).

## Global climate change effects and hotspots of African biodiversity

To understand potential effects of climate change on African birds, we must understand the predicted effects on climate of rising $CO_2$ levels. In their extensive review of climate change effects across the globe the Inter-governmental Panel on Climate Change (IPCC) predicted that in Africa global warming will have five major effects (IPCC 2001):
- increased mean seasonal temperatures;
- decreased rainfall in most areas;
- increased frequency of El Niño Southern Oscillation (ENSO) effects in southern Africa;
- increased frequency of severe weather anomalies;
- increased frequency of fires, as a result of increased temperatures and decreased rainfall.

Several studies have employed climatic variables ('envelopes'), especially temperature and rainfall, to predict the existing and future distribution limits of species (e.g. Midgley *et al.* 2001, 2003, Githaiga-Mwicigi *et al.* 2002, Pearson and Dawson 2003). These can be used to predict likely shifts for any individual species for which current distributions can be adequately described. However, these techniques provide a first-cut assessment only, because they are correlative and not causative, and because the change in potential range projected by these models interacts with life history characteristics which may amplify species' sensitivity to shifts in geographic range.

Increasing temperatures and sharply decreasing rainfall are expected to move the winter-rainfall dominated Succulent Karoo Biome southwards by about 2050, and diminish its size, putting severe selective pressures on plant species in this biome (Midgley *et al.* 2001). The Succulent Karoo is the world's only arid-zone biodiversity hotspot (Myers *et al.* 2000), and extends from central-western South Africa to south-western Namibia. It is dominated by dwarf succulents highly adapted to a winter rainfall regime. The Fynbos Biome, part of the most densely speciose floral kingdom in the world (Cowling and Richardson 1995, Cowling *et al.* 1998) is similarly expected to shift southwards, diminishing habitats especially on its western and northern boundaries (Midgley *et al.* 2003). Climate shifts are predicted to 'push' certain habitats and biomes, such as the temperate Fynbos Biome, off the southern end of the continent and threaten high-altitude communities. This is predicted in other landscapes too (e.g. Peterson *et al.* 2002).

Such boundary shifts in other ecosystems have already contributed to the extinction of one Cloud Forest toad by reducing cloud persistence (Pounds *et al.* 1999), impacted on montane plant species (Grabbherr *et al.* 1994) and shifted the ranges of 15 temperate butterfly species poleward (Parmesan *et al.* 1999). Collectively, such shifts are predicted to exacerbate the extinction risk of a further 15–37% of species, based on a sample of 20% of the earth's surface including Africa (Thomas *et al.* 2004). The prediction of Thomas *et al.* (2004) that this will likely cause the extinction of over 1 million species has received considerable media coverage, but also some criticism of the assumptions used. Briefly, these criticisms emphasise that not all organisms

forced out of their present range will automatically become extinct (Pearson and Dawson 2003, Ferguson 2004). Some organisms may (and currently do) survive under the new range of conditions.

Africa and its islands feature some of the most biodiverse regions anywhere in the world, many of which are already profoundly threatened by land-clearing and degradation through fragmentation, biotic invasions, desertification, urbanisation and overexploitation (Myers *et al.* 2000, Fishpool and Evans 2002, Balmford *et al.* 2003). In their global assessment of the world biodiversity hotspots — areas with high endemism under serious threat — Myers *et al.* (2000) identified 25 hotspots, of which five are in Africa and two in southern Africa. These are:

- Eastern Arc and coastal forests of Tanzania/Kenya (121 endemic vertebrates, representing 0.4% of global vertebrates);
- West African forests (270 endemic vertebrates, representing 1.0% of global vertebrates);
- Cape Floristic Province (Region) (53 endemic vertebrates, representing 0.2% of global vertebrates);
- Succulent Karoo (45 endemic vertebrates, 0.2% of global vertebrates);
- Madagascar (771 endemic vertebrates, 2.8% of global vertebrates).

Many of these hotspots are so designated because of high plant diversity and endemism (e.g. 69% of 8 200 species in the Cape Floristic Region are endemic). The Eastern Arc mountains have 1 500 endemic plants in a mere 2 000km².

Bird endemism in most biodiversity hotspots is much lower than that of plants. This could reflect a greater overall adaptability of birds to paleoclimatic change, or selection for generalism and adaptive mobility (e.g. nomadism) in dynamic ecosystems. For example, less mobile taxa in Namibia show much higher rates of endemism (plants 17%, insects 24%, arachnids 12%, frogs 12% and reptiles 24%) than do fish (3%), mammals (7%) or birds (2%) (Simmons *et al.* 1998). This may reflect greater palaeo-climatic stability in the Namib-Angolan escarpment than on the surrounding plains (Barnard *et al.* 1994, 1998, Simmons *et al.* 1998). As found by Erasmus *et al.* (2002), this may mean that birds are likely to have a lower extinction risk than species with limited mobility.

All five African biodiversity hotspots have endemic birds: Madagascar — 199 endemics of 359 total birds; Eastern Arc mountains — 22 endemics of 585 birds; West African forests — 90 endemics of 514 birds; Cape Floristic Region — six endemics of 288 birds; Succulent Karoo — 1 endemic of 269 birds (Stattersfield *et al.* 1998, Myers *et al.* 2000). In areas such as Madagascar with high human population densities, where more than 90% of the country's primary vegetation has been lost (Myers *et al.* 2000), climate change is likely to be devastating as species confined to habitat fragments are forced southwards into agricultural deserts. This is one reason why ecologists interested in the effects of climate change have focused on biodiversity hotspots. However, other areas with large numbers of restricted-range species, for example Africa's Important Bird Areas (Fishpool and Evans 2001), are also under serious threat from climate change. The arid Nama and Succulent Karoo biomes, for example, hold 76% of southern Africa's endemic birds (Siegfried 1992). The bioclimatic envelope for this region is expected to suffer a major range reduction and move southeastwards under mid-range climate change scenarios (Midgley *et al.* 2001).

**Climate change and birds: options available**

As mobile organisms, birds should respond to climate change more rapidly than sessile plants or terrestrial animals which require contiguous habitat corridors for dispersal. Plants rely on dispersal of propagules and a potentially lengthy period of population establishment to migrate in response to environmental change, while terrestrial vertebrates and many invertebrates rely on habitat cover and resources in corridors for physical movement across landscapes; they should be considerably more limited in their responses to climate change than are most birds. This assumes that suitable habitat remains in areas outside present species limits. Where landscapes have been profoundly transformed by agriculture, urbanisation, biotic invasions or fragmentation, adaptive responses by species to climate change are less likely to occur (Midgley *et al.* 2001, 2003). Land transformation and development will severely constrain the adaptive capacity of many species, even birds, to move, particularly in the intensively-farmed and densely-populated countries of southern, eastern and western Africa.

Apart from the stark threat of extinction, climate change will influence many aspects of the ecology of species as they attempt to adapt or move with the changing climate. The unanswered and difficult question is how many species in Africa are likely to face extinction as a result of the speed of habitat change. In other words, is it possible that some species will exhibit rapid adaptation to a new climate? Recent reviews of the speed of genetic and morphological change in the face of intense (typically anthropogenic) environmental change suggests that some organisms do react much faster than anticipated and show evolutionary change within a few generations (Stockwell *et al.* 2003). Some examples of rapid evolutionary change in the face of selection pressures include: (i) morphological and fat storage responses by Mosquito Fish *Gambusia affinis* to changes in their thermal environment; (ii) development, growth and reproductive timing changes by Pacific Salmon *Oncorhynchus* sp. to temperature; (iii) Pitcher Plant Mosquitos' (*Wyeomyia smithii*) photoperiod responses to global warming; among birds, (iv) Darwin's Finch *Geospiza fortis* body size and bill size changes in response to climatic changes and seed size abundance (Grant and Grant 2002, review in Stockwell *et al.* 2003). This gives conservationists some hope that the pace of climate change will be slow enough to enable some species to adapt to changes in temperature (cf. 'Migration' below).

Most of the species for which rapid evolutionary change has been shown have short generation times (Stockwell *et al.* 2003). This may be an artifact of the ability to study such species in the lab or wild over short time periods. However, it may also be reasonable to assume that such species can respond rapidly *because* of shorter generation times. If this

is the case, then larger, slower-breeding species may be less likely to respond rapidly enough to climatic change (Table 1).

Conservation scientists should also be aware that selection should be strongest, and potential adaptation most rapid, soon after major climate change (Stockwell *et al.* 2003). Hence species may adapt quickly to new conditions, or perish quickly. This should be measurable in the field for short-generation birds under strong selection.

## Demographic and life history variables influencing birds' vulnerability to climate change

What factors might determine the vulnerability of African birds to climate change? Evolutionary specialisation tends to foreclose options in times of strong directional selection (Endler 1986, Schluter 2000). Using the ecological comparison of alien birds introduced into new environments, the degree of specialisation of a species in its native habitat is not a strong predictor of its invasiveness (Veltman *et al.* 1996, Williamson 1996, Duncan 1997). However, generalist, granivorous or omnivorous species tend to be more successful invaders, especially those commensal with humankind, in at least one African country (Dean 2000a). However, other more specialised species have also been successful, making it difficult to predict vulnerability to climate change or extinction risk based on one trait. In a unique data set on introduced alien birds in New Zealand, Veltman *et al.* (1996) found that successful invasive species were those with a higher birth-to-mortality ratio. A similar conclusion was reached by Dean (2000a) for southern Africa's alien birds. Both findings are compatible with the result (Stockwell *et al*. 2003) that species with short generation times can evolve most rapidly.

Most of the traits likely to increase birds' vulnerability to climate change reflect some sort of specialisation, although they may not always be obvious (Table 1). Here we explore some of them in greater detail, and then test some predictions.

## Body size

What differences in vulnerability to climate change might we expect between large-bodied and small-bodied species, over and above the effects of generation time? Large species may be better able to withstand 'lean' periods than small birds, given their slower metabolic rates and ability to hold larger body fat reserves (Schmidt-Nielsen 1983). Smaller species are less likely to survive, as a result of their higher metabolic rates and reduced ability to sustain substantial fat reserves.

## Nomadism and residency

Many nomadic species which are found in the arid Nama Karoo and Succulent Karoo biomes are expected to be heavily impacted by climate change (Midgley *et al.* 2001), and they are especially common where variation in rainfall is highest (Dean 2004). If rainfall variability increases under climatic change (IPCC 2001, Midgley *et al.* 2001), then nomadic birds may not only move more frequently, or further, but may be 'pre-adapted' to the change. Nomadism is an adaptation allowing animals to move away from poor environmental conditions and seek out more productive patches of habitat with particular characteristics (Dean 2004). As arid conditions push southward and eastward, nomadic birds would probably adjust their nomadic patterns to keep moving away from unsuitable habitats, and thus have a higher chance of survival in the face of unpredictable conditions. Such species in southern Africa include the bustards, sandgrouse, sparrowlarks and Lark-like Buntings *Emberiza impetuani*.

However, those species that are resident even in the face of arid conditions (Dean 2004) are adapted to environ-

**Table 1:** Demographic and life-history traits likely to increase birds' vulnerability to climate change (examples in parentheses)

---

**Demographic/ecological traits**
- Restricted range (Knysna Warbler)
- Limited to islands (Cape Gannets)
- Limited to mountain tops (Mountain Pipit)
- Specific niche requirements, i.e. dietary specialist (Palm-nut Vulture, sugarbirds), limited roosting or breeding sites, i.e. salt pans
- Reliance on vulnerable habitats e.g. ephemeral wetlands (Chestnut-banded Plover)
- Obligate co-evolutionary relationship with other (non-food) species (oxpeckers, host-specific brood parasites)
- Limited dispersal tendencies (Blue Cranes)
- Sedentary and territorial (eagles)
- High population saturation, leading to limited places for dispersing sub-adults (most long-lived birds)
- Existing conservation threat(s) (African Penguin)

**Life history/behavioural traits**
- Slow reproductive rates (long-lived species)
- Small clutch size (large, long-lived species)
- Extended parental care (long-lived species)
- Sensitivity to human disturbance/settlement (raptors, wetland birds)
- Morphological and behavioural traits affecting heat stress e.g. dark plumage, exposed nest site, feathered tarsi, reliance on limited nest holes
- Sensitivity to storms and floods (small passerines with open cup nests, flamingos on salt pans)
- Tendency to stay in parents' territory (co-operative breeders)
- Migrants (Palearctic travelling long distances)

---

ments with generally low production, and can survive both stochastic events that suddenly increase production and/or prolonged droughts with very little primary production. They are also behaviourally adapted to deal with high temperatures (Dean 2000b). Their survival would also depend, to some extent, on the effects of climate change on other bird species in the community. Differential survival by species in communities brings in new sets of ecological assembly rules (Cody 1999), so for some species there may be increased competition in the new species assemblages, whereas for other species there may be competitive release. What is probably predictable here is not which species will survive, but that there will be changes in bird community species' composition with climate change. So while we cannot conclude whether arid-zone nomads or residents will best cope, some are predicted to disappear, given that in arid areas across the globe, species richness is significantly positively correlated with high rainfall (Dean 2004) and absolute mean rainfall is likely to decrease in these areas in Africa (IPCC 2001).

Can we link the issues of body-size and nomadism? We suggest that larger-bodied, highly nomadic species are likely to best deal with new conditions, as they are able to shift range and are buffered against poor conditions elsewhere. Small-bodied species can shift range, but do not have the physiological buffer. Small-bodied resident species may be more likely to adapt evolutionarily because of their shorter generation times (multiple broods while conditions are favourable), while large-bodied species are physiologically buffered, but are less likely to show an evolutionary response. Either way, larger-bodied species may be better able to deal with climate shifts in the short-term but not in the long-term.

### Migration

Truly migrant species living in climate-impacted regions may be adversely affected for two reasons. First, in their analysis of successful alien bird introductions to New Zealand, Veltman *et al.* (1996) noted that species that were migratory in their country of origin were significantly less likely to be successful than non-migratory species. This may arise because migration direction is genetically controlled (Berthold 2003) and birds displaced to a new locality in their breeding areas may migrate to an inhospitable non-breeding area. Some attention should thus be given to intra-African migrants pushed eastwards by climatic factors. Indeed recent evidence suggests micro-evolutionary shifts towards sedentariness in response to climatic warming for passerine species that usually migrate to Africa (Coppack *et al.* 2003). Second, if a species' migratory timing is under the control of photoperiod while the emergence of their main food is under the control of spring temperatures, the two may become decoupled. Breeding migrants may find themselves in a situation where their typical arrival month is too late for their food, which has already emerged as a result of warmer spring temperatures (Both and Visser 2001). This scenario was painted for temperate-breeding species but it has recently been shown that decoupling is unlikely because migrants respond by shortening their migratory distances

away from breeding grounds (Coppack *et al.* 2003) and advance their spring migration behaviour and testicular activity in order to arrive earlier on breeding grounds (Berthold 2001). In Africa, where breeding and temperature are less inter-dependent than breeding and rainfall (e.g. Lloyd *et al.* 2001), such decoupling is also less likely. However, the flush of seeds, insects and small mammals that Palearctic migrants depend on in southern Africa is triggered by rainfall (e.g. Lloyd *et al.* 2001, Dean 2004) and this may be less predictable given the likelihood of reduced and less dependable rainfall (IPCC 2001).

### Food specialisation

Food-specialised birds and other organisms may be vulnerable for two reasons. Cape Sugarbird *Promerops cafer* and Gurney's Sugarbird *Promerops gurneyi* are highly reliant on the flowering of plants in the Proteaceae for food resources (including invertebrates associated with the flowers) during breeding, and leave their territories only during the dry season when flowers are absent (Rebelo *et al.* 1984, De Swardt 1997, Fraser 1997, Calf *et al.* 2003). Thus their entire life history is adapted to the Proteaceae, a family which is predicted to face range contractions (17 of 28 species) or, for five species, extinction as climate conditions shift them completely out of their present range (Midgley *et al.* 2003). Climate change could therefore accelerate the extinction of one or both sugarbird species. Frequency of fire, which is likely to increase as soil moisture drops and temperatures increase (IPCC 2001), is also predicted to markedly reduce plant biomass (Bond *et al.* 2003), and will probably adversely influence slow-growing and maturing plants. Slow-maturing proteas therefore are especially vulnerable to climate change (J Midgley pers. comm.).

Sugarbirds are thought to be important pollinators of proteoids (Rebelo *et al.* 1984, Collins and Rebelo 1987). If the birds' own physiological temperature tolerances force them away from that of dependent proteoid flowers, the proteoid-sugarbird link may be broken. Thus not only might sugarbird populations be detrimentally influenced, but rare or specialised proteoid species may also show reduced seed set and reduced population size, over and above any direct climatic-induced shifts they may suffer. The likelihood of extinction depends on the strength of the pollinator-plant mutualism. While many plants can self-fertilise or re-sprout, fire-dependent fynbos species including the Proteaceae are at risk because few sprout after fire and the seeds are few and large (Le Maitre and Midgley 1992, Bond 1994). Indeed, almost 50% of 300 species in the Cape Floristic Region are expected to go extinct if mutualisms collapse (Bond 1994). For those that survive through re-sprouting, genetic out-crossing through pollination may decrease and thus long-term genetic viability will probably decrease (J Midgley pers. comm.). This is just one example of many that may involve intimate links between mutualists with complex climate change effects in space and time (Bond 1994).

## Other avian examples from Africa

While there is increasing focus on the impact of climate change on biomes and their associated plants in South Africa (Midgley *et al.* 1995, 2001, 2003, Hulme 1996, Rutherford *et al.* 1996), only two studies to date have assessed the likely influence of climatic change on African vertebrates.

Erasmus *et al.* (2002) assessed the likely response of a guild of 179 species (including 34 birds, 19 mammals and 50 reptiles) under changing climate envelopes in South Africa. They showed that 17% of species expanded their ranges, 78% displayed range contractions of between 4% and 98%, and 2% became locally extinct. These predicted extinctions (none of which were birds) were either in restricted-range species or those found predominantly in the west of South Africa, where greatest range changes are predicted (Midgley *et al.* 2001, Erasmus *et al.* 2002). The majority of range shifts were in an easterly direction, as also predicted by other models (Midgley *et al.* 2001). Few of these vertebrates were birds, as many species retained over 50% of their present range. Among threatened species, Red Data species were more likely to shift their ranges by 90% than were non-threatened species. The authors concluded that while few species were likely to become extinct as a result of predicted climatic change, fragmentation of their ranges meant that local extinctions were likely (Erasmus *et al.* 2002).

Wichmann *et al.* (2003) assessed the probable impact of climate change on an arid savanna raptor, the Tawny Eagle *Aquila rapax*, and predicted that even a slight change in the inter-annual variation in rainfall would have a marked effect on the population persistence of this species. A less than 10% change in mean annual precipitation would probably result in extinction. This is in agreement with the scenarios above, where large and mainly resident species dependent on rainfall are most at risk from changing climatic conditions.

## Other birds vulnerable to climate change: restricted-range species

How many species are likely to be threatened with extinction if restricted-range species are more likely to become extinct under climate change shifts than other species (Erasmus 2002, Table 1)? In Africa, endemic birds that occur in <44 1° grid cells number 398 species and tend to cluster in the Cameroon mountains, along the Albertine Rift, in the Kenyan and Tanzanian mountains, along the Angolan Escarpment, in the Ethiopian highlands and in the southern Cape (Fjeldså 2003). In southern Africa, 33 birds were designated by Barnes (1998) as restricted-range species with a global range of less than 50 000km². Most of these are larks or smaller passerines occurring in specialised arid or montane habitats. Those species that are both restricted in range and specialised on at least one other vulnerable topographical feature or habitat, such as mountain slopes, islands or ephemeral wetlands (IPCC 2001) are given priority as species in need of monitoring. An additional criterion would be their westerly or southerly location on the subcontinent, given that climatic envelopes are expected to move fastest in westerly areas or force biomes southward off the conti-

nent (Midgley *et al.* 2001, Midgley *et al.* 2003). If they additionally occur in the Fynbos or Succulent Karoo biomes, which are expected to suffer greatest area loss (Midgley *et al.* 2001), they are ranked higher. Some of the obvious at-risk species occurring on mountain slopes are Herero Chat *Namibornis herero*, rock-jumpers *Chaetops* spp., Orange-breasted Sunbird *Anthobapthes violacea* and Drakensberg Siskin *Crithagra symonsi*. An expanded list of 41 restricted-range species (Table 2) indicates that three Fynbos specialists (Victorin's Warbler *Cryptillas victorini*, Cape Rock-jumper *Chaetops frenatus* and Orange-breasted Sunbird) are ranked as the most susceptible to climate change in southern Africa. None are currently on the South African Red Data list (Barnes 2000). All occur on mountain tops and slopes in the southern parts of the Fynbos Biome, which puts them at particular risk of extinction. Four species are ranked just below them as high risk: Drakensberg Rock-jumper *Chaetops aurantius*, Kynsna Warbler *Bradypterus sylvaticus*, Yellow-breasted Pipit *Anthus chloris* and Mountain Pipit *A. hoeschi*. The latter three species have very restricted ranges of <50 quarter-degree squares, according to bird atlas data (Harrison *et al.* 1997). Seven other species are ranked as facing medium-high risk, three of which are Namibian near-endemics (Table 2).

It should be noted that some additional species are potentially at risk, which are not strictly range-restricted (ranges somewhat greater than 50 000km²). These are typically near-endemics, have small populations, breed in montane areas or on near-shore islands, or are resident and associated with specific soil types, such as Red Lark *Calendulauda burra*, Dune Lark *C. erythrochlamys*, Gray's Lark *Ammomanopsis grayi*, and various subspecies of Spike-heeled Lark (*Chersomanes albofasciata*) and Eastern Clapper Lark (*Mirafra fasciolata*). These latter taxa may indeed be high risk, as their distributions appear tightly linked to restricted soil type. Other species include the Bearded Vulture *Gypaetus barbatus* (Brown 1997) and Bald Ibis *Geronticus calvus* (Allan 1997), both of which breed in highlands around the Drakensberg escarpment and have specialised ecological requirements. Those limited to breeding on a few near-shore islands or mainland sites include African Penguins *Spheniscus demersus*, Cape Gannets *Morus capensis*, the Benguela cormorants *Phalacrocorax capensis* and *P. neglectus* (Crawford and Whittington 1997, Crawford 1997a, 1997b, 1997c). How they will be affected is poorly understood, but global warming is expected to increase the frequency of ENSO events (Timmerman *et al.* 1999). Increasingly frequent ENSO events are seen as conservation threats to many predators dependent on the Benguela Current, through storms, warm-water events and sulphur eruptions disrupting breeding and feeding (Du Toit *et al.* 2003, Roux 2003, Weeks *et al.* 2003).

Other regions in Africa predicted to be particularly vulnerable to climate change are those biodiversity hotspots (Myers *et al.* 2000) which are predominantly highland areas (Eastern Arc mountains, central highlands in Madagascar, Cape Fold mountains in the Fynbos Biome). Endemic species within these regions, such as the 37 Albertine Rift restricted-range species which occur on mountain tops (e.g. Regal Sunbird *Cinnyris regius* and Kungwe Apalis *Apalis*

**Table 2:** Southern African restricted-range species with global ranges of <50 000km² which also occur in vulnerable areas (mountain slopes and islands) or at southern or western edge of species range in southern Africa. Where species ranges or core habitat fall into both categories they are ranked as high-risk

| Species | Mountain slopes or islands | Southern or western regions of S Africa** | Risk to climate change |
|---|---|---|---|
| Hartlaub's Spurfowl* | Slopes | Western | Medium-high |
| Cape Parrot* | Afro montane | No | Medium |
| Violet Wood-hoopoe* | Namibian highlands | Western | Medium-high |
| Knysna Turaco | No | Southern | Medium |
| Knysna Woodpecker | No | Southern | Medium |
| Benguela Long-billed Lark* | No | West Succulent Karoo | Medium |
| Cape Long-billed Lark | No | West Succulent Karoo | Medium |
| Short-clawed Lark | No | No | Low |
| Barlow's Lark* | No | West Succulent Karoo | Medium-high |
| Dune Lark* | No | Western | Medium |
| Red Lark | No | Western | Medium |
| Rudd's Lark* | No | No | Low |
| Botha's Lark* | No | No | Low |
| Blue Swallow* | Highlands | No | Medium |
| Bush Blackcap | Slopes | No | Medium |
| Chorister Robin-Chat | No | No | Low |
| Swynnerton's Robin* | Slopes | No | Medium |
| Cape Rock-jumper | Slopes/tops | Southern Fynbos | **Highest** |
| Drakensberg Rock-jumper | Tops | No | **High** |
| Brown Scrub-Robin | No | No | Low |
| Herero Chat* | Slopes | West | Medium-high |
| Knysna Warbler* | No | Southern Fynbos | **High** |
| Victorin's Warbler | Slopes | Southern Fynbos | **Highest** |
| Chrindra Apalis* | Slopes | No | Medium |
| Rudd's Apalis* | No | No | Low |
| Cinnamon-breasted Warbler | Hillsides | Western | Medium-high |
| Brier Warbler* | Slopes | No | Medium |
| Yellow-breasted Pipit* | High slopes | No | **High** |
| Mountain Pipit* | Tops | No | **High** |
| Gurney's Sugarbird | Slopes | No | Medium |
| Cape Sugarbird | No | Southern Fynbos | Medium |
| Orange-breasted Sunbird | Slopes | Southern Fynbos | **Highest** |
| Neergard's Sunbird* | No | No | Low |
| Pink-throated Twinspot* | No | No | Low |
| Cinderella Waxbill | No | No | Low |
| Lemon-breasted Canary | No | No | Low |
| Forest Canary | No | Southern | Low |
| Cape Siskin | Slopes | South-western | Medium-high |
| Drakensberg Siskin* | Slopes | No | Medium |
| Protea Canary | Slopes | South-western | Medium-high |

\*   recorded in fewer than 50 quarter-degree squares
\*\* southern populations are highlighted here because of the danger of them being forced out of all remaining habitat

*argentea* — Baker and Baker 2001), may be most at risk as increasing temperatures push them farther up the mountains. Restricted-range endemics that occur on islands are also at risk, as their only refuge may be on adjacent mainlands where sister species are likely to occur. African endemic bird areas, where two or more endemics overlap with ranges <50 000km² (Stattersfield *et al.* 1998) which are small islands include Cape Verde, Tristan da Cunha, Gough, Annobón, São Tomé, Principe, the Seychelles group, Aldabra, Pemba and St. Helena (Fishpool and Evans 2001). Each area and its endemics should be assessed in detail for vulnerability to climate change.

**Testing range shift responses in southern African species using bioclimatic niche modelling**

We tested some of the above predictions using bioclimatic niche modelling on six species representing contrasting habitat, body size and life history traits. This method has been extensively used to develop first assessments of species' responses to climate change (e.g. Peterson *et al.* 2002, Peterson 2003). In southern Africa, Githaiga-Mwicigi *et al.* (2002) found that climatic variables among a suite of other potential dependent variables best explain the distribution of arid-region birds. The bird species selected were chosen based on their distribution range, estimated extinction risk and particularly whether or not the species had

been well covered by contributors to the Southern African Bird Atlas Project (SABAP) (Harrison 1992, Harrison *et al.* 1997). We ultimately selected six species as follows: (i) two medium-risk species (Table 2) restricted to South Africa's fynbos habitat (Cape Sugarbird and Orange-breasted Sunbird), (ii) two high-risk species with restricted ranges in high altitude slopes or grasslands (Drakensberg Rock-jumper and Blue Swallow *Hirundo atrocaerulea*) and (iii) two non-risk species, one with a wide range in the arid Karoo Biome (Mountain Wheatear *Oenanthe monticola)* and the frugivorous winter-rainfall species the Cape Bulbul *Pycnonotus capensis*. Other high-risk, large-bodied species (Table 2) were not covered sufficiently well to model the effects of climate changes on possible shifts in distribution. Presence-absence data were provided from the SABAP database (Harrison *et al.* 1997) at a 15' x 15' (quarter-degree square) resolution for southern Africa.

Key environmental variables (annual and winter temperature, annual and winter potential evapotranspiration, annual, winter and summer precipitation) representing the current climate were constructed from the CRU CL 2.0 dataset (New *et al.* 2000) at a quarter-degree resolution. From within the BIO-MOD modelling framework (Thuiller 2003, 2004), we selected and ran Generalized Additive Models: GAM (Midgley 2003, Thuiller *et al.* 2004b) using the seven selected climatic variables to predict the distribution of each of the six bird species. This framework also allows the projection of potential future range, given an anticipated change in climate.

The predictive accuracy of each model for current range simulation was assessed using the area under the curve (AUC) of a received operating characteristic (ROC) plot of sensitivity against (1-specificity) (Swets 1988). Sensitivity is defined as the proportion of true positives correctly predicted, whereas specificity is the proportion of true negatives correctly predicted. A guide to the accuracy of the model is: 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; 0.50–0.60 = fail (Swets 1988). We transformed the probability of occurrence derived from the GAM to presence/absence using a probability threshold maximising the percentage of presence and absence correctly predicted (Pearce and Ferrier 2000).

Future projections for the 2050 time period (averages for 2040–2065) were derived using predicted climatic changes from a General Circulation Model (Hadley Centre Model, HADCM3) downloaded from the IPCC Data Distribution Centre (http://ipcc-ddc.cru.uea.ac.uk/dkrz/dkrz_index.html). The projections we used are based on the A2 greenhouse gas emissions scenario, representing a low- to mid-range emissions scenario. The A2 scenario is based on an economically heterogeneous world in which the underlying theme is self-reliance and preservation of local identities. Economic development is primarily regionally-oriented and *per capita* economic growth and technological changes are more fragmented and slower than in the other scenarios.

The GAM-derived range projections captured current distributions well, with AUC index generally much higher than 0.91. This result supports the finding of Githaiga-Mwicigi *et al.* (2002) that macroclimate exerts an appreciable direct control on species distributions. The projections for future potential range shifts indicate that bioclimatic space is strongly reduced for all species under the HadCM2 A2 scenario. The six species modelled suffer an average reduction of about 40% in current potential geographic range (Table 3, Figure 1). Even with the predicted marginal expansion into new range for one species, the Blue Swallow, the results suggest a dramatic decline in the potential persistence of all species in significant portions of their current ranges.

Surprisingly, the two nectar specialists show the lowest potential range loss (Table 3), in contrast to the significant range reductions of their major nectar source (Proteaceae) predicted by Midgley *et al.* (2003). This result may be due to the broad topographic range of habitats occupied by these species, and their predicted persistence could be explained by their reliance on a wider range of plant species for nectar. This may be an artifact of single-species modelling without additive effects of proteoid range shifts. Further modelling may reveal shifts in sugarbird ranges because they are highly reliant on proteoids, while the sunbird may show no such shifts because they feed from aloes and ericas (Rebelo *et al*. 1984).

The highest range loss (69%) was, as predicted, found in the high-altitude specialist Drakensberg Rock-jumper (Table

**Table 3:** A summary of the present and predicted future (2050) ranges of six species of southern African birds. Each range is given in units of quarter-degree squares (qds) and % decrease (lost range) or increase (expanded range). Models were generated using a Generalized Additive Modelling (GAM) approach, based on species' distributional data (SABAP) (Harrison 1992, Harrison *et al.* 1997). Climate projections for ~2050 (averages for 2040–2065) were derived from a General Circulation Model (Hadley Centre Model, HADCM3) sourced from the IPCC Data Distribution Centre (http://ipcc-ddc.cru.uea.ac.uk/dkrz/dkrz_index.html). The projections are based on the A2 greenhouse gas emissions scenario, representing a low- to mid-range greenhouse gas emissions scenario. The AUC statistic is an indication of the model's significance: 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; 0.50–0.60 = fail (Swets 1988)

| Species | AUC statistic | Present modelled range | Lost range | | Retained range | Range expansion | | Future potential range |
|---|---|---|---|---|---|---|---|---|
| | | qds | qds | % | qds | qds | % | qds |
| Orange-breasted Sunbird | 0.99 | 203 | 44 | 21.7 | 159 | 4 | 2.0 | 163 |
| Cape Sugarbird | 0.99 | 233 | 65 | 27.9 | 168 | 2 | 0.9 | 170 |
| Blue Swallow | 0.91 | 162 | 53 | 32.7 | 109 | 19 | 11.7 | 128 |
| Cape Bulbul | 0.98 | 328 | 121 | 36.9 | 207 | 2 | 0.6 | 209 |
| Drakensberg Rock-jumper | 0.99 | 161 | 111 | 68.9 | 50 | 2 | 1.2 | 52 |
| Mountain Wheatear | 0.91 | 1 174 | 601 | 51.2 | 573 | 0 | 0.0 | 573 |
| Means | | | | 39.9 | | | 2.7 | |

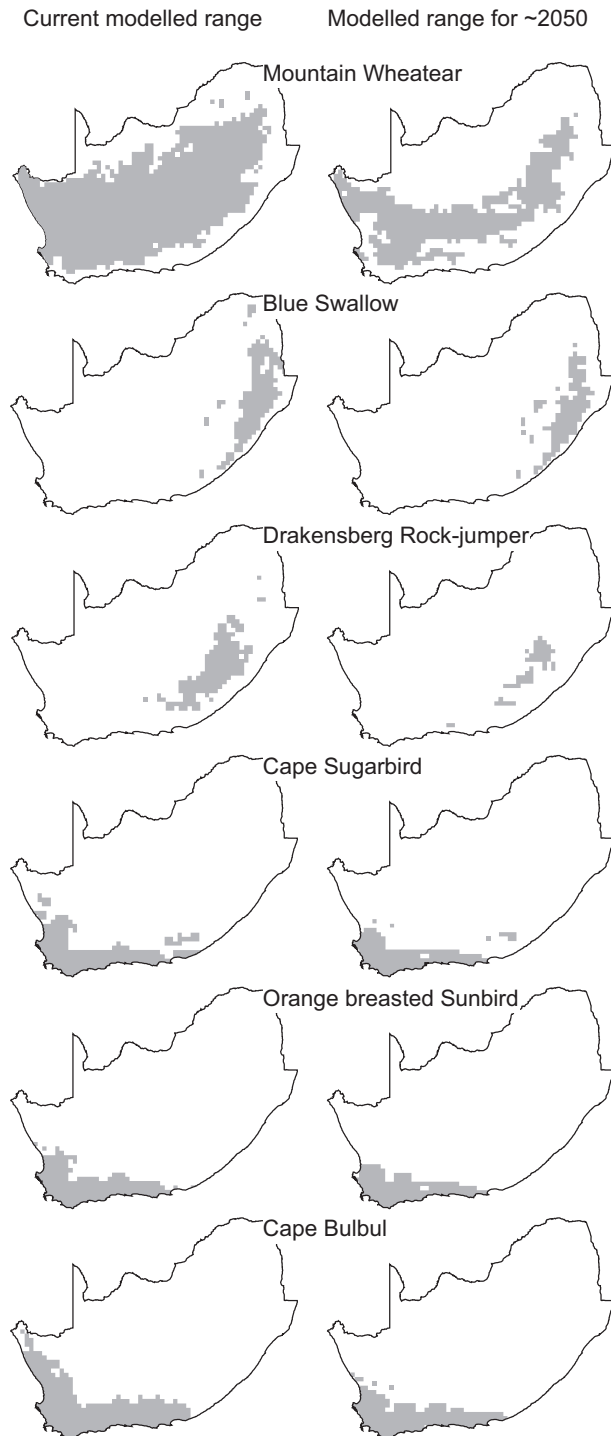Current modelled range    Modelled range for ~2050



**Figure 1:** Modelled ranges of six selected southern African bird species under current climate conditions, and in response to projected climate change. Models were generated using a Generalized Additive Modelling (GAM) approach, based on species distributional data (SABAP) (Harrison 1992, Harrison *et al.* 1997) (see Table 3 for statistics). Climate projections for ~2050 (averages for 2040–2065) were derived from a General Circulation Model (Hadley Centre Model, HADCM3) sourced from the IPCC Data Distribution Centre (http://ipcc-ddc.cru.uea.ac.uk/dkrz/dkrz_index.html). The projections are based on the A2 greenhouse gas emissions scenario, representing a low- to mid-range greenhouse gas emissions scenario

3), a result which illustrates the impact of warming in cool, high-altitude zones. The Blue Swallow is projected to shift its range closer to the east coast of southern Africa, which results in a relatively modest overall range loss. However, this also results in a potentially biologically untenable shift out of favoured high-altitude grasslands (Allan and Earle 1997) into afforested and human-impacted habitats to the east (Figure 1). This highlights the importance of combining climate change models with land-use mapping to predict future extinction risk. The wide-ranging Nama Karoo species, the Mountain Wheatear, suffered a surprisingly high loss of range (51%), largely the result of range contraction in the north-central parts of South Africa — matching earlier findings for biome contraction in the Savanna and Nama-Karoo Biomes in this region (Rutherford *et al.* 2000). This surprisingly high range contraction matches findings for plains species elsewhere (Peterson 2003). The frugivorous winter-rainfall Cape Bulbul showed a predicted range loss of 37%, generally southwards as expected. Overall these results match earlier biome level modelling carried out with an earlier version of the Hadley Center GCM (HadCM2) (Rutherford *et al.* 2000, and see http://www.cru.uea.ac.uk/ link/experiments/1b_experi_contents.html for climate projection details), and average range contractions here match modal values predicted for plains species (35%) in North America (Townsend 2003).

**Future research**

Given the potential areas where birds are most at risk, and the potential species most likely to suffer population reduction or extinction, how can we best measure changes or assess those species at risk? We propose that the montane biodiversity hotspots of southern and eastern Africa (e.g. the Fynbos and Succulent Karoo, Eastern Arc mountains and Albertine Rift) should be the most urgent priority for research, with two major themes: (1) what birds can tell us about the speed and effects of change (i.e. their possible use as early and sensitive indicators of change) and (2) what species are most at risk to population reduction, fragmentation and extinction as a result of such change. Birds at risk which additionally play a critical role in essential ecological processes (e.g. pollinators or seed dispersers) in these biomes should be a particular focus.

Specific questions that could be addressed include:
- Is the known recent distributional change of resident species (e.g. Hadeda Ibis *Bostrychia hagedash* and Black Sparrowhawk *Accipter melanoleucos*) an indication of current and recent climate change in South Africa? This could be assessed comparing historical records (from the 19th century cf. WRJ Dean unpubl. data), atlas data from the 1980s (Hockey *et al.* 1989) and present distributions (Harrison *et al.* 1997). This will allow an assessment of the speed of spread of such species, and correlations with known changes in climatic features through climatic modelling.
- Modelling of climatic envelopes (Midgley *et al.* 2001) will also allow us to understand whether temperate species now breeding in the Southern Hemisphere (e.g. White Stork *Ciconia ciconia*, European Bee-eater *Merops api-*

*aster* and Steppe Buzzard *Buteo buteo vulpinus*) are recent additions to the breeding southern African avifauna, and if their breeding coincided with appropriate local environmental conditions.

- Is the ecology of essential pollinators and dispersers of seeds within the Fynbos (sugarbirds, sunbirds, small mammals) affected by increased frequency of fire, or by reduced ability to forage or breed in an hotter, drier environment, and if so, does this threaten the long-term persistence of rarer plants?
- Are the rare, range-restricted, endemic birds identified in Table 2, or longer-lived, sedentary and slow-breeding species (e.g. raptors and seabirds — Pearson and Dawson 2003) at risk of habitat fragmentation or imminent extinction because of the speed of climate shifts?
- Are coastal seabirds that depend on the strong upwellings associated with the Benguela Current at risk?
- What are the expected changes in diversity, and what might they tell us as early indicators of perturbations within this dynamic marine system (Shannon 1985, Crawford and Dyer 1995, Du Toit *et al.* 2003)?
- Which species are most sensitive to climate change and thus potential indicators of the speed of change? For example, empirical and modelling comparisons should be made of high-altitude restricted-range species, coastal seabirds, nomadic, migrant and resident species, longlived and short-lived species. Assessments could include determining species' temperature tolerances through

physiological laboratory testing.

At each stage it will be important to separate global climate change effects on species distributions, fragmentation or population decline from more direct anthropogenic effects such as habitat degradation This is extremely difficult to do because short-term trends of less than a decade could represent short-term responses to the variable rainfall which characterises much of southern Africa (e.g. Tyson 1986, Mendelsohn *et al.* 2002) and only long-term avian datasets offer a reasonable chance of success (IPCC 2001, Root *et al.* 2003). The variables most likely to determine vulnerability to climate change in birds (IPCC 2001) are listed in Table 4. Many trends probably lie hidden in existing data sets, the most useful of which are those spanning more than 8–10 years (Table 5).

Where feasible, individuals or populations at the northern or western distributional limits (those areas predicted to change most) of their range should be assessed for behavioural change, increased mortality or breeding frequency relative to those at the centres and southern limits of their distribution. The analysis of these aspects from transects across species' ranges is a promising approach because populations in the west or north of the range should already show the demographic and behavioural characteristics expected to occur in the core of the range in several decades' time.

Particular emphasis should be focused on protected areas in vulnerable regions which have been established to

**Table 4:** Variables of potential use in detecting bird species' sensitivity to climate change and testable predictions of how they may change. Adapted from examples reviewed by IPCC (2001)

| Sensitive variable | Possible change |
| --- | --- |
| Timing of breeding | earlier in temperate climates |
| Latest nest initiation | season is shortened or fragmented |
| Presence of birds | new records in areas where not found previously (especially non-breeding); stay-overs by northern migrants in their (southern) non-breeding range |
| Egg size (volume) | in colder springs eggs may be smaller, reducing hatchability |
| Incidence of double-brooding | may be more frequent where day length longer |
| Frequency of breeding | large species less than annual breeding reduced to bi-annual breeding. Episodic breeders wait longer for optimal (rain) conditions |
| Body size | population response to warmer springs, hotter summers |
| Peak egg-laying date | shifts with earlier spring warming, away from peak food resources? |
| Number of fledged young | reduced in colder springs, higher frequency of storms |
| Range extensions | overall movement of birds towards poles (out of protected areas) |
| Peak fledging date | shifts with warmer springs, retarded with wetter springs |
| Population size | reduced as source populations turn to sinks |
| Extinctions | populations of range-restricted species reduced to point of extinction |

**Table 5:** Characteristics of datasets on African birds potentially useful for the study of climate change impacts

Long-term study (8+ years)*
Includes body and/or egg morphology data
Includes accurate demographic data — e.g. range size, core and peripheral populations
Use of fixed transects over long periods (e.g. SABAP and BIRP datasets)
Includes life history and reproductive data e.g. phenology of breeding
Cover a range of habitats e.g. suburban/rural, terrestrial/marine, alien/natural vegetation
Includes effects of the abiotic environment (especially temperature, rainfall) on breeding or adult/juvenile survival

\* datasets should ideally be adjusted for the generation time of species in question, e.g. flamingoes 40 years, passerines 5–10 years

conserve particularly rare or threatened species. Without provision for corridors, or naturally-occurring higher ground, it is likely that some such species will be forced into marginal habitat already significantly influenced by humans and thus face a high probability of extinction. More sophisticated future analyses should devise an approach for modelling the cumulative impacts of multiple anthropogenic pressures.

## Testable hypotheses on climate change impacts on African birds

We end by suggesting testable hypotheses that can be used to discriminate climate change effects on southern African birds from other anthropogenic influences:

- Species will shift southwards in response to the global trend of temperature profiles and biomes shifting poleward (IPCC 2001). Climate envelope modelling will predict how far south species should move over several decades (e.g. Midgley *et al.* 2003).
- Sub-population fragmentation or extinction will occur first at the westernmost or northernmost edge of a susceptible species' range; range constrictions and population declines are expected in the southern coastal areas.
- Egg and body size of south-temperate passerine species in mesic habitats will increase, as warmer temperatures allow greater resources to be allocated to body maintenance or egg-formation.
- Mortality at all life stages may increase in passerine species in all habitats, particularly those with exposed nest sites, as warmer temperatures, droughts and fires exceed individuals' physiological thresholds.
- Timing of breeding (earliest nests and population means) in south-temperate passerines will move forward as spring temperatures become warmer (cf. Winkler *et al.* 2002).
- Arid-zone species dependent on rainfall events to initiate breeding may experience increasing breeding failure, as aseasonal rainfall events, followed by prolonged dry spells, increase.
- Breeding frequency may decline in species reliant on ephemeral wetlands (e.g. flamingos and rails) as the length of time between major rainfall events increases. For long-lived species currently breeding less than once per year (e.g. eagles), lowered rainfall may decrease the chances of future breeding (Wichmann *et al.* 2003).
- Second broods may decrease for multi-brooded species as climate change shortens the effective length of breeding seasons.
- For subtropical species pushed south, breeding seasons may be lengthened as day length increases, allowing second broods.
- Nest-failure rates for passerines may increase as parents spend more time away from nests foraging.
- Extinction probabilities of range-restricted species in western regions should be higher than those of more widespread species, particularly those identified as high-risk (Table 3).
- Large-bodied nomadic species such as sandgrouse will be less likely to experience reduced populations or local extinctions than small-bodied resident species.
- Species with specialised feeding associations will have significantly higher extinction probabilities than will generalist species.

## Conclusions

This review and prospectus for future research on climate change effects on African birds is necessarily speculative. Few published papers exist on the predicted or known effects of climate change on African organisms, on a continent widely recognised as the world's most vulnerable. This needs to change, and soon. We predict that suites of range-restricted species will be especially prone to climatic change, and list life history, behavioural and ecological traits which may pre-dispose species to population declines, fragmentation or extinction.

Several species falling into one or more high-risk categories occur in southern Africa. It is revealing that several of these species are not currently on Red Data lists (e.g. Barnes 2000). These species may be ideal indicators of climate change, and it remains for future research to target these species and their habitats in detail to determine exactly how they are being affected.

Conservation biologists face several challenges for the future in this area. The first challenge is to re-think the planning of protected areas and other natural landscapes to accommodate the future effects of climate change to effectively protect vulnerable birds and other components of Africa's rich biodiversity. We recognise the immense pressures which make this difficult on a continent-wide scale. However, the South African government has recently declared a number of new protected areas, expanded areas and incentives for biodiversity-compatible management of land outside protected areas, based on the results of innovative landscape-level planning (e.g. Cowling *et al.* 2003, Driver *et al.* 2004). It did this by demonstrating how protecting such 'living landscapes' supports human socio-economic aspirations rather than limiting them. It is therefore within the realm of possibility that climate-change planning can occur even in regions such as southern Africa which face serious socio-economic pressures. A second challenge for conservation biologists, therefore, is to demonstrate to governments across the continent that sound landscape-level planning is also one of the single most cost-effective ways to support lasting human development and the well-being of Africa's riches.

## References

**Allan DG** 1997. Bald Ibis *Geronticus calvus*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 104–105. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Allan DG and Earle RA** 1997. Blue Swallow *Hirundo atrocaerula*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 52–53. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Baker N and Baker L** 2001. Tanzania. In: Fishpool LDC and Evans MI (eds) Important Bird Areas in Africa and Associated Islands: Priority Sites for Conservation. BirdLife International. Newbury & Cambridge, UK

**Balmford A, Gaston KJ, Blyth S, James A and Kapos V** 2003. Global variation in terrestrial conservation costs, conservation benefits and unmet conservation needs. Proceedings of the National Academy of Sciences 100: 1046–1050

**Barnard P (ed)** 1998. Special issue: the biological diversity of Namibia. Biodiversity and Conservation 7: 415–559

**Barnard P, Robertson A, Simmons R, Brown CJ and Jarvis A** 1994. Endemism hotspots and the Pleistocene refuge model: an odd case from arid Africa. Poster presentation. Jacques Monod Conference on Evolutionary and Ecological Processes Underlying Biodiversity, CNRS, Aussois, France

**Barnosky AD** 1986. "Big game" extinctions caused by late Pleistocene climate change: Irish Elk (*Megalocerus giganteus*) in Ireland. Quaternary Research 25: 128–135

**Berthold P** 2001. Bird migration: a novel theory for the evolution, the control and the adaptability of bird migration. Journal fur Ornithologie 142: 148–159

**Berthold P** 2003. Genetic basis and evolutionary aspects of bird migration. Advances in the Study of Behaviour 33: 175–229

**Bond WJ** 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society, London B 344: 83–90

**Bond WJ, Midgley GF and Woodward FI** 2003. What controls South African vegetation — climate or fire? South African Journal of Botany 69: 79–91

**Both C and Visser ME** 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 296–298

**Brown CJ** 1997. Bearded Vulture *Gypaetus barbatus*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 154–155. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Calf KM, Downs CT and Cherry MI** 2003. Territoriality of Cape Sugarbirds (*Promerops cafer*) between and within breeding seasons. Ostrich 74: 125–128

**Cody ML** 1999. Assembly rules at different scales in plant and bird communities. In: Weiher E and Keddy P (eds) Ecological Assembly Rules. pp 165–205. Cambridge University Press, Cambridge

**Collins BG and Rebelo T** 1987. Pollination biology of the Proteacea of Australia and southern Africa. Australian Journal of Ecology 12: 387–421

**Coppack T, Pulido F, Czisch M, Auer DP and Berthold P** 2003. Photoperiod response may facilitate adaptation to climate change in long-distance migratory birds. Proceedings of the Royal Society, London B 270: S43–S46

**Cowling R and Richardson D** 1995. Fynbos: South Africa's Unique Floral Kingdom. Fernwood Press, Cape Town, South Africa

**Cowling RM, Rundel PW, Desmet PG and Esler KJ** 1998. Extraordinarily high regional-scale plant diversity in southern African arid lands: subcontinental and global comparisons. Diversity and Distributions 4: 27–36

**Cowling RM, Pressey RL, Rouget M and Lombard AT** 2003. A conservation plan for a global biodiversity hotspot — the Cape Floristic Region, South Africa. Biological Conservation 112: 191–216

**Crawford RJM** 1997a. Cape Gannet *Morus capensis*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 28–29. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Crawford RJM** 1997b. Bank Cormorant *Phalacrocorax neglectus*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 34–35. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Crawford RJM** 1997c. Crowned Cormorant *Phalacrocorax coronatus*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 38–39. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Crawford RJM and Dyer BM** 1995. Responses by four species of seabirds to a fluctuating availability of Cape Anchovy *Engraulis capensis* off South Africa. Ibis 137: 329–339

**Crawford RJM and Whittington PA** 1997. Jackass (African) Penguin *Spheniscus demersus*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 4–5. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Dean WRJ** 2000a. Alien birds in southern Africa: what factors determine success? South African Journal of Science 96: 9–14

**Dean WRJ** 2000b. Factors affecting bird diversity patterns in the Karoo, South Africa. South African Journal of Science 96: 609–616

**Dean WRJ** 2004. Nomadic Desert Birds. Adaptations in Desert Organisms Series. Springer-Verlag, Berlin, Heidelburg and New York

**De Swardt DH** 1997. Gurney's Sugarbird *Promerops gurneyi*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 486–487. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Driver A, Cowling RM and Maze K** 2004. Planning for living landscapes: perspectives and lessons from South Africa. Centre for Applied Biodiversity Science, Washington DC, and Botanical Society of South Africa, Cape Town

**Duncan RP** 1997. The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. American Naturalist 149: 903–915

**Du Toit M, Boere GC, Cooper J, De Villiers MS, Kemper J, Lenten B, Petersen SL, Simmons RE, Underhill LG, Whittington PA and Byers OP (eds)** 2003. Conservation Assessment and Management Plan for Southern African Seabirds. Avian Demography Unit, Cape Town and Conservation Breeding Specialist Group, Apple Valley, California, USA

**Endler JA** 1986. Natural Selection in the Wild. Princeton University Press, Princeton

**Erasmus BFN, Van Jaarsveld A, Chown SL, Kshatriya M and Wessels KJ** 2002. Vulnerability of South Africa animal taxa to climate change. Global Change Biology 8: 679–693

**Ferguson R** 2004. Extinction Risk from Climate Change? Website Centre for Science and Public Policy, Washington DC, USA

**Fishpool LDC and Evans MI (eds)** 2002. Important Bird Areas in Africa and Associated Islands: Priority Sites for Conservation. BirdLife International. Newbury and Cambridge, UK

**Fjeldså J** 2003. Patterns of endemism in African birds: how much does taxonomy matter? Ostrich 74: 30–38

**Fraser MW** 1997. Cape Sugarbird *Promerops cafer.* In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The Atlas of Southern African Birds. pp 484–485. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Githaiga-Mwicigi JMW, Fairbanks DHK and Midgley G** 2002. Hierarchical processes define spatial pattern of avian assemblages restricted and endemic to the arid Karoo, South Africa. Journal of Biogeography 29: 1067–1087

**Grabbherr G, Gottfried M and Pauli H** 1994. Climate effects on mountain plants. Nature 369: 448

**Grant PR and Grant BR** 2002. Unpredictable evolution in a 30-year study of Darwin's Finches. Science 296: 707–711

**Harrison JA** 1992. The Southern African Bird Atlas Project databank: five years of growth. South African Journal of Science 88: 410–413

**Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds)** 1997. The Atlas of Southern African Birds. Avian Demography Unit and BirdLife South Africa, Johannesburg

**Hockey PAR, Underhill LG, Neatherway M and Ryan PG** 1989. Atlas of the Birds of the South-western Cape. Cape Bird Club, Cape Town, South Africa

**Hulme M (ed)** 1996. Climate change and southern Africa: an exploration of some potential impacts and implications in the SADC region. WWF report, Climate Change Group UEA, Norwich, UK

**IPCC (Intergovernmental Panel on Climate Change)** 2001. Climate Change 2001: Impacts, Adaptation and Vulnerability. Cambridge University Press, Cambridge, UK

**Le Maitre DC and Midgley JJ** 1992. Plant reproductive ecology. In: Cowling RM (ed) The Ecology of Fynbos: Nutrients, Fire and Diversity. pp 135–174. Oxford University Press, Cape Town

**Lloyd P, Little RM, Crowe TM and Simmons RE** 2001. Rainfall and food availability as factors influencing the migration and breeding activity of Namaqua Sandgrouse *Pterocles namaqua*. Ostrich 72: 50–62

**Mendelsohn J, Jarvis A, Roberts C and Robertson T** 2003. Atlas of Namibia: a portrait of the land and its people. Directorate of Environmental Affairs, Windhoek, Namibia

**Midgley GF, Stock WD and Juritz JM** 1995. The effects of elevated $CO_2$ on Cape Fynbos species adapted to soils of different nutrient status: nutrient- and $CO_2$ responsiveness. Journal of Biogeography 22: 185–191

**Midgley G, Rutherford M and Bond W** 2001. The heat is on…: impacts of climate change on plant diversity in South Africa. National Botanic Institute, Cape Town, South Africa

**Midgley GF, Hannah L, Millar D, Thuiller W and Booth A** 2003. Developing regional and species-level assessments of climate change impacts on bio-diversity in the Cape Floristic Region. Biological Conservation 112: 87–97

**Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB and Kent J** 2000. Bio-diversity hotspots for conservation purposes. Nature 403: 853–858

**New M, Lister D, Hulme M and Makin I** 2000. A high-resolution data set of surface climate over global land areas. Climate Research 21: 1–25

**Overpeck JT, Whitlock C and Huntley B** 2003. Terrestrial biosphere dynamics in the climate system: past and future. In: Alverson K, Bradley R and Pedersen J (eds) Paleoclimate, Global Change and the Future (IGBP Synthesis Volume). pp 81–111. Springer-Verlag, Berlin

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

**Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent J, Thomas JA and Warren M** 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 578–583

**Pearce J and Ferrier S** 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133: 225–245

**Pearson RG and Dawson TP** 2003. Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? Global Ecology and Bio-geography 12: 361–371

**Peterson AT** 2003. Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of bio-diversity consequences. Global Change Biology 9: 647–655

**Peterson AT, Ortegu-Huerta MA and Bartley J** 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416: 626–629

**Petit JR, Jouzel J and Raynaud D** 1999. Climate and atmospheric history of the past 420 000 years from the Vostok ice core, Antarctica. Nature 399: 429–436

**Pounds JA, Fogden MPL and Campbell JH** 1999. Biological responses to climate change on a tropical mountain. Nature 398: 611–615

**Rebelo AG, Siegfried WR and Crowe AA** 1984. Avian pollinators and the pollination syndromes of selected Mountain Fynbos plants. South Africa Journal of Botany 3: 285–296

**Rogers DJ and Randolph SE** 2000. The global spread of malaria in a future warmer world. Science 289: 1763–1766

**Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C and Pounds JA** 2003. Fingerprint of global warming on wild animals and plants. Nature 421: 57–60

**Roux JP** 2003. Risks. In: Molloy F and Reinikainen T (eds) Namibia's Marine Environment. Directorate of Environmental Affairs, Ministry of Environment and Tourism, Windhoek

**Rutherford MC, O'Callaghan M, Powrie LW, Hurford JL and Schulze RE** 1996. Predicting survival in new environments through analytical GIS application. Environmental Software 11: 113–121

**Rutherford MC, Midgley GF, Bond WJ, Powrie LW, Roberts R and Allsopp J** 2000. Plant biodiversity. In: Kiker G (ed) Climate Change Impacts in Southern Africa. Report to the National Climate Change Committee, Department of Environmental Affairs and Tourism, Pretoria, South Africa

**Schluter D** 2000. The Ecology of Adaptive Radiation. Oxford University Press, Oxford

**Schmidt-Nielsen K** 1983. Animal Physiology: Adaptation and Environment. Cambridge University Press, Cambridge

**Shannon LV** 1985. The Benguela ecosystem, part I: evolution of the Benguela, physical features and processes. Oceangraph and Marine Biology Annual Review 23: 105–182

**Siegfried WR** 1992. Conservation status of South African endemic avifauna. South African Journal of Wildlife Research 22: 61–64

**Simmons RE, Griffin M, Griffin RE, Marais E and Kolberg H** 1998. Endemism and diversity in Namibia: patterns, processes and predictions. Biodiversity and Conservation 7: 513–530

**Stattersfield AJ, Crosby MJ, Long AJ and Wege DC** 1998. Endemic Bird Areas of the World — Priorities for Bio-diversity Conservation. BirdLife Conservation Series 7. BirdLife International, Cambridge, UK

**Steyn P** 1982. Birds of Prey of Southern Africa. David Philip, Cape Town, South Africa

**Stockwell CA, Hendry AP and Kinnison MT** 2003. Contemporary evolution meets conservation biology. Trends in Ecology and Evolution 18: 94–101

**Swets KA** 1988. Measuring the accuracy of diagnostic systems. Science 240: 1285–1293

**Thuiller W** 2003. BIOMOD: optimising predictions of species distributions and projecting potential future shifts under global change. Global Change Biology 9: 1353–1362

**Thuiller W** 2004. Patterns and uncertainties of species' range shifts

under climate change. Global Change Biology 10: 2020–2027

**Thuiller W, Araújo MB, Pearson RG, Whittaker RJ, Brotons L and Lavorel S** 2004a. Biodiversity conservation: Uncertainty in predictions of extinction ris. Nature 430: doi:10.1038/nature02716

**Thuiller W, Araújo MB and Lavorel S** 2004b. Do we need land-cover data to model species distributions in Europe? Journal of Bio-geography 31: 353–361

**Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M and Roeckner E** 1999. Increased El Nino frequency in a climate model forced by future greenhouse warming. Nature 398: 694–696

**Tyson PD** 1986. Climate Change and Variability in Southern Africa. Oxford University Press, Cape Town, South Africa

**Veltman CJ, Nee S and Crawley MJ** 1996. Correlates of introduction success in exotic New Zealand birds. American Naturalist 147: 542–557

**Weeks SJ, Currie B and Bakun A** 2003. Massive emissions of toxic gas in the Atlantic. Nature 415: 493–494

**Wichmann MC, Jeltsch W, Dean WRJ, Moloney KA and Wissel C** 2003. Implications of climate change for the persistence of raptors in arid savanna. Oikos 102: 186–202

**Williamson M** 1996. Biological Invasions. Chapman and Hall, London

**Winkler DW, Dunn PO and McCulloch CE** 2002. Predicting the effects of climate change on avian life-history traits. Proceedings of the National Academy of Sciences 99: 13595–13599

**Woodward FI** 1987. Climate and Plant Distribution. Cambridge University Press, Cambridge, UK