Southern African geography: its relevance to birds

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THE ATLAS OF SOUTHERN AFRICAN BIRDS

VOLUME 1: NON-PASSERINES

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Southern African geography: its relevance to birds

INTRODUCTION

The southern African subcontinent has a diversity of habitats probably unsurpassed by any other region of comparable size. Seven major terrestrial biomes are represented: forest, woodland (or savanna), grassland, fynbos, Nama Karoo, succulent Karoo and desert (Rutherford & Westfall 1986). A recent vegetation map delineated 68 vegetation types in South Africa, Lesotho and Swaziland alone (Low & Rebelo 1996). There is also an array of freshwater and marine habitats. Because of this diversity of habitats, the region regularly hosts close to 800 bird species or *c.* 9% of the world's total in an area that covers 1.67% of the world's land surface.

Most of the distributions presented in this atlas can be understood in terms of associations with one or more geographical variables, of which vegetation type is the most useful for terrestrial species. Patterns are repeated again and again across families and orders. Some closely related species occupy niches in different biomes and consequently have very different distributions. By the same token, species with completely different taxonomic and physical characteristics can have similar distributions when adapted to the same biome. Recognition of the small number of typical patterns is one of the rewards of studying the maps in this atlas. On the other hand, the deviations from those patterns are as important and interesting as the patterns themselves. Every distribution, no matter how 'typical', holds its own peculiarities which pose questions and clues relating to species' ecology and history. The information held in these maps should provide grist to the mills of research for many years.

The objective of this chapter is to provide an overview of the key geographical factors affecting bird distributions; in other words, an introduction to the biogeography of southern African birds. Both natural and anthropogenic factors are considered. It was the last chapter to be written, and it highlights some of the recurring themes detected by the editors as they processed the species accounts. Bird names follow the nomenclature adopted elsewhere in the atlas; for scientific names, refer to the systematic lists in each volume.

TOPOGRAPHY

A simplified model of southern African topography (Figure 13) would be of a shallow bowl occupying the central bulk of the subcontinent, the sides of this bowl falling away steeply around the edges to a low-lying coastal margin (Wellington 1955). The bowl has an asymmetrical tilt such that the edge in the east is higher than in the west, with the highlands associated with these edges being wider and higher in the east. The interior of the bowl, including the peripheral highlands, is known as the Central Plateau; its steep edges are the Great Escarpment. The width of the coastal margin varies from *c.* 50–200 km; it is widest in the south and narrowest in the east, but broadens out from northeastern KwaZulu-Natal northwards to become the 'lowveld' of the eastern Transvaal, eastern Swaziland, and most of Mozambique. It extends into a few valleys in the extreme eastern edge of Zimbabwe, most notably at the confluence of the Haroni and Rusitu rivers (2033AA), where a number of tropical lowland bird species marginally enter the atlas region.

This simple model is disrupted by a number of major features. The continuity of the Central Plateau is broken by a number of broad river valleys, principal amongst these being the Limpopo and Zambezi valleys in the east. These low-lying areas introduce hot, dry, tropical conditions, similar to those prevailing on the coastal plains in the northeast, deep into the interior of the subcontinent and provide corridors for some species (e.g. Longtailed Starling) while being barriers for others (e.g. Yellowrumped Widow). These river valleys have the effect of dividing Zimbabwe into three zones corresponding to the Zambezi Valley in the north, a central plateau and the Limpopo Valley in the south. Other important river valleys in the east, although not at the same scale, are those of the Umfolozi (*c.* 28.5°S) and Tugela (*c.* 29°S) rivers which constitute a north–south cut-off point for a number of distributions (e.g. Threestreaked Tchagra) and an intrusion of arid woodland into the otherwise grassy midlands of KwaZulu-Natal.

The Orange River valley extends from the eastern escarpment westwards. In the west, its broad low-lying valley is linked to the fossil or near-fossil river valleys of the Koa, Nossob and Molopo, to form a large shallow basin which is principally filled with deep deposits of sand, forming the plains of Bushmanland and the South African portion of the southern Kalahari. The lower reaches of the Orange River are incised and characterized by the eroded rocky hills to the south (Richtersveld) and north. The Fish River which drains into the Orange River from the north has created a deep canyon in southern Namibia.

Another disruptive feature is the ranges of fold mountains which occupy much of the coastal margin in the south and southwest. These extend from the Cedarberg range at *c.* 32°S in the southwest, southward to the complex and extensive ranges in the extreme southwest between 33° and 35°S, and from there eastwards, for the most part in three or four parallel ranges, to *c.* 27°E. The rain shadow created by these mountains restricts the fynbos biome to the seaward slopes and plains of the southwestern Cape Province and, further inland, creates parallel strips with dramatically different vegetation types. For example, the Little Karoo (succulent Karoo biome) lies between the Swartberg range to the north and the Langeberg and Outeniqua ranges to the south; further north, between the Swartberg and the Great Escarpment, lies the Great Karoo (Nama Karoo biome), a flat expanse visible as a 'hole' in the distribution maps of several montane species (e.g. Ground Woodpecker, Black Eagle, Palewinged Starling). The arid Tanqua Karoo (3219), lying between the Cedarberg range in the west and the Great Escarpment in the east, forms a corridor which allows a southward extension in distribution of some species of arid habitats (e.g. Tractrac Chat).

On the Central Plateau, the eastern highlands extend as a broad band of high-altitude mountains and broken terrain from the northeastern Cape Province, through Lesotho, western KwaZulu-Natal, northeastern Free State and the eastern Transvaal. This stretch of highlands and associated escarpment is known as the Drakensberg. Particularly in the Transvaal, the distributions of many species can be seen either to follow (e.g. Bluemantled Flycatcher, Longtailed Wagtail) or avoid (e.g. Longtailed Shrike, Glossy Starling) the narrow band of the Great Escarpment. The highlands find their most dramatic expression in the Lesotho massif where peaks of over 3500 m fall to the deeply incised valleys of the Orange River and its tributaries. These highlands, together with adjacent areas to the west having an elevation above 1500 m, are often collectively referred to as the 'highveld'.

North of the Limpopo Valley, the highlands reappear in eastern Zimbabwe with the Chimanimani, Vumba and Inyanga mountains running roughly south to north along the border with Mozambique, with a west-facing escarpment *c.* 260 km in length. These highlands provide an important link between the Afromontane Forests to the north of the Zambezi Valley and to the south of the Limpopo Valley, and also have a number of endemic species (e.g. Chirinda Apalis and Brier Warbler).

Portions of central and northeastern Zimbabwe are also relatively elevated (>1200 m) and are variously referred to as highveld, the central watershed or as the Mashonaland plateau.

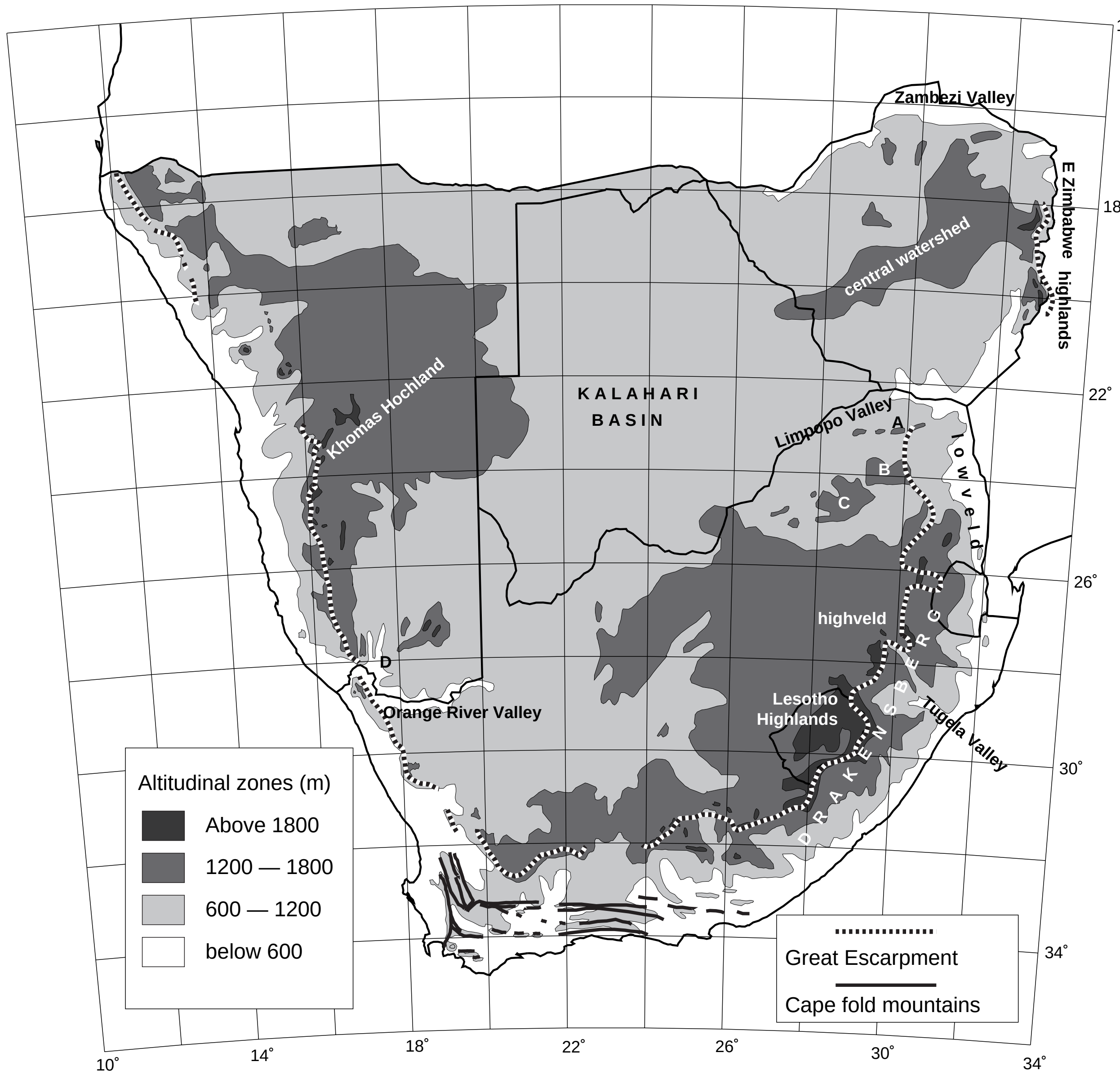


FIGURE 13. The principal altitudinal zones and topographical features of the atlas region. Features A, B, C and D are the Soutpansberg range, Pietersburg Plateau, Waterberg Mountains and Fish River Canyon, respectively.

The western highlands and escarpment take on more modest proportions but nevertheless form an important divide between the interior and coastal areas. In northwestern Namibia, the escarpment is a broad band of broken terrain with characteristics distinct from the Namib Desert to the west and the woodlands to the east, and having a number of associated endemic species (e.g. Herero Chat and Whitetailed Shrike).

The interior of the Central Plateau is also not uniform; the altitude, geological formations and patterns of erosion vary. Much of the Karoo is characterized by numerous mesas ('koppies' and 'tafels') which reflect differential patterns of erosion and provide habitat for species which prefer broken terrain but do not require the moisture typical of more substantial mountains to the south and east (e.g. Cinnamonbreasted Warbler, Mountain Chat and Rock Pipit).

Other inland mountains of importance to birds are those in the northern Transvaal: the Magaliesberg, Waterberg, Strydpoortberg and Soutpansberg ranges (e.g. Cape Batis); the granite hills of southern Zimbabwe, particularly the Matobo Hills (e.g. Black Eagle, Boulder Chat); the Tswapong Hills of eastern Botswana (e.g. Cape Vulture) and the inselbergs of the Tsodilo and Gubatcha hills on the northern Kalahari plains (e.g. Freckled Nightjar); and below the Great Escarpment, the Lebombo Mountains of northern KwaZulu-Natal and eastern Swaziland (e.g. Jackal Buzzard). Elevated plateaus of equal importance are the Pietersburg Plateau (2329) in the northern Transvaal and the Waterberg Plateau and Khomas Hochland of Namibia.

In addition to these elevations on the Central Plateau, there are a number of significant depressions, over and above the river valleys discussed above. By far the largest and most important of these is the central depression of the 'bowl', namely the Kalahari Basin. This basin is exceptionally large and flat, and the greater part of it is filled with deep deposits of alluvial sand which form the substrate of the Kalahari proper which covers most of Botswana, an eastern portion of Namibia, a western portion of Zimbabwe, and a portion of the northern Cape Province. These Kalahari sands are responsible for a lack of surface water. Most granivorous species, unlike insectivorous birds, need to drink regularly and therefore are absent from areas that are without surface water for at least part of the year, and a 'Kalahari hole' is evident in the distributions of many mainly granivorous, species (e.g. Greenspotted Dove, Melba Finch, Blue Waxbill and Blackthroated Canary).

In eastern Botswana, the Kalahari sands give way to the firm substrate of the 'hardveld' which extends into the western Transvaal. Water availability and vegetation differ strikingly between

FIGURE 14. The main river systems and oceanographic features of the atlas region.

the hardveld and the Kalahari, and the distributional boundaries of many species coincide with this divide (e.g., in addition to the examples of water-dependent birds above, Natal Francolin, Redbilled Hornbill, Blackheaded Oriole, Familiar Chat, Whitethroated Robin, Rattling and Tinkling Cisticolas, Chat Flycatcher, Paradise Flycatcher and Puffback).

Three much smaller, but nevertheless large and well-defined depressions have significance for bird distributions: the Etosha Pan in northern Namibia, the Okavango Delta in northwestern Botswana and the Makgadikgadi Pans of northeastern Botswana. These are the sites of important wetlands, discussed below.

OCEANS AND COASTLINE

The oceans are vast, rich and, despite their featureless appearance, complex. Marine communities, like all others, depend on food, which is dependent on factors such as temperature, salinity, nutrient content and exposure to sunlight. These in turn are ultimately controlled by winds, earth-spin, and global climate which are responsible for currents, upwellings and other phenomena, such as the degree to which waters with different properties become mixed. Seabird assemblages are influenced at different spatial and temporal scales by oceanographic processes which affect the availability, distribution and abundance of their marine prey (Schneider & Piatt 1986; Hunt & Schneider 1987).

Two major current systems affect the waters of the southern African coast (Payne & Crawford 1989): the Agulhas Current flows southwestwards along the Indian Ocean coast, and the Benguela Current flows northwards along the Atlantic Ocean coast (Figure 14). The Benguela is a cold coastal current with an offshore flow component due to persistent and strong southeasterly winds; these drive a nutrient-rich upwelling system which supports the complex Benguela Ecosystem. This cold current has a profound effect on the climate of the adjacent coastline. Air flowing from the cold ocean to the hot land does not yield precipitation; consequently the west coast of southern Africa, from about St Helena Bay to the Kunene River, is arid, semi-desert or desert.

The 1000 m depth contour is considered the offshore boundary of the Benguela Current (Berruti *et al.* 1989), so that it encompasses the continental shelf of the west coast of southern Africa. High concentrations of seabirds occur along the offshore divergence belt near the edge of the continental shelf (Summerhayes *et al.* 1974), as well as along the nearshore waters of the Benguela (Hockey *et al.* 1983a). Bird concentrations on the continental shelf seem to be independent of such oceanic features as temperature and masses of upwelled waters (Abrams &

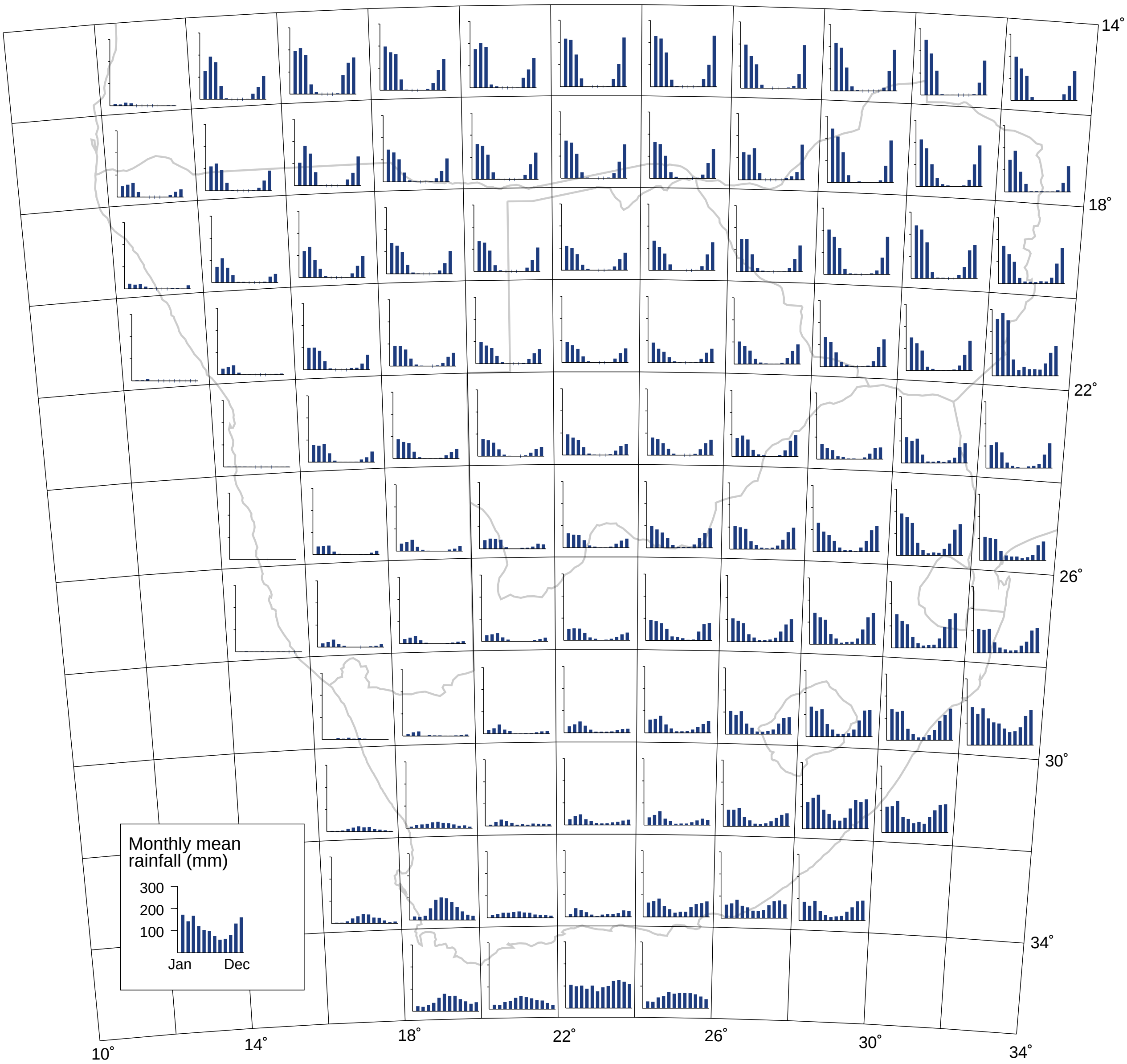


FIGURE 15. Histograms of mean monthly rainfall (mm) for 2° x 2° grid cells in southern Africa. The plotted data refer to one weather station within the grid cell or are interpolated from neighbouring grid cells, especially in central Botswana. Data obtained from Lebedev (1970), Müller (1982), Weather Bureau (1986) and Bhalotra (1987).

Griffiths 1981). The patchiness of their distribution is most probably related to that of their prey (Schneider & Duffy 1985).

The Agulhas Current is part of a huge wind-driven gyre circulating anticlockwise in the southern Indian Ocean, moving southwards along the east coast of Africa. The water mass splits when it reaches Madagascar; west of this island it flows through the Mozambique Channel as the Mozambique Current. The part that moves along the east coast of Madagascar reunites with the Mozambique Current along the coast of KwaZulu-Natal, forming the Agulhas Current. This current brings warm water from the tropics to the east coast of South Africa, following the contour of the continental shelf. From near Port St Johns (3129DA) westwards, the edge of the shelf swings away from the shore forming a wide bulge known as the Agulhas Bank, off Cape Agulhas (3420CC). This deflects the Agulhas Current away from the coast; close inshore, cooler water flows parallel to the coast but in the opposite direction to the Agulhas Current. Thus from the Transkei westwards, cooler coastal waters support a set of marine plants and animals different to that which occurs in the warmer water along the KwaZulu-Natal and Mozambique coasts. The counter-current is squeezed and overpowered by the Agulhas Current off the coast of KwaZulu-Natal. In midwinter, cooler water extends farther east along the KwaZulu-Natal coast, in which shoals of Pilchard *Sardinops ocellatus* move northwards as far as about Durban (2931CC), a phenomenon known as the 'sardine run'. Many seabirds follow the sardine run (Berruti *et al.* 1989); this can be discerned in the seasonal occurrence models for several species (e.g. Whitechinned Petrel, Cape Gannet, Cape Cormorant and Subantarctic Skua).

A string of rocky islands are scattered offshore, from Hollam's Bird Island (2414DB) north of Lüderitz to Bird Island (3326CD) in Algoa Bay. These provide platforms for seabird breeding colonies (Berruti 1989). For six seabird species, Jackass Penguin, Cape Gannet, Cape, Bank and Crowned Cormorants and Hartlaub's Gull, the majority of their global populations breed on these offshore islands. Over 50% of the population of one shorebird, the African Black Oystercatcher, breeds on these islands.

The coastline of South Africa and Namibia is *c.* 4000 km in length, with about 25% in Namibia. The sea–land interface is characterized by exposed shorelines with strong wave-action. The mean tidal range is *c.* 1 m, so the intertidal zone is narrow. There are few embayments that are sufficiently protected to provide totally sheltered shorelines; the largest are Walvis Bay Lagoon (2214C), Sandwich Harbour (2314AD), Langebaan Lagoon (3318AA), Durban Harbour (2931CC) and Richards Bay (2832CC). These localities have, or had in their pristine state,

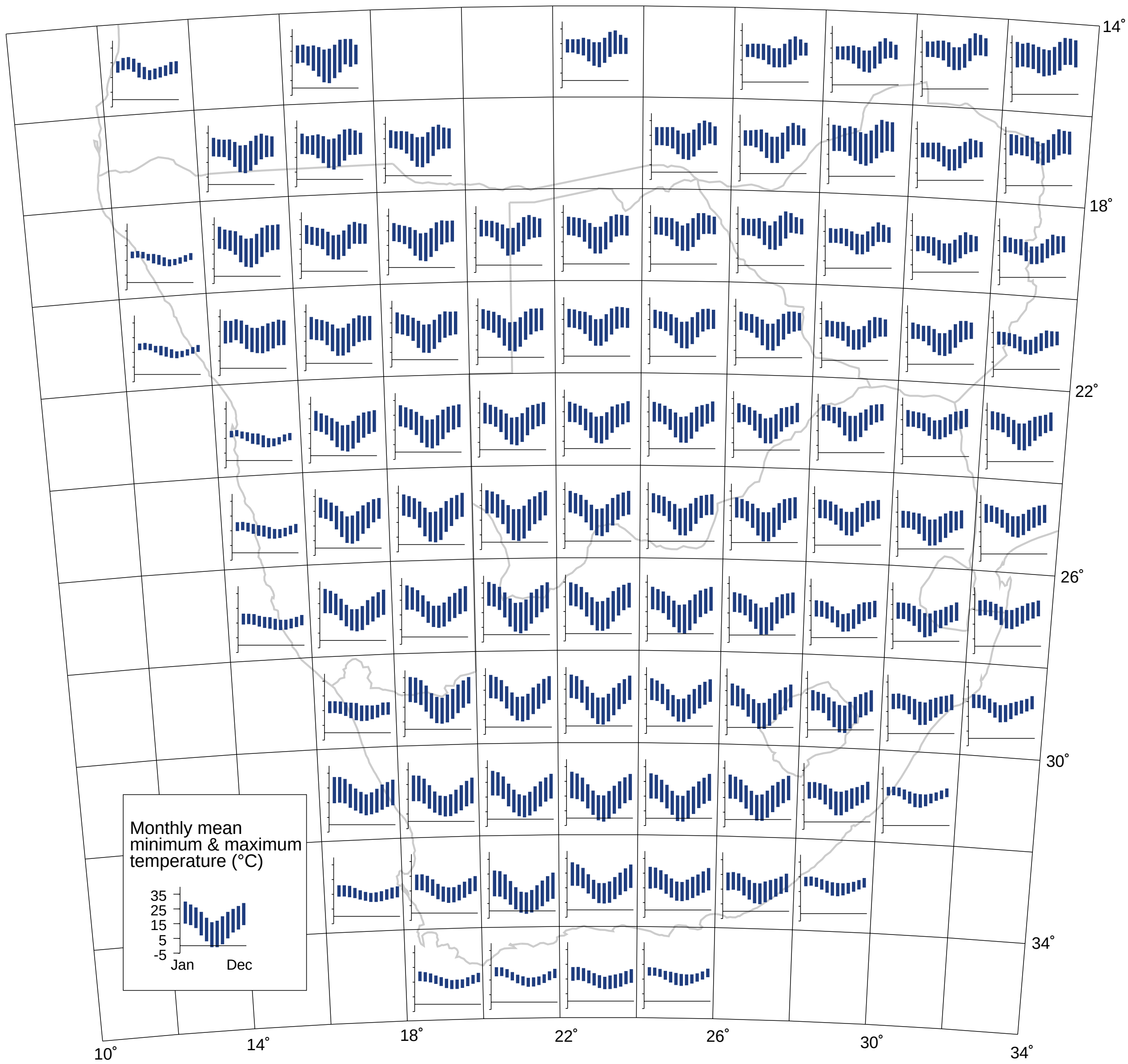


FIGURE 16. Histograms of monthly mean minimum and maximum temperatures (°C) for 2° x 2° grid cells in southern Africa. The plotted data refer to one weather station within the grid cell, or are interpolated, where possible, from neighbouring grid cells, especially in central Botswana. Data obtained from Lebedev (1970), Müller (1982), Weather Bureau (1986) and Bhalotra (1987).

the largest areas of intertidal sandflats in the atlas region, and support large concentrations of migrant waders, of which the Curlew Sandpiper is the most abundant. The coastline consists mainly of alternating stretches of sandy beaches, rocky shorelines, cliffs, and wave-cut platforms. Where exposure on the shoreline is reduced at low tide by the occurrence of offshore reefs or beds of kelp, mainly *Ecklonia maxima,* the abundance of shorebirds increases. Shorebird densities increase further where rotting kelp, deposited on the shoreline by wave action, attracts large numbers of invertebrates on which they feed. In parts of southern Namibia, the dunes of the Namib sand-sea drop directly into the ocean, providing inhospitable habitat for shorebirds, and many coastal species, e.g. Curlew Sandpiper, exhibit a gap in their distributions here.

RAINFALL

Rainfall has a profound effect on the distribution and abundance of birds, and indeed of most non-marine biota. Rainfall, as the primary determinant of water availability, is arguably the most important factor in the biogeographical patterns shown by most terrestrial life-forms. Southern Africa is largely semi-arid to arid, with most regions having mean annual rainfall below 500 mm (Figure 15). True desert occurs in the Namib and vast areas of the western and central parts of the subcontinent fall below the 500 mm isohyet. Mesic conditions occur only in the east and extreme south of the subcontinent; the Limpopo Valley forms a major semi-arid corridor through the eastern half of the region. The southwestern fringe of the subcontinent receives winter rainfall, with relatively dry summers, while the interior receives summer rains; rain occurs throughout the year along the south coast and in a transitional strip between winter- and summer-rainfall zones inland. Most high-altitude areas along the eastern escarpment also receive rainfall throughout the year.

The direct influence of rainfall on terrestrial birds is mostly through its role in determining botanical structure. For example, forests, and therefore forest birds, occur only in areas of southern Africa with rainfall of more than *c.* 800 mm/annum. Total rainfall is not the sole determinant of vegetation structure; seasonality and variability of rainfall are also critical. The fynbos and succulent Karoo biomes are characterized by winter rainfall, which militates against the widespread growth of grasses and trees, and promotes an abundance of sclerophyllous shrubs (Rutherford & Westfall 1986). Most arid and semi-arid environments in southern Africa are characterized not only by low rainfall, but also by highly unpredictable rainfall. Despite the huge year-to-year variation in rainfall in the arid and semi-arid areas, there is a tendency for series of below-average or above-average years to follow each other in cycles (Tyson 1986). When regions receive well below average rainfall for consecutive years, they become drought-stricken.

The period covered by the atlas (1980s to early 1990s) largely spanned a period of below-average rainfall in southern Africa. This has several implications. The distribution and abundance of waterbirds as shown by the atlas is likely to be biased against the arid and drought-prone western parts of the subcontinent, which probably support larger waterbird populations during moister periods. Many other bird species may have retracted or expanded their ranges in the face of these dry conditions compared with higher-rainfall conditions. Future bird atlas projects, during wetter conditions, will provide further insights in this regard.

The most obvious and widespread effect of differential rainfall patterns on the atlas data is apparent in the breeding seasonality models. A large proportion of species that occur in both the winter-rainfall (mainly Zone 4 in Figure 7) and summer-rainfall (especially Zones 5–8) regions show earlier and more truncated breeding in the former region. These species breed after the wet season in the winter-rainfall region; rapidly deteriorating conditions reduce the suitability of this region for breeding as the dry summer progresses. By contrast, breeding in the summer-rainfall region frequently starts just prior to the rains and continues until the main rainfall peak as conditions presumably improve. To what extent the longer breeding season in the summer-rainfall region represents greater opportunities for multiple brooding, and/or repeat breeding attempts after failure, is worthy of further investigation.

Differential patterns of breeding seasonality are also often apparent within the summer-rainfall region. On average, peak rainfall comes later in an anticlockwise fashion from east, via north, to west through the region (Griffiths 1972; Taljaard 1986; Tyson 1986). Rainfall in the east tends to peak about December–January, shifting later to about March in the west. This is often reflected in the atlas breeding data for species with wide east–west distributions in the summer-rainfall region, with later breeding occurring in the west (mainly Zones 1–2) compared with the east (Zones 5–8) (e.g. Cape Turtle Dove and Masked Weaver). In addition, the unpredictable nature of rainfall in the drier regions promotes opportunistic breeding during much of the year, compared with regions with higher and more predictable rainfall. North–south variations in breeding seasons apparent in breeding seasonality models may be related more to temperature than rainfall.

Good rainfall in summer results in remarkable food gluts, such as immediate massive emergences of termite alates, while later in the season, outbreaks of grasshoppers, army worm caterpillars and rodents (particularly multimammate mice *Mastomys* spp.) usually follow; these may develop locally into ‘plagues’. Many species, in particular nonbreeding migrants, wander opportunistically in southern Africa, exploiting any such outbreak of potential food. For many migrant species which are present in the atlas region during the austral summer, their occurrence, distribution and abundance in a particular year and area are to a large extent determined by the location and magnitude of major rainfall events and consequent food gluts. Such species include White, Abdim’s and Marabou Storks, and some Palearctic raptors (e.g. Lesser, Eastern Redfooted and Western Redfooted Kestrels, and Lesser Spotted and Steppe Eagles) (e.g. Brooke *et al.* 1972; Jensen 1972).

TEMPERATURE

Temperature is intimately linked to other aspects of climate in southern Africa and its effects on birds are generally masked by what are often interpreted as more ecologically significant seasonal events, such as rainfall. Consequently, direct temperature effects on birds are infrequently reported, apart from catastrophic events such as mass mortality during unusually cold spells (e.g. Steyn & Brooke 1971; Herremans *et al.* 1994b).

Temperatures in the region vary geographically, seasonally, and diurnally. The coastal lowland areas are mostly frost-free and are characterized by relatively limited seasonal and diurnal variations in temperature, although day-to-day variations may be large and unpredictable, with frequent changes between cool and hot days. On the Central Plateau, both seasonal and day/night changes become dramatic, but day-to-day variation is smaller, i.e. temperatures become more predictable, with winter days being almost invariably cool to mild and winter nights cold with frequent frost, while summer days are invariably (very) hot and nights mild (Tyson 1986). The absence of the moderating influence of the oceans on temperature in the arid interior is evident in the fact that average daily temperature changes (typically 20–25°C), particularly in winter, are larger than the differences between summer mean maximum and winter mean minimum at the coast (Figure 16).

Temperatures have significant effects on the activities of birds. Species which forage from exposed perches in open country during most of a mild day in winter (e.g. Whitecrowned Shrike and Marico Flycatcher) only do so during the cooler hours of the morning in summer, while the hot hours are spent under the canopy of a shady tree. In the drier interior of the region, Forktailed Drongos converge to associate conspicuously with prey-beaters (e.g. livestock, game, flocks of terrestrially foraging birds) during winter and to a lesser extent during cool morning hours in summer; they mostly forage solitarily, and much less conspicuously, on warm summer days (Herremans & Herremans-Tonnoeyr in press).

Such changes in activity pattern and behaviour, possibly combined with subtle differences in habitat occupation between summer and winter, have an impact on a species’ conspicuousness throughout the year and affect the reporting rate statistics used in this atlas (see ***Introduction and methods***). There is evidence from elsewhere in the Afrotropics that diurnal rhythms and differences in activity patterns may also be involved in a temporal separation of potentially competitive activities (such as foraging) between resident species and Palearctic migrants (Leisler 1992).

With regard to temperature, most of the inland areas south of the Tropic of Capricorn can be described as having two distinct seasons, summer and winter, with short transitional periods of about a month. North of the Tropic there are also two temperature seasons; however, rainfall peaks progressively later in the north and west of the subcontinent (Taljaard 1986), resulting in three seasons: a cool, dry winter (May to mid-August), a hot, dry spring (mid-August to mid-October) and a hot, moist summer (mid-October to April). Lower average maximal temperatures with the onset of the rains in November are a feature of many of the graphs north of 22°S (Figures 15 and 16).

The most reliable indication of spring in the semi-arid Kalahari basin is a sharp rise in night temperatures (Herremans 1994d). Some plants respond to this by flowering in late August or early September, and many insects appear well before any ecologically significant rain is likely to fall. Early-arriving migrant birds, mostly intra-African breeding species (e.g. Yellowbilled Kite, Wahlberg’s Eagle, Carmine Bee-eater, Rufouscheeked Nightjar and Redbreasted Swallow), arrive August–September, coincident with this early spring temperature change; they do not use rainfall as a proximal cue for timing their arrival. Late-arriving migrants on the other hand, mostly from the Palearctic and arriving after October (e.g. Whitethroat and European Marsh Warbler), need veld conditions to be improved by rainfall, and are therefore delayed during a drought spring (Herremans in press). Most insectivorous species have peak breeding during the pre-rain spring period (Skinner 1995a), allowing time to complete moult while insects are abundant during summer (M.H. unpubl. data). Most granivorous birds breed in mid- to late summer, in response to seed crops resulting from rains several weeks earlier (Skinner 1995a), and they moult during the dry winter season (M.H. unpubl. data).

In the northwest of the region, the hot, dry spring season is generally inimical to plant growth; for example, *Acacia mellifera* blooms in the Karoo and the southern part of the Kalahari basin in late August to early September; farther north, it blooms late in October in response to the first significant rains. In the northern regions, breeding of some insectivorous species still starts in response to spring temperatures, which recover from less cold winter minima than farther south, but others wait until conditions improve with the rains. Thus, the former show a pattern of later breeding with increasing latitude (e.g. Forktailed Drongo, Blackheaded Oriole, Southern Black Tit, Chinspot Batis and African Pied Wagtail), while the latter show earlier breeding in the southwest and southeast, and later breeding in the northwest and northeast (e.g. Fantailed and Rattling Cisticolas and Neddicky).

In the arid areas of the Karoo and Namib, breeding becomes almost entirely dependent on irregular rainfall events, both in granivorous and insectivorous species, though some still breed in response to spring temperature, regardless of rainfall (e.g. Rufouseared Warbler: Maclean 1970b).

Cold winter temperatures with severe frost in mountainous areas cause altitudinal migration in many species, particularly along the Drakensberg escarpment (Johnson & Maclean 1994). Here, severe frost, and more temperate conditions in the KwaZulu-Natal midlands, may occur within distances of a few kilometres. Although such short-distance movements are not well documented by the atlas, some examples of altitudinal migration – albeit usually only partial migration – in the high Drakensberg escarpment are well known (e.g. Ayres' Cisticola, Barratt's and Broadtailed Warblers, Yellowbreasted Pipit, Dusky Flycatcher and Sentinel Rock Thrush). The highlands of Zimbabwe have milder winters than the South African highveld; altitudinal migration, mainly onto the Mozambique coastal plain, is nevertheless noted or suspected for many species, e.g. for Natal and Starred Robins (Irwin 1981).

Sudden downhill movements induced by irregular snowfalls are also temperature-related events because if temperatures had been a few degrees warmer the same precipitation would have fallen as rain and would not have had the same effect. Other species migrate longer distances from their mountainous summer distribution and may reach coastal areas or disperse widely over the plateau in the interior during winter (e.g. Sentinel Rock Thrush, Shorttoed Rock Thrush, Stonechat and Fairy Flycatcher). Cold winters and late springs, sometimes in combination with migratory behaviour, cause high-altitude populations of some species to breed later than their conspecifics close by at lower altitudes, and this has sometimes resulted in well-marked isolation and subspeciation (e.g. Layard's Titbabbler, Fairy Flycatcher and Southern Grey Tit).

VEGETATION

The influence of vegetation patterns on the distribution and abundance of birds has long been recognized, both in Africa (e.g. Chapin 1923; Moreau 1966) and elsewhere (Cody 1985). Vegetation patterns, specifically plant form and vegetative structure, are determined by a myriad of climatic and edaphic factors, of which the former are the more decisive (Rutherford & Westfall 1986). Total rainfall, its predictability and seasonality, and temperature are the most important climatic factors (Walter 1979); they determine moisture availability.

Although attempts have been made to relate African bird distribution patterns directly to climatic factors (e.g. Bowen 1933), these have not been widely accepted. This is largely because associations between distribution patterns and climatic factors in one part of the continent often do not apply in other parts (Winterbottom 1978), or because of methodological problems (Stuckenberg 1969). By contrast, many analyses relating bird distribution patterns to vegetation types, both in Africa and elsewhere, have proved both reliable and illuminating (Winterbottom 1978; Cody 1985). This is because vegetation type and structure reflect and integrate numerous climatic factors and non-climatic factors, e.g. latitude, height above sea-level, topography, atmospheric circulation and the impact of ocean currents (Chapin 1923; Tyson 1986; Gentilli 1992).

Examples of some African, especially southern African, studies that have successfully related selected bird distribution patterns to vegetation types include Benson & Irwin (1966d), Moreau (1966), Winterbottom (1968a,b, 1972a), Tarboton (1980), Hockey *et al.* (1988a), Dean & Hockey (1989), Osborne & Tigar (1992) and Bruderer & Bruderer (1993).

It is widely accepted that vegetation structure, rather than plant species composition, is the critical habitat parameter for most birds (Elton & Miller 1954; MacArthur & MacArthur 1961; MacArthur *et al.* 1962; Gentilli 1992). At least two studies confirm this in southern Africa (Pianka & Huey 1971; Herremans 1993c).

Winterbottom (1959b, 1972b, 1974a, 1978) provided the most comprehensive analysis and review relating the distribution patterns of the southern African avifauna to vegetation types. He identified two major shortcomings of such analyses. Firstly, the paucity of bird distribution data for large areas, especially emphasized by Winterbottom (1956a) and, secondly, the lack of an authoritative and comprehensive vegetation map for the region. The atlas data have largely solved the former problem, and a comprehensive vegetation map used in the vegetation analysis (see ***Introduction and Methods***) was compiled from numerous sources. The rationale and methods used are discussed below, followed by a brief description of the vegetation types used and examples of their associated avifauna.

Vegetation types and sources of botanical information

The key criterion for the recognition of the vegetation types was that they be recognized as botanically distinct. The approach was to take existing vegetation maps and reorganize their vegetation units into an appropriate set of vegetation types. The criteria used to amalgamate botanically defined vegetation units, or to keep them separate, were (1) the existence of clear differences in vegetation structure, likely to be relevant to birds, and (2) the results of published community studies on bird/vegetation associations. For example, Benson & Irwin (1966d) demonstrated that there is a distinct Miombo avifauna.

A classification intermediate between Acocks' 70 'Veld Types' and Rutherford & Westfall's seven 'biomes' was found to be appropriate. No previously unpublished vegetation-unit boundaries were created to correspond with known bird distributions.

Where more than one vegetation map was available for an area, all were examined. The interpretation that seemed the most reliable and appropriate was employed, taking into account factors which included how recently the map had been compiled, to what extent it had been based on field examinations, and the

TABLE 3. The allocation of the 70 Acocks' (1953) Veld Types in South Africa, Lesotho and Swaziland to the vegetation zones.

Vegetation zones	Acocks' Veld Types
Succulent Karoo	25 (part), 26 (part), 28, 31 (part), 33 (part), 34 (part), 39 (part), 43 (part)
Nama Karoo	16 (part), 17 (part), 24, 25 (part), 26 (part), 27, 29, 30, 31 (part), 32, 33 (part), 35, 37, 38, 39 (part), 40, 42
Grassy Karoo	36, 41
Fynbos	4 (part), 34 (part), 43 (part), 46, 47, 69, 70
Sweet Grassland	50, 51, 52
Mixed Grassland	21, 48, 49, 53, 55, 56 (part), 59, 60, 64, 65, 67, 68
Sour Grassland	3, 5, 8, 22, 44, 45, 54, 56 (part), 57, 61, 62, 63, 66
Alpine Grassland	58
Southern Kalahari	16 (part), 17 (part)
Central Kalahari	16 (part), 17 (part)
Arid Woodland	6, 10, 11, 12, 13, 14
Valley Bushveld	7, 23
Mopane	15
Moist Woodland	9, 18, 19, 20
East Coast Littoral	1, 2
Afromontane Forest	4 (part)

present authors' first-hand knowledge. Detailed botanical descriptions of the vegetation regions will not be repeated here, as they are available in the original sources.

South Africa, Lesotho and Swaziland: The revised vegetation map for these three countries (Low & Rebelo 1996) was in preparation and therefore unavailable at the time the vegetation types were being compiled; earlier sources had therefore to be used. The main source was Acocks (1953); his 70 Veld Types were allocated to 16 vegetation types (Table 3). Moll & Bossi (1983) was used for delineating the boundaries of the fynbos and adjacent vegetation types. The area of the Cape Province north of the Orange and Vaal rivers was not well covered by Acocks (1953), and Gubb's (1980) vegetation map was used. Because the clear differentiation between Nama and Succulent Karoo has been appreciated only relatively recently (Rutherford & Westfall 1986), the boundaries between these two biomes were used to subdivide some of Acocks' Veld Types into vegetation types (Table 3).

An unpublished map, compiled by the Forest Biome Project, was used to locate, and determine the sizes of, forest patches in South Africa. The location and extent of forests in Swaziland was extracted from Hesse *et al.* (1990), with amendments and additions from Masson (1991) and V. Parker (pers. comm.). There are no true forests in Lesotho.

Namibia: The Namibian vegetation types were delineated using the vegetation map of Geiss (1971), modified by Brown *et al.*'s (1987a) map of 'bioclimatic regions'. The three Namib vegetation units of Geiss' map were combined into one Namib vegetation type. Similarly, three of his savanna units (Mountain Savanna and Karstveld, Thornbush Savanna, and Highland Savanna) were treated as part of the Arid Woodland vegetation type. The Etosha Pan region was combined with the Mopane vegetation type. His Semi-desert and Savanna Transition or Escarpment Zone vegetation units were extended northwards to the Kunene River and classified as the Namibian Escarpment vegetation type (see also Brown *et al.* 1987a). Geiss (1971) already indicated this change as possibly appropriate. In the eastern Caprivi Strip, Koen's (1988) vegetation types were followed. Unlike all the vegetation maps for other regions, on which 'exact' boundaries of vegetation units were delineated, Geiss's (1971) map simply classified each quarter-degree grid cell; the vegetation boundaries may therefore be inaccurate by as much as 25 km. However, this is adequate because the vegetation patterns of Namibia are relatively uncomplicated.

Botswana: The vegetation types for Botswana were based on the map of Bekker & De Wit (1991). One modification was the division of the Kalahari into Southern and Central Kalahari vegetation types along a boundary shown in Wild & Fernandes (1968) and Weare & Yalala (1971). This separates the largely treeless dunes of the Southern Kalahari from the better-developed woodland of the Central Kalahari; this boundary is likely to influence bird distribution patterns. The Makgadikgadi Pan region was combined with Arid Woodland.

Zimbabwe: The vegetation types were based on the vegetation map in Wild & Fernandes (1968). An isolated patch of Miombo near the confluence of the Save and Runde rivers was reclassified as Arid Woodland (C. Hustler *in litt.*). The Zimbabwe Forestry Commission supplied a map of the Afromontane Forest patches in eastern Zimbabwe (J. Timberlake *in litt.*).

The boundaries of the 22 vegetation types recognized for southern Africa, simplified to quarter-degree-grid-cell format, are shown in Figure 17. Major groups of vegetation types are shown in Figure 18, and illustrations of habitat types are shown in Figures 19–66.

Many grid cells contain more than one vegetation type and this is reflected on the grid maps.

Real and potential shortcomings

Given the multiplicity of sources used, the boundaries of vegetation units did not always coincide precisely across national boundaries, but generally there was good consistency. There remain, however, some disjunctions; no attempt was made to artificially manipulate boundaries because such an approach would have been arbitrary.

In western areas, the northern Cape Province and most of Botswana and Namibia, the number of vegetation types is small and they are distributed in relatively large, homogeneous units. This contrasts with the situation in eastern and southern South Africa and in Zimbabwe where the pattern of vegetation types is complex, often forming interdigitations and mosaics reflecting variation in rainfall and topography over short distances. These small-scale features resulted in many grid cells containing two, three or more vegetation types, with consequent problems for the analysis of associations between species occurrence and vegetation type.

No attempt was made to account for the vast areas where natural vegetation has been largely removed or extensively modified by human activities. So, for example, the extensive areas now occupied by alien trees and commercial afforestation, monocultures of crops such as cereals, maize and sugar-cane, urbanization and other dense settlements have been treated as if they were still in their natural state. This is largely dictated by the source vegetation maps which, apart from Moll & Bossi (1983) for the fynbos, do not delineate such alterations. This shortcoming, however, is unlikely to degrade the analysis of the distributions of most species because relict patches of the original natural vegetation, and their associated birds, usually persist in even the most radically modified grid cells. Similarly, the spread or planting of alien trees in areas which originally had few, if any, trees has not been taken into account. It would be useful if future vegetation mapping efforts attempted to delineate these anthropogenic zones.

The distribution patterns of terrestrial birds are not all determined primarily by vegetation. Examples of species that show no obvious, or puzzling, vegetation-related patterns in their distribution in southern Africa include Secretarybird, Martial Eagle, Orange River Francolin, Spotted Eagle Owl, Pearl-breasted Swallow, Black and Pied Crows, Stonechat and Fiscal Flycatcher.

Descriptions of the vegetation types and examples of their characteristic avifaunas

Nineteen of the 22 vegetation types are encompassed by seven biomes, similar to those of Huntley (1984) for South Africa, Lesotho and Swaziland, and Rutherford & Westfall (1986) for the area south of 22°S.

The seven biomes within the atlas area, and their associated vegetation types, are:

(1) Desert biome (Namib vegetation type);
(2) Succulent Karoo biome (Succulent Karoo vegetation type);
(3) Nama Karoo biome (Nama Karoo and Grassy Karoo vegetation types);
(4) Fynbos biome (Fynbos vegetation type);
(5) Grassland biome (Sweet, Sour, Mixed and Alpine Grasslands vegetation types);
(6) Woodland (or savanna) biome (Southern, Central and Northern Kalahari, Arid Woodland, Namibian Escarpment, Valley Bushveld, Moist Woodland, Mopane, and Miombo vegetation types);
(7) Forest biome (Afromontane Forest vegetation type).

Those vegetation types which consist of complex mosaics are treated separately.

Desert biome

The **Namib** (Figure 22) is on the coastal plain of Namibia and is 100–150 km wide. It is an extremely arid desert with a mean annual rainfall below 85 mm, with high annual variability (>50%), and annual evaporation far exceeding precipitation (Lovegrove 1993).

The Namib contains three distinct bird habitats: rolling sand dunes, frequently referred to as the 'sand sea', gravel plains, and watercourses, normally dry drainage lines which are delineated by trees, the most impressive of which is the Camel thorn *Acacia erioloba*. Away from watercourses, vegetation is sparse and consists primarily of grasses, e.g. *Stipagrostis* spp., and low shrubs, including the unique *Welwitschia mirabilis* (Geiss 1971).

The Namib biome supports several endemic bird species: Dune Lark occurs in the sand dune areas, and Rüppell's Korhaan and Gray's Lark in the gravel plains.

Sporadic rainfall events in this biome result in explosive growth and seeding of annual plants, which attract huge flocks of seed-eating birds, such as finchlarks and Larklike Buntings (Lovegrove 1993). The Namib also provides a regional stronghold for the threatened Lappetfaced Vulture (Brown 1986).

Succulent Karoo biome

The **Succulent Karoo** (Figures 23 and 24) falls within the winter-rainfall region in the far west, and is characterized by succulent shrubs, particularly Mesembryanthemaceae and Crassulaceae (Low & Rebelo 1996), and a particular paucity of grass cover and trees, except in the Little Karoo of the southern Cape Province, where tree cover is relatively well developed (Rutherford & Westfall 1986).

Nama Karoo biome

The **Nama Karoo** (Figure 26) vegetation of the semi-arid Karoo region largely comprises low shrubs and grasses; peak rainfall occurs in summer. Trees, e.g. *Acacia karroo* and alien species such as Mesquite *Prosopis glandulosa,* are mainly restricted to watercourses where fairly luxuriant stands can develop, especially in the southeastern Karoo (eastern Cape Province) and along the Orange River. In comparison with the Succulent Karoo, the Nama Karoo has higher proportions of grass and tree cover.

The **Grassy Karoo** (Figure 27) can be viewed as an ecological transition zone between the Nama Karoo and grassland biomes; although also primarily a dwarf-shrub habitat, it shows higher proportions of grass and, in places, tree cover.

The 'Karoo', used here loosely to refer to the amalgamation of the Succulent Karoo and Nama Karoo biomes, supports a particularly high diversity of species endemic to southern Africa (Clancey 1986a). Its avifauna characteristically comprises ground-dwelling species of open habitats, but the many tree-lined watercourses allow penetration of several species typical of Arid Woodland. This is particularly apparent along the Orange River (e.g. Scimitarbilled Woodhoopoe) and in the eastern Cape Province where, for example, the Kori Bustard and Scalyfeathered Finch are common in woodland patches in open Karooveld. The Namaqua Warbler is unique in that it is restricted to riverine woodland in the Karoo; its range does not extend into similar habitat in neighbouring biomes. The distribution of the Karoo Korhaan clearly follows that of the amalgamated Karoo biomes. Some species typical of the Karoo also occur in the Namib and/or the Namibian Escarpment vegetation types (e.g. Karoo Chat and Cinnamonbreasted Warbler).

Several species typical of the Karoo are also found in the highlands of Lesotho in the grassland biome, often being represented there by at least partially isolated populations and by distinct subspecies: Thickbilled Lark, Southern Grey Tit, Sicklewinged Chat, Layard's Titbabbler, and Blackheaded and Whitethroated Canaries. Indeed, Rutherford & Westfall (1986) differed from Acocks (1953) and Huntley (1984) in including the Lesotho highlands in the Nama Karoo, rather than the grassland biome, because of the scrubby nature of the alpine vegetation.

The ecotonal nature of the Grassy Karoo is apparent from the presence of species typical of both grasslands and Karoo in this region, e.g. Karoo and Blue Korhaans, often the only place where such species overlap. Indeed, it would appear that several grassland species which have suffered major reductions in abundance in the grassland biome now ironically find a remaining stronghold in the Grassy Karoo, at the edge of their range, e.g. Blue Crane (Allan 1992b).

Many species show clear differences in relative abundance between the Succulent Karoo and the Nama Karoo vegetation types. For example, the Thickbilled and Karoo Larks and the Karoo Eremomela show a clear preference for the former, while the Red and Sclater's Larks are entirely restricted to the latter, with the Red Lark having a particularly circumscribed range confined to the Bushmanland region south of the Orange River.

Rainfall in the Nama Karoo is mainly in summer while the Succulent Karoo falls within the winter-rainfall region. This provides opportunities for birds to migrate between the Succulent Karoo during winter and the Nama Karoo during summer to exploit the enhanced conditions associated with rainfall. This has been little researched but was found for Ludwig's Bustard (Allan 1994b) and is also apparent in the atlas data for the Larklike Bunting.

Grassland biome

This biome encompasses the open grassland regions of the eastern interior plateau of South Africa, Lesotho and Swaziland (Figure 18); open montane grassland also occurs in the Eastern Zimbabwe Highlands. The dominant vegetation comprises grasses, with geophytes and herbs also well represented (Low & Rebelo 1996). These grasslands are maintained largely by a combination of relatively high summer rainfall, frequent fires, frost and grazing, which preclude the presence of shrubs and trees. Much of the grassland biome has been transformed by crop farming, afforestation and dense human settlement (described further under **Human Activities**).

Sweet Grasslands (Figure 28) are found in lower-rainfall areas, are taller and less dense, have a lower fibre content and retain nutrients in the leaves during the winter.

Sour Grasslands (Figures 29 and 30) occur in the higher-rainfall regions (>625 mm/annum) and on acidic (leached) soils, and are characterized by being shorter and denser in structure, having a high fibre content and a tendency to withdraw nutrients from the leaves to the roots during the winter, rendering the grazing largely unpalatable to stock during this time (Rutherford & Westfall 1986).

Mixed Grasslands represent a transition or combination of Sour and Sweet Grassland types.

Alpine Grasslands (Figure 31) occur at altitudes above 1850 m, mainly in Lesotho and the eastern Cape Province, and can be described as sweet to mixed in nature (Acocks 1953). The low temperatures partially negate the effect of the relatively high rainfall and result in a more arid vegetation than otherwise expected. Some scrubby, karroid botanical elements are present in Alpine Grassland (see also Acocks 1953 and Low & Rebelo 1996).

The southern African range of the Longtailed Widow neatly delineates the boundaries of the grassland biome (plus the ecotonal Grassy Karoo). Many grassland birds, several of which are endemic to southern Africa, show a clear preference for Sour over Sweet and Mixed Grasslands, and some of these are essentially absent from the latter two grassland types, e.g. Bald Ibis (Manry 1985), Redwinged Francolin, Blackwinged Plover, Rudd's Lark (Hockey *et al.* 1988a), Botha's Lark (Allan *et al.* 1983), Blue Swallow, Buffstreaked Chat, Palecrowned Cisticola and Yellowbreasted Pipit. Examples of grassland species preferring Sweet and Mixed Grasslands appear fewer but include Melodious Lark and South African Cliff Swallow.

The presence of several Karoo bird species in the Alpine Grasslands has been noted above. This vegetation type is also characterized by an absence or scarcity of some common grassland (and more widespread) species at these high altitudes, despite their abundance in surrounding regions, e.g. Cattle Egret, Blackshouldered Kite, Cape Turtle Dove, European Swallow and Fiscal Shrike. By contrast, the Sentinel Rock Thrush shows particularly high reporting rates in Alpine Grasslands, and the threatened Bearded Vulture finds its last southern African stronghold in this region (Brown 1991). Three species are restricted to this vegetation type: Orangebreasted Rockjumper, Mountain Pipit and Drakensberg Siskin.

Fynbos biome

The **Fynbos** (Figure 32) is dominated by low shrubs and has two major vegetation divisions: fynbos proper, characterized by restioid, ericoid and proteoid components; and renosterveld, dominated by Asteraceae, specifically Renosterbos *Elytropappus rhinocerotis*, with geophytes and some grasses (Low & Rebelo 1996). Renosterveld has now been largely replaced by agricultural cropfields and planted pastures throughout the region. This biome is characterized by a high level of diversity and endemism in its botanical composition (Cowling & Richardson 1995).

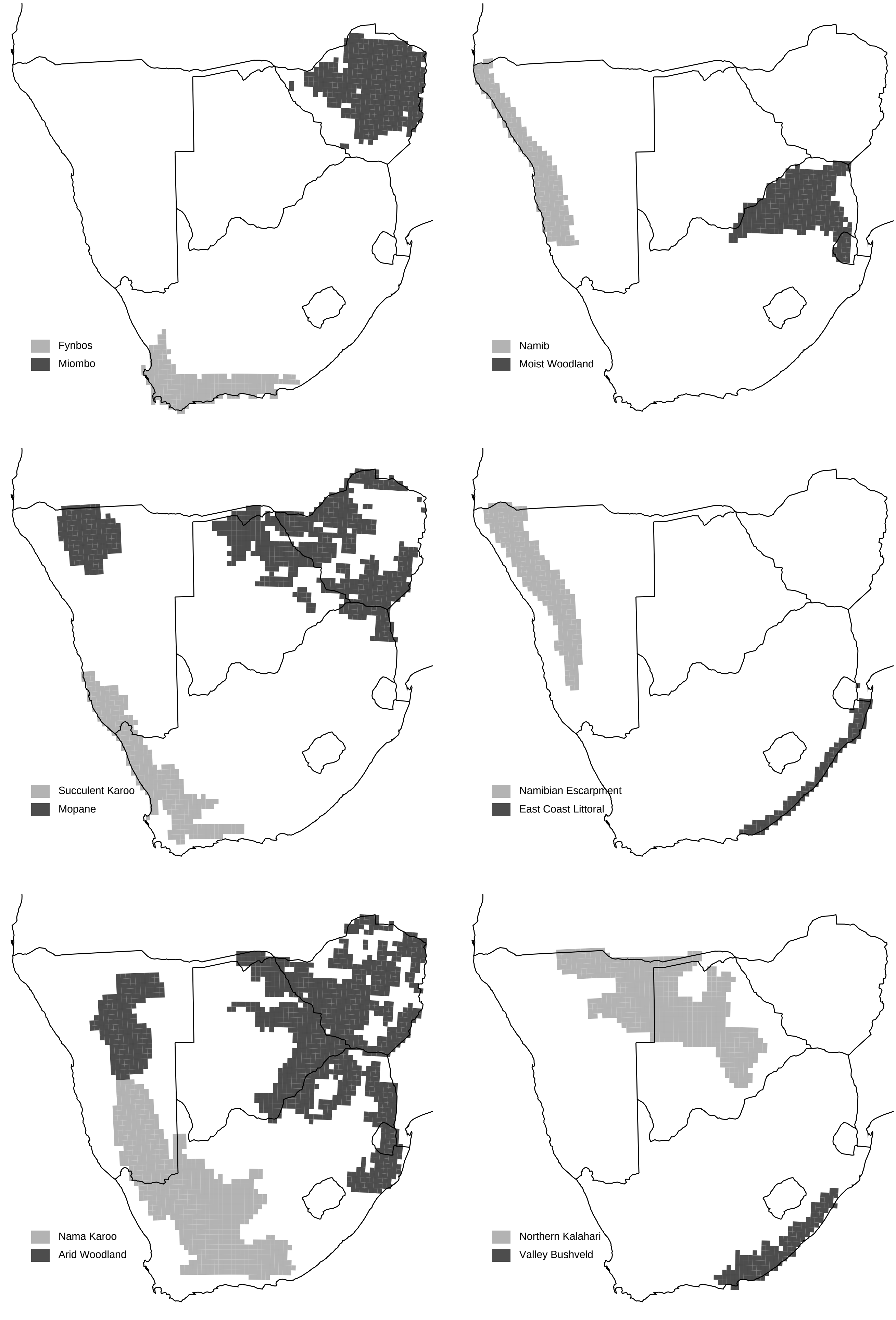


FIGURE 17. Grid maps of the distributions of vegetation types.

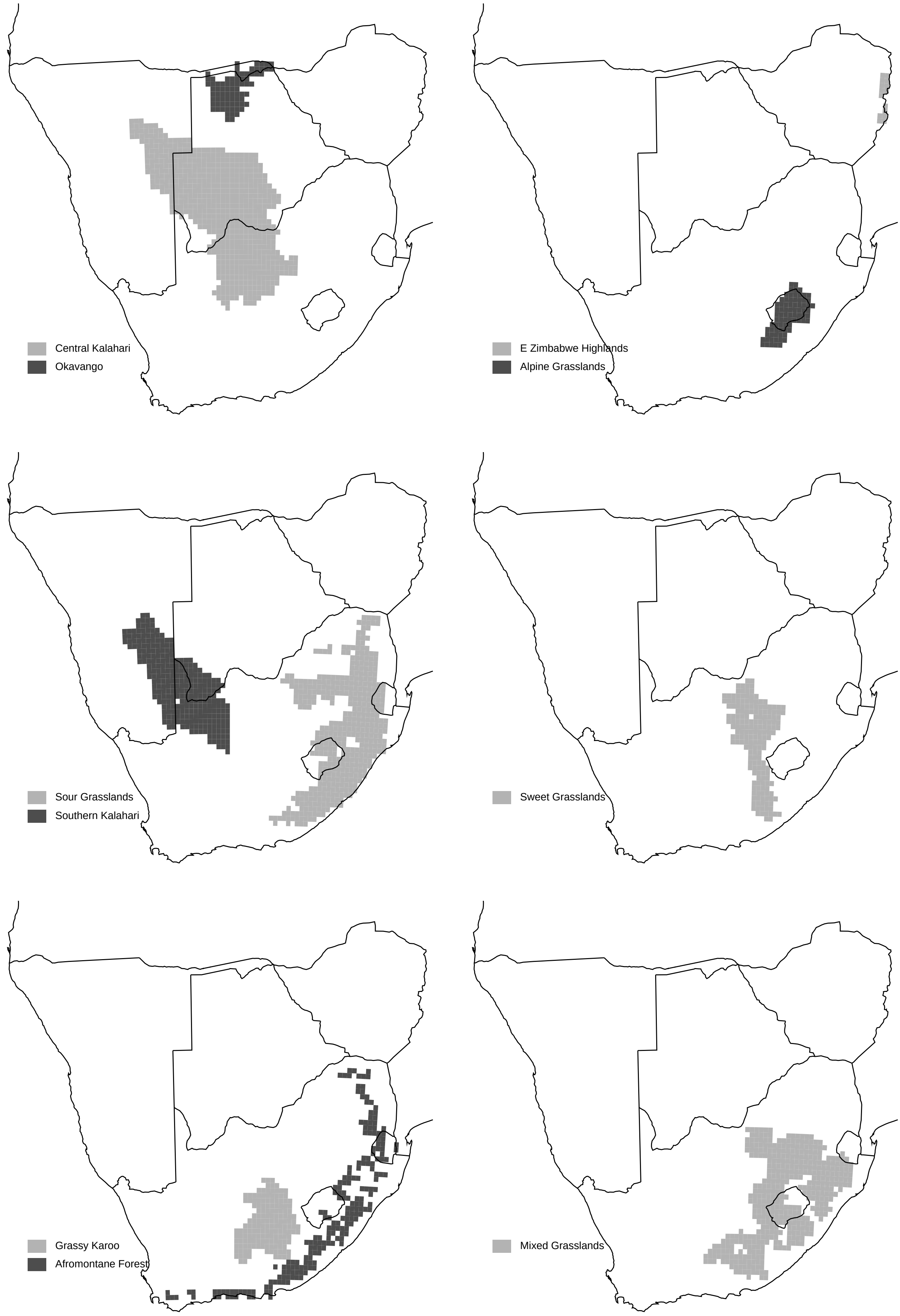


FIGURE 17 (continued).

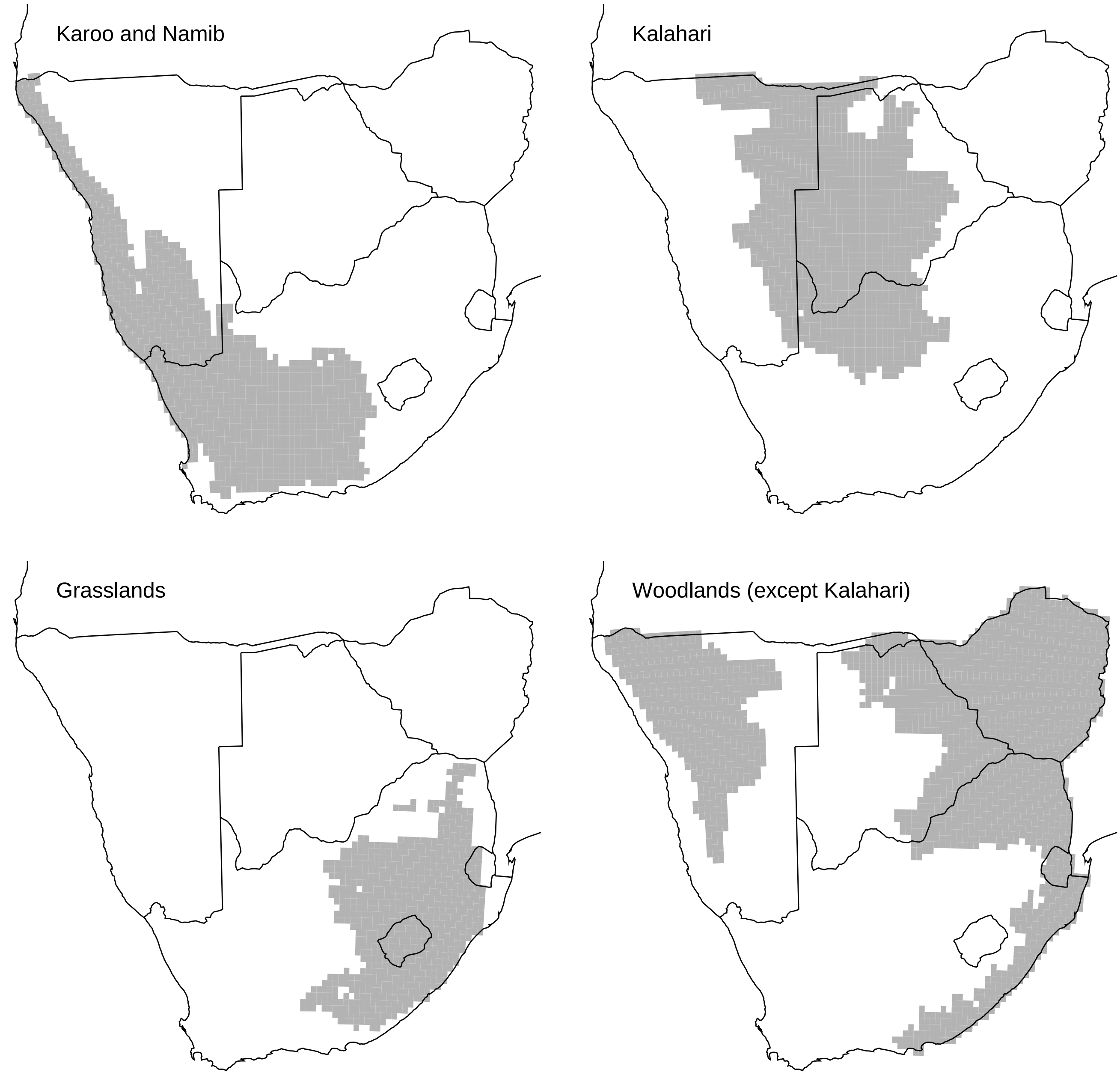


FIGURE 18. Grid maps of the major groups of vegetation types.

The plant diversity of fynbos is not paralleled in its terrestrial avifauna which is depauperate in species relative to other southern African biomes. The endemic avifauna consists of Cape Rockjumper, Victorin's Warbler, Cape Sugarbird, Orange-breasted Sunbird, Protea Canary and Cape Siskin. The distributional limits of the sugarbird and sunbird closely follow those of the fynbos biome. The Black Harrier, endemic to southern Africa, is likely to have most of its breeding grounds in the fynbos. The Knysna Warbler is largely confined to the fynbos but is associated with forest-edge habitats and extends farther along the east coast beyond the limits of the fynbos.

The rockjumper and siskin have their sole congeners restricted to the highlands of Lesotho, in the grassland biome. The Cape Sugarbird has its sole congener, Gurney's Sugarbird, in the high-lying grasslands farther north in southern Africa. The fynbos also shares some species with the Karoo (e.g. Greybacked Cisticola and Karoo Prinia). These examples suggest a biogeographical connection between the avifaunas of the fynbos, grassland and Karoo biomes and an ancient link between them, being quite distinct from the woodland and closed forest biomes farther north and east in the region.

The introduction of alien trees and the establishment of crop fields and planted pastures in the fynbos has resulted in numerous bird species colonizing or increasing in abundance in these areas (Hockey *et al.* 1989) (see **Human Activities** below).

Woodland (savanna) biome

The woodland biome covers most of the northern and eastern parts of southern Africa (Figure 18). We have recognized nine vegetation types in this biome. Woodland is defined here as having a grassy understorey and a distinct woody upperstorey of trees and tall shrubs (Rutherford & Westfall 1986). Tree cover can range from sparse, in the Southern Kalahari and Namibian Escarpment, to almost closed-canopy cover, as in well-developed Miombo woodland. There is an important dichotomy in woodland vegetation types: the arid, fine-leaved, typically *Acacia*-dominated woodlands and the mesic, predominantly broadleaved woodlands (Rutherford & Westfall 1986). The relatively arid woodland types, e.g. the three Kalahari vegetation types and Arid Woodland, typically occur on nutrient-rich, often alluvial, soils in the drier (<650 mm/annum) western regions, and the relatively mesic woodlands, e.g. Miombo and Moist Woodland, typically occur on nutrient-poor (leached) soils in the wetter eastern regions. These two basic types, however, are often closely interdigitated, with *Acacia* woodland on alluvial plains and broadleaved woodland on higher slopes.

Miombo (Figure 33) is broadleaved, relatively tall and dense and, in its well-developed form, approaches closed canopy cover. It is dominated by *Brachystegia* spp. It occurs mainly on the central plateau of Zimbabwe, mostly at altitudes between *c.* 900 m and *c.* 1400 m.

Moist Woodland (Figure 34) comprises predominantly broadleaved, winter-deciduous woodland. A wide variety of plant species form diverse communities, including characteristic species such as *Combretum apiculatum*, *Acacia caffra* and *Faurea saligna.* Grass cover is determined by fire and grazing. Soil types are varied but are generally nutrient-poor; average rainfall ranges between 350–1000 mm.

Mopane (Figure 35) woodland is dominated by *Colophospermum mopane*, a broadleaved tree, generally winter-deciduous, but evergreen near permanent water. The growth habit varies from dense shrubland to tall, open woodland with an open understorey and few grasses. Monospecific stands of Mopane occur on seasonally waterlogged soils in tropical, poorly drained areas with average rainfall >450mm, but the Mopane vegetation type consists typically of a complex mosaic of monospecific Mopane, arid woodland and riparian vegetation. Summers are hot and wet, and winters cool.

Arid Woodland (Figures 36 and 37) comprises predominantly fine-leaved, semi-deciduous *Acacia*-dominated woodlands on rich soils. Broadleaved, winter-deciduous *Baikiaea* woodland on deep Kalahari sands were included in this vegetation type. Arid Woodland occurs where there is intermediate, though variable, rainfall (average 250–650 mm), with hot, wet summers and cool, dry winters.

The **Namibian Escarpment** (Figure 38) is hilly and supports a varied vegetation cover of grasses, shrubs and trees, such as *Euphorbia guerichiana* and several species of *Commiphora*. It is a transitional zone between the woodland biome to the east, the Namib to the west and the Nama Karoo to the south; rainfall averages 100–250 mm.

Valley Bushveld (Figure 39) is a dense, closed shrubland with poorly developed grass cover; virtually impenetrable thickets of thorny shrubs, trees, succulents and creepers, mainly in hot, dry valleys along the east coast. Large euphorbias and aloes are conspicuous features.

The **Northern Kalahari** (Figure 41) consists mostly of dense shrubland or woodland on deep Kalahari sands dominated by semi-deciduous to deciduous *Acacia*, *Terminalia* and *Combretum* trees, and *Acacia*, *Grewia* and *Catophractes alexandri* shrubs. Grass cover is variable dependent on rain, grazing and fires. There are no watercourses, but fossil river valleys and some pans on calcrete, which irregularly hold water. There are hot summer and cold winter seasons; rainfall is in summer (average 400–550 mm), but variable between years.

The **Central Kalahari** (Figure 42) is characterized by sparse to dense shrubland or parkland woodland dominated by semi-deciduous *Acacia*, *Boscia albitrunca*, *Terminalia sericea* and *Lonchocarpus nelsii* trees and *Acacia* and *Grewia* shrubs on deep Kalahari sands. Grass cover is variable dependent on rain, grazing and fires. There are no watercourses, but there are fossil river valleys and many pans, predominantly on calcrete, some of which irregularly hold water. Summers are hot and winters cold, with highly variable rainfall (average 250–450 mm), mostly in summer.

The **Southern Kalahari** (Figure 43 and 44) is on deep Kalahari sands with rolling dunes, and consists of open shrubland with semi-deciduous *Acacia* and *Boscia albitrunca* trees along intermittent fossil watercourses and in interdunal valleys. Grass cover is very variable dependent on rain and grazing. Summers are hot, winters cold; rainfall, averaging <250 mm/annum, is very variable and mostly, but not exclusively, in summer.

The Goldenbreasted Bunting inhabits all vegetation types in the woodland biome, although it is scarce in the Southern Kalahari. Woodland species, the most species-rich community in southern Africa, show complex patterns of presence and absence, and substantially differing reporting rates, between the various woodland vegetation types. The most discrete group is the *c.* 20 species confined to the Miombo woodlands of Zimbabwe, e.g. including Spotted Creeper, Miombo Rock Thrush and Miombo Doublecollared Sunbird. Tarboton (1980) identified the avifauna of Moist Woodland in the Transvaal as being a depauperate subset of that in Miombo. Although the avifauna of Miombo is particularly species-rich, several widespread woodland birds appear to avoid this vegetation type, e.g. Redcrested Korhaan, Pearlspotted Owl and Violeteared Waxbill. Indeed, the Miombo woodlands of Central Africa are a major biogeographical barrier separating the avifaunas characteristic of the dry savanna woodlands found to the north and south in East and southern Africa respectively (Benson & Irwin 1966d); for example, two populations considered subspecies of the Kori Bustard are separated by the Miombo belt.

Even though the Namibian Escarpment is a transition zone between the Namib Desert and the arid woodlands farther inland, it holds endemics such as Hartlaub's Francolin, Herero Chat and Rockrunner. There are also several woodland species which are endemic to the Namibian Escarpment and the adjacent woodlands: Rüppell's Parrot, Monteiro's Hornbill, Carp's Black Tit and Whitetailed Shrike.

The avifauna of the three dry Kalahari woodland types is also characteristic, with many species which are widespread in moister woodlands avoiding the Kalahari, with perhaps the absence of surface water in most of the Kalahari providing the major constraint (see examples above under topography). This is not matched by the presence of any species truly endemic to the Kalahari vegetation types, as all Kalahari birds also extend into other woodland types where patches of *Acacia*-dominated woodland occur. Nevertheless, the Fawncoloured Lark and Kalahari Robin are two examples of species with their ranges obviously centred on the three Kalahari vegetation types. Within the Kalahari, many species also show clear differences between the Southern and Central Kalahari. For example, the Namaqua Sandgrouse and Sociable Weaver are widespread and common in the former but are uncommon in the latter, and the reverse applies to the Lilacbreasted Roller, Forktailed Drongo and Marico Flycatcher.

Over most of the central and western Transvaal, the woodland and grassland biomes abut at *c.* 26°S, and numerous species of both biomes have remarkably linear boundaries at this latitude. Crested Francolin, Greenspotted Dove, Yellowfronted Tinker Barbet, Blackheaded Oriole and Blackcrowned Tchagra are examples of woodland species with part of their southern limits here; Spikeheeled Lark, Cloud Cisticola and South African Cliff Swallow are species typical of the grassland biome reaching their northern limit here.

Valley Bushveld, which extends southwards along the east coast to the eastern Cape Province, supports a depauperate subset of woodland species. The reporting rate presentation used on the distribution maps shows that the southern limits of many woodland species 'fade out' south of central KwaZulu-Natal (e.g. Natal Francolin and Southern Black Tit).

Forest biome

Two forest vegetation types are present in southern Africa, namely **Afromontane Forest** (Figures 45 and 46) and coastal forest (Geldenhuys & MacDevette 1989). All forest patches east of, and including, Alexandria Forest (3326CB) and located within *c.* 40 km of the coast were classified as coastal forests and incorporated in the **East Coast Littoral** vegetation type (Figure 47). Forest patches west of Alexandria Forest, irrespective of their distance from the coast, and those to the east and located farther inland than *c.* 40 km, were classified as Afromontane Forest. The tree-canopy cover in forests is continuous and mainly comprises evergreen tree species (Rutherford & Westfall 1986). Below the canopy, vegetation is multi-layered. Epiphytes and lianas are common in both Afromontane and coastal forests but herbaceous vegetation, especially ferns, are only common in the former. There is, however, little structural difference between the two forest types. The tall, dense trees result in little ground vegetation and a thick leaf litter. Forests only occur in frost-free regions with relatively high rainfall and protected from fires.

The **Afromontane Forest** (Figures 45 and 46) vegetation type occurs at sea-level in the south, but at progressively higher altitudes northwards. It is often confined to moist valleys which are protected from fire, and surrounded by Sour Grasslands in the east and north, or by Fynbos in the south.

The Cape Batis shows a distribution typical of a southern African forest bird, although this species is occasionally found outside true forest in alien plantations and other dense growth (including fynbos). There are clear differences in the avifauna of Afromontane and coastal forests. Many species occurring in the latter are absent from the former, e.g. Green Coucal, Spotted Thrush and Grey Sunbird, and a smaller proportion are present in the former but largely lacking from the latter, e.g. Forest Buzzard, Orange Thrush and Forest Canary. Several species largely breed in Afromontane Forest but undergo altitudinal migration in the winter to coastal forest, e.g. Chorister and Starred Robins (Cyrus & Robson 1980).

Seven species associated mainly with Afromontane Forest are endemic to South Africa, Lesotho and Swaziland: Forest Buzzard, Knysna Woodpecker, Bush Blackcap, Chorister Robin, Knysna Warbler, Forest Canary and Knysna Lourie, recently awarded specific status from forms found farther north (Clancey 1989d). Three additional southern African endemic forest species are Barratt's Warbler (Afromontane Forest), which also inhabits forests in the Eastern Zimbabwe Highlands, Olive Bush Shrike (Afromontane and coastal forests) which also occurs in the forests of the Eastern Zimbabwe Highlands and in southern Mozambique, and Brown Robin (Afromontane and coastal forests), which extends into southern Mozambique. The Afromontane Forests of the Eastern Zimbabwe Highlands support several forest species either endemic to that region or present in southern Africa only there, e.g. Stripecheeked Bulbul, Swynnerton's Robin, Chirinda Apalis, Brier Warbler and Whitetailed Flycatcher. In addition, the only true tropical lowland forest occurring in the atlas region is found in the Haroni–Rusitu region (2033AA) of eastern Zimbabwe, and several lowland forest birds occur there and nowhere else in southern Africa, e.g. Barred Cuckoo, Vanga Flycatcher and Chestnutfronted Helmetshrike.

Vegetation mosaics

Three of the vegetation types, Okavango, Eastern Zimbabwe Highlands and East Coast Littoral, do not fit within the seven biomes listed above.

The **East Coast Littoral** (Figure 47) is a mosaic of coastal forest, sand forest, coastal thicket, coastal grasslands and mangroves. It is typically moist and tropical to subtropical.

The **Eastern Zimbabwe Highlands** is a rugged area having a total relief of *c.* 2000 m (Irwin 1981). The natural vegetation is a complex mosaic of montane grassland, montane heathland, Afromontane Forest, lowland forest and Miombo woodland. Superimposed on this are subsistence and commercial agriculture and extensive afforestation with alien trees. The avifauna has representatives of all the vegetation types included, together with species that have expanded their ranges as a result of anthropogenic factors.

The **Okavango** (Figure 53) vegetation type was kept separate because of its large size, botanical distinctiveness (Bekker & De Wit 1991) and characteristic avifauna (Penry 1994). It is a complex mosaic of a variety of wetland habitats (rivers, lagoons, reed and papyrus swamps, inundated grasslands, seasonal floodplains) and adjacent dry floodplain and riparian swamp-fringing woodland (with evergreen, deciduous broadleaved and semi-deciduous fine-leaved components). Similar habitat combinations are present upstream along the Kavango River in Namibia and along the Kwando–Linyanti and Chobe rivers and to some extent along the (now dry) Savuti Channel. These similar areas were combined into one vegetation type; hence, the Okavango vegetation type extends much wider than merely the swamps of the Okavango Delta. The former comprises the mosaic of wetland, grassland and riverine woodland communities of the Okavango Swamps and the associated floodplains of the Savuti, Linyanti and the area between the confluence of the Zambezi and Chobe rivers in Botswana and the Caprivi Strip in Namibia.

Although they occur further north, beyond the boundaries of the atlas region, several species, including Hartlaub's Babbler, Greater Swamp Warbler, Chirping Cisticola, Swamp Boubou and Brown Firefinch, prefer lush mixed woodland and do not occur outside the Okavango vegetation type in southern Africa. Numerous waterbirds have strongholds in this region; this is discussed further in the following section.

WETLANDS AND RIVERS

Although southern Africa is largely arid, and the total area of wetlands is small, there is a large variety of wetland habitats. Wetland characteristics are dependent on the varied rainfall regimes in their catchments, which may be hundreds or thousands of kilometres distant. This adds major wetland systems to arid areas as another element in wetland diversity; examples are the lower Orange River and the Okavango Delta. Natural wetlands are described in this section; artificial wetlands are considered in the section on **Human Activities**.

Estuaries, lagoons and lakes

Estuaries and lagoons are coastal wetlands typically associated with the mouths of rivers. They are most abundant along the higher-rainfall east and south coasts of southern Africa, although the west coast has several large estuaries, at the mouths of the Kunene, Orange (2816CB), Olifants and Berg (3218CC) rivers. Walvis Bay Lagoon, Sandwich Harbour and Langebaan Lagoon, also on the west coast, are embayments rather than estuaries.

Estuaries and lagoons are the interface between inland freshwater ecosystems and the marine environment; their direct connection to the ocean plays a major role in their ecological functioning and in the species composition and abundance of their avifauna. Estuaries (e.g. Berg River estuary) are defined as being permanently subject to tidal influences, while lagoons typically have closed mouths that are intermittently, sometimes annually, breached by flooding, wave action or human activities (e.g. Bot River Lagoon (3419AC), Verlorenvlei (3218AD)) (Begg 1978).

The inland regions of southern Africa are virtually devoid of true natural freshwater lakes; the few examples include Lake Fundudzi (2230CD) in the far northeast of South Africa, Lake Oponono (1815BB) in northern Namibia and Lake Liambezi (1724CD) in the eastern Caprivi Strip of Namibia. Most of the other large, natural and static waterbodies in the interior fall within the definition of pan ecosystems or are man-made dams (see below). Therefore virtually all of the region's true freshwater lakes occur along the coastline, where they can be differentiated from estuaries and lagoons by being permanently isolated from any seawater influences, which is again important in determining their waterbird communities. Similar to the situation with estuaries and lagoons, the majority of coastal lakes are found along the east and south coasts of southern Africa.

There are more bird species at east coast wetlands than on the west coast; this is largely due to a greater diversity of ciconiiform birds, with sedentary, fish-eating species dominant; on the west coast, the dominant species are migratory, invertebrate feeders (Siegfried 1981). West coast wetlands tend, however, to have greater bird densities than on the east coast.

An important wetland dichotomy is the presence or absence of mangroves; these occur as far south along the east coast as the Nahoon estuary (3227DD) in the eastern Cape Province; there are no mangroves on the west coast (Brown & Jarman 1978; Steinke 1995). There is, however, only one 'mangrove specialist' waterbird, the Mangrove Kingfisher, although several waterbirds find mangrove areas suitable for foraging, e.g. Terek Sandpiper (Siegfried 1981) and Whimbrel (Hockey & Douie 1995).

The difference, in terms of their aquatic avifauna, between tidally influenced estuaries and lagoons, and freshwater coastal lakes, is profound. For example, most Palearctic waders are common at either tidal sites or freshwater lakes, but rarely at both. Little Stint, Ruff and Wood and Marsh Sandpipers prefer the freshwater conditions of coastal lakes, and are also common at inland waterbodies, while Sand and Grey Plovers, Turnstone, Terek Sandpiper, Sanderling, Knot, Curlew, Whimbrel and Bartailed Godwit are largely restricted to tidal mudflats, and are uncommon inland. Ringed Plover, Common and Curlew Sandpipers and Greenshank occur regularly in both saltwater and freshwater environments. A pattern evident from the atlas maps (and confirmed by count data) is that seven of the nine Palearctic waders restricted to tidal habitats are more common along the west coast, becoming progressively less common along the south coast and east coasts; the exceptions are Sand Plover and Terek Sandpiper.

Pans

Pans are endorheic wetlands having closed-drainage systems; water usually flows in from small catchments but with no outflow from the pan basins themselves (Allan *et al.* 1995c). They are typical of poorly drained, relatively flat and dry regions. Water loss is mainly through evaporation, sometimes resulting in saline conditions, especially in the most arid regions. Their shape is usually circular to oval. Water depth is shallow (<3 m), and flooding is characteristically ephemeral. They vary in diameter from a few metres to many kilometres.

The extensive Etosha (in northern Namibia) and Makgadikgadi (in northeastern Botswana) pan ecosystems (Figures 51 and 52) provide critical global breeding sites for both Greater and Lesser Flamingos, the latter considered globally near-threatened (Collar *et al.* 1994). These are the only places in southern Africa where these species breed in large numbers more or less regularly (i.e. every time flooding conditions are right). Indeed, the largest known African breeding colony of the Greater Flamingo occurs at Sua Pan in the Makgadikgadi (Penry 1994). The White Pelican breeds at both localities (Berry *et al.* 1973; Penry 1994); the Caspian Tern breeds at Makgadikgadi, as well as at Barberspan (2625DA) (Cooper *et al.* 1992). The Chestnutbanded Plover has major strongholds at Etosha and Makgadikgadi (Hockey & Douie 1995). These pans, when flooded, support massive populations of a wide diversity of other waterbirds. Etosha and Barberspan are listed as wetlands of international importance under the Ramsar Convention (Cowan 1995; Dodman & Taylor 1996), and the Makgadikgadi would also qualify if Botswana were a signatory.

The 'panveld' of southern Africa is situated on the Central Plateau (e.g. Noble & Hemens 1978), especially in the Nama Karoo (Verneukpan, Grootvloer and Vanwyksvlei all are located near Brandvlei (3020AD)), in the southern Kalahari (Parris 1984; Hines 1996), and in the grassland biome (e.g. Geldenhuys 1982; Allan *et al.* 1995). Pans, however, can also be found along the coastline, e.g. Yzerfontein Pan (3318AC) north of Cape Town (Hockey *et al.* 1989). Innumerable tiny pans are found in woodland regions in the north of the Kalahari basin, particularly on poorly drained soils such as 'black cotton soils' in Mopane veld. There are larger pan systems in the Hwange National Park, Zimbabwe (Irwin 1981), and in the Bushmanland (1920) and Grootfontein (1918CA) regions of northern Namibia (Hines 1996), although the latter may be more akin in ecology and avifauna to tropical floodplains (e.g. Hines 1989). The pans in grassland and Mopane woodland are frequently inundated (usually annually) and only rarely develop saline conditions, owing to the high-rainfall regime; in contrast, those in the drier west (Karoo and Kalahari) are only flooded in occasional, exceptionally wet years. In the eastern parts of the grassland, e.g. in the Lake Chrissie region (2630A), regular high rainfall means that some pans are essentially permanent and are more similar to lakes in their ecological functioning. Such semi-permanent freshwater pans support a greater diversity of aquatic vegetation, and associated waterbirds, than the ephemeral and saline western pans.

A feature of many atlas distribution maps for waterbirds is the concentration of high reporting rates on the eastern plateau of South Africa. This region corresponds with the grassland panveld. The atlas data therefore emphasize the critical importance of this region, and its pans, for southern Africa's waterbird populations to an extent not previously fully appreciated. However, the atlas period was mostly dry, and the western pan ecosystems did not receive adequate rainfall for (sustained) inundation in most years of data collection. During a higher-rainfall period, waterbirds may be spread more evenly across the subcontinent into western regions. During dry periods it is likely that the eastern panveld serves as an important drought refuge. In many cases the atlas maps show waterbird species to have two core areas in South Africa: the southwestern Cape Province and the Central Plateau panveld (e.g. Great Crested Grebe, Cape Shoveller, Southern Pochard and Maccoa Duck). The hypothesis, suggested by the atlas maps, that some species may migrate annually between the winter-rainfall and summer-rainfall regions provides a fruitful avenue for future research. The highly erratic nature of rainfall in the drier regions generally results in nomadic lifestyles.

No southern African waterbird is so specialized that it can be classed as being exclusive to pan habitats. The avifauna of pans is fairly typical of inland static waterbodies generally. The frequent desiccation of pans and their closed drainages, however, are prejudicial to the survival of fish, and piscivorous waterbirds are uncommon at most pans. The ephemeral nature of pans results in rapid nutrient cycling during the short periods for which they hold water, and these habitats can support high densities of waterbirds, and sustain breeding activities; this is particularly noteworthy for ducks and geese, some of which breed relatively scarcely at estuarine and lake habitats (e.g. Geldenhuys 1980a for the South African Shelduck). Inland pans are also important habitats for Palearctic migrant waders, especially Ringed Plover, Common, Wood, Marsh and Curlew Sandpipers, Greenshank, Little Stint and Ruff.

Waterbirds apparently preferring brackish waters and typical of pan ecosystems are Blacknecked Grebe, South African Shelduck, Cape Teal, Greater and Lesser Flamingos and Avocet. Whiskered Tern is largely restricted to breeding at pans (e.g. Allan 1988b) and the breeding sites of the important Greyheaded Gull population centred on the East Rand are at pans, albeit highly modified ones.

Vleis, marshes, dambos, sponges and floodplains

These wetlands are characterized by static or slow-flowing water and are extensively covered with tall emergent wetland vegetation. Sponges are marshes associated with the upper catchments of watercourses and relatively high altitudes. Floodplains are typically associated with the lower reaches of larger rivers, where these enter level terrain and waterflow becomes slow, and the rivers break their banks during flooding to inundate adjacent regions (Figure 56). Floodplains are therefore most typical of coastal flats but can also arise under suitable conditions far inland, e.g. the Okavango Delta, Linyanti and Chobe floodplains and Nylsvlei (2428DA). The terms 'vlei' and 'dambo' are used in South Africa and Zimbabwe, respectively, to describe (mostly seasonally wet) marshy depressions. As with most other wetlands in southern Africa, these aquatic habitats are most common in the higher-rainfall east and extreme south.

No comprehensive map of these types of wetlands is available for all of southern Africa, although their location has been documented to a greater or lesser extent (Noble & Hemens 1978; Begg 1989; Rogers 1995). Despite their significance for waterbird populations, little has been published on the waterbird communities present at individual sites, especially in comparison with coastal wetlands. Among the few examples are Tarboton (1987b) for Nylsvlei (in addition Higgins *et al.* (1996) provided a detailed review of the ecology of this system) and Kok & Roos (1979) for Seekoeivlei.

Botswana and Namibia are largely too arid to support these types of wetlands, although the Cuvelai drainage (1715,1815) into the Etosha Pan functions as an inland delta and is important for waterbirds (Lindeque & Archibald 1991; Hines 1996). The major exception to this, however, is the extensive wetland system of the Okavango Delta, an inland delta or 'fan'. There are similar floodplain wetlands associated with the Kwando, Linyanti, Savuti and Chobe rivers, and in the triangle formed by the Zambezi River at its confluence with the Chobe River. This wetland complex covers much of northern Botswana and the adjacent Caprivi Strip of Namibia. The Okavango Delta, with an area of 16 000 km^2, is probably the single most important wetland in southern Africa, rivalled only by the Lake St Lucia–Mkuzi Swamps–Mfolozi complex in KwaZulu-Natal. Two southern African wetlands in this category are listed as wetlands of international importance under the Ramsar Convention: the Cuvelai drainage (along with Lake Oponono and Etosha Pan) and Blesbokspruit (Dodman & Taylor 1996), though the Okavango would also qualify if Botswana were a signatory.

The list of waterbirds for which vleis and floodplains provide significant habitat is long, and only key species are highlighted here. The Wattled Crane, a globally threatened species (Collar *et al.* 1994), is in South Africa restricted to relatively high-altitude sponges and marshes of the eastern grassland regions (Tarboton *et al.* 1987b). It is also found in the larger dambos of Zimbabwe (Morris 1987), as well as having a major stronghold in the Okavango Delta and associated floodplains of northern Botswana and the Caprivi Strip (Brown 1992; Mangubuli & Motalaote 1996). The Crowned Crane, another crane of conservation concern (Meine & Archibald 1996), shares many of the same wetlands with the Wattled Crane in South Africa and Zimbabwe (e.g. Morris 1987; Johnson 1992; Tarboton 1992a). The globally threatened (Collar *et al.* 1994) Whitewinged Flufftail is restricted in the region to a few high-altitude sponges in South Africa; e.g. Middelpunt (2530CA), Wakkerstroom and Franklin vleis (Taylor 1994).

The vleis and floodplains of Zimbabwe, northern Botswana and northern Namibia are characterized by a suite of tropical waterbirds, a few of which extend into South Africa at Nylsvlei (Tarboton 1987) and some wetlands of northern KwaZulu-Natal: Rufousbellied Heron, Dwarf Bittern, Pygmy Goose, Streaky-breasted Flufftail (Tarboton 1996a), Striped Crake (Tarboton 1996a), Lesser Moorhen, Lesser Gallinule, Lesser Jacana, Natal Nightjar and Pinkthroated Longclaw. Well-vegetated vleis and floodplains are major strongholds of the skulking Rallidae (crakes and rails), although further research in this regard is needed (Taylor 1997a,b).

The Okavango Delta and the associated wetlands of northern Botswana and the Caprivi Strip support a rich waterbird community perhaps best characterized by large populations of numerous species of herons and aquatic storks, especially the Saddlebilled Stork (Mangubuli & Motalaote 1996). The Slaty Egret, a globally threatened species (Collar *et al.* 1994), has a major proportion of its world population centred on these wetlands. Major breeding sites of herons and storks in this complex were described by Fraser (1971a), Child (1972), Fothergill (1983a), Fry *et al.* (1986), Randall (1988b), Hines (1992) and Randall & Herremans (1994). The Pygmy Goose (Brown & Seeley 1973) and African Fish Eagle have their major southern African strongholds in this region. Other key species include Wattled Crane (mentioned above), Western Banded Snake Eagle (Brown & Hines 1987), Longtoed Plover and Pel's Fishing Owl (Liversedge 1980). Two small passerine wetland birds, Greater Swamp Warbler and Chirping Cisticola, are restricted to these wetlands in southern Africa. Many waterbirds, however, are surprisingly absent or scarce in the Okavango, most noticeably many ducks, geese and the Redknobbed Coot, but also species such as Bittern, Crowned Crane and African Finfoot. These patterns of abundance and scarcity are readily apparent in the atlas maps.

Rivers

Along the moist southern and eastern coasts of South Africa there are numerous river courses draining south and east, usually with relatively small catchments due to the close proximity of the Great Escarpment. Most of the western and central interior of South Africa is drained to the west by the extensive Orange–Vaal system. The Fish River catchment covers a large proportion of southern Namibia and drains into the Orange River. The northern Transvaal, eastern Botswana and southern Zimbabwe drain eastwards through the Limpopo–Shashi system into Mozambique. In southeastern Zimbabwe, the Runde and Save rivers drain into Mozambique. Most of northern Zimbabwe falls into the Zambezi River catchment, as does the eastern Caprivi via the Kwando and Chobe systems. In the western Caprivi, the Kavango River flows southeast from Angola into the extensive Okavango Delta of Botswana. In northwestern Namibia, the Kunene River flows west from Angola into the Atlantic Ocean.

Most rivers are in the higher-rainfall east and extreme south of southern Africa and, not surprisingly, there is a gradient of increasingly intermittent river flow with increasing aridity farther west. Most rivers in areas of rainfall below 500 mm are seasonal or flow only for short periods after heavy rain, but they may have pools for most of the year. The Zambezi and Orange rivers have the longest river courses; the Orange River is 1950 km in length, with a catchment area of 852 000 km^2 (Van Zyl 1991) covering 47% of South Africa (Figure 54).

The courses of many of southern Africa's major rivers can be discerned on the atlas maps by the linear distribution of records following the routes of these rivers. This is most striking for the lower Orange River as it passes through the otherwise arid western parts of the region; good examples are Darter, Goliath Heron, Hamerkop, African Black Duck, African Fish Eagle, Cape Francolin, Pied and Malachite Kingfishers, Swallowtailed Bee-eater, African Pied Wagtail and Cape Robin.

There are 13 species of waterbird that are mostly restricted to riverine habitats: Whitebacked Night and Greenbacked Herons, Black and Saddlebilled Storks, African Black Duck, African Finfoot, Whitecrowned Plover, Green Sandpiper, African Skimmer, Rock Pratincole, Pel's Fishing Owl, Half-collared Kingfisher and Longtailed Wagtail (although the Black and Saddlebilled Storks, and the Pel's Fishing Owl are also regular on some floodplain and estuary habitats). The atlas maps for these species mirror the courses of the river systems within their ranges.

HUMAN ACTIVITIES

Human activities, or 'anthropogenic factors', have had a dramatic impact on bird distributions in southern Africa, and this is clearly visible in many of the atlas maps. Some species have benefited by association with man-made habitats; others have declined as a result of destruction of their natural habitats.

One of the frequent impacts of anthropogenic factors is to obscure the association between bird distribution patterns and natural vegetation types. Species may become so reduced in distribution and/or density, owing to some anthropogenic factor, that former close associations between their distributions and vegetation types are no longer apparent. Conversely, but with the same result, anthropogenic factors may lead to species expanding their distributions beyond the vegetation types in which they occurred naturally.

Poisons

Poisons have had severe negative impacts on bird populations; in the atlas, this is best illustrated in the current distribution patterns of the vultures and large eagles.

After the first wave of explorers and hunters, southern Africa was occupied, mainly during the 19th century, by European settlers who sought to make a living off the land. With little insight into the role of vultures in nature, they regarded them, along with all other scavengers and predators, as requiring extermination. The favoured technique was to poison carcasses with strychnine, and vultures, as scavengers of dead meat, were among the most heavily impacted (Mundy *et al.* 1992). The result is that the present distributions of all the vultures in southern Africa are mere relict fragments of their former ranges, confined to the larger protected areas, and to areas where subsistence farming continues, in the former 'homelands' of South Africa and Namibia, the 'tribal trust lands' of Zimbabwe, and Botswana.

In many places, this attitude to predators and scavengers still prevails. So-called 'problem-animal' control measures continue to be a widespread feature of commercial farms in southern Africa. Blackbacked Jackal *Canis mesomelas* and Caracal *Felis caracal* are the usual target species on stock farms and are combated with a variety of poisoning techniques, e.g. poisoned carcasses and the random spreading of small poisoned baits. These poisoned carcasses prevent vultures recolonizing areas where they might well be able to survive on the natural mortality of domestic herds. Other carrion feeders (e.g. Bateleur and Tawny Eagle) have also been eradicated from commercial stock-farming areas. In the case of the Bateleur and the Whiteheaded Vulture, their vulnerability is believed to have been aggravated by their searching rapidly at low altitudes, causing them to be first at small poisoned baits (Watson 1986; Mundy *et al.* 1992).

Marine habitats: The open ocean is the habitat of pelagic seabirds which feed on fish, squid and offal from fishing boats. A small number of offshore islands provide important breeding habitat for some of these species.

Figure 19. ***Pelagic seabirds****, albatrosses, petrels and gannets, at sea off the Cape Peninsula.*

K.N. Barnes

R.A. Navarro

Figure 20. *Roosting Cape Gannets on Malgas Island, one of the islands on which colonial seabirds breed. The headland of Saldanha Bay (3317BB) is visible in the background.*

J.A. Harrison

Figure 21. *The* ***coastline and its shores****, both sandy and rocky, are the habitat of shorebirds. The Robberg Peninsula (3423AB), southern Cape Province.*

R.A. Navarro

Desert biome: The **Namib** Desert is a true desert with less than 100 mm of rainfall per annum. It does receive significant amounts of moisture in the form of fog which is adequate for a small amount of plant growth and a specialized fauna. The landscape is dominated by sand dunes and gravel plains – both visible in the illustration – and very sparse vegetation in areas with a stable substrate.

Figure 22. *Naukluft National Park, Namibia.*

Succulent Karoo biome is characterized by winter rainfall, very little grass cover, an abundance of flowering annuals in late winter and spring, and a dominance of dwarf, succulent shrubs. The succulent Karoo veld of the **Little Karoo** (parallel to the south coast) is tall and dense relative to that in the west, with a tree component in places.

K.N. Barnes

Figure 23. ***Succulent Karoo** veld in the Tankwa Karoo, near Katbakkies Pass (3219DC).*

D.M. Richardson

Figure 24. Aloe ferox *near Calitzdorp (3321DA) in the **Little Karoo**.*

Strandveld is relatively dense scrub vegetation near the coast, often on permanent dunes. It contains a large number of fruiting shrubs which attract some species which are absent or scarce further inland. For the purposes of the vegetation analysis, strandveld was included with Fynbos and Succulent Karoo along the west coast, and with Fynbos along the south coast.

Figure 25. ***Strandveld*** *vegetation south of Lambert's Bay (3218AB), western Cape Province.*

D.M. Richardson

C.N. Spottiswoode

The **Nama Karoo biome** is characterized by predominantly summer rainfall, variable but significant grass cover, and a variety of dwarf shrubs, but not as many succulent species as in the Succulent Karoo. The **Grassy Karoo** is transitional between the Nama Karoo biome and the Grassland biome, but belongs to the former. The grass cover is relatively dense, especially after good rains.

Figure 26. ***Nama Karoo*** *veld with typical Karoo 'koppies', near Three Sisters (3123CC).*

D.G. Allan

Figure 27. ***Grassy Karoo*** *veld east of Victoria West (3123AC).*

The **Grassland biome** is restricted to eastern South Africa, Lesotho and western Swaziland. (Relatively small, isolated patches of tropical grassland occur in Zimbabwe.) It is a centre of plant and animal endemism in southern Africa, and many species are threatened owing to the high levels of human activity and habitat alteration which prevail.

Sweet grasslands are relatively dry and nutrient rich and occur primarily on the plains. Originally they were the ecological base for large roving herds of game, but the vegetation type has been largely converted to agriculture and what remains is fragmented.

D.M. Richardson

Figure 28. *Red Hartebeest in* Cymbopogon–Themeda *veld (Acocks Veld Type 48), Faan Meintjies Nature Reserve(2626DA), southern Transvaal.*

Sour grasslands are generally associated with relatively high altitudes and rainfall. Here, as in other grasslands, there is a marked contrast in the seasonal appearance of the veld, being lush and green after summer rains, dry and brown during winter.

G. Holtshausen

Figure 29. *A summer aspect on the escarpment, eastern Transvaal . . .*

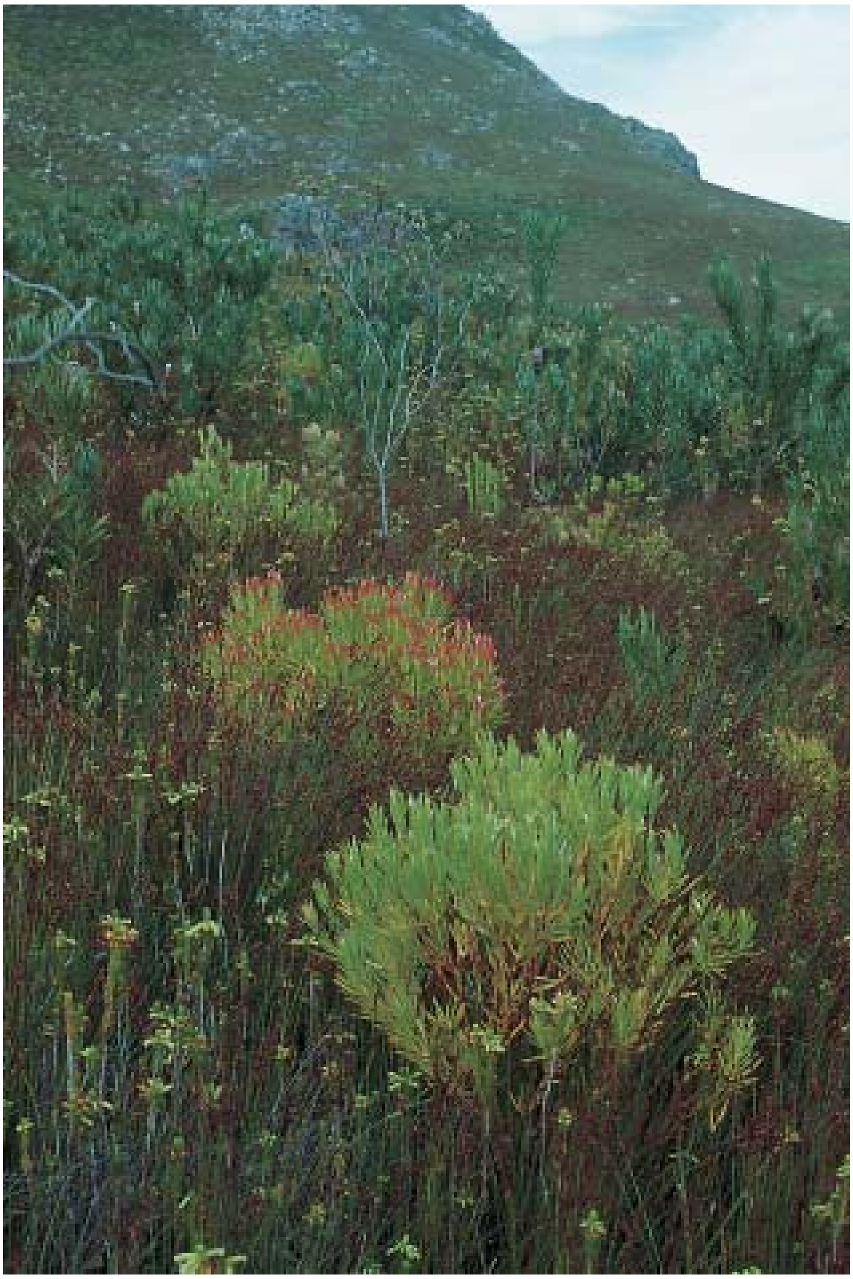
J.A. Harrison

Figure 30. *. . . and a winter aspect, Loteni Nature Reserve (2929BC), Drakensberg, KwaZulu-Natal.*

D.Butchart

Figure 31. ***Alpine grasslands*** *occur on high-altitude (>1800 m) peaks and plateaus and comprise sour grasses and dwarf shrubs. Severe frosts and snowfalls are regular winter occurrences which pose important ecological constraints on the vegetation and its associated fauna. Highlands at Bokong (2928AC), Lesotho.*

J.A. Harrison



The **Fynbos biome** is characterized by macchia vegetation of varying height. Important components of these exceptionally species-rich shrublands are species of the families Proteaceae (proteas, conebushes, etc.), Restionaceae (reed-like tussocks) and Ericacae (heaths).

Figure 32. *Montane* ***fynbos*** *near Kleinmond (3419AC).*

G. Holtshausen

The **woodland** or **savanna biome** is a combination of trees, scrub and grass. Important variables in determining the type of woodland are the height of the trees, the distance between trees, and the mix of tree species, particularly whether most are fine-leaved acacia or broadleaved deciduous species. The condition of the grassy understorey varies dramatically with seasonal rainfall and grazing pressure.

Figure 33. ***Miombo woodland*** *consists mainly of broadleaved species, particularly* Brachystegia *spp. The interior of Miombo woodland in Zimbabwe.*

Figure 34. ***Moist woodland*** *is a mixture of broadleaved and fine-leaved species, with the broad-leaved component tending to dominate. A moist woodland south of Mbabane (2631AD), Swaziland.*

C.N. Spottiswoode

P. Steyn

Figure 35. ***Mopane woodland****, in Moremi Game Reserve, northern Botswana, here consisting of a monotypic stand of the broadleaved species,* Colophospermum mopane, *and a typically sparse grassy understorey.*

C.N. Spottiswoode

Figure 36. ***Arid woodland****, consisting of a mixture of species, mainly of the genus* Acacia. *An arid woodland near Gaborone (2425D), southeastern Botswana, after good rains; note the tall grass.*

M. Herremans

Figure 37. *A potentially similar arid woodland, near Maun (1923C), northern Botswana, but during a* ***drought*** *period. The trees have lost their leaves and the ground is denuded by grazing (including by termites).*

C.N. Spottiswoode

Figure 38. *The vegetation of the* ***Namib Escarpment*** *is equivalent to an arid savanna on broken terrain. The structure and species composition of the woodlands vary, becoming more stunted and sparse in the south. Landscape near Omaruru (2115BA), Namibia.*

D.M. Richardson

Valley bushveld, also known as 'subtropical thicket', is tall and dense with arborescent euphorbias and aloes as dominant features.

Figure 39. ***Valley bushveld*** *near Suurberg (3325A), eastern Cape Province.*

Palm savanna is patchily distributed on floodplain soils in the moister tropics and subtropics, e.g. the Okavango, Owambo and Makgadikgadi.

Figure 40. Hyphaene ***palm savanna*** *on an island in the Okavango Delta.*

M. Herremans

M. Herremans

The Kalahari, although relatively arid, is not a true 'desert' but a variety of arid savannas on deep sands, and is therefore part of the woodland biome. As in Arid Woodland, the condition of these woodlands varies dramatically between periods of good rains and drought, particularly with regard to the amount of leaf and ground cover.

Figure 41. *Mixed* ***Northern Kalahari*** *woodland, near Phuduhudu (2024B), northern Botswana, after good rains.*

In the **Central Kalahari** woodland scrub is dominant and trees are relatively sparse.

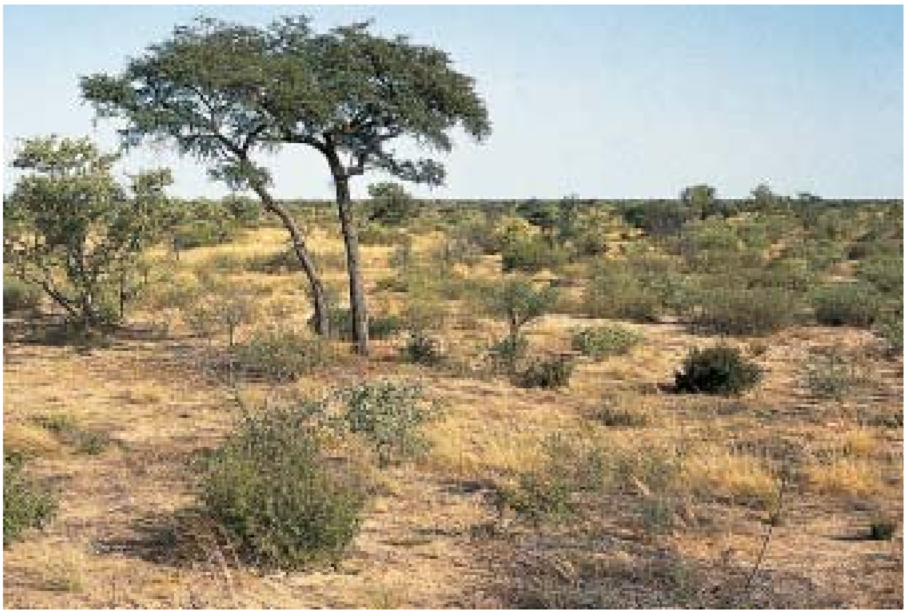


Figure 42. *Khutse Game Reserve (2324A), central Botswana.*

M. Herremans

The **Southern Kalahari** is based largely on a substrate of permanent sand dunes. Depending on the depth of sand and the availability of ground water, *Acacia* parklands or stunted scrublands tend to predominate.

Figure 43. *Dune veld north of Upington (2821AC).*

D.G. Allan

R.A. Navarro

Figure 44. Acacia *parkland along Nossob River, Kalahari Gemsbok Park (2520DA).*

D.G. Allan

The **Forest biome** comprises evergreen forests which occupy a relatively tiny area of southern Africa, but provide indispensable habitat for several forest specialist species, including a few southern African endemics, such as the Chorister Robin. The forests are of two types, Afromontane and coastal. Coastal forest is largely confined to the tropics and subtropics along the east coast. Afromontane forest occurs at relatively high altitudes, but at progressively lower altitudes further south, down to sea-level on the south coast.

Figure 45. *The closed canopy of a patch of **Afromontane forest** surrounded by sour grasslands in the midlands of KwaZulu-Natal.*

K.N. Barnes

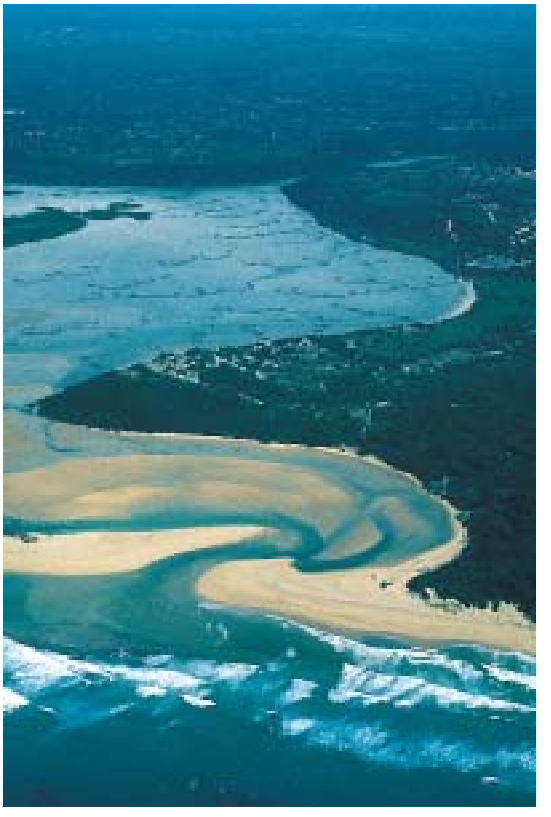
Figure 46. *The moist, dark interior of an **Afromontane forest**, Tsitsikamma (3323D), southern Cape Province.*

D. Kirkwood

Figure 47. *An example of the **East Coast Littoral** vegetation mosaic, here showing coastal grassland with dune forest in the background, St Lucia (2832B), northern KwaZulu-Natal.*

Freshwater wetlands occur in a variety of forms, an important variable being the amount and density of emergent aquatic vegetation. They provide habitat for waterfowl, waders and reedbed dwellers, such as rails. Endorheic pans are seasonal wetlands which have no outflow point. Their size ranges from tiny to enormous. They are very numerous in parts of southern Africa and because they dry up slowly by evaporation, they provide important wetland habitat in otherwise arid areas. Some particularly large pans are situated in arid areas and contain water very irregularly, e.g. Etosha Pan in northern Namibia and the Makgadikgadi Pans in northeastern Botswana; after good rains they can provide ideal breeding conditions for large waterbirds, e.g. flamingos and pelicans.

An **estuary** is that part of a river which is affected by the tides and by seawater. Estuaries and lagoons provide food-rich habitats for shorebirds and some other waterbirds.



L.G. Underhill

Figure 48. *Kosi Bay, northern KwaZulu-Natal.* (*Traditional fish traps are visible.*)

D. Butchart

Figure 49. *A* ***palustrine wetland****, or 'vlei', with plenty of emergent vegetation, in Pinda Game Reserve (2732CB), northern KwaZulu-Natal.*

D. Kirkwood

Figure 50. *Emergent vegetation and coastal forest on the fringes of a freshwater coastal lake, Lake Sibaya (2732BC), in northern KwaZulu-Natal.*

Figure 51. *Aerial view of part of* ***Sowa Pan****, in the* ***Makgadikgadi Pans*** *area, northeastern Botswana. Note the veterinary cordon fence in the foreground and the small body of water with waterbirds. The large pale-coloured areas are salty crust which becomes inundated after good rains.*

P. Mundy

Figure 52. ***Etosha Pan****, northern Namibia, in dry condition with giraffes in the distance. Typical halophilic fringing vegetation visible in the foreground.*

D.M. Richardson

P. Steyn

Figure 53. *The* ***Okavango*** *swamps in northern Botswana constitute the inland delta of the Okavango River. The swamps provide a wealth of wetland and moist habitats, including well-developed gallery woodland and palms, in the midst of the relatively arid northern Kalahari.*

Rivers, both perennial and seasonal, provide a range of habitats, including riverine scrub, gallery woodland, reedbeds, sandy beaches and islands, and sometimes steep, incised banks of rock or sand which afford nesting sites for birds.

P. Steyn

Figure 54. *The **Orange River** provides a ribbon of moisture and trees through an arid region, and several species have linear distributions along it.*

G. Holtshausen

Figure 55. ***Perennial rivers in subtropical regions** are flanked by strips of tall, dense riverine woodland. The Luvuvhu River (2231A) in the northeastern Transvaal.*

P. Steyn

Figure 56. ***Floodplains** are the relatively broad, flat areas on either side of riverbeds which are inundated seasonally when rivers come down in flood. They provide rich, seasonal habitat for waterbirds. The Chobe floodplain near Kasane (2832B), northern Botswana.*

M. Herremans

Anthropogenic habitat changes: human activites are destructive to natural habitats but they create new habitats. Some species tend to suffer while others tend to benefit.

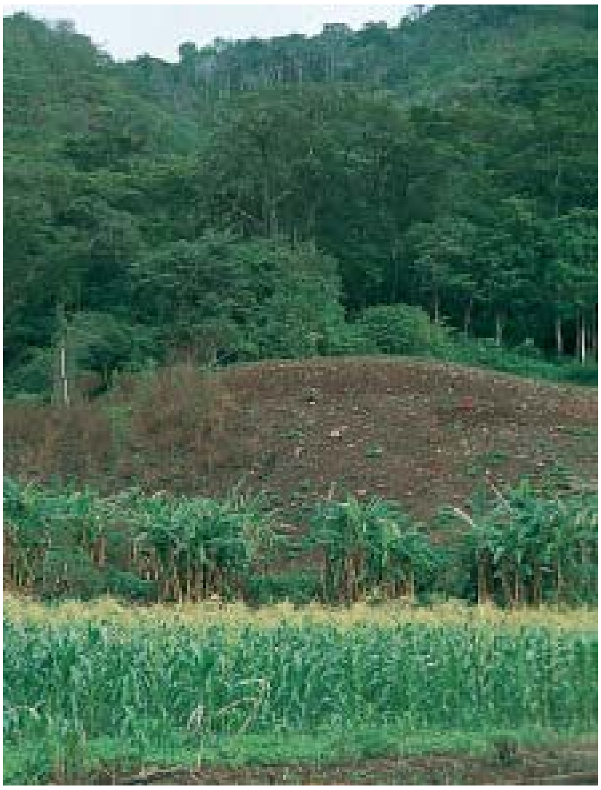
Figure 57. *A typical* ***grazing*** *contrast along the 'buffalo fence' near Maun (1923C), Botswana. The degraded veld on the right is the result of overgrazing by livestock; the conservation area on the left is grazed by wildlife.*

Figure 58. *Severe* ***soil erosion*** *near Maseru (2927AD), Lesotho. This area lies in the headwaters of the Caledon River which flows into the Orange River and contributes to its silt load.*

K.N. Barnes

J.A. Harrison

Figure 59. ***Burnt*** *Mixed Grassland in the eastern Free State.*



C.N. Spottiswoode

D.M. Richardson

D.H. de Swardt

Figure 60 *(top left). Small-scale* ***subsistence farming*** *at the expense of the lowland Vhimba Forest (2032BB), Haroni–Rusitu, Zimbabwe.*

Figure 61 *(top right).* Pinus pinaster *(right) invading montane fynbos (left) in the Cape fold mountains, near Villiersdorp (3319CD). Manual clearing of* ***invasive aliens*** *(centre) is difficult and costly.*

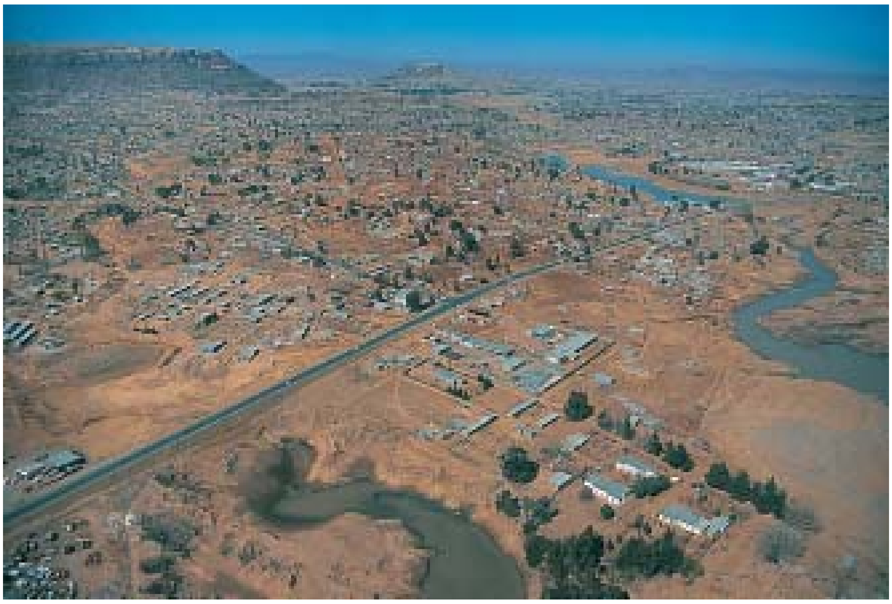
R.A. Navarro

Figure 62 *(above).* ***Afforestation*** *with pines; a plantation in the background contrasts sharply with the grassland and open* **Protea** ***woodland*** *in the foreground. Lydenburg (2530AB) district.*

Figure 63 *(right).* ***Commercial crop agriculture*****:** *wheatlands with some fragmented renosterveld fynbos, southern Cape Province. Cape fold mountains visible in the background.*

G. Holtshausen

Figure 64. *A typical water* ***impoundment****, near Eshowe (2831CD), KwaZulu-Natal.*



K.N. Barnes

Figure 65. ***Urban sprawl****; Maseru (2927AD), Lesotho.*

J.A. Harrison

Figure 66. ***Powerlines*** *crossing strandveld near the Koeberg nuclear power station, outside Cape Town (3318CB).*

The effects of the use of DDT and other organo-chloride insecticides in the past have not been well documented in southern Africa, but can be assumed to have been as serious as in the developed world. Of concern is that many of these chemicals, including DDT and Dieldrin, are still being used in southern Africa, often illegally (Allan 1989b).

The Redbilled Quelea causes serious damage to small-grain crops and is the target of large-scale control operations (Bruggers & Elliott 1989; Mundy & Jarvis 1989). These are directed at roosts and breeding colonies, and usually involve either aerial spraying with Queleatox poison, or fire-bombing with explosives and flammable fuels. These measures inevitably result in mortality of non-target species, especially as quelea nests attract a wide range of avian predators, including large raptors (Allan *et al.* 1995b). Where these operations are frequent, the impact on local populations of non-target species must be severe.

Accidental and deliberate poisoning of birds with poisoned seed is a frequent occurrence on agricultural lands, and has occasionally caused mass mortality of, for example, Blue Cranes (e.g. Allan 1993). Many unexplained local changes in abundance of species (e.g. the disappearance of Cape Wagtail from many city suburbs) may have been caused by the use of poisons or other chemicals, but the lack of monitoring programmes and detailed investigations makes it difficult to draw firm conclusions.

The so-called 'purple-label' dips to kill ticks on domestic animals contained arsenic and were lethal to oxpeckers; the distributions of the two species were limited to the protected areas within their ranges. With the introduction of non-toxic (to oxpeckers) 'green label' dips, both species have expanded their ranges, in places by deliberate translocations (Lockwood 1995).

Hunting, exploitation and disturbance

Most raptorial birds, particularly the large eagles, have in the past been perceived as threats to domestic animals and have been actively hunted by farmers. Eagles and even smaller raptors have been accused of taking lambs and poultry. This undoubtedly led to a reduction in the numbers of many species, but probably did not greatly change distribution patterns (e.g. Martial Eagle). The taking of lambs has been exaggerated in the past and campaigns to educate farmers are having positive results (G.H. Verdoorn, EWT Raptor Conservation Group pers comm.); more enlightened attitudes towards these birds have begun to take hold in recent years and it is possible that a reversal of population declines will occur in some areas. The Black Eagle preys on Rock Hyrax *Procavia capensis* (Gargett 1990), and farmers have found that a pair of Black Eagles can help to control the damage to grazing caused by these small herbivores by restricting the foraging range of the hyraxes to the vicinity of rocky outcrops (Davies 1994).

The Black Eagle also provides an example of a raptor whose distribution appears to have been altered by the hunting-out of its prey base. One would expect this montane species to be common in the Lesotho highlands, but the reverse is true. As it is largely dependent on the availability of its favoured prey, hyraxes, its absence is almost certainly due to the absence of prey which, in turn, is due to the widespread hunting of hyraxes for food by herdsmen and their dogs (Osborne & Tigar 1990).

Licensed hunting of game birds for sport continues, but is not believed to have any large-scale negative effects (e.g. Little & Crowe 1993b). However, it appears that the unregulated exploitation of wild birds by poor rural communities may be having an important impact on some species. Atlas reporting rates for the Helmeted Guineafowl drop markedly across the border from the Transvaal to Botswana, suggesting that the species is being exploited extensively for food in Botswana.

The latter species, along with many other ground-nesters (e.g. Blue Crane, Stanley's Bustard and Crowned Plover), has a distinct 'hole' in its distribution in Lesotho and Transkei, both areas with dense human populations (up to 78 persons/km^2: Macdonald 1989; O'Connor 1991) of poor rural people engaged in subsistence farming. It is not possible at present to know whether direct exploitation or incidental disturbance by people and livestock, or both, is the primary reason for this absence, but the effect is clearly anthropogenic.

The over-exploitation of marine fish resources affects pelagic seabirds (Crawford & Dyer 1995). The fisheries based on the rich Benguela ecosystem off the west coast have already depleted stocks of some species such as Pilchard, and others may soon follow. This has had an impact on the Jackass Penguin which also suffered from exploitation of its eggs until 1968 (Shelton *et al.* 1984).

The practice of guano scraping on offshore islands not only disturbs seabirds, but prevents Jackass Penguins from burrowing into the guano to build their nests. Penguins nesting in surface nests are exposed both to the elements (sun, wind and rain) and to predation of eggs and small chicks by Kelp Gulls (Berruti 1989). Guano is no longer collected at these islands.

Several pelagic seabird species, including albatrosses and petrels, are vulnerable to incidental mortality as a by-catch of longline fisheries (e.g. Brothers 1991; Barnes *et al.* in press). The birds are hooked and drowned as they take baits at the surface and are dragged underwater. The affected species are generally long-lived and reproduce slowly; hence the impact of the deaths of tens of thousands of birds per annum is likely to be severe.

The practice of discarding offal overboard from fishing trawlers has led to the phenomenon of seabirds, especially Whitechinned Petrels and Mollymauks, following such vessels in thousands. One consequence of this practice is to break down the migratory patterns of, for example, the Cape Gannet. In the 1950s and 1960s, significant numbers of recoveries of ringed gannets were made along the West African coast in winter; nowadays it seems that their food requirements at this time of the year are met by discards (Oatley 1988; Berruti *et al.* 1993).

Another form of direct exploitation is the capture of wild birds for the cage-bird trade. Attractive seed-eating species, such as the waxbills, are particularly sought after. This is done legally under a quota system in Botswana; the extent of the illegal trade in southern Africa is unknown but could be considerable and has the potential to reduce populations locally. The species probably needing the greatest protection from illegal trapping are the parrots and lovebirds, particularly the threatened Cape Parrot.

Ranching, grazing and burning

Grazing by domestic livestock is usually a relatively low-impact form of land-use. Provided stocking densities are kept at levels appropriate to the carrying capacity of the land, more-or-less natural plant communities are maintained. Social and economic factors, and the dynamics in the carrying capacity of the land itself, frequently encourage such levels to be exceeded, however, and this can have severe consequences (Figure 57). Particularly in drought periods, overgrazing leads to a virtual eradication of grasses, and damage to the structure of the soil through trampling (Figures 37 and 58). Soil erosion by wind and rain is one negative consequence, bush encroachment in the savanna regions is another. The absence of grass favours the germination and survival of trees and shrubs which then tend to grow in dense thickets (Campbell & Child 1971; Van Rensburg 1971; Werger 1978; McLeod 1992; Ringrose *et al.* 1992).

Such a change in vegetation structure favours species which forage in scrub, and puts species which forage on the ground or in grass, or which require open spaces in which to hunt prey, at a disadvantage. The consequences of bush encroachment on bird communities are particularly prevalent in the Kalahari of Botswana where thornbush-loving species (e.g. Titbabbler, Pied Barbet, Redeyed Bulbul, Blackchested Prinia, Marico Flycatcher and Crimsonbreasted Shrike) are more common on rangeland than in conservation areas, while the reverse is true for a number of the larger species preferring open grassy patches (e.g. Whitewinged Black Korhaan, Kori Bustard, Ground Hornbill, Ostrich and Secretarybird) (M. Herremans unpubl. data).

The burning of grass (Figure 59) is one means by which farmers attempt to maintain the balance between grass and bush because fire kills bush seedlings and stimulates new growth of grass. Burning is also used in pure grasslands to remove senescent grass cover and produce a burst of succulent new growth. However, too-frequent burning followed by heavy grazing can lead to impoverishment of the soil and to shifts towards the dominance of unpalatable species (Macdonald 1976). Too-frequent burning also decimates valuable scrub, such as protea scrub in montane grasslands and montane fynbos, upon which nectarivores such as sugarbirds and sunbirds are dependent (Kruger & Bigalke 1984).

There are several bird species which must leave when grasslands are burnt, and may lose eggs and chicks if burning takes place during breeding (e.g. game birds). Other species are attracted to freshly burnt areas (e.g. dryland plovers), or even to the moving fronts of fires (e.g. Forktailed Drongo), to exploit flushed and incapacitated insects. Grassland birds also tend to be sensitive to the height and density of the grass cover (e.g. Hockey *et al.* 1988a). In general, a mosaic of relatively small patches with grasses at different stages of grazing and recovery from fire is ideal for maintaining biodiversity as it offers a wide range of conditions.

Crop agriculture and deforestation

The tilling of the soil is often thought of as an 'improvement' of the environment but it is in fact one of the most drastic and irrevocable alterations wrought on natural systems (Figures 60 and 63). It completely destroys the structure and species composition of the natural vegetation, either temporarily or permanently, and thereby has a massive impact on the birds which are dependent on that vegetation. This is as true in grassland and fynbos as in scrubland or woodland. On the other hand, species which are able to exploit monocultures of cultivated crops, or some by-product of cultivation (e.g. bare ground), may benefit substantially. However, the ecology of cultivated lands is essentially unstable because it is intensively managed and subject to the vicissitudes of market forces and agricultural policies, and therefore even species which benefit in the short term may be disadvantaged later on.

The vegetation types most impacted by conversion to croplands are renosterveld (a subset of fynbos) to wheatlands in the Overberg and Swartland regions of the southwestern Cape Province (Figure 63); Sweet Grassland to maize and wheat in the central and northern Free State and the southern Transvaal; grass lands and thickets of the East Coast Littoral to sugar-cane; and riparian forests and woodlands in many regions to vineyards, orchards and various irrigated crops.

The extensive human pressures on the grassland biome as a whole have severe conservation implications for its avifauna; no less than 11 of the 14 globally threatened species present on the mainland of South Africa, Lesotho and Swaziland (Collar *et al.* 1994) have major strongholds in the grassland biome and five of these (Bald Ibis, Whitewinged Flufftail, Rudd's and Botha's Larks, and Yellowbreasted Pipit) are entirely restricted to this biome in the region.

The birds least likely to show the effects of these transformations are the small species which are able to persist in small, fragmented remnants of undisturbed habitat. Conversely, the species most likely to show disrupted patterns of distribution are large species with large home ranges. This can be seen in the distribution of the Blue Crane which shows evidence of a major decline in the Sweet Grasslands. Ironically, the Blue Crane has also benefited from agriculture in that it is able to exploit the conditions which prevail in fallow lands, pastures and fields of wheat stubble in the Overberg. It did not originally occur in the fynbos scrub of this region, but cultivated lands, as they are currently managed in the Overberg, offer it a suitable type of secondary grassland, to the extent that this area now sustains an important concentration of the species (Allan 1992b).

Many itinerant species benefit from croplands and orchards as they are able to exploit different stages in the agricultural cycle, e.g. sowing, fruiting, harvesting, fallow periods, etc. Some noteworthy examples are White Stork, Egyptian and Spurwinged Geese, Steppe Buzzard, Blackshouldered Kite, Barn Owl, Cattle Egret, Hadeda Ibis, Helmeted Guineafowl, Blue Korhaan, Crowned Plover, Yellowthroated Sandgrouse, Rock Pigeon, mousebirds, Redcapped Lark, Grassveld Pipit, Fantailed Cisticola, European and Wattled Starlings, Cape Sparrow, Masked and Cape Weavers, Red Bishop and Redbilled Quelea. Some of these, such as Blue Korhaan and Helmeted Guineafowl, do not necessarily move long distances but are able to utilize a mosaic of adjacent habitats in such a way as to meet all their needs. The Red Bishop and Redbilled Quelea are of significance as pest species of small-grained cereals; particularly the quelea can occur in devastating numbers.

Irrigation makes cultivated lands attractive to some species as the moisture of the soil allows probing for invertebrates (e.g. Hadeda Ibis and European Starling).

A large proportion of the indigenous forests, both coastal and montane, have been cleared during the past 300 years, making way for plantations of alien trees, subsistence and commercial agriculture, and urbanization (Geldenhuys & MacDevette 1989). Although much of the remaining forest falls within protected areas, it is severely fragmented; further losses of forest are likely to reduce the viability of the small populations in each 'island' of forest.

A deforestation-related impact, mainly in the woodland biome, is the collection of firewood, mainly by rural communities. The potential negative impact is the loss of dead and decaying branches and trunks, utilized as nest sites by obligate treehole nesters. This applies to primary hole excavators, to secondary hole users, and to species that make use of natural holes in decaying wood (e.g barbets, woodpeckers, woodhoopoes and hornbills).

Afforestation and alien plants

Commercial afforestation is a specialized type of crop farming and as such causes a similarly radical transformation of the vegetation (Figure 62). In natural grasslands it represents an extreme transformation because not only the species composition but also the macro-structure of the vegetation is totally altered. In addition, the concentration of large numbers of trees has profound consequences for the hydrology of the area with the drying up of streams and wetlands being a common result, even when the trees are some distance from the waterbody (Versfeld & Van Wilgen 1986).

Most of the areas identified as suitable for commercial afforestation in South Africa lie within the grassland biome and, more particularly, within the high-rainfall Sour Grasslands (e.g. Allan *et al.* 1997). There is conclusive evidence from atlas data that commercial afforestation has already had a major impact on grassland birds, and the potential for further negative impacts on endemic and threatened species (e.g. Bald Ibis, Whitebellied Korhaan, Rudd's Lark and Yellowbreasted Pipit) is serious (Allan *et al.* 1997). Woodland species (e.g. Black Sparrowhawk, Hoopoe, and Crested Barbet, none of which are endangered) tend to benefit from plantations of alien trees (Allan *et al.* 1997).

A form of uncontrolled afforestation takes place through the spread of invasive alien species of tree and shrub. There are many examples in southern Africa but probably the worst are to be found in the fynbos biome of the southwestern Cape Province where *Pinus* spp. and Australian *Acacia* spp. have invaded the fynbos (Figure 61). The spread of alien plants has allowed many woodland and forest birds to extend their distributions into areas which were previously unsuitable for them (e.g. Allan & Tarboton (1985) for sparrowhawks and Macdonald (1986b) for the Pied Barbet). The spread of some alien plants is aided by dispersal of seed by birds (e.g. Bugweed *Solanum mauritanum* by Rameron Pigeons, and Rooikrans *Acacia cyclops* by Redwinged Starlings and even European Swallows: Oatley 1984; Hofmeyr 1989). Some species have spread into areas where alien *Acacia* thickets have become established in areas of natural dwarf scrubland (e.g. Pied Barbet in the southwestern Cape Province and, subsequently, its brood parasite, the Lesser Honeyguide: Macdonald 1986b; Underhill *et al.* 1995). Swainson's Francolin is an example of a species that has benefited in the grassland biome from both crop planting and alien trees (Clancey 1965c; Tarboton *et al.* 1987b; Osborne & Tigar 1990).

Another mode of afforestation with alien plants is the planting of trees and shrubs in parks and gardens. Where this occurs in formerly treeless areas, a transformation to a form of secondary woodland takes place. The northern suburbs of Johannesburg provide an example; areas which were originally mainly open grassland now appear as woodland. Most of the original grassland species no longer occur in gardens in the area, but several woodland species are now common residents (e.g. Grey Lourie and Crested Barbet). The treed and irrigated farmsteads and small towns which occur at intervals throughout the Karoo have made it possible for a number of species to establish themselves as resident breeders in regions where they were probably absent or sparse before (e.g. Redeyed Dove, Blacksmith Plover, Cape Wagtail, Hoopoe and Pied Barbet).

Impoundments and other artificial wetlands, drainage, and river and wetland pollution

The river systems of southern Africa are characterized by copious numbers of man-made dams, ranging in size from large state impoundments many square kilometres in area to small farm dams of less than 1 ha (Figure 64). Most are in the higher-rainfall east and extreme south. In South Africa, 517 major reservoirs had been constructed by July 1986 (Macdonald 1989, with further details being provided elsewhere: Bowmaker *et al.* 1978; Noble & Hemens 1978; Department of Water Affairs 1986; De Wet 1991; Van Zyl 1991).

The largest impoundment in the atlas region is Lake Kariba (1628BD) on the Zambezi River in northern Zimbabwe; it is *c.* 290 km long and *c.* 5250 km^2 in area and almost twice the combined area of all the 517 major impoundments in South Africa. Lake Kariba inundates a major portion of the Middle Zambezi valley, as well as having profound downstream impacts on the Lower Zambezi system (Davies 1986). The aquatic avifauna of this dam has been investigated (e.g. Donnelly & Donnelly 1983; Eriksson 1984), especially with regard to the impact of piscivorous birds on fisheries (e.g. Hustler & Marshall 1996) and the level of contamination of waterbirds by pesticides (e.g. Douthwaite 1992; Douthwaite *et al.* 1992c).

The total number of small earthen dams on farms and other private land in southern Africa is thought to be many tens of thousands (e.g. Benade & Gaigher 1987 for the Cape Province). Zimbabwe had over 7100 such dams by 1974 (Bowmaker *et al.* 1978) and there are about 400 in Namibia (De Wet 1991). The number of farm dams in KwaZulu-Natal doubled between 1956 and 1986 (Macdonald 1989). Despite the ubiquity of farm dams in the southern African landscape, the significance of these habitats to waterbirds has attracted little research attention. It is certain, however, that they have encouraged the expansion of many waterbird species into areas which would normally be too arid, especially in the Karoo and central Namibia. However, many of these species may have visited these areas irregularly in years of exceptionally good rainfall. Their major significance might be as near-permanent drought refuges and the largest change may be in increased population sizes in formerly inhospitable areas, and possibly in the breakdown of more-or-less regular patterns of movement between mesic and arid areas.

Although dams frequently inundate riverine and wetland ecosystems, the extent of the areas actually flooded by dams along most river systems is relatively small. A major ecological impact of these impoundments occurs downstream, through reducing river flow, attenuating flood peaks and altering seasonality and temperature of flow, sediment loads, channel morphology and water chemistry (Macdonald 1989; O'Keeffe *et al.* 1989).

Many thousands of natural wetlands in southern Africa have been drained for urbanization and agriculture (Coetzee 1995; Kotze *et al.* 1995). Wetland loss is attributable not only to such obvious on-site destruction but also to more subtle upstream activities. The most important are those, including dam construction and afforestation described above, that disrupt waterflow into the wetland; all forms of water abstraction reduce flows, whereas stormwater from adjoining built-up areas produces flash floods. Other negative factors include inflows of water containing suspended sediments, heavy metals and other pollutants and inflows of eutrophic run-off from agricultural activities (fertilizers and dung), sewage works and nutrient-rich effluents. In addition, the use of groundwater has lowered watertables and thereby contributed to the dessication of wetlands.

These upstream factors impact not only the wetlands, but the rivers which flow into them. The Orange River bears its name because of the huge quantities of silt carried downstream from its catchment (Figure 58). Contributing factors to the silt load in this and many other rivers are overgrazing in catchments and deforestation of riverbanks. In some cases the deforestation of banks, and the destruction of mangrove swamps, is caused by violent flooding which results from increased and more rapid run-off, which are themselves consequences of a denudation of catchment areas. Eutrophication of river waters causes algal blooms which do damage to food chains, particularly in streams where ecosystems and species are adapted to relatively low nutrient levels and clear waters (e.g. Longtailed Wagtail). These factors, together with altered flow regimes caused by impoundments and water abstraction, have caused the degradation of many rivers and their estuaries. This can be seen most clearly in the disrupted distributions of riverine species (e.g. Halfcollared and Mangrove Kingfishers) in KwaZulu-Natal where the fast-flowing nature of the rivers have made them particularly vulnerable to damage. The beleaguered position of river ecosystems is highlighted by the fact that seven of the 13 species which are more or less dependent on rivers are included in the South African Red Data book (Brooke 1984b).

Some waterbirds, usually those favouring deep, open-water conditions, have benefited from the construction of dams (e.g. Siegfried 1970; McLachlan 1971), but this has been at the cost of a larger guild of waterbird species, including many threatened species, which have lost habitat through the inundation of marshy and riverine habitats, and through the deleterious downstream impacts on riverine, floodplain and estuarine environments. The creation of impoundments has tipped the balance towards wetlands with deep, permanent waters, as opposed to those which are shallow and seasonal. The species for which the construction of deep impoundments is detrimental are those which require marshy and muddy conditions with complex mosaics of wetland vegetation (e.g. crakes, rails, flufftails, bitterns, snipe and some herons, ducks and waders).

An example of a waterbird benefiting from dams is the African Fish Eagle in the Transvaal, where an estimated 25% of the total breeding population occurs at impoundments (Tarboton & Allan 1984). Williams & Randall (1995) demonstrated the beneficial effects of dams for the pelecaniforms (pelicans, darters and cormorants). Large dams provide moulting sites for waterfowl (e.g. Geldenhuys 1975) and dry-season/drought refuges for waterbirds (e.g. Junor & Marshall 1987). For example, at least 70% of the global population of South African Shelduck gathers to moult at only 23 localities in South Africa; all but two of these are large dams (Geldenhuys 1981). They can also serve as important breeding sites for some species, e.g. waterfowl (Geldenhuys 1976b). These habitats therefore support significant populations of many waterbird species and these include a few species of conservation concern (Brooke 1984b). For example, fifty pairs or more of the White Pelican breed at Hardap Dam (Williams & Randall 1995), the Pinkbacked Pelican has nested at Jozini Dam (2732AC) on the Pongolo River (Tarboton *et al.* 1987a) and Caspian Terns breed at the Vaal and Kalkfontein (2925AC) dams (Cooper *et al.* 1992).

A class of artificial wetlands which are important for waterbirds are waste water treatment (sewage) works. These wetlands can support particularly high densities of aquatic birds owing to the rich nutrient cycling in these systems. Although the water at sewage works is eutrophic, it is of a relatively benign nature, partly because nutrient levels decrease through a series of settlement ponds. Most towns and all cities in southern Africa have associated sewage works; there are likely to be several thousand such sites. Many waterbirds find sewage ponds attractive places to forage and as such these waterbodies have also contributed to the spread of waterbirds into formerly inhospitable areas. Well-known examples of sewage works are at Strandfontein (3418BA) (Cape Town) and Diepsloot (2527DD) (Johannesburg) in South Africa; at Swakopmund (2214DA) and Rundu (1719DD) in Namibia; Phakalane (2426CA) (Gaborone) and at Francistown (2127AD/BA) in Botswana; and at Aisleby (2028BA) (Bulawayo) and Crowborough (1730DD) (Harare) in Zimbabwe. Of these, the Strandfontein Sewage Works probably supports the largest number of waterbirds; the number and diversity of aquatic birds at this site rivals that at many of the major natural wetlands in southern Africa (e.g. Allan *et al.* 1990). Examples of important waterbird populations at sewage works include Maccoa Duck at Phakalane sewage works (Bishop 1994a). These man-made wetlands can also provide habitat for some threatened waterbirds (Brooke 1984b), e.g. Strandfontein for White Pelican, Greater Flamingo and Caspian Tern, and Paarl Sewage Works for Lesser Flamingo.

Saltworks are a further important class of artificial wetland. They are found mainly within a few kilometres of the coast, with clusters near Swakopmund and Walvis Bay in Namibia, at the Berg River estuary and near Algoa Bay. Some saltworks are located at pans in the interior. Chestnutbanded Plovers frequently benefit from commercial saltworks (Allan *et al.* 1995; Hockey & Douie 1995). Dams associated with mining activities also create wetlands supporting, at times, large numbers of waterbirds; this occurs most notably on the Free State goldfields, where highly mineralized seepage water pumped to the surface cannot be used for agriculture (Liversidge 1958; Brooke 1960).

In areas where impoundment of run-off is impractical, groundwater is frequently brought to the surface by innumerable windpumps, and used for stock watering points and gardens in semi-arid regions. This provides permanent drinking water. As a result, many terrestrial species have permanently colonized regions that were previously unsuitable or only seasonally available to them. This too has had an impact on distributions and the permanence of a greater diversity of species in arid areas (Knight 1989). For example, in the Central Kalahari vegetation type, which straddles South Africa and Botswana, many species are shown by the atlas maps to be common in South Africa but absent or scarce in Botswana (e.g. Laughing Dove and Cape Sparrow). This probably relates, at least partially, to the abundance of man-made watering points in South Africa compared with Botswana.

Water brought to the surface by windpumps is frequently stored in small circular reservoirs with vertical walls; these can act as traps for birds drinking at them, and many large raptors are drowned in them (McLachlan 1971; Anon. 1992c).

Urbanization, man-made structures and roads

In addition to the transformations of natural vegetation in towns and cities (Figure 65), man-made structures themselves have affected birds. Buildings, pylons, culverts, bridges, telegraph poles, windpumps, etc., all offer potential nesting sites and, for some species, have become the most commonly used sites (e.g. the South African Cliff Swallow nesting under bridges and culverts).

Pylons for high-tension cables (Figure 66) are a major hazard for large birds (e.g. vultures, eagles and storks) attracted to them as perches and being electrocuted when they span the wires with their wings on take-off or landing (e.g. Mundy *et al.* 1992). Declines of some species in some areas may be primarily due to this phenomenon. Progress has been made in improving designs to alleviate these effects, but many old-fashioned structures still exist. On the other hand, some pylons have been designed specifically to offer birds nesting sites and such structures have the potential to boost populations of species (e.g. Martial Eagle and Whitebacked Vulture) in areas where suitable nest sites are lacking (Allan 1988a). Large birds which are relatively unmanoeuvrable in flight (e.g. flamingos, cranes and bustards) are vulnerable to flying directly into utility wires and cables and breaking their necks or limbs, particularly if the cables are strung close to points of take-off and landing, such as near wetlands (e.g. Longridge 1986).

Fences, fence posts and utility poles have become almost ubiquitous features of rural landscapes and are used extensively by birds as perches and aids in still-hunting. The proximity of these perches to roads is probably a further benefit as cars tend to flush insect and rodent prey. Road verges themselves are often important linear refugia for wild plants and therefore also for prey species of birds. Scavengers are attracted to roadkills. These attractive features of roads probably contribute to the number of birds killed by collisions with moving vehicles (Macdonald 1989). The total number of birds killed in this manner must be vast and may be an important factor for the populations of some nocturnal species (e.g. Spotted Eagle Owl, Spotted Dikkop and several nightjar species). Utility poles and windpumps, substituting for trees, have enabled the Sociable Weaver and Black and Pied Crows to expand their ranges into treeless areas, and also Greater Kestrels, which recycle the nests of these species.

Quarries and rock cuttings for roads and railway lines substitute for cliffs for some ledge-nesting species, and have enabled them to expand their ranges. Cuttings through sand and soft substrates provide banks for some hole-nesting species (e.g. bee-eaters, martins, kingfishers and starlings).

Conservation

Conservation, unlike most of the other human activities discussed here, has had mainly positive impacts on bird populations, although many of these have been by-products rather than direct objectives of conservation planning. Perhaps the most significant achievement has been the continued existence of viable populations of some of the large raptors in the region. Particularly in South Africa, there are species which have viable populations inside the large protected areas, namely Kruger and Kalahari Gemsbok National Parks, and the parks of northern KwaZulu-Natal (Ndumu, St Lucia, Umfolozi, Hluhluwe and Mkuzi) but have become almost extinct outside them. These large reserves (Figure 11), and others (e.g. Etosha in Namibia, Hwange in Zimbabwe, Chobe, Moremi and Central Kalahari in Botswana) have unequivocally demonstrated the importance of large protected areas as refugia, particularly for large raptorial birds (e.g. Liversidge 1984; Tarboton & Allan 1984; see also distribution maps for vultures, Bateleur, Tawny Eagle, etc.).

On the other hand, the extremely uneven spread of protected areas – particularly large ones – in the various biomes of the region (see Figures 11 and 17) has benefited some groups and left others vulnerable. Mountain fynbos, evergreen forest and, to a lesser extent, the natural woodlands of the north and north-east, and the arid biomes of the west, are examples of vegetation types which, for historical and economic reasons, have been either well-protected or left relatively undisturbed, so that large parts of these habitats still exist in near-pristine condition. The distribution maps for the species dependent on these habitats show patterns which largely correspond to the geographical extent of the relevant vegetation types, i.e. 'natural' patterns of distribution.

Conversely, there are biomes which are relatively poorly protected and have also been severely impacted by agriculture and other human activities. Foremost amongst these are lowland fynbos and the grassland biome (Siegried 1989). This atlas indicates that the species endemic to the grassland biome are, collectively, the most threatened group in the region and that some (e.g. Rudd's Lark, Botha's Lark, Yellowbreasted Pipit) face imminent extinction if degradation and destruction of natural grasslands continues at the present rate (Allan *et al.* 1997). These species typically show disrupted patterns of distribution. Their ranges do not correspond to the former extent of the grasslands and also tend to be fragmented (e.g. Whitebellied Korhaan); these species now persist as collections of isolated populations, probably with little gene flow; each population is vulnerable to extinction because of the relatively small number of individuals in it.

The plight of the grassland birds highlights the urgent need for implementation of conservation policies on privately owned land. It is unlikely that new, large, state-owned protected areas will be established in future; the survival of many species will depend on the land uses and management practices of farmers and other landowners.

Very few areas in southern Africa are in a condition completely unaffected by human activity, even those thought of as 'unspoilt' or 'pristine'. Human beings shape their environment to suit their needs and thereby shape the destinies of all other living things. Conservation is also a human activity subject to man-made values, policies and management decisions. Through this atlas, birds provide us with numerous pointers to the effects that our activities are having on the broader environment. Macdonald (1992) considered that monitoring bird distributions through atlas projects should be an ongoing and continuous activity. We have not achieved this. But future bird atlas projects will show whether the messages contained in the first southern African bird atlas project have been understood and taken seriously.

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